Long term change in arid zone vegetation

at

Koonamore, South Australia

by

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Summary

The investigation at Koonamore Vegetation Reserve is known
world-wide as a long and comprehensive study in vegetation
change. Two neglected areas of this investigation were
developed for the present studies. The first of these was
cross-fence comparisons between the Reserve (grazed by sheep
from 1870 - 1925 ; ungrazed i.e. protected from 1925) and
South Lake Paddock (grazed continuously from 1870). The
second area concerned under- and un-evaluated data records,
especially photographs, which had accumulated since 1925.

Initial cross fence comparisons revealed
significant compositional differences in all strata of the
vegetation examined, namely soil cryptogams, ephemerals and
low shrubs. Irrigated small plots were used to investigate
possible mechanisms of development of the observed differences
between the two sites in two ephemeral grasses. Abundance
of *Stipa nitida,* as measured by biomass, density of plants
and density of seeds in the soil was greater in the protected
area, and abundance of *Schismus barbatus* by the same criteria
was greater in the grazed area. The soils in the protected
area were more fertile, less compacted, apparently higher
in organic matter content, and had a better developed lichen
crust than the grazed area. Except for the lichen crust these
differences were slight. The difference in *Stipa* was attributed
to direct grazing selection and in *Schismus* to physical or
chemical lichen crust properties retarding its germination and
growth.

Summary (Cont.)

The irrigated plots were used also to make a study
of seasonal pattern in several ephemeral species. Most species
were capable of germinating and establishing in most seasons
except mid-summer and mid-winter.

Using the unevaluated data records, longevity and
survivorship of three perennials were examined. *Atriplex
vesicaria* lives to a maximum age of 30 years, *Acacia aneura*
to 300 years and *Kochia sedifolia* to an unknown maximum of
hundreds of years. In the latter two species mortality exceeds
replacement even in the protected area, and it is predicted
that under grazing they will ultimately be eliminated from the
landscape.

The value of long term investigations and the future
of the one at Koonamore are discussed in relation to my studies.

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fruitful and stimulating discussion. I thank Chris. Evans
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Finally I must thank my wife, Leeanne, for her many roles :
as field assistant, draughtsman, typist and most of all for
her continuing support.

Declaration

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

Michael D. Crisp.

CONTENTS

Contents,
Page 2.

Contents,
Page 3.

Contents

Page 4.

Contents
Page 5.

Contents
Page 6.

1.   Introduction

This project results from the revival of a unique study in vegetation dynamics. The Koonamore Vegetation Reserve[†] in arid South Australia has its roots in the historical traditions of research in the Botany Department, Adelaide University; of land usage in South Australia; and of early 20th century ecology.

In the mid 1920's Professor Osborn and his colleagues extended their interests in ecology and field physiology of vegetation to the arid zone of South Australia (Osborn and Wood 1923; Wood 1923; Wood 1924). They soon became aware of serious degradation of the soils and vegetation resulting from pastoralism and other alien influences in the region (Osborn 1929), which had been a cause of alarm up to 30 years before (Dixon 1892). Equally important to the origin of KVR was the new theory of vegetation succession (Clements 1916; Cooper 1926). Osborn (1929, p 168) was particularly concerned with the question as to whether overgrazing by domestic and feral herbivores resulted in return of the vegetation to recognisable seral stages or whether they were

> "artificial, mere destructions and as such outside
> the ecologist's proper field".

Although the concepts of 'succession' are now modified to the extent that such a question is irrelevant (Knapp 1974a) nevertheless they gave the initial impetus to KVR and many other long-term vegetation studies from that time.

[†] Now named the 'T.G.B. Osborn Vegetation Reserve', after its founder. For the purpose of this thesis the name is abbreviated to 'KVR'.

In 1925 a badly overgrazed area of 400 ha on Koonamore (see chapter 2) was fenced to exclude permanently sheep and (hopefully) rabbits. The background to, and initiation of KVR were described in detail by Osborn (1925, 1928). The aims were stated by Osborn (1927):

" (i) To study the regeneration of natural vegetation, particularly of saltbush and trees in an over-grazed area, when all grazing influences, including those of rabbits, are removed.

(ii)To study the effect of grazing of known intensity on the process of regeneration.

(iii)To study the ecology of the area, and particularly the autecology of the species that are most valuable economically".

The theory of vegetation succession gave rise to the permanent charted quadrat as a technique for observing vegetation change (Weaver 1918; Cooper 1923). An extensive series of permanent quadrats was set up on KVR, and supplemented by a series of fixed photopoints, in order to pursue the first aim. Although many of these were allowed to lapse within 5 years, many were sampled annually for 35 years, and three publications describing the progress of vegetation change resulted (Osborn et al 1935; Wood 1936; Hall et al 1964). Nothing was ever done towards the second aim but some autecological studies were made (Osborn et al 1931; Osborn et al 1932; Carrodus and Specht 1965).

After 50 years KVR is well known as a uniquely long and comprehensive investigation (see chapter 7). However after 1950 the rate of sampling had begun to decline, and in the mid 1960s ceased altogether (Fig 1.1).

The reasons for this are discussed in chapter 7. Because of the very fact of its long history, it is important that KVR be kept going, especially since many questions about arid zone vegetation and the impact of pastoralism upon it remain unanswered (Perry 1967), and can only be answered from long term studies. Thus in 1970 it was suggested to me that I undertake research at KVR towards my honours degree and so revive the KVR investigations. This work (Crisp and Lange 1975) laid the foundation for my doctoral studies by revealing considerable potential for further research.

In planning my doctoral program I used as criteria the unique attributes of KVR as a situation for arid zone vegetation research. These were

(i)   the permanent quadrat and photopoint data records on 45 years of vegetation change, and

(ii)   that it was a site with a known history (section 2.1) of grazing and protection from grazing.

There was plenty of scope for further research by exploiting both these situations. The data records covered such a time span that many variables could be measured meaningfully that could not have been 10 or more years before. Furthermore, the photopoint records, although more numerous and continuous than the quadrat charts, had never been used as a source of quantitative data. A preliminary investigation using both sets of records produced some very useful data about the longevity and population dynamics of 3 of the most important Australian arid zone perennials.

Another area inadequately researched by previous KVR workers was comparison of the regenerating vegetation in KVR with that in adjacent grazed paddocks. Comparisons of KVR with South Lake Paddock[†] would have been particularly relevant, because these two sites had identical grazing histories until the fencing of KVR in 1925 (section 2.1). Comparisons of KVR with the other adjacent paddocks (Mustering No. 3 and Koonamore Cross), with less similar but nevertheless known histories, would also have been useful. In the first years of KVR a few quadrats and photo-points were established in the adjacent paddocks, but all were abandoned within 5 years. The only published comparisons are in Osborn et al (1931). Thus, in a second preliminary investigation I made comparisons between KVR and S. Lake in all the lower vegetation strata (chapter 3).

Both of the areas of preliminary investigation showed potential for further development as the main theme of my Ph.D. program. The studies from the KVR records could be developed in various ways. First, the work on the 3 species in chapter 6 could be expanded by field studies, the question of longevity of *Kochia sedifolia* and its lack of regeneration on KVR being especially interesting. Second, the age studies could be extended to other species, such as *Myoporum platycarpum* and *Casuarina cristata*. Finally, there was potential for phenological and growth studies of various species by using the photographs.

[†] Hereafter abbreviated to S. Lake.

On the other hand the cross-fence comparisons could be expanded into an intensive investigation into the mechanisms of development of the observed differences. Although many studies have been made, all revealing changes in vegetation composition under changed stocking pressure (Ellison 1960), little is known except in very broad terms about the mechanisms of change.

Having decided to develop one of these areas thoroughly rather than both partially in the limited time available, I chose the cross-fence comparisons for further work. I had already developed this area further than the other and it had been more neglected than any other area in previous research at KVR. On the other hand, I doubted whether suitably rapid and accurate methods of determining age for field studies of population dynamics of shrubs and trees, most of which had anomalous or irregular growth habits, could be found. Furthermore, Noble (1975) required data on the growth and phenology of shrubs and ephemerals for his thesis, and I left it to him to obtain those data. However, the age and population studies were rounded off with a brief field study of *Acacia aneura* (chapter 6).

The principal investigation was an intensive study of cross-fence differences in soils, microclimate and two ephemeral grasses (chapter 4). All further details about the particular course of action taken may be found in section 4.0.

Simultaneously, a study of seasonal pattern in several ephemeral species was made (chapter 5). Finally, in chapter 7, I discuss the value of long term investigations and the future of KVR in the light of my studies there. A schematic representation of the development of my Ph.D. thesis and its structure appears in Fig 1.2.
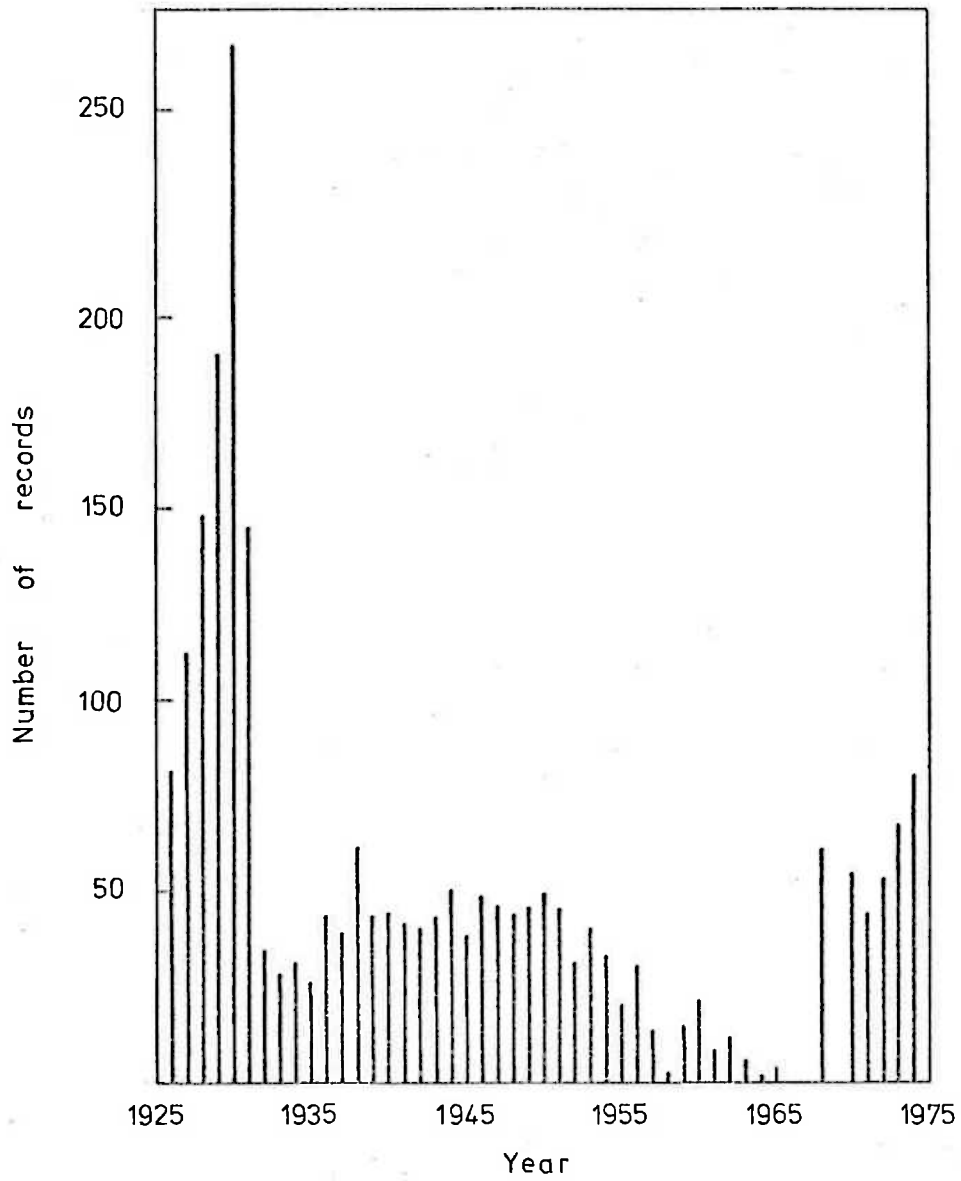
Fig 1.1   Number of records made annually at KVR, 1926-74.
One record is one quadrat charting or one photograph.
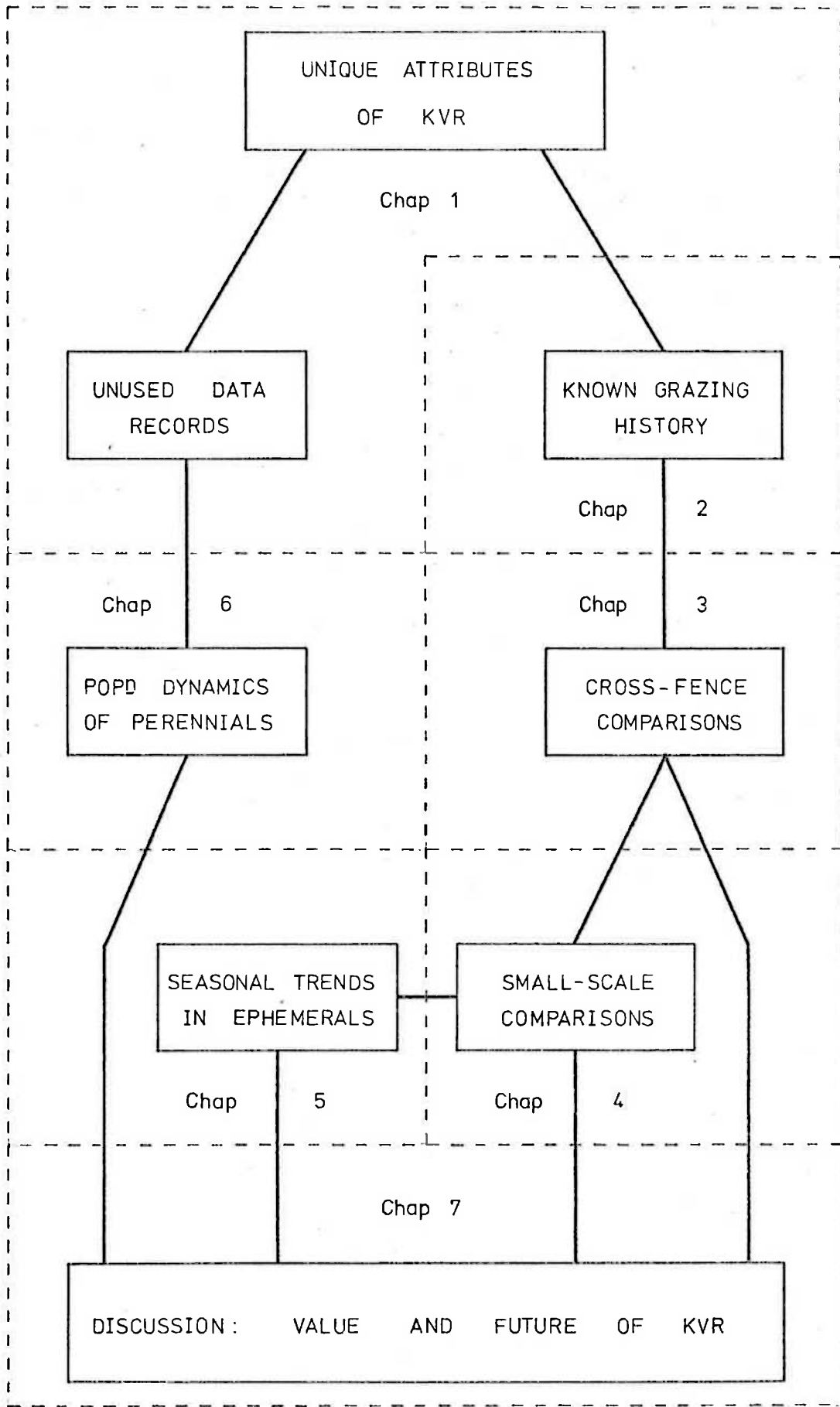
Fig 1.2   Schematic representation of the development and
           structure of this thesis.

2.   Study Area

2.0   Introduction

The arid rangelands of Australia and their history of pastoralism
are described in detail in Slatyer and Perry (1969) and Alexander
and Williams (1973). The South Australian rangelands have been
described by Barker (1972). Koonamore Station, a sheep grazing
property of 1200 km^2, is located at 32° 05'S, 139° 25'E near
to the southern edge of the winter rainfall arid rangelands[†] The
landscape, climate, vegetation and soils of Koonamore are
described by Carrodus et al (1965), and the lichen flora of KVR
by Rogers (1974). Because previous descriptions of the grazing
history, soils and vegetation of KVR and its surrounds have
inadequacies for some purposes of this thesis, they are
supplemented here.

2.1   Grazing history

2.10   Introduction

It is a truism that in order to interpret effects on vegetation
of grazing and protection from grazing it is necessary to know
as much as possible about the nature of the grazing pressure.
However the history of grazing on and around KVR has been
poorly documented in previous publications.

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† Defined by Perry (1967).

Estimation of sheep stocking pressure from stocking rates
requires a knowledge of various site factors which influence sheep
behaviour (McBride et al. 1967). In the arid zone the most
important factor is the water point. Stocking pressure tends to
attenuate with distance from a water point because of the
dependence of the sheep on water. This results in the development
of a 'piosphere', a tendency for radial pattern of grazing
influences on soils and vegetation (Lange 1969; Barker and
Lange 1969). Secondary influences on sheep behaviour include
wind, into which sheep tend to graze; position of shelter, such as
trees, which they use for camping; temperature; topography and
many others (McBride et al 1967). Such factors are mentioned where
appropriate in section 2.11.

Diverse sources of information have been used to reconstruct
the grazing history. The only data available were the detailed
records kept by the present lessee of Koonamore since 1954, and a
small amount of data in the KVR records. No other records from
Koonamore appear to exist. Much of the early history has been
inferred from a knowledge of management practices and social and
economic influences upon them as described in more general
histories such as Ratcliffe (1936) and Barker (1972).

2.11 Sheep grazing

The first pastoral leases were taken up at Koonamore in 1862-3.
A major impediment to pastoral occupation of the arid zone of
South Australia at that time was the lack of permanent surface
water (Ratcliffe 1936; Barker 1972).

Artificial water points (dams and wells) were very time consuming
and expensive to construct. Thus although the original holding
at Koonamore was huge, incorporating almost all of the present-
day surrounding stations, the number of water points and hence
the amount of land grazed were small for many years. Fencing
was probably also minimal. The only water point in the vicinity
of KVR dating back to this period was Finn's Dam, constructed in
1870, 5 km to the southwest. It is probable that early grazing
on the KVR site, as registered in *Acacia burkittii* age structures
(Crisp and Lange 1975), was done by sheep watering at this dam.

In the first two decades of the 20th century considerable
development occurred on Koonamore by fencing of paddocks and
construction of water points. Lake Paddock (Fig 2.1) had one
water point, Hills Well, constructed on its northern boundary
in 1905. The future site of KVR was in the southeastern corner
of Lake Paddock, 10 km from Hills Well. Although sheep do not
usually travel more than a few km from a water point in the arid
zone, two factors led to heavy use of the KVR site by sheep
(Osborn et al 1931). The first was the prevailing south to
southwesterly winds into which the sheep tended to graze. Secondly,
the major concentration of trees in Lake Paddock was in the
southeastern corner, which the sheep used for camping. There is
no direct information about stocking rates on Koonamore in this
pre-KVR period. Ratcliffe (1936, section 12) records that in the
northeast district of South Australia stocking rates remained very
high despite early mistakes and a disastrous drought in 1902. A
rate per paddock of 15 sheep/km^2 was considered to be very
conservative.

This rate was higher (in terms of intensity of stocking pressure) than it seems by comparison with present rates because of the sparsity of water points at that time. Stocking at this rate in Lake Paddock (95 km^2) would result in 1425 sheep on a single water point, which is heavy set stocking by current standards. In those days the pastoralists used continuous[†] grazing systems with fixed area-based stocking rates, unless forced by drought to move or sell stock. Thus it is probable that the sites of S. Lake and KVR were grazed continuously and at a much heavier rate than is indicated by the 15 sheep/km^2 'minimum'.

In 1926, immediately following the fencing of KVR, a new bore was put down at Southern Cross (Fig 2.1), opening up hitherto little grazed areas in three paddocks, namely Lake, Finn's and Milang (Fig 2.1). Although this was a time of severe drought, stocking rates in many paddocks on Koonamore were very high, as is shown by an isolated record from the KVR files (Table 2.1) for 1926-7. Southern Cross Bore was stocked with 6100 sheep, of which 1400 were in Lake Paddock. The remainder had access to both Finn's and Milang Paddocks, where the effect was devastating. Within 44 days a dense stand of saltbush (*Atriplex vesicaria*) and bluebush (*Kochia sedifolia*) was reduced to dust for a radius of at least 2 km (see photographs in Wood 1936). During 1926-7 most of the stock on Koonamore were moved or sold because of the drought (Table 2.1). From 1926-54 sheep grazing in Lake Paddock around KVR watered at Hills Well and Southern Cross Bore.

[†] Definition of Heady (1970).

The grazing pressure was apparently still high (Osborn et al 1931). Nothing is known about actual stocking rates over most of this period, when the station was reduced to its present size.

When the present lessee took over Koonamore in 1954, paddocks were reduced in size and new water points constructed (Fig 2.2). Lake Paddock was divided in two. From this time all grazing around KVR was centred on Southern Cross Bore. This and the reduction of stocking rates in the three decades since the fencing of KVR have greatly reduced the grazing pressure adjacent to the reserve (compare Table 2.1 and Table 2.2). The present management system is a two year grazed/one year ungrazed rest-rotation[†] cycle, with destocking during drought (Table 2.2). Thus not only KVR, but also S. Lake has had an opportunity to recover from over-grazing, especially over the last 20 years.

2.12 Rabbit grazing

Rabbits were introduced to the Koonamore district in about 1880 (Myers 1970). Since that time they have probably grazed the sandy areas and adjacent loam plains on and around KVR more or less continuously, with population numbers fluctuating according to rainfall. Introduction of myxomatosis in the 1950's reduced the rabbit populations temporarily until resistance to the disease became widespread. In 1970 rabbits were eradicated from KVR, and numbers have been very low since that time.

_____

[†] Definition of Heady (1970).

2.13   Conclusions

The history of sheep grazing in KVR and adjacent present-day paddocks (Fig 2.2) may be summarized as follows. The whole area was grazed at an unknown rate (probably light) from 1870 to 1905. S. Lake and KVR were heavily overgrazed as continuous parts of the one paddock from then until 1925, when sheep were permanently excluded from the KVR area. Grazing pressure continued to be heavy in S. Lake, but by 1954 was reduced to present rates. Koonamore Cross Paddock was lightly grazed until 1926 when it was severely overstocked. From then until the present its history was similar to that of S. Lake. Mustering Paddock no. 3 has been used since ca 1900 for the purpose which its name suggests. Thus grazing has been intermittent but heavy, the paddock being stocked for only a few days at shearing time each year.

2.2   Soils and vegetation

KVR is situated on a plain over which sand dunes and shallow silty depressions are irregularly scattered (Fig 2.3). A shallow watercourse runs parallel to the western fence of KVR, between 50 and 100 m outside of it. An extensive saline depression lies a few hundred metres north of it.

The soil of the plain is a solonised loam with limestone nodules throughout the profile, but concentrated into a dense layer from a depth of ca 20 cm. The dunes are predominantly siliceous and show little profile development. Although the

surface soils grade continuously from silty loam through loam
to sand, they are classified for convenience (Fig 2.3). Represent-
ative profiles are described by Carrodus et al (1965) and
Carrodus and Specht (1965) under the "Bindy-eye soil family".

The vegetation of the loam plain belongs to the low
shrubland formation (Specht 1972) which is of considerable
importance to the pastoral industry of arid southern Australia.
The dominant species, *Atriplex vesicaria* (saltbush) and *Kochia*
sedifolia (bluebush) were virtually eliminated from KVR by
overgrazing before 1925. Now the saltbush is largely re-
established but only a few surviving bluebushes remain. Various
ephemerals, notably *Stipa nitida* and *Bassia* spp, are associated
with the shrubland. The tree *Myoporum platycarpum* forms a sparse
overstorey. The dunes carry a tall shrubland (Specht 1972)
of *Acacia aneura* (mulga), *A. burkittii* and *Eremophila sturtii,*
with *Enneapogon* spp dominating the ephemeral layer. Several
species of ephemeral forbs and a few tall shrubs, including mulga,
occur on the silty flats. Groves of the trees *Casuarina cristata*
and *Heterodendrum oleaefolium* occur irregularly on all soil types.
Most of the trees and tall shrubs are survivors of the original
KVR populations. The vegetation intergrades in the same way as
do the soils.
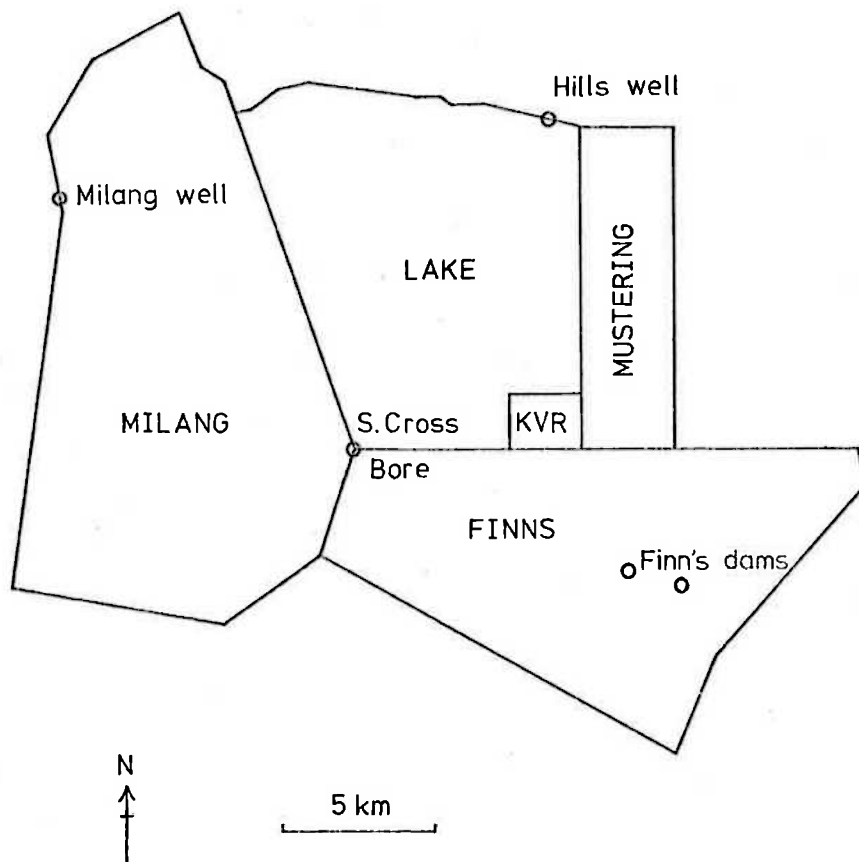
Fig 2.1   Part of Koonamore Station in 1926, showing
           paddocks and water points around KVR.
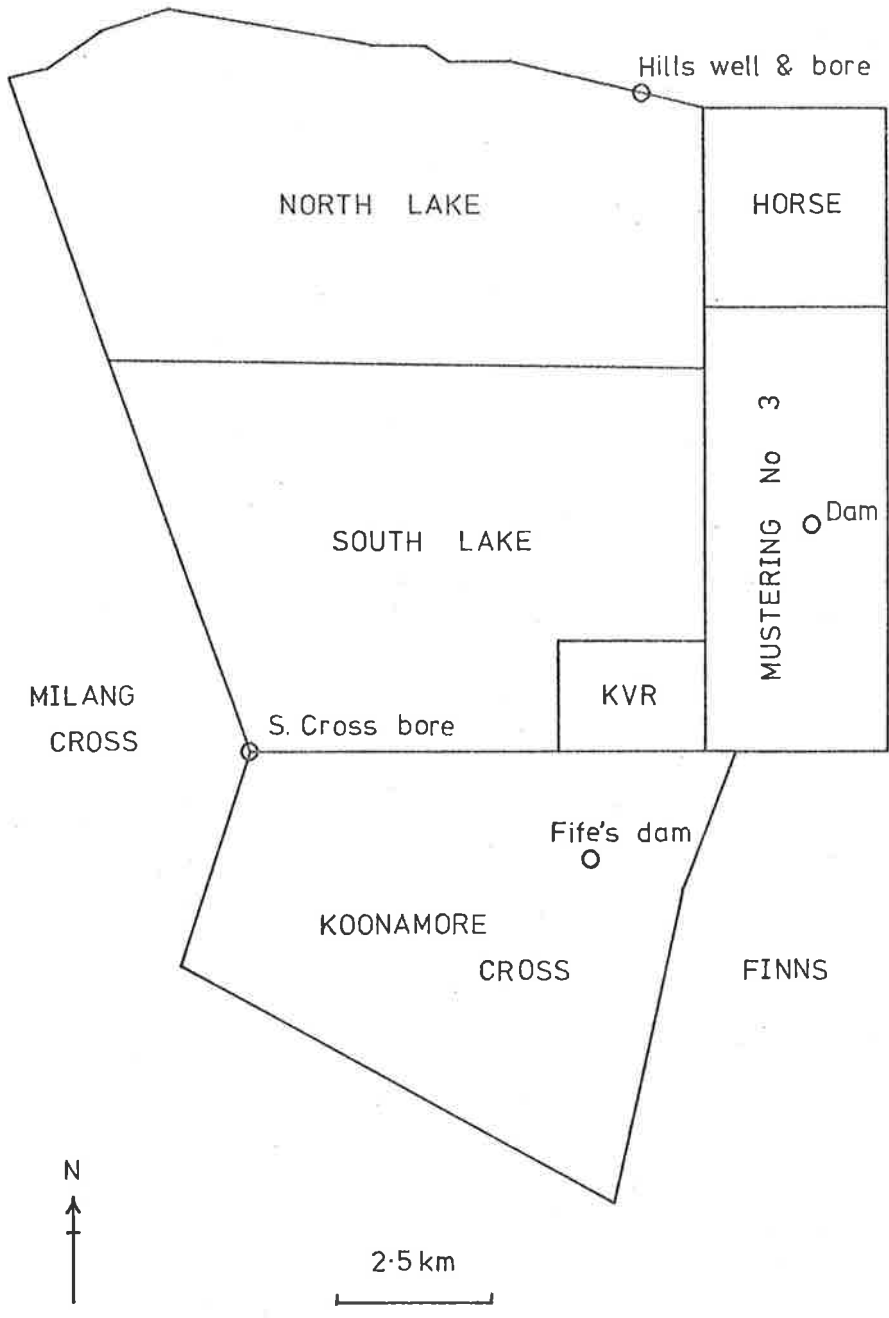
Fig 2.2   Paddocks and water points adjacent to KVR, 1975.

Salt Swamp

S. LAKE

KVR

200m

N

deep sand   shallow sand

calcareous loam   silty loam depression
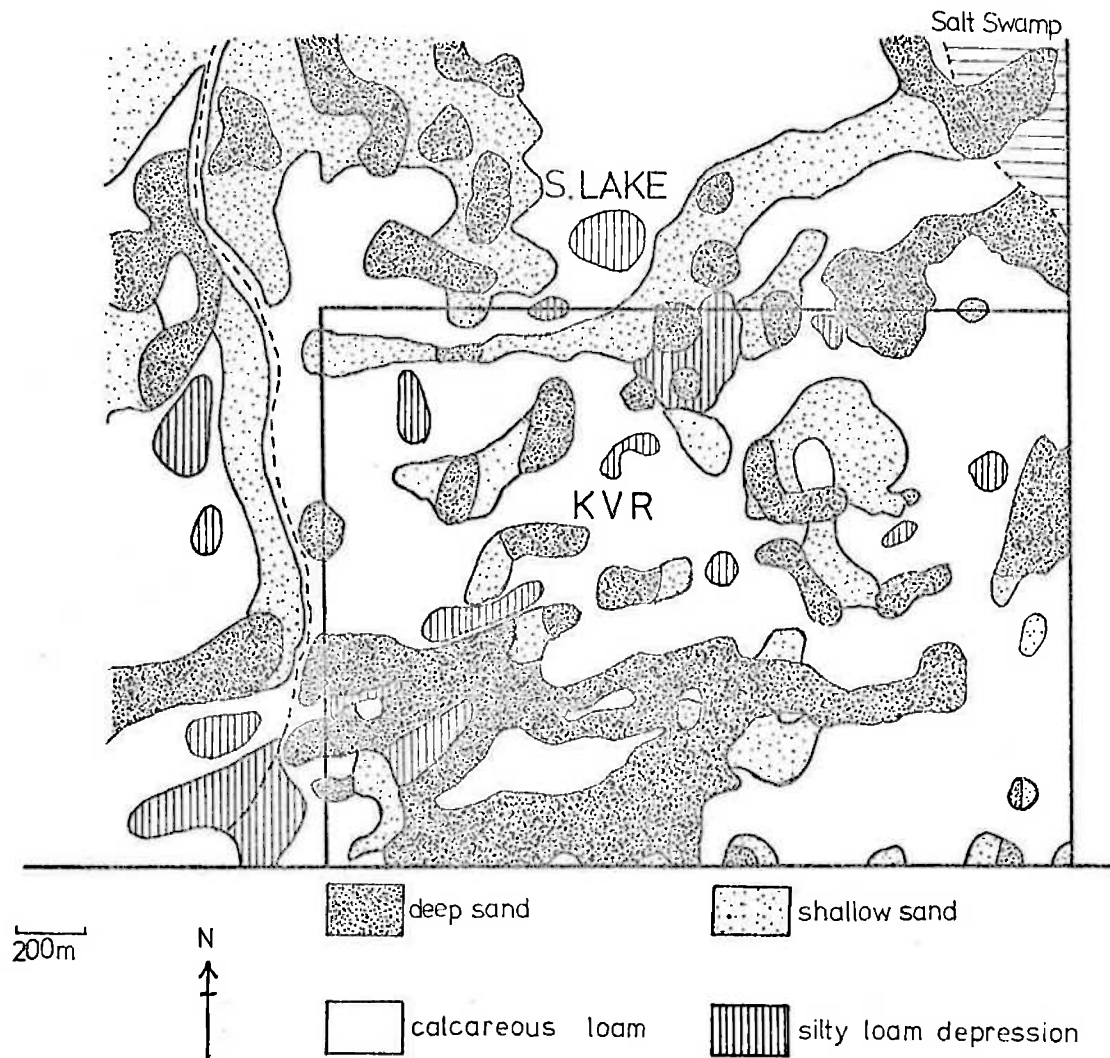
Fig. 2.3   Soils of KVR and adjacent areas in S. Lake.
A watercourse is shown immediately west of KVR.

Paddock	Period		Sheep		Comment
	Dates	Days	No.	Type	
Hills	4/ 9/26 to 4/ 9/27	366	822	wethers	killed for meat
Milang & Finns	7/ 9/26 to 20/10/26	44	5067	wethers	sold
Koonamore Toolaby	9/ 9/26 to 1/11/26	53	4076	ewes	
Springs	1/11/26 to 1/12/26	30	1697	ewes	
Old Station	1/11/26 to 1/12/26	30	1151	ewes	
Black Hill (Nillinghoo)	1/11/26 to 23/ 8/27	296	1584	ewes	
Upper Toolaby (Nillinghoo)	1/12/26 to 23/ 8/27	265	1549	ewes	
Station	8/ 3/27 to 23/ 8/27	168	945	ewes	
Lake	9/ 9/26 to 20/10/26	42	1443	cull ewes	sold
	14/ 9/26 to 20/10/26	36	1444	cull aged ewes	sold
Toms	14/ 9/26 to 27/10/26	43	2482	ewes	
	14/ 9/26 to 27/10/26	43	1040	lambs	
	27/10/26 to 16/ 1/27	81	1000	ewes	
Creek	9/ 9/26 to 27/10/27	315	1439	ewes	
Chimney	27/10/26 to 21/ 3/27	124	1040	lambs	
Oopina	17/ 9/26 to 5/ 9/27	353	1810	ewes	
Aldermans	17/ 9/26 to 8/12/26	82	2000	ewes	
	20/ 8/27 to 5/ 9/27	15	2000	ewes	
Johnsons	8/12/26 to 20/ 8/27	255	2000	ewes	

Table 2.1   Stock distribution on Koonamore Station, 1926 - 27.
Some of the paddocks referred to appear in Fig 2.1

Year	Stock		Comment
	Number	Type	
1954	no stock		
1955	no stock		
1956	no stock		
1957	1171	wethers	June, for 5 months
1958	no stock		
1959	no stock		drought
1960	no stock		drought
1961	no stock		drought
1962	no stock		drought
1963	no stock		drought
1964	1151	wethers	June 25, removed Sept 30
1965	481	ewes	March 15 -
1966	no stock		
1967	284	ewes	
1968	1084	ewes	
1969	no stock		
1970	790	weaners } cattle	
1971	60	cows	
1972	no stock		
1973	1500	wethers	mid June for 4 weeks
1974	409		
1975	no stock		

Table 2.2   Stock numbers in South Lake Paddock, Koonamore, 1954 - 75.

3.   Cross-fence comparisons

3.0   Introduction

This chapter describes the initial work of the project. The
purpose of this work was to detect differences between the
protected (KVR) and grazed (S. Lake) areas with respect to
as much of the flora as was feasible. A floristic survey
was made (section 3.1). Four groups, each requiring a
separate sampling approach, were distinguished in the flora, viz:
cryptograms (section 3.3), ephemerals (section 3.2), low shrubs
(section 3.4) and tall shrubs and trees (section 3.5).

3.1   Floristics

A floristic survey was made in S. Lake and KVR early in 1971 so
as to provide a basis for the cross-fence comparisons. Over the
period 1971 - 1974 this survey was extended to include all of
Koonamore Station with the aim of updating the list of Carrodus
et al (1965). Results appear in Appendix 1 and are summarised
in Table 3.1.

Although statistics are not useful in cross-fence
comparisons at the level of mere occurrence of species, some
useful indications may be found in these data. For example, 33%
(56) of the taxa found in KVR were not found in S. Lake while
only 14% (19) of the S. Lake taxa were not found in KVR. This
suggests that protection from grazing has resulted in relatively
greater diversity in the flora. Further, the majority (56%)
of the 'KVR-only' taxa were indigenous annual herbs but only 7%

were alien weeds. These groups comprised 15% and 42% respectively
of the 'S. Lake-only' taxa. Hence, it appears that indigenous
annual herbs have been favoured by protection and that alien
weeds have been favoured by continued grazing.

3.2   Ephemerals

3.20   Introduction

For the purpose of this thesis an ephemeral is defined as a species
which germinates and grows in response to a sufficient fall of
rain, but which dies out at the onset of drought, leaving no
living aerial parts. Such growth periods are irregular and may
not occur at all in a given year. The entire growth period occurs
within a few weeks or months for most species in this class, but
a few at Koonamore such as *Stipa* spp, *Enneapogon* spp and *Bassia* spp
may persist for 2 to 3 years under favourable conditions (thus
being 'biennial' or 'perennial' under alternative definitions).

3.21   Sampling

Following heavy rains in early to mid 1971 the ephemerals were
sampled twice : in May, just after the summer growth peak and
in August at the winter growth peak. There was no grazing by
domestic stock in S. Lake adjacent to KVR during 1971 ; in other
words, there was no differential stocking effect to confound
comparisons of ephemeral production during this period.

Aerial biomass, the most useful measure of abundance
(Ellison 1960), was the variable used.

It was determined by clipping and weighing. The area sampled was
a strip (400m x 1800m) with the northern fence of KVR running
along its central long axis (Fig 3.1). A reconnaissance revealed
no discontinuities in soils or topography coinciding with this
fence. The western fence was not used because of the watercourse
just outside of KVR (Fig 2.3).

Because high variance is always a problem in sampling arid-
zone vegetation (Amer. Soc. Range Mgmt. 1962) a trial was conducted
to determine the largest size and number of quadrats that were
feasible in the time available. The quadrats were deliberately
chosen to be long and narrow (0.5m x 10m) to further reduce variance,
but not so narrow as to cause large 'edge-effect' errors. The
sample area was divided into 96 equal cells and a quadrat placed
at random in each cell (Figs 3.2a and 3.3a). Quadrats were
oriented at 90° to the KVR fence to minimise the influence of
any 'fence-effect' gradients. No such gradient was detected in
the data. All ephemerals on each quadrat were harvested, sorted
by species, oven-dried at 85°C and weighed.

3.22 Data analysis problems

Despite the aforesaid attempt to minimise variance (section 3.21),
it was still sufficiently high to be a major limitation to the
power of student's t test. I considered using a powerful non-
parametric test of comparison between two means such as the
"randomisation test for two independent samples". However, when
values of n are large (e.g. >20) the computations involved are
extremely tedious, and in any case the randomisation distribution
approximates the t distribution (Siegel 1956). Thus in this

chapter and throughout the thesis I have used the *t* test whenever n >20.

However, I have taken the attitude that although only consistently significant differences (probability < 0.05) may be accepted without reservation as indicating real differences, a situation where mean values consistently show the same trend (with occasional significance) probably indicates a real difference. This view was supported by Leppard[†] (pers. comm.).

3.23   Results

Figs 3.2 and 3.3 show the distributions of total biomass and biomass of the more abundant ephemerals for May and August respectively.   *T* tests were used to compare S. Lake and KVR with respect to mean biomass values (Tables 3.2 and 3.3).

Despite my earlier observation that the north fence of KVR followed no natural boundary, it is possible that the particular samples used were biassed in relation to soils, thus confusing the cross-fence comparisons.   Therefore, the quadrats were classified into those with predominantly loamy soil and those with pre-dominantly sandy soil.   In the May sample the numbers of sand quadrats were 21 in S. Lake and 23 in KVR.   In the August sample these numbers were 17 and 24 respectively. χ^2 tests from 2 x 2 contingency tables revealed no significant cross-fence difference in either sample.   Even so, the more abundant species were tested for association with soil type, and tested separately for cross-fence differences on each soil type (Tables 3.4 and 3.5).

[†] P. Leppard, Consultant Statistician, Statistics Dept., University of Adelaide.

3.24   Discussion

There was no significant difference in total biomass between the two areas either in May or in August ; in fact the mean values were remarkably similar. However, there were differences in composition.

Four species showed large and consistently significant differences. Of these, the grass *Stipa nitida* was more abundant in KVR, while the grass *Schismus barbatus* and the bassias *Bassia obliquicuspis* and *B. patenticuspis* were more abundant in S. Lake. In May I was unable to differentiate the last two species satisfactorily and lumped them together. Separate sampling of these species in August revealed that each was significantly more abundant in S. Lake. In this group of species only *B. patenticuspis* was strongly associated with one soil type. On its preferred type (loam) the cross-fence difference was highly significant.

Five species showed consistent trends in mean values, without consistently achieving significance, but probably having real differences in biomass (see section 3.22). Of these, *Salsola kali* var *strobilifera, Bassia sclerolaenoides* and *Chenopodium cristatum* had higher means in S. Lake while *Bassia diacantha* and *Zygophyllum aurantiacum* var *eremaeum* had higher means in KVR.

Thus of the more abundant species, only *Enneapogon* spp and *Bassia paradoxa* did not show consistent cross-fence differences.

Throughout the previous discussion I have ignored possible differences due to season between the May and August samples.

In fact they differed mainly in occurrence of minor species
(Tables 3.2 and 3.3). Of the major species only *Salsola* and
Enneapogon appeared to show marked seasonality, both being
summer growing species (see chapter 5). Most of the standing
biomass of these species was dead in August, but distribution
patterns were similar to those in May.

3.3 Cryptogams

3.30 Introduction

Cryptogamic crusts play an important role in stabilising the soil
surface in the arid shrublands of southern Australia (Rogers and
Lange 1971b). Rogers (1974) reported 20 taxa of soil surface
lichens on KVR. In the field I was readily able to identify 12
of these and the liverwort *Riccia lamellosa* Raddi. The soil-crust
mosses, which were difficult to identify, were not used in this
survey.

3.31 Sampling

In May 1972 I sampled the soil crust for cross-fence comparisons
at the same sites as were used in the May 1971 ephemeral harvest.
Because of the diffuse nature of lichen thalli it was difficult to
define an individual for sampling. The possibility of estimating
biomass from chlorophyll or organic matter content was considered
but discarded because of problems in separating litter and other
organic matter from the soil crust.

Eventually frequency was chosen as the most useful sampling variable. For each sampling site 50 contiguous quadrats (20 cm x 23 cm) were laid along the 10 m base line of the harvest strip and occurrence of all 13 cryptogam species recorded for each quadrat-unit.

3.32 Results

The distributions of frequency of the more abundant species appear in Fig 3.4. T tests for comparisons between KVR and S. Lake of mean frequency were made for all quadrats (Table 3.6) and for the two soil types separately (Table 3.7). Comparisons of frequency between the different soil types were made separately for KVR and for S. Lake (Table 3.7).

3.33 Discussion

Three of the soil cryptogams were not found outside KVR. These were *Chondropsis semiviridis, Parmelia convoluta* and *Diploshistes scruposus*. The remainder all showed strong and consistent associations with KVR and loam soil. In other words the cryptogams tend to cluster strongly under the soil and stocking influences such that either many are present (crust) or none are present (bare soil). Rogers and Lange (1971a) made very similar findings in a nearly identical flora under grazing at Whyalla.

This general, rather than selective, effect of stocking pressure suggests that trampling is the major cause of decrease in frequency of cryptogams.

This is suggested also by the brittle nature of the crust and the sight of sheep tracks cut deeply into it. The very brittle fruticose form of *Aspicilia calcarea* was reduced in frequency in S. Lake to a much greater extent than the crustose form. These forms are illustrated by Rogers and Lange (1971b).

3.4   Low shrubs

3.40   Introduction

This important category includes *Atriplex vesicaria* (saltbush) and *Kochia sedifolia* (bluebush), the dominant species of the low shrubland formation (section 2.2). However, bluebush is considered not here but in section 3.5 because its scarcity on KVR and its great longevity make biomass sampling inappropriate. Three other species, *Atriplex stipitata* (mallee saltbush), *Kochia georgei* and *Bassia diacantha*, were sufficiently abundant for sampling. *Bassia diacantha* had previously been included in the sampling of ephemerals. This species, being a very low shrub, did not fall easily into either category and was included in both.

An initial reconnaissance revealed obvious differences in the saltbushes between KVR, throughout which they were abundant, and S. Lake where they were virtually absent. The stands in KVR were the result of invasion after 1925 from the paddocks to the south and east (Hall et al 1964). Either this invasion had not reached S. Lake or it had been prevented by continued grazing. There was no point in sampling merely to establish the fact of such obvious differences, but I considered documentation of the degree of difference to be relevant.

3.41 Sampling

Both density and biomass of the low shrubs were sampled. Biomass
of the herbaceous tips only of the shrubs was used, this being
a better expression of current production than whole shrub weight.
Because an extensive survey was intended, a visual estimate
method was used rather than a time consuming clipping technique.

The method of biomass estimation was essentially as
described by Pechanec and Pickford (1937) ; that is, estimation
in multiples of hand-held, known-weight units. Each species
required a separate approach. An intensive training period was
carried out before commencement of sampling. Calibrations of
actual versus estimated biomass were made during the course of
sampling to minimise the effect of systematic errors. A calibration
involved estimation of a range of shrub biomass, followed by
hand stripping of the shrubs and weighing the yield.

The initial training period was used to establish whether
wet weight or dry weight should be estimated. Error associated
with the latter was generally lower (Fig 3.5, Table 3.8) except in
the case of *Bassia diacantha* whose green foliage was so dense
as to obscure the dead. Much of the *Atriplex stipitata* foliage
was dead. This was sampled, but calibrated separately.

The choice of reference unit size required careful consideration.
There is an upper limit to estimation beyond which the ability to see
all the plant material breaks down. For example the data of Tadmor
et al (1975) clearly show that quantities of more than 50 g dry weight
of herbage are increasingly under-estimated, yielding a logarithmic
calibration relationship.

In addition, variance increases sharply. In practice I found units of between 20% and 50% of the average sized shrub (depending upon species) most useful. These shrubs rarely exceed 50 cms in height or diameter.

Although Amer. Soc. Range Mgmt. (1962) suggests a plot size of 192 square feet for "sparse desert vegetation", I used a 2 m x 30 m (600 square feet) quadrat because of the large scale of pattern in shrub distribution. The area sampled was all of KVR and a slightly larger area adjacent in S. Lake (Fig 3.6a). It was divided into 160 equal cells and a quadrat placed at random in each. The salt swamp northeast of KVR and the water-course west of it were avoided.

In each quadrat density and estimated biomass of all shrubs more than 10 cm tall were recorded by species. An individual of *B. diacantha* was difficult to define, and density was not sampled for this species.

3.42 Results

Dry weights were predicted from the daily calibration curves. Fig 3.6 shows the distributions of biomass (dry weight) and density for each species. *T* tests for comparisons between KVR and S. Lake were made for all quadrats (Table 3.9) and for sand and loam quadrats separately (Table 3.10). Comparisons of density and biomass between the different soil types were made separately for KVR and S. Lake (Table 3.10).

3.43 Discussion

All species were more abundant in KVR in both variables although
the degree of difference ranged from near-absence of saltbush
in S. Lake to barely significant difference in the *Bassia* and
Kochia. A similar result was obtained with the *Bassia* in the
ephemeral harvests, although mean biomass was locally higher there.
The saltbushes and the *Kochia* were strongly associated with loam
soil, and this tended to confound the cross-fence comparisons for
all quadrats in the case of *A. stipitata* and *K. georgei*. The
proportions of loam quadrats in KVR and S. Lake were 50% and 67%
respectively.

A further interesting difference between KVR and S. Lake
lies in the ratio of biomass to density (i.e. mean weight per
shrub). This ratio was higher in S. Lake for both saltbushes
and the *Kochia*. This may be a result of under-estimation of
the higher biomass values, but no evidence of this was found in
the calibrations. If real, it may be a result of density-
dependent competition. It is also possible that the KVR
populations have higher proportions of juvenile plants. Because
the shrubs were not chosen for further work (section 4.01) these
last two possibilities were not investigated.

3.5 Tall shrubs and trees

A study of cross-fence differences in tall shrubs and trees
requires a different approach from that used with the lower
vegetation strata. Biomass is not a useful measure of response
to grazing or protection in these species. Their longevities are

such that most of the individuals on KVR are survivors from before

fencing of the reserve in 1925. Further, the lack of juveniles

in their populations on Koonamore generally suggests that they

are survivors from before the advent of pastoralism to the area

(i.e. from before 1870). A much more useful approach is the

study of their age structures and population dynamics, as I have

demonstrated for *Acacia burkittii* in earlier work (Crisp and Lange

1975). Age studies of three additional species are described in

chapter 6.

3.6   Summary of vegetation differences between KVR and S. Lake

This section is not a discussion of the meaning of the observed

differences in relation to history of grazing or protection, but

merely a summary of those differences. Discussion is postponed

to chapter 7. The flora in KVR is qualitatively richer than in

S. Lake. The excess in KVR is chiefly made up of indigenous

annual herbs and soil lichens. There are more alien weeds in

S. Lake.

All soil surface cryptogams are far more frequent in KVR

than in S. Lake. The difference is so great that whereas a lichen

crust is the dominant surface feature on loam soils in KVR, it is

rarely seen in S. Lake.

In a wet year there was no difference between KVR and S. Lake

in total ephemeral production after summer growth nor after winter

growth. Composition of the herbage differed to some extent. Some

species showed no consistent differences ; some showed marginal

differences, and a few showed large and consistent differences.

The dominant grass *Stipa nitida* was much more abundant in KVR while the grass *Schismus barbatus* and two spiny *Bassia* spp were far more abundant in S. Lake.

The two principal low shrub species, including the important *Atriplex vesicaria,* were abundant in KVR but virtually absent in S. Lake. *Kochia georgei* and *Bassia diacantha* were more abundant in KVR but not consistently significantly so. Mean weight per shrub was higher in S. Lake for both *Atriplex* spp and the *Kochia*.
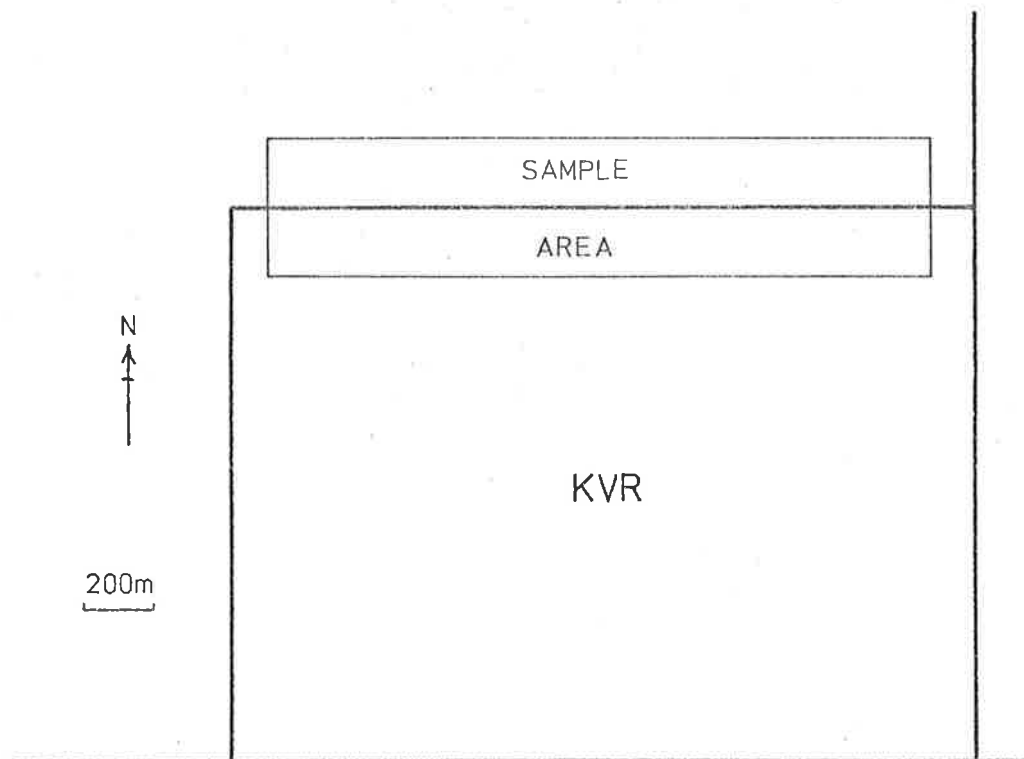
Fig 3.1   Location of area sampled in biomass harvests
           (May and August, 1971) and in lichen frequency
           count (May 1972).

BASE MAP

0   200 M
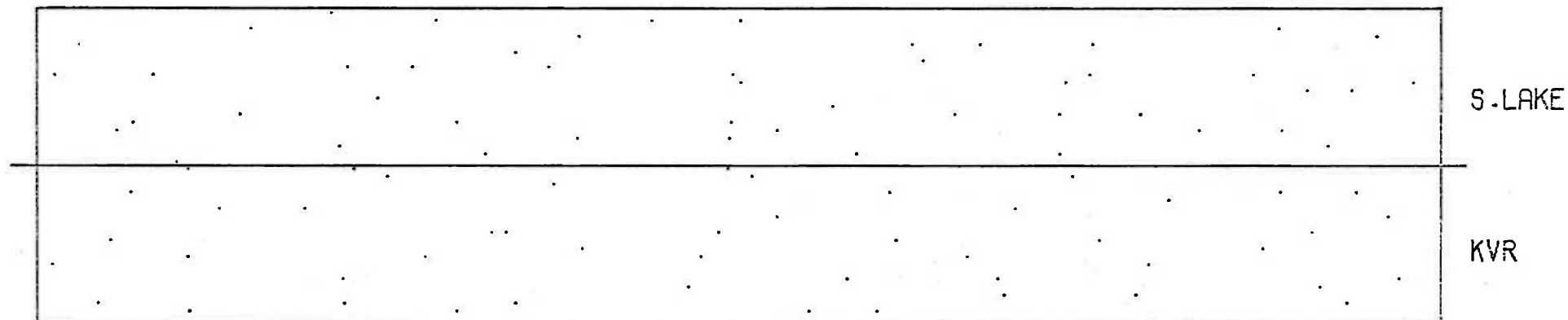
S-LAKE

KVR

TOTAL BIOMASS

1000   100   10   KG/HA

S-LAKE

KVR
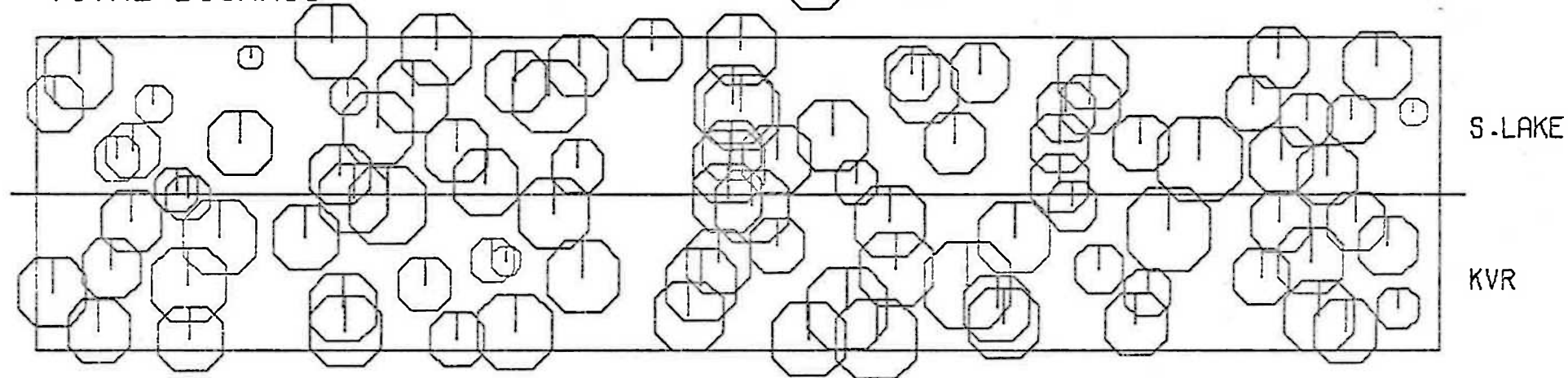
Fig 3.2a   Distribution of biomass of ephemerals in KVR and S. Lake, May 1971.
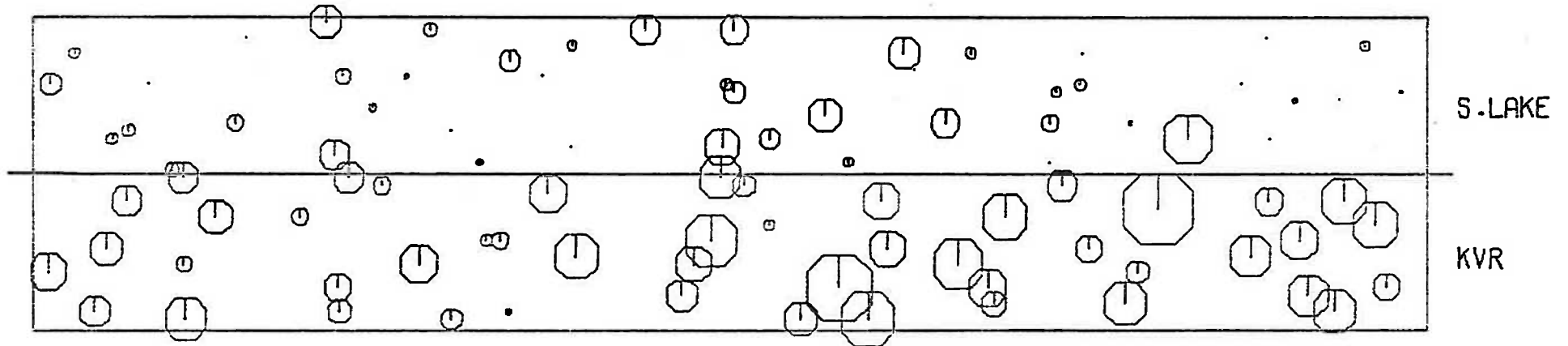
Table 3.2b   Distribution of biomass of ephemerals in KVR and S. Lake, May 1971.

TRIBULUS TERRESTRIS

0   200 M

S.LAKE

KVR
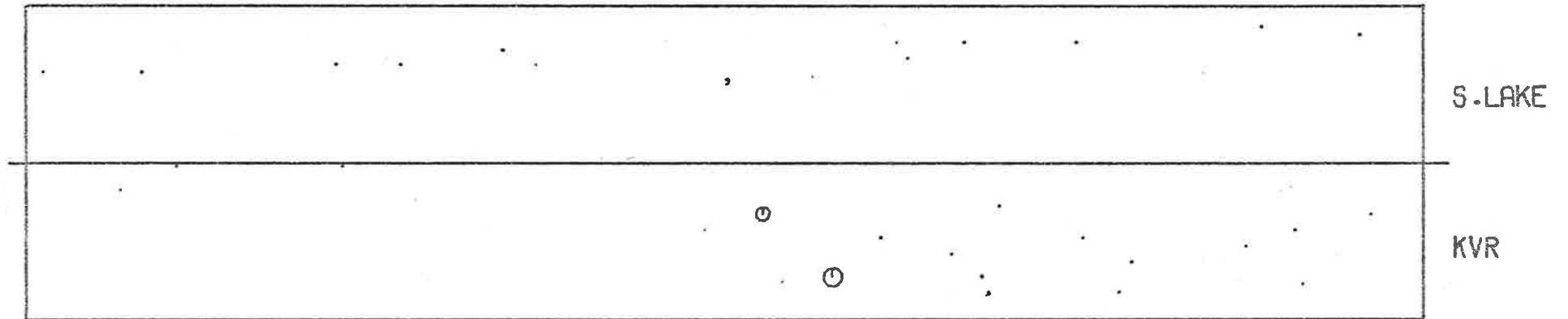
B. OBLIQUICUSPIS/PATENTICUSPIS   1000   100   · 10   KG/HA

S.LAKE

KVR
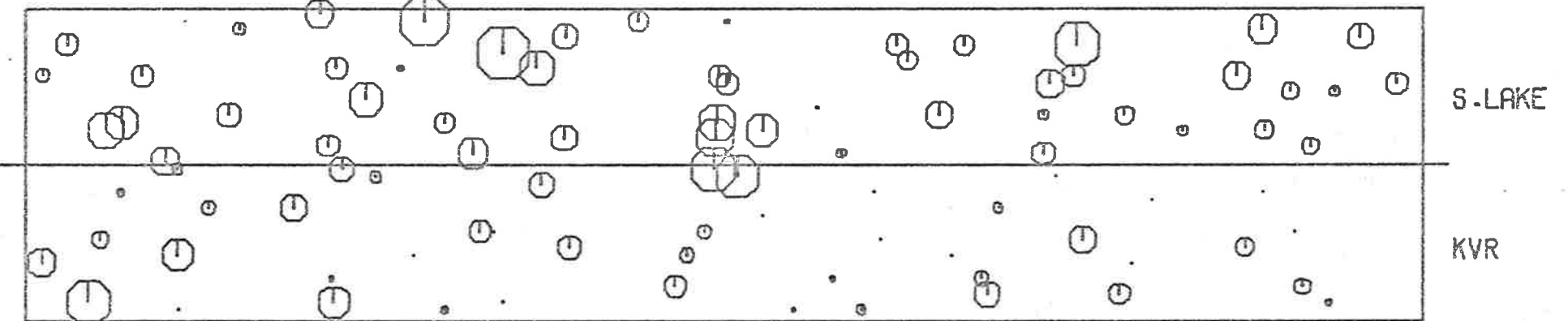
Fig 3.2c   Distribution of biomass of ephemerals in KVR and S. Lake, May 1971.

SALSOLA KALI

0   200 M

S.LAKE

KVR

BASSIA PARADOXA

1000   100   10   KG/HA

S.LAKE

KVR

Fig 3.2d   Distribution of biomass of ephemerals in KVR and S. Lake, May 1971.
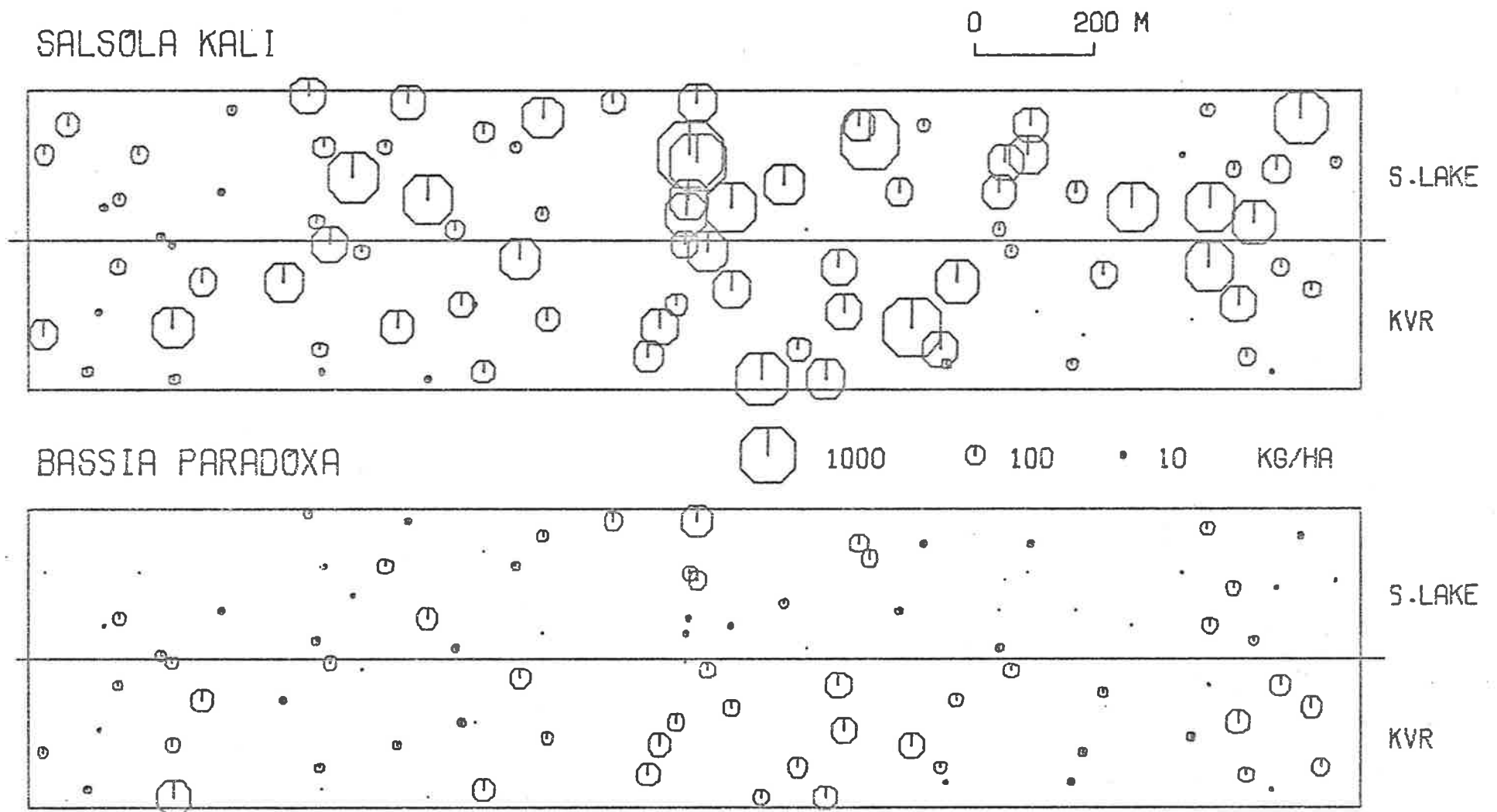
Fig 3.2e   Distribution of biomass of ephemerals in KVR and S. Lake, May 1971.

BASE MAP

0   200 M

S.LAKE

KVR

TOTAL BIOMASS   1000   100   10   KG/HA

S.LAKE

KVR
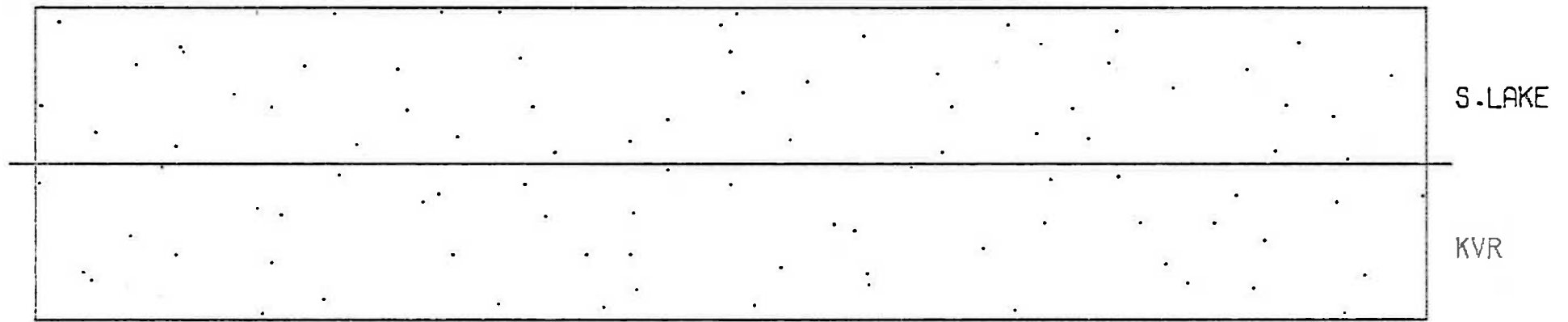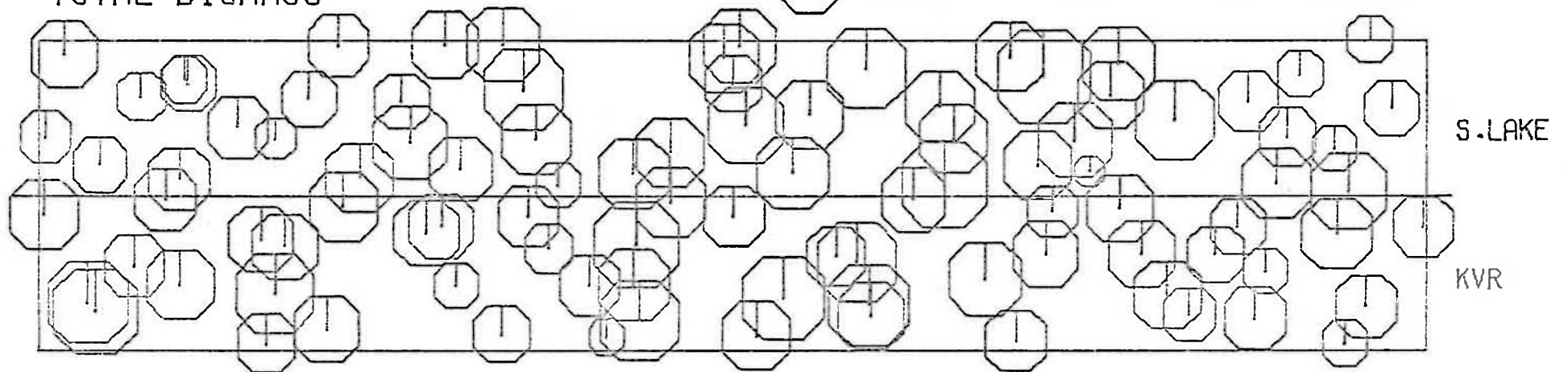
Fig 3.3a   Distribution of biomass of ephemerals in KVR and S. Lake, August 1971.
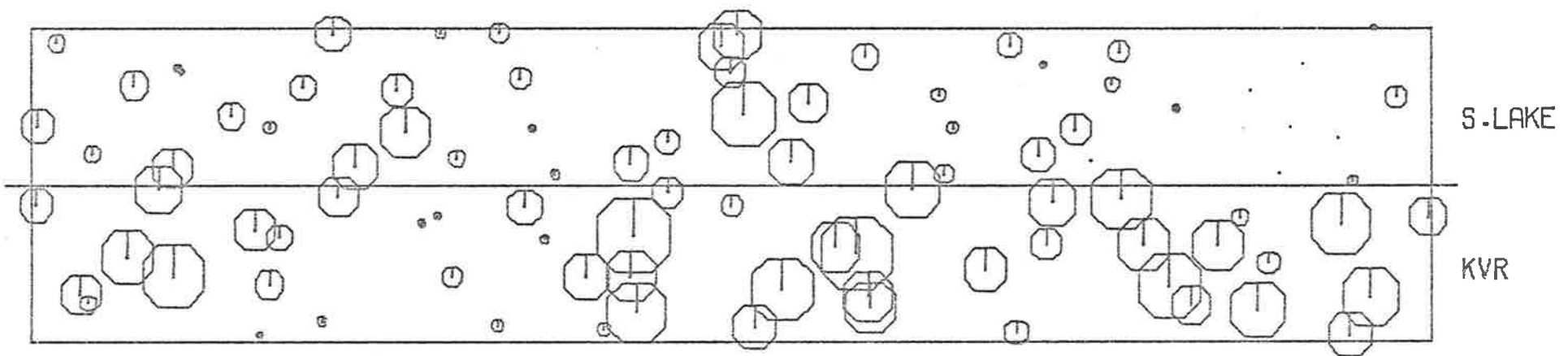
Fig 3.3b   Distribution of biomass of ephemerals in KVR and S. Lake, August 1971.
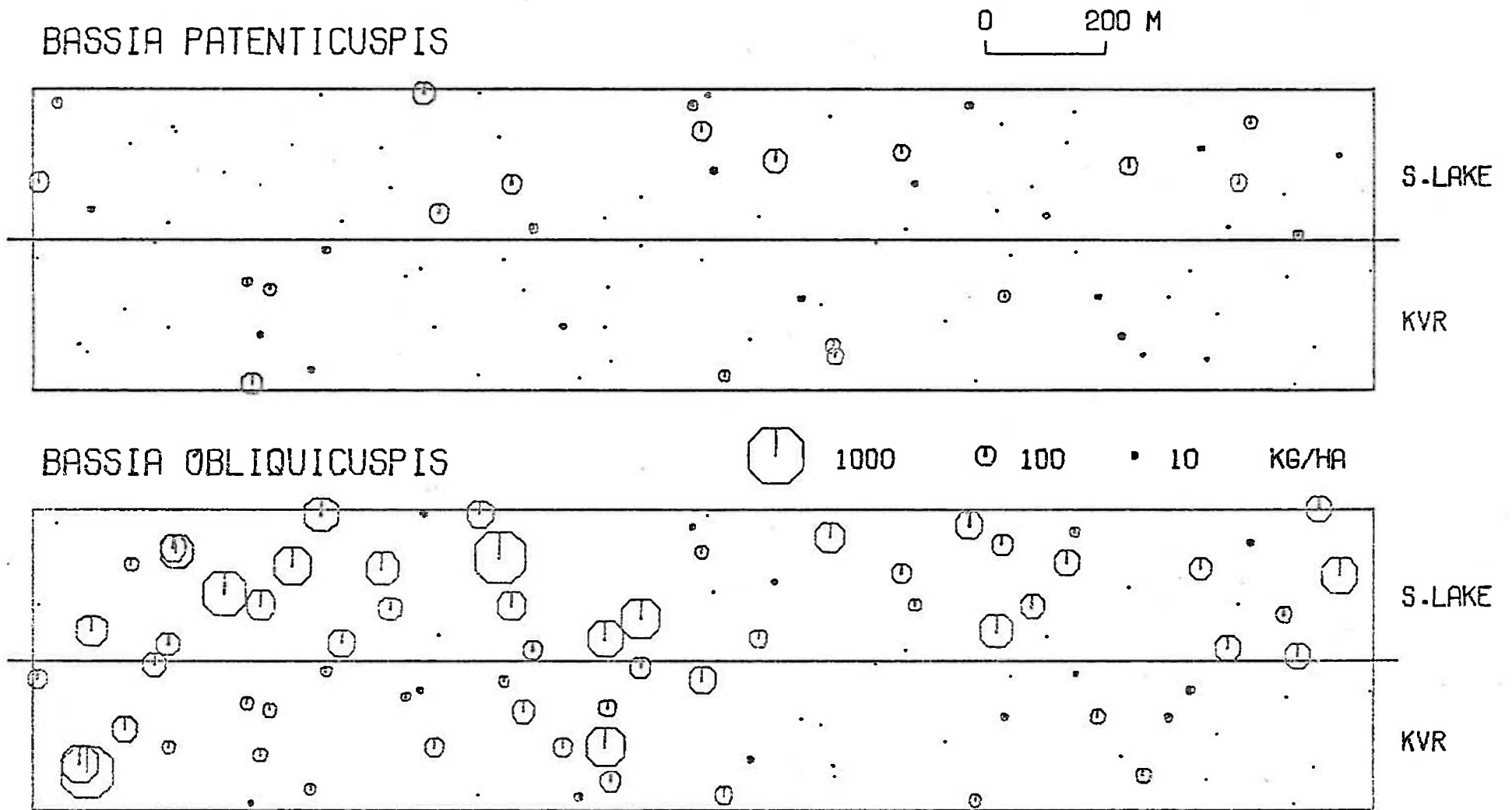
BASSIA PATENTICUSPIS

S-LAKE

KVR

BASSIA OBLIQUICUSPIS

S-LAKE

KVR

Fig 3.3c   Distribution of biomass of ephemerals in KVR and S. Lake, August 1971.

SALSOLA KALI

SALSOLA KALI

BASSIA PARADOXA

S·LAKE

KVR

S·LAKE

KVR

0   200 M

1000   ① 100   • 10   KG/HA
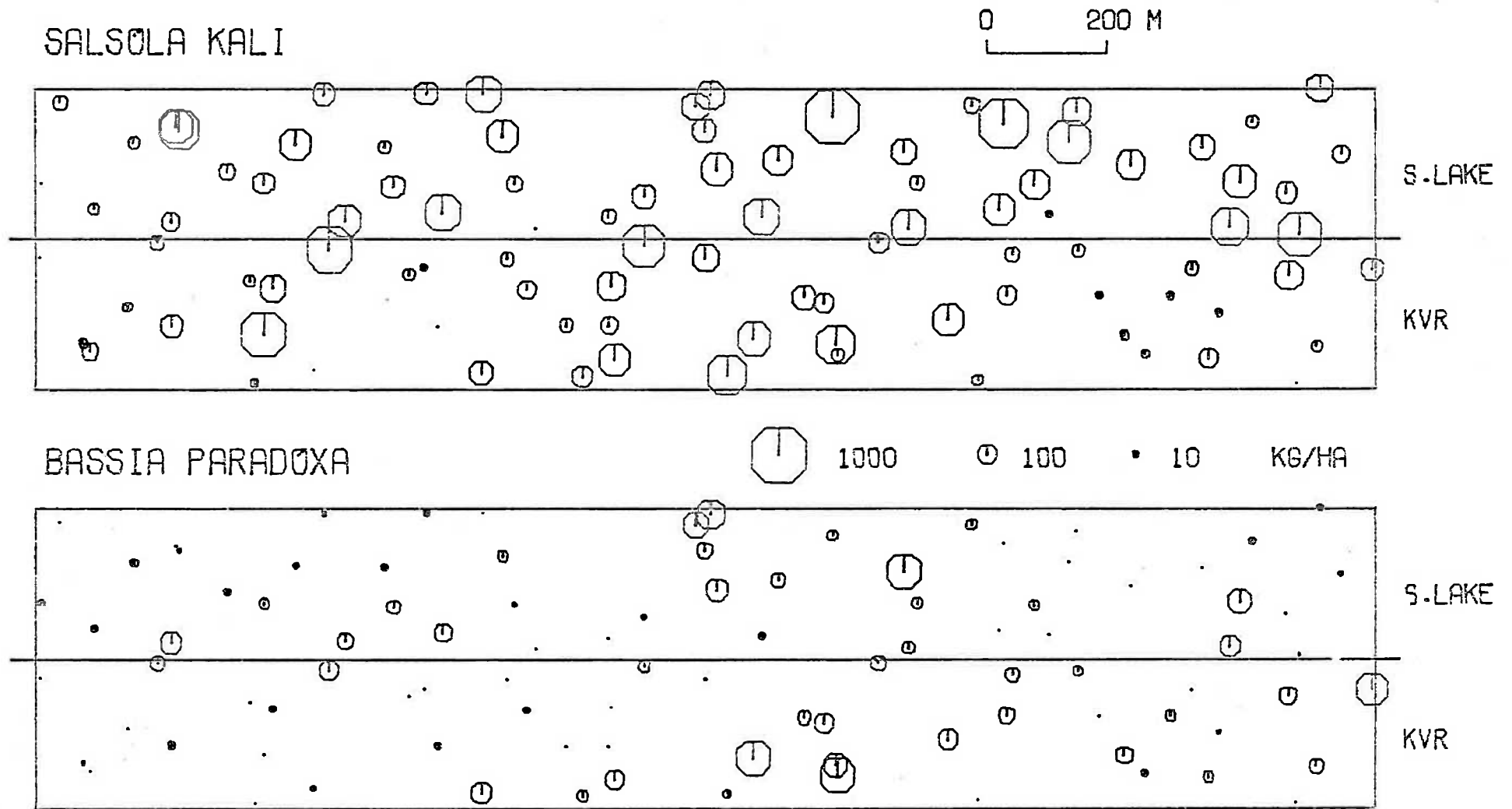
Fig 3.3d   Distribution of biomass of ephemerals in KVR and S. Lake, August 1971.
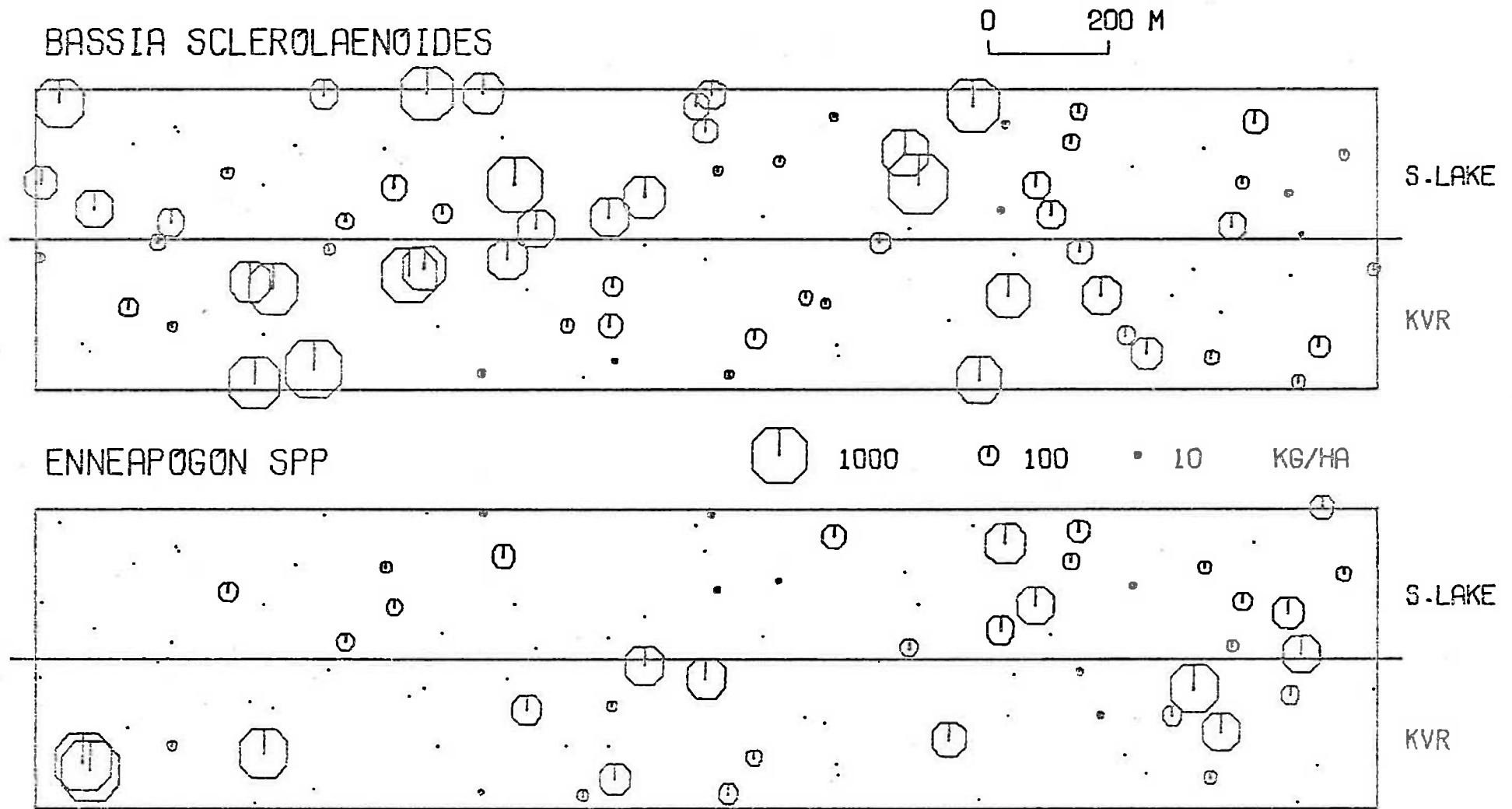
Fig 3.3e   Distribution of biomass of ephemerals in KVR and S. Lake, August 1971.
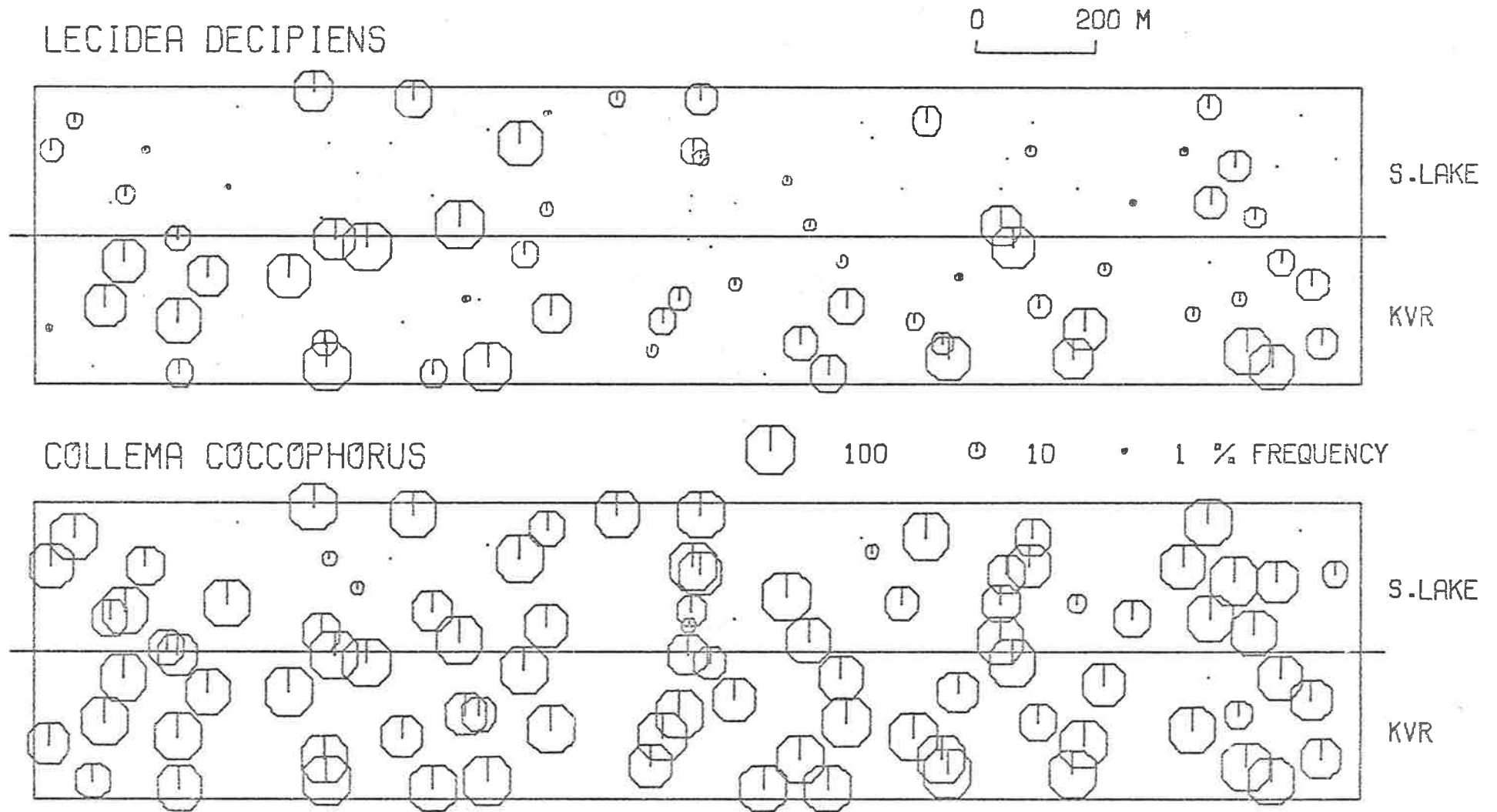
Fig 3.4a   Distribution of frequency of soil cryptogams in KVR and S. Lake, May 1972.

ASPICILIA CALCAREA (CRUSTOSE)

S.LAKE

KVR

ASPICILIA CALCAREA (FRUTICOSE)

100   10   1 % FREQUENCY

S.LAKE

KVR
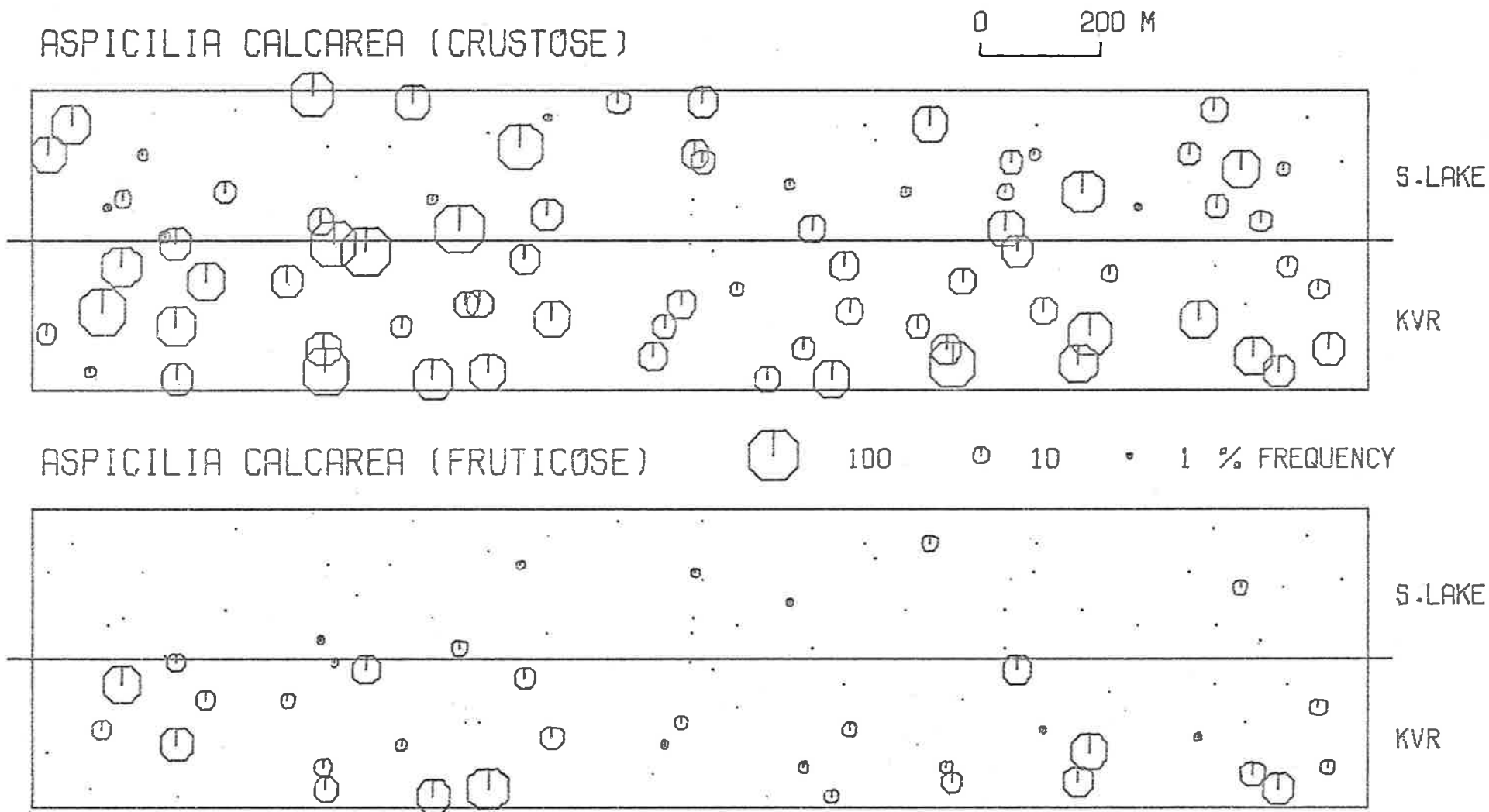
Fig 3.4b   Distribution of frequency of soil cryptogams in KVR and S. Lake, May 1972.

FULGENSIA BRACTEATA

TONINIA CAERULONIGRICANS

S.LAKE

KVR
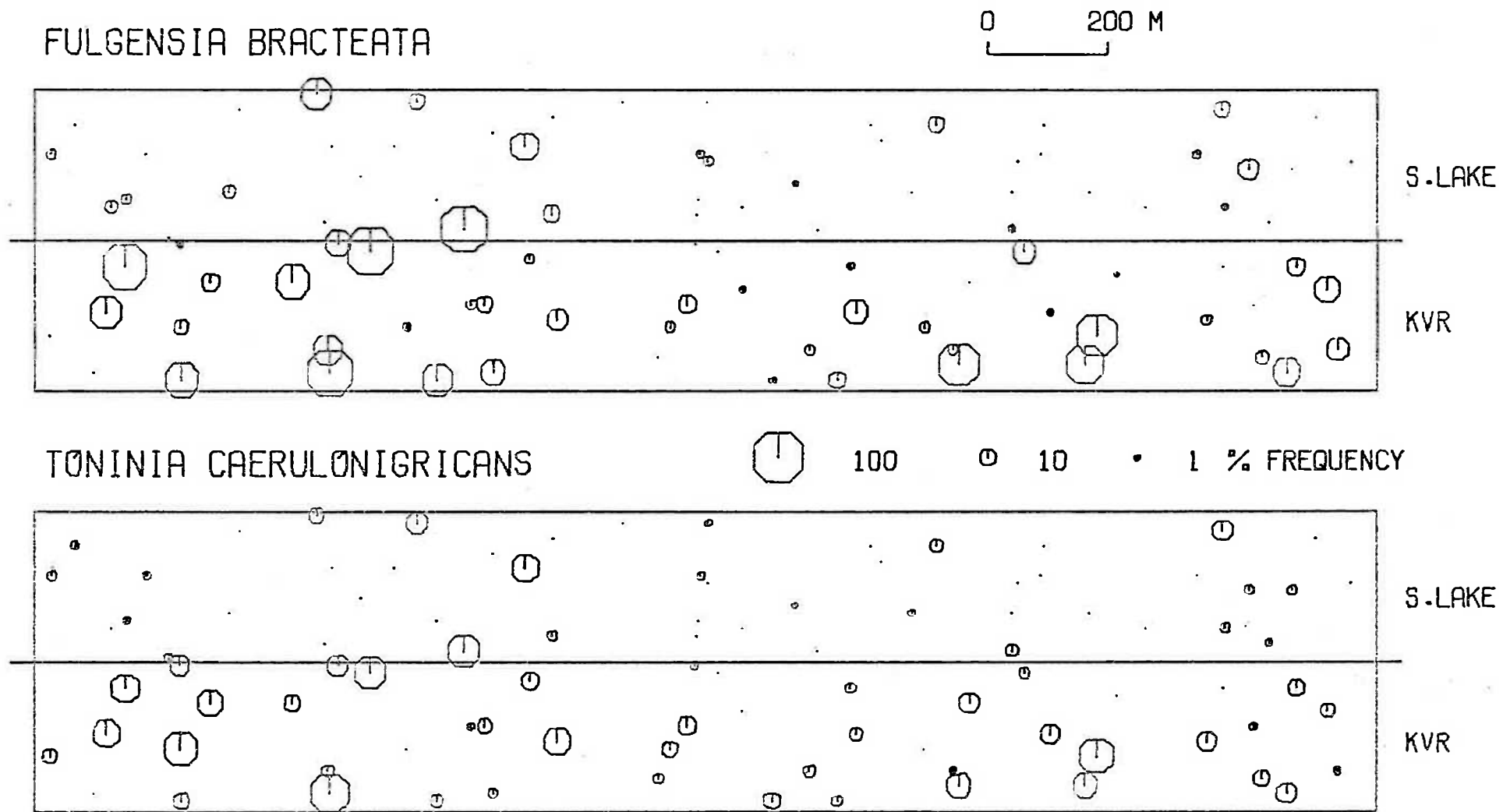
100 ⊙ 10 • 1 % FREQUENCY

Fig 3.4c   Distribution of frequency of soil cryptogams in KVR and S. Lake, May 1972.
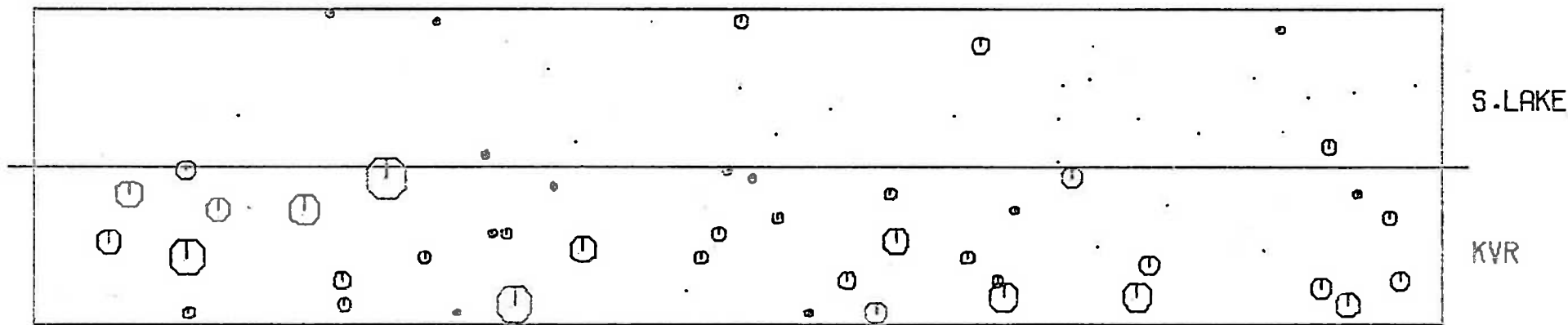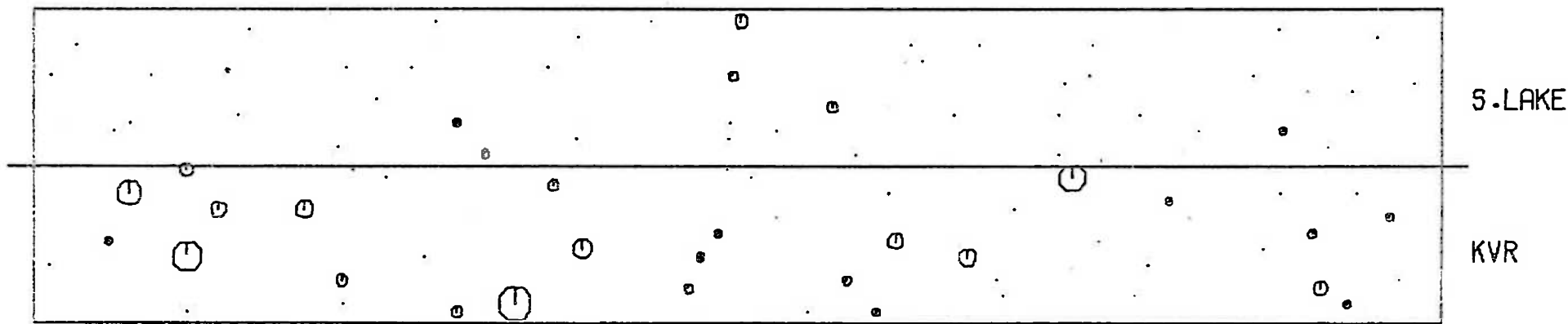
Fig 3.4d   Distribution of frequency of soil cryptogams in KVR and S. Lake, May 1972.
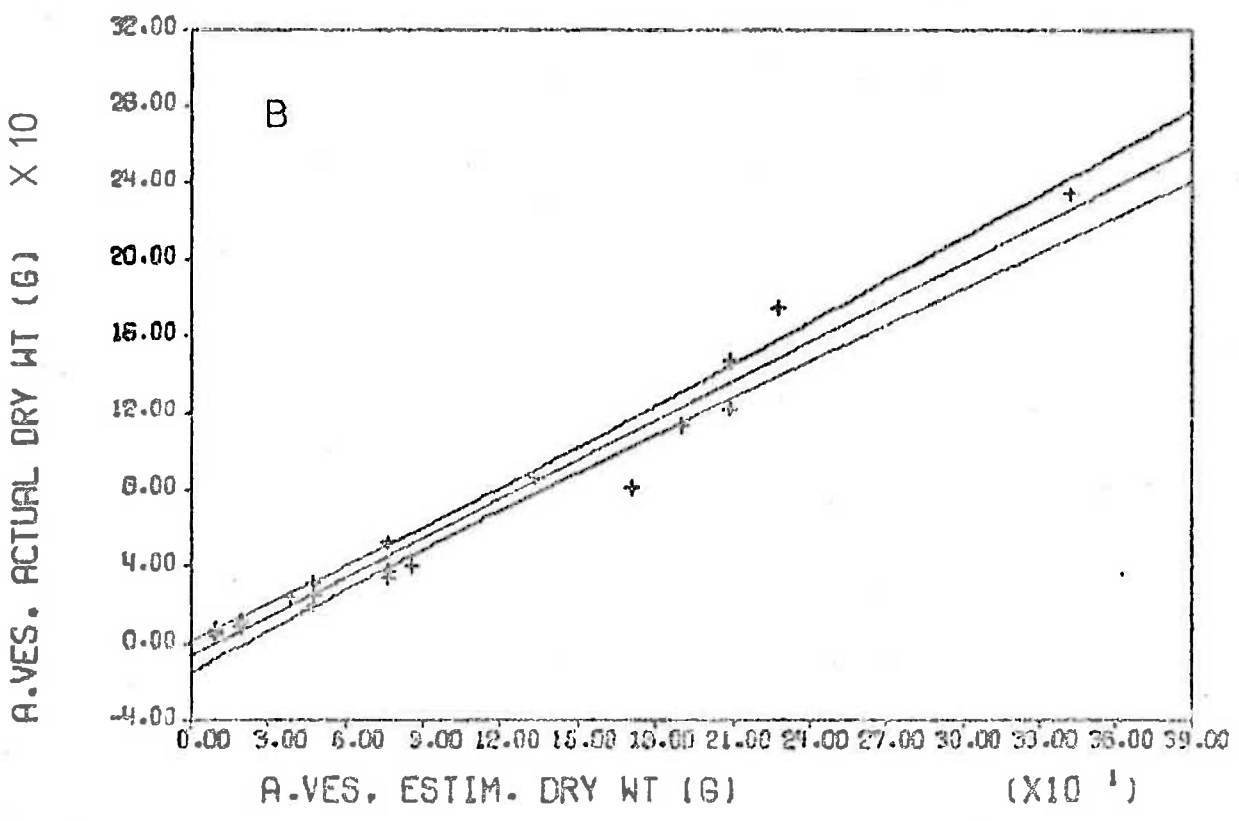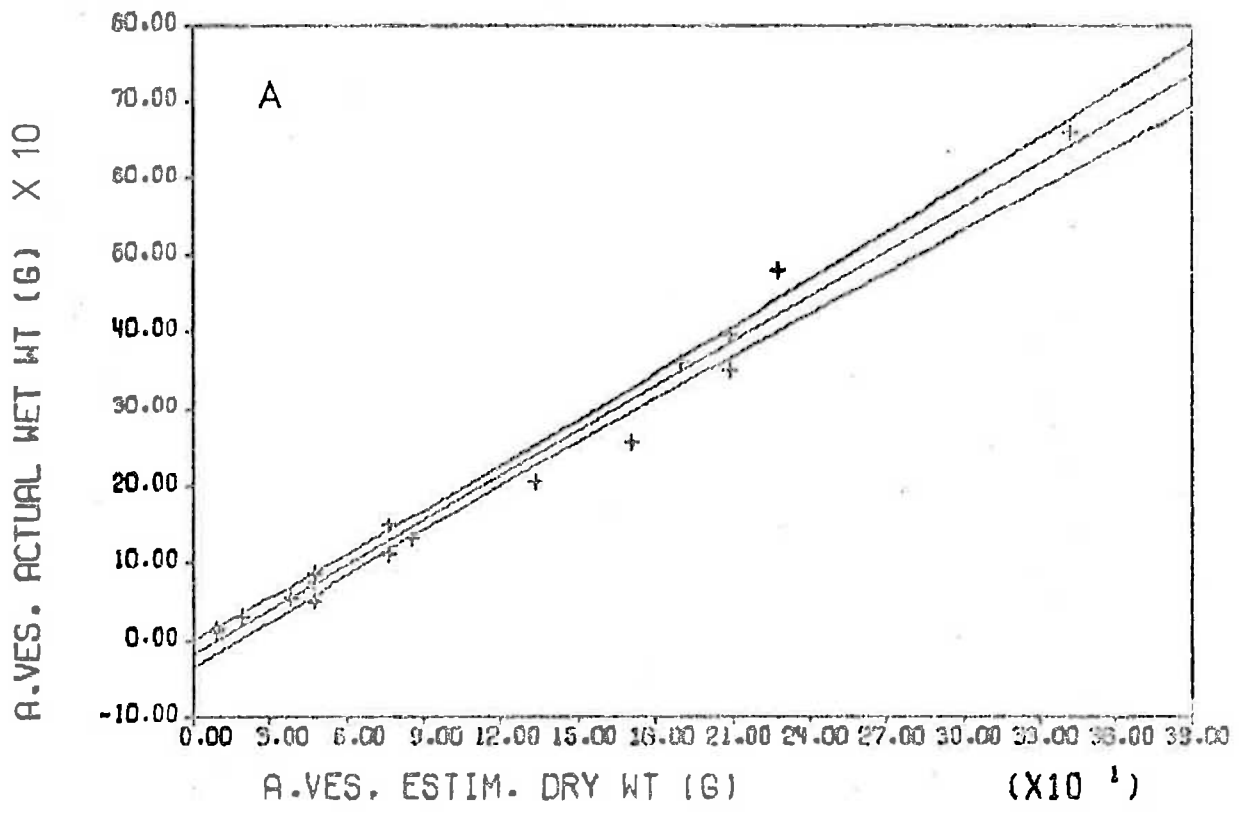
Fig 3.5   Calibration lines for biomass estimation of *Atriplex
           vesicaria*, comparing estimation of wet weight (a) with
           estimation of dry weight (b). Details of linear regressions
           are in Table 3.8. 95% confidence limits are shown.
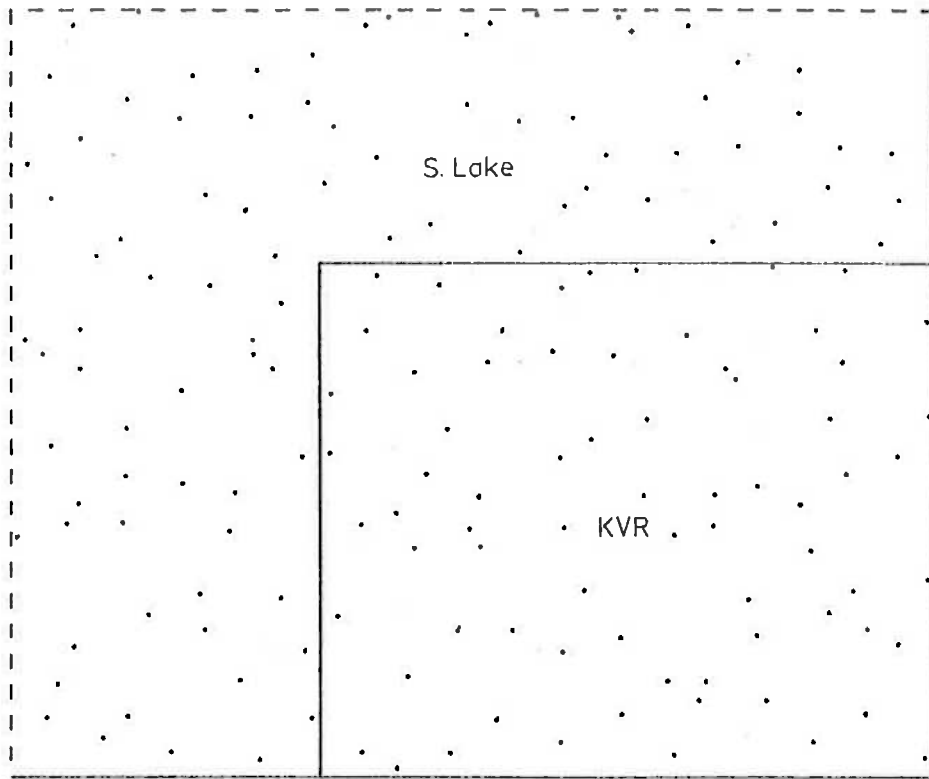
Base map

500 m

Bassia diacantha

[biomass]

```
  o       O        O      kg/ha
  2       20      200
```
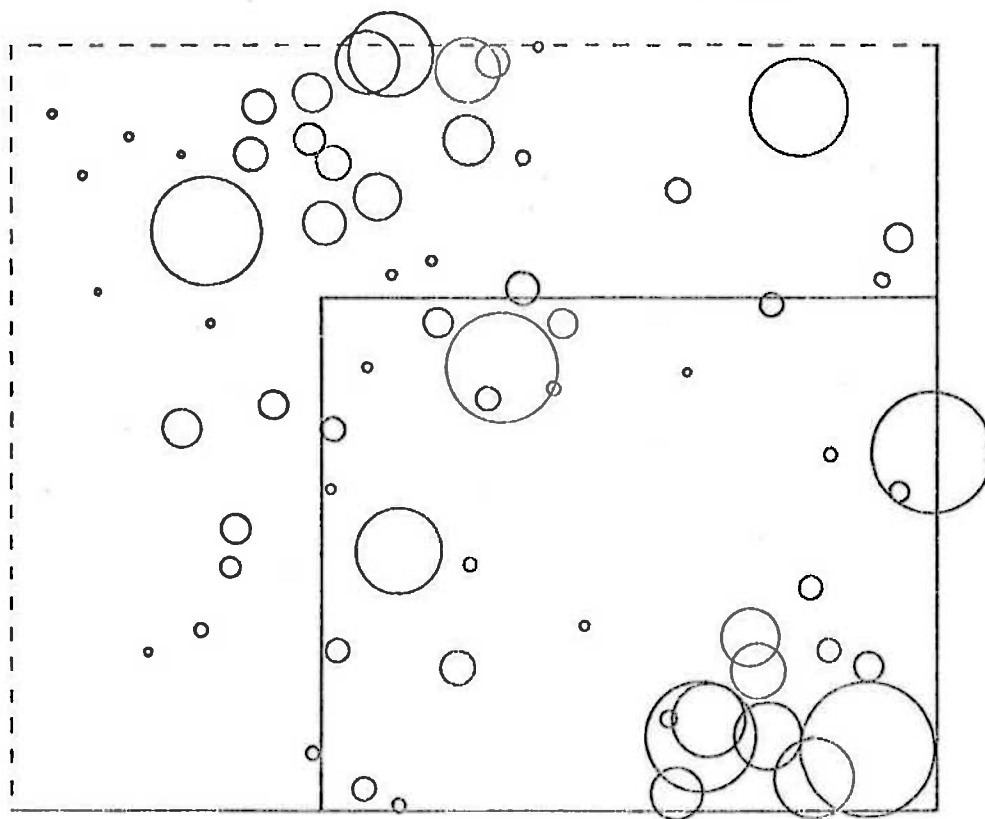
Fig 3.6a   Base map and distribution of biomass of
            Bassia diacantha in KVR and S. Lake, July
            1971.

Atriplex vesicaria
[density]

500 m

200   2000   20000 no/ha

Atriplex vesicaria
[biomass]

2   20   200 kg/ha
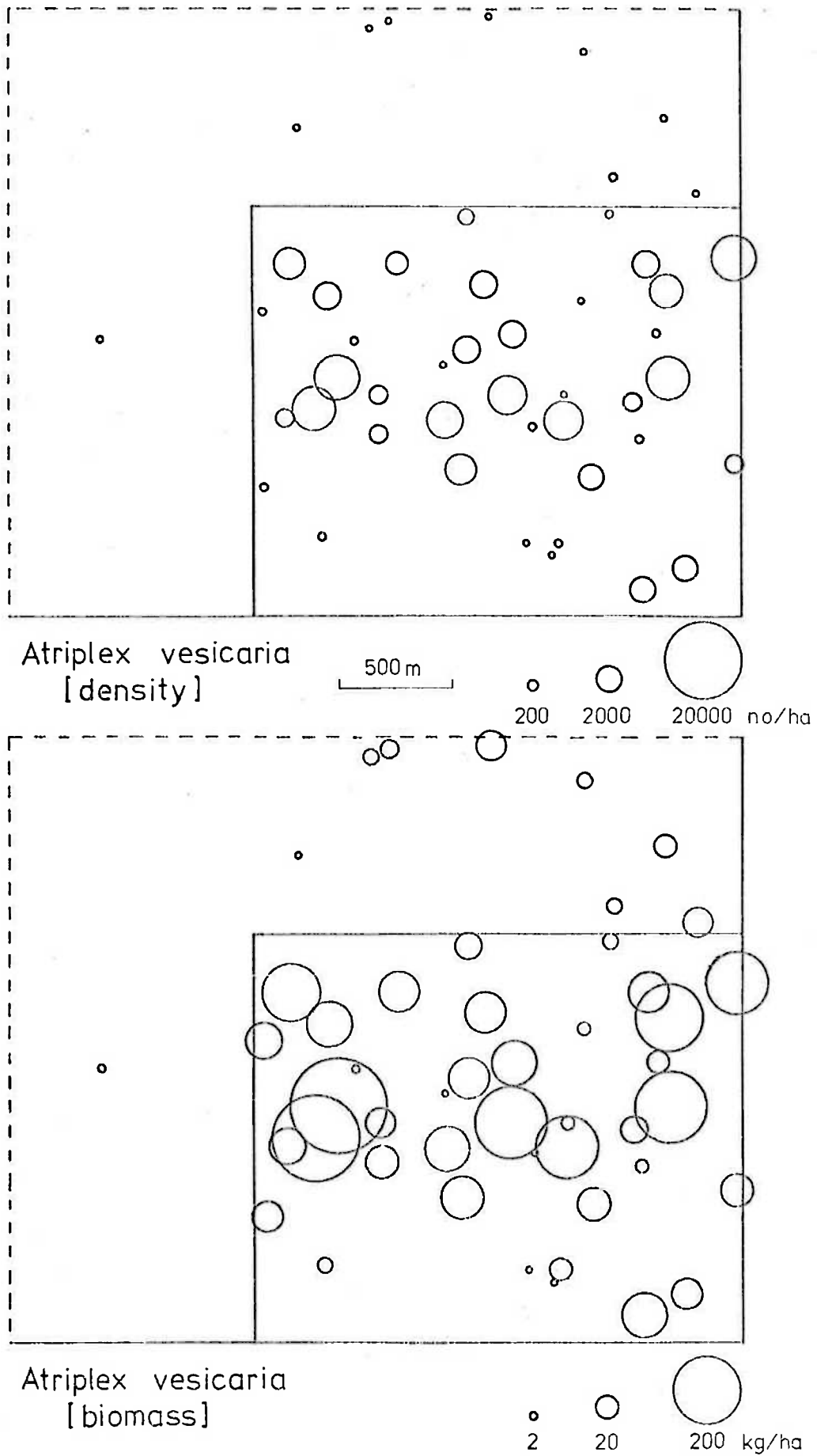
Fig 3.6b   Distribution of density and biomass of
             Atriplex vesicaria in KVR and S. Lake,
             July 1971.

Atriplex stipitata
[density]

500m

200   2000   20000 no/ha

Atriplex stipitata
[biomass]

2   20   200 kg/ha
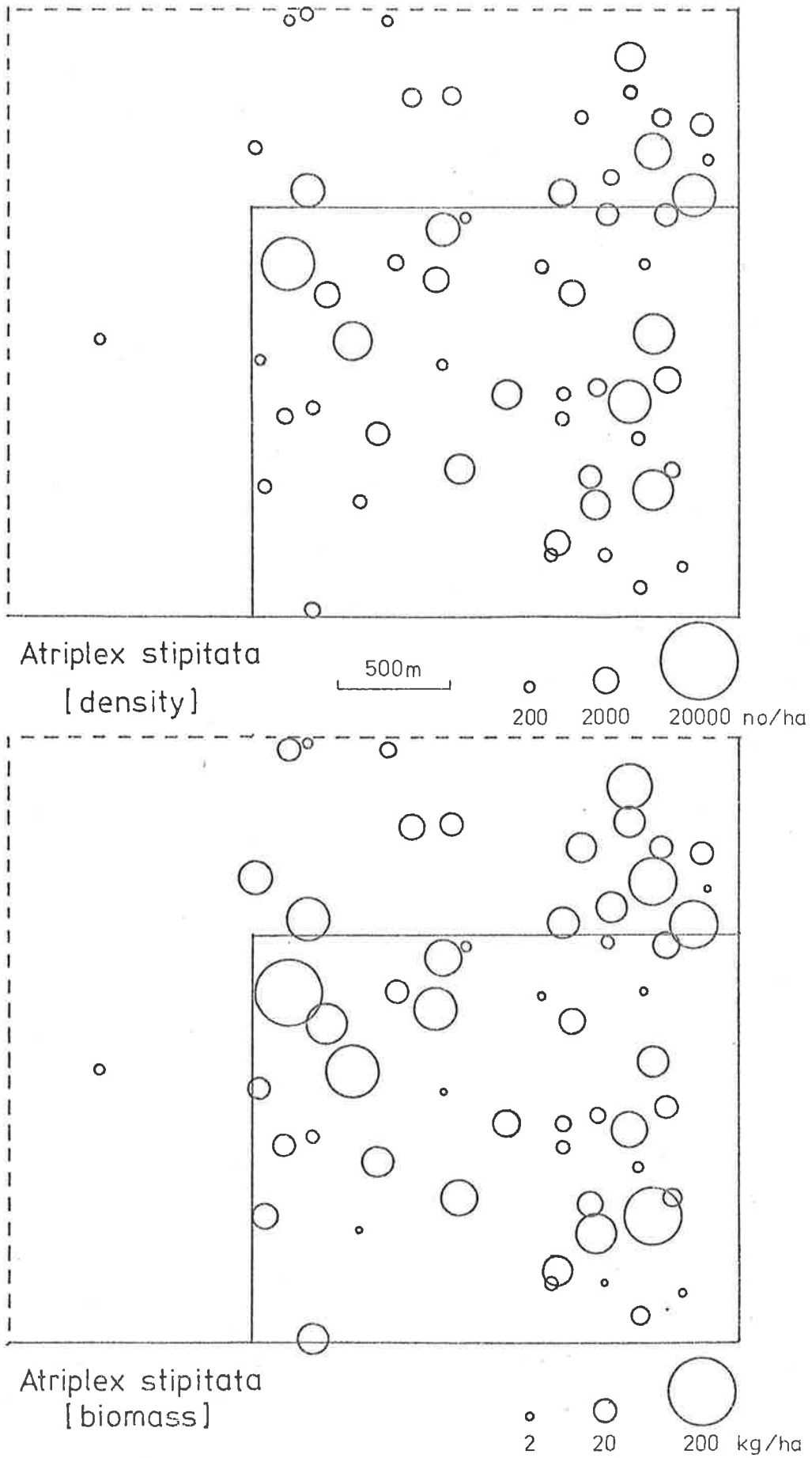
Fig 3.6c   Distribution of density and biomass of
            Atriplex stipitata in KVR and S. Lake,
            July 1971.

Kochia georgei
[density]

500m

200   2000   20000 no/ha

Kochia georgei
[biomass]

2   20   200 kg/ha
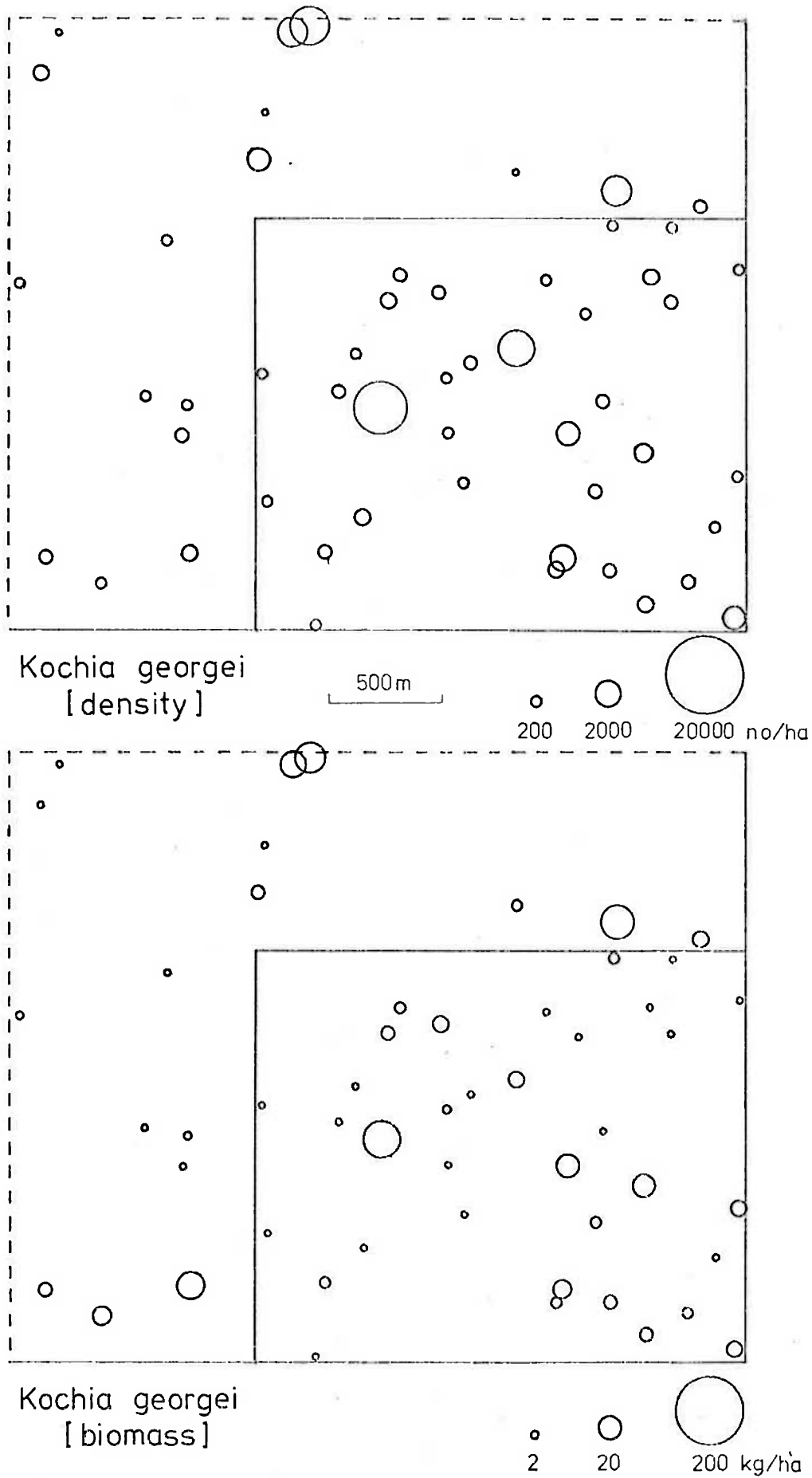
Fig 3.6d   Distribution of density and biomass of
Kochia georgei in KVR and S. Lake,
July 1971.

Total no. of taxa recorded for Koonamore   356

No. of new taxa recorded by Crisp   150

No. of taxa recorded by Carrodus, not
    recorded by Crisp   32

No. of taxa in KVR   175

No. of taxa in KVR, not found in S. Lake   56

No. of taxa in S. Lake, not found in KVR   19

Table 3.1   Summary of the results of the floristic survey.
                Full details are in Appendix 1.

Species	Mean_o	Mean_i	S_o	S_i	t	Prob
Total biomass	1000	1080	408	491	.03	
Stipa nitida	84	373	136	291	6.24	3
Salsola kali var *strobilifera*	346	248	352	256	1.57	
Bassia sclerolaenoides	167	106	219	166	1.55	
B. obliquicuspis } *B. patenticuspis*	187	91	166	140	3.06	2
Enneapogon spp	64	69	118	100	.22	
Bassia diacantha	67	66	199	172	.01	
Schismus barbatus	20	1.4	50	4	2.61	2
Bassia paradoxa	32	74	52	78	3.13	2
Erodiophyllum elderi	18	1.7	78	10	1.44	
Chenopodium cristatum	6.7	5.5	16	21	1.77	
Zygophyllum aurantiacum var.	.2	4.5	1.4	14	2.09	2
Erodium spp	.04	.4	.04	1.5	1.81	
Helipterum moschatum	.2	1.2	1.1	4.7	1.46	
Tribulus terrestris	.2	2.8	1.2	14	1.25	
Nicotiana goodspeedii	2.6		15		1.23	
Calotis cymbacantha		.9		5.6	1.18	
Boerhavia diffusa	.7	.03	4.9	.05	1.02	
Euphorbia drummondii	.5	.1	1.9	.6	1.52	
Zygophyllum iodocarpum	.2	.1	1.7	.8	.48	
Vittadinia triloba		.1		.5	1.77	
Convolvulus erubescens	.02	.01	.3	.03	.90	
Sonchus oleraceus	.01		.02		1.00	
Podocoma nana		.01		.1	1.00	
Eragrostis dielsii						
Omphalolappula concava						

Table 3.2.   Cross-fence comparisons – ephemerals in May 1971.
Means are dry weight in kg/ha. Species are ranked
in approximate order of biomass, and ranking matches
Table 3.3. Subscripts signify S. Lake (o) and KVR
(i). S is standard deviation. t is the value from
the t test. Prob is the probability from t : blank
means $P > 0.05$; 2 means $0.01 > P > 0.001$; 3 means
$P < 0.001$.

Species	Mean$_o$	Mean$_i$	S$_o$	S$_i$	t	Prob
Total biomass	1280	1290	482	422	.14	
Stipa nitida	207	546	253	427	4.73	3
Salsola kali var *strobilifera*	246	143	198	168	2.75	2
Bassia sclerolaenoides	227	183	302	283	.74	
B.obliquicuspis	181	80	181	151	2.95	2
B. patenticuspis	26	10	45	24	2.17	1
Enneapogon spp	71	138	125	278	1.54	
Bassia diacantha	30	91	94	195	1.95	
Schismus barbatus	196	24	311	56	3.79	3
Bassia paradoxa	45	55	76	89	.58	
Erodiophyllum elderi	42	13	220	86	.84	
Chenopodium cristatum	5.1	.3	12	1.7	2.67	2
Zygophyllum aurantiacum var.		5.3		26	1.39	
Erodium spp		4.1		17	1.70	
Helipterum moschatum	2.4	.7	15	3.6	.77	
Tribulus terrestris						
Nicotiana goodspeedii						
Calotis cymbacantha						
Boerhavia diffusa						
Euphorbia drummondii						
Zygophyllum iodocarpum						
Vittadinia triloba						
Convolvulus erubescens						
Sonchus oleraceus						
Podocoma nana						
Eragrostis dielsii	2.0		8.3		1.68	
Omphalolappula concava	.3	.4	1.0	1.7	.59	

Table 3.3. Cross-fence comparisons - ephemerals in August, 1971.
Means are dry weight in kg/ha. Ranking of species
matches Table 3.2. Subscripts signify S. Lake (o)
and KVR (i). S is standard deviation. t is the
value from the t test. Prob is the probability from
t : blank means P > 0.05 ; 1 means 0.05 > P > 0.01 ;
2 means 0.01 > P > 0.001 ; 3 means P < 0.001.

Species	S. Lake		KVR	
	Loam	Sand	Loam	Sand
Stipa nitida	49.1(78.3)	32.8(51.5)	178(145)	196(149)
Salsola kali var.	146(189)	208(156)	102(132)	147(122)
Bassia sclerolaenoides	135(119)	17.4(40.1)	93.3(96.7)	9.1(25.5)
B. obliquicuspis } *B. patenticuspis*	82.3(70.0)	108(96.5)	40.0(46.3)	51.6(89.5)
Enneapogon spp.	12.0(32.6)	57.8(78.7)	6.3(16.5)	65.2(56.5)
Bassia diacantha	25.9(85.9)	42.8(117)	44.1(103)	21.1(67.1)
Schismus barbatus	2.0(4.9)	20.4(34.9)	.15(.47)	1.3(2.7)
Bassia paradoxa	21.0(31.4)	9.6(14.5)	34.7(34.3)	39.8(43.8)
Erodiophyllum elderi	16.0(51.3)		1.7(6.7)	
Chenopodium cristatum	.3(1.1)	7.3(10.9)	2.3(11.2)	3.3(10.1)
Z. aurantiacum var.	.17(.90)		.58(1.8)	4.1(9.9)

Table 3.4a   Ephemerals in May, 1971 - mean biomass and standard deviation calculated for each side of the fence, and for each soil type, separately. Entries are of the form : mean (standard deviation), expressed in kg/ha.

Species	Soils comparisons		Cross-fence comparisons	
	S. Lake	KVR	Loam	Sand
Stipa nitida			3	3
Salsola kali var.				
Bassia sclerolaenoides	3	3		
B. obliquicuspis } *B. patenticuspis*			2	1
Enneapogon spp.	1	3		
Bassia diacantha				
Schismus barbatus	1		1	1
Bassia paradoxa				2
Erodiophyllum elderi				
Chenopodium cristatum	2			
Z. aurantiacum var.				1

Table 3.4b   Ephemerals in May, 1971 - results of *t* tests for comparisons of mean biomass, with soils comparisons made separately for each side of the fence and cross-fence comparisons made separately for each soil. Entries are probability ratings as for Table 3.3.

Species	S. Lake		KVR	
	Loam	Sand	Loam	Sand
Stipa nitida	117 (148)	90 (102)	306 (220)	214 (192)
Salsola kali var.	84.9 (64.7)	161 (113)	53.4(70.0)	104 (99)
Bassia sclero-laenoides	184 (175)	42.8(75.6)	138 (158)	6.9(17.3)
B. obliquicuspis	59.9(98.3)	121 (72)	23.5(45.4)	71 (107)
B. patenticuspis	24.9(26.7)	1.0(3.5)	7.0(13.8)	1.5(5.3)
Enneapogon spp.	8.3(20.8)	62.3(77.7)	2.2(5.6)	191 (179)
Bassia diacantha	18.0(57.3)	12.2(34.8)	62.2(117)	15.3(25.8)
Schismus barbatus	67.8(154)	128 (154)	3.4(9.5)	26.9(41.5)
Bassia paradoxa	35.9(48.7)	8.9(3.0)	27.5(44.9)	27.0(45.3)
Erodiophyllum elderi	42.0(155)		10.2(53.8)	
Chenopodium cristatum	.3(1.5)	4.8(8.2)		.4(1.5)
Z. aurantiacum var.			2.9(15.9)	2.1(5.9)

Table 3.5a Ephemerals in August, 1971 - mean biomass and standard deviation calculated for each side of the fence, and for each soil type, separately. Entries are of the form : mean (standard deviation), expressed in kg/ha.

Species	Soils comparisons		Cross-fence comparisons	
	S. Lake	KVR	Loam	Sand
Stipa nitida			3	1
Salsola kali var.	2	1		
Bassia sclero-laenoides	3	3		1
B. obliquicuspis	1			
B. patenticuspis	3	1	2	
Enneapogon spp.	2	3		1
Bassia diacantha		1		
Schismus barbatus		1	1	2
Bassia paradoxa	2			
Erodiophyllum elderi				
Chenopodium cristatum	1			1
Z. aurantiacum var.				

Table 3.5b Ephemerals in August, 1971 - results of *t* tests for comparisons of mean biomass, with soils comparisons made separately for each side of the fence and cross-fence comparisons made separately for each soil. Entries are probability ratings as for Table 3.3.

Species	$Mean_o$	$Mean_i$	S_o	S_i	t	Prob
Collema coccophorus	63.6	81.4	35.6	21.0	3.89	3
Lecidea decipiens	15.1	38.7	24.6	33.8	3.95	3
Aspicilia calcarea (crustose)	20.6	39.4	26.2	26.0	3.24	3
A. calcarea (fruticose)	1.1	13.6	2.4	18.2	4.84	3
Fulgensia bracteata	5.0	20.0	14.2	25.2	3.56	3
Toninia caerulonigricans	3.8	13.1	7.6	13.8	4.11	3
Lecidea crystallifera	.7	11.4	2.0	13.8	5.30	3
Riccia lamellosa	.4	4.2	1.2	8.2	3.28	3
Acarospora smaragdula	.5	2.4	2.2	7.6	1.70	
Diploschistes scruposus		.6		2.4		
Chondropsis semiviridis		.08		.1		
Parmelia convoluta		.04		.1		

Table 3.6   Cross-fence comparisons - cryptogams in May, 1972.
Means are frequency (%). All other entries have the
same meaning as in Table 3.3.

Species	S. Lake		KVR	
	Loam	Sand	Loam	Sand
Collema coccophorus	40.2 (11.3)	17.4(16.6)	46.7(5.4)	36.4(12.0)
Lecidea decipiens	12.7 (14.3)	.7(2.0)	32.6(12.4)	5.0(5.7)
Aspicilia calcarea (crustose)	18.0 (13.6)	2.1(3.6)	27.4(11.7)	11.3(8.3)
A. calcarea (fruticose)	.7 (1.5)		12.1(9.9)	1.0(2.0)
Fulgensia bracteata	4.6 (9.0)	.1(.1)	16.4(13.9)	3.1(5.7)
Toninia caerulonig-ricans	2.8 (4.8)	.2(.5)	9.4(8.1)	3.0(2.8)
Lecidea crystallifera	.4 (1.1)	.2(.9)	9.5(7.7)	1.6(1.7)
Riccia lamellosa	.3 (.7)		3.7(5.1)	.4(.8)
Acarospora smaragdula	.4 (1.4)		2.2(5.2)	.2(.5)

Table 3.7a   Soil cryptogams in May, 1972 - mean frequency (%) and standard deviation calculated for each side of the fence, and for each soil type, separately. Entries are of the form : mean (standard deviation).

Species	Soils comparisons		Cross-fence comparisons	
	S. Lake	KVR	Loam	Sand
Collema coccophorus	3	3	2	3
Lecidea decipiens	3	3	3	2
Aspicilia calcarea (crustose)	3	3	2	3
A. calcarea (fruticose)	1	3	3	1
Fulgensia bracteata	1	3	3	1
Toninia caerulonig-ricans	2	3	3	3
Lecidea crystallifera		3	3	3
Riccia lamellosa	1	2	2	1
Acarospora smaragdula				

Table 3.7b   Soil cryptogams in May, 1972 - results of t tests for comparisons of mean frequency, with soils comparisons made separately for each side of the fence and cross-fence comparisons made separately for each soil. Entries are probability ratings as for Table 3.3.

Species	y	a	b	$S_{\bar{y}}$	Prediction error (%)	$C_{x.y}$ (%)
A. vesicaria	dry weight	- 6.8	0.682	2.66	21	19
	wet weight	-19.0	1.93	5.88	31	14
A. stipitata (green)	dry weight	- 6.4	0.930	1.96	22	15
	wet weight	- 8.8	1.88	4.86	28	18
A. stipitata (dead)	dry weight	0.8	1.11	1.22	27	16
	wet weight	- 1.0	1.38	2.07	39	23
K. georgei	dry weight	- 3.7	1.09	0.73	32	21
	wet weight	-11.9	3.44	3.90	39	36
B. diacantha	dry weight	0.1	1.29	1.93	36	21
	wet weight	- 8.5	3.08	3.06	21	16

Table 3.8   Details of regressions of actual biomass on estimated

biomass.   Regression equation is $y = a + bx$.   X is

always estimated dry weight. $S_{\bar{y}}$ is the standard error

of the estimate of $\bar{y}$.   Prediction error is the 95% limit

of the prediction of y_i from x_i (k=1) as a percentage

of $\bar{x}$.   (Sokal and Rohlf 1969, chap.14). $C_{x.y}$ is the

standard deviation as a percentage of the mean (Tadmor

et al 1975).

Species	Variable	Mean_o	Mean_i	S_o	S_i	t	Prob
Atriplex vesicaria	biomass	1.5	43.7	6.0	79.1	4.51	3
	density	18.9	1060	58.9	762	5.04	3
Atriplex stipitata	biomass	8.2	18.5	22.3	36.5	2.11	1
	density	290	910	949	1670	2.80	2
Kochia georgei	biomass	2.1	2.9	7.7	7.9	.62	
	density	174	309	13.2	19.7	1.43	
Bassia diacantha	biomass	17.4	36.4	51.9	94.8	1.52	

Table 3.9   Cross-fence comparisons - low shrubs in July, 1971.
Biomass values are dry weight (estimated) in kg/ha.
Density values are individuals/ha. All other entries
have the same meaning as in Table 3.3.

Name	Variable	S. Lake		KVR	
		Loam	Sand	Loam	Sand
A.vesicaria	density	20.2(63.1)	5.5(28.9)	1650(2050)	472(1100)
	biomass	2.2(7.3)	0.3(1.5)	73.2(96.0)	14.4(35.6)
A.stipitata	density	333(1080)	108(428)	828(1750)	990(1610)
	biomass	9.1(23.9)	6.4(18.9)	15.7(37.1)	21.0(36.1)
K.georgei	density	215(740)	105(458)	760(1500)	185(380)
	biomass	2.8(8.9)	0.8(4.4)	5.5(10.4)	1.5(3.8)
B.diacantha	biomass	9.2(28.1)	33.4(78.6)	22.3(32.3)	50.3(69.0)

Table 3.10a   Low shrubs in July, 1971 - mean biomass and density with standard deviation calculated for each side of the fence, and for each soil type, separately. Entries are of the form : mean (standard deviation), expressed in kg/ha.

Name	Variable	Soils comparisons		Cross-fence comparisons	
		S. Lake	KVR	Loam	Sand
A.vesicaria	density		2	3	1
	biomass	3	3	3	1
A. stipitata	density				2
	biomass				1
K.georgei	density		1	1	
	biomass		1		
B.diacantha	biomass		3	3	

Table 3.10b   Low shrubs in July, 1971 - results of t tests for comparisons of mean biomass and density, with soils comparisons made separately for each side of the fence and cross-fence comparisons made separately for each soil. Entries are probability ratings as for Table 3.3.

4.   Small scale cross-fence comparisons of soils and
       two ephemeral grasses

4.0   Introduction

4.01   General

This chapter describes the further development of the cross-
fence comparisons, the aim being to investigate how some of the
observed differences (chapter 3) might have arisen. In chapter
1 the reasons for developing this, rather than the other area
of initial work (chapter 6) are discussed. The intention was
to carry out detailed measurements and comparisons of vegetation
soil and micrometeorological variables - an approach similar in
scope to those of Langlands and Bennett (1973) and Smoliak et al
(1972). The approach was basically observational so as to build
a sound basis for hypothesis formulation.

4.02   Choice of species

Although there were striking differences between KVR and S. Lake
in all strata of the vegetation (section 3.6), it seemed best
to limit further work to a few species and study these in depth.

Lichens and their response to stocking pressure have been
studied well by Rogers and Lange (1971a) and Rogers (1972).
My initial findings were in no way inconsistent with theirs
(section 3.33).

The saltbushes had shown large cross-fence differences also
(section 3.43). Many Australian workers have investigated the
impact of grazing by sheep on *Atriplex* shrublands (Osborn et al
1932; Knowles and Condon 1951; Jessup 1951; Barker and Lange 1970;
Lay 1972). The consensus of these is that except at the most
moderate rates, stocking pressure is deleterious to survival of
Atriplex. Leigh and Mulham (1971) have investigated survival
of shrubs in relation to degree of damage and much has been
published already from the KVR data records concerning recolon-
isation of denuded areas by *Atriplex* (Hall et al 1964).

Much less is known about the role of ephemerals in
chenopod shrublands, the most notable work having been done on
the Riverine Plain in New South Wales (Williams 1966, 1968b, 1969,
1970a, 1970b; Wilson and Leigh 1964) and in the Murchison region
of Western Australia (Mott 1972, 1974; Mott and McComb 1974).
Both these areas differ markedly from Koonamore in flora, soils
and microrelief.

There is no doubt that the ephemerals form an important
component of the Koonamore vegetation. In the wet year of 1971
the ratio of peak ephemeral biomass to low shrub biomass (green
shoots) was approximately 20:1 in KVR and 100:1 in S. Lake.
Much of Koonamore and the surrounding district resembles S. Lake
in lacking most of the original shrubs, leaving ephemerals (when
present) as the principal vegetation.

Systems comparable with Koonamore both in general structure
and in composition of their ephemeral floras occur over a wide
area e.g. at Whyalla (Noble 1975), in the 'Northwest' of South

Australia (Jessup 1951; Lay 1972), and at Broken Hill (Pidgeon
and Ashby 1940; Beadle 1948). Little is known about the phenology
of the response to stocking pressure of these ephemeral floras.
I concluded that they were a logical choice for further study at
Koonamore.

In particular the species *Stipa nitida* and *Schismus barbatus*
were chosen for detailed study. These provided an interesting
contrast in response to protection from stocking (section 3.63)
and had shown greater cross-fence differences than any other
ephemerals. *Stipa* is an important pasture species across a wide
area of southern arid Australia. It produced a greater biomass
than any other ephemeral at KVR (Tables 3.2 and 3.3). *Schismus,*
although introduced to Australia had established itself in the arid
zone so quickly that Osborn (1929) commented that

> "it is hard to realise that... (it is) not native
> to the (arid) district".

Its present distribution extends through most of arid South
Australia.

Concurrently with the present small scale cross-fence
studies of *Stipa* and *Schismus* a phenological investigation of
several ephemeral species was made (chapter 5).

4.1   Methods

4.10   Introduction

The occurrence of arid zone ephemerals is dependent upon unreliable
rainfall and therefore intermittent.

Given the unpredictability of rain at Koonamore (Hall et al 1964)
it seemed best to artificially stimulate germination and growth
of *Stipa* and *Schismus* by irrigation. Watered field plots were
initiated at regular intervals throughout one year because the
seasonal conditions for establishment of these species (given
adequate moisture) were largely unknown. At the same time
information about germination and establishment in relation to
season of other ephemerals was obtained (chapter 5). Irrigation
and sampling were done 9 times between February 1973 and January
1974 i.e. at intervals of ca 6 weeks (Fig 4.3).

4.11 Choice of sites and plot design

Two sites were used to represent the sand and loam soil types
respectively. Each site was a long homogeneous strip (50 m x
20 m) designed to allow placement of 'matched' pairs of plots
a few feet apart on either side of the KVR/S. Lake fence. The
sites were located halfway along the northern fence (loam soil)
and halfway along the western fence (sandy soil) of KVR.

Each site was fenced to exclude rabbits, sheep, cattle
and kangaroos (Fig 4.1). Kangaroos can damage severely a low
fence in gaining access to a small exclosure, which they may
graze heavily. Perry[†] (pers. comm.) and Fatchen[*] (pers. comm.)
both experienced this problem. However, the height (2.5 m) of
my fences apparently deterred kangaroos from attempting to enter.
The other grazing mammals also were successfully excluded.

[†] R.A. Perry, Chief, Division of Land Resources Management, C.S.I.R.O.

[*] T.J. Fatchen, Scientific Officer, National Parks and Wildlife
  Service, South Australia.

New plots were used at each time. On a single plot repeated
irrigation might have drained the reservoir of seeds in the soil.
Each plot was placed 3 m away from the KVR/S. Lake fence to
avoid the well-worn animal tracks running along the fence. The
plots were compact in shape so as to minimise exposure of the area
sampled to the dry surrounding environment. In this situation
the usual quadrat shape, long and narrow to cut across pattern
and minimise variance, could not be used. All sampling was done
at least 50 cm within the irrigated area to avoid edge effects.
The plots were square to match the pattern of the irrigation
system (section 4.12) and were 16 m^2 in area because of limitations
on the amounts of water which could be transported to the sites.

4.12 Irrigation

The plots were sprayed rather than flooded so as to more nearly
simulate natural rainfall. A great variety of rainfall simulators
have been invented (Amer. Soc. Range Mgmt. 1962) but the ones
which imitate best the velocity, drop size distribution and rate
of rainfall are elaborate and expensive. In any case, little is
known about the detailed characteristics of rainfall at Koonamore.
A similar system to Costin and Gilmour's (1970) was used, but with
fixed rather than hand-held nozzles. Nine commercially available
sprinklers were tested in various combinations for uniformity
of water distribution over a grid of 50 small raingauges on an
area of approximately 20 m^2. The most useful system incorporated
4 semicircular pattern nozzles (Rain-bird '1800') yielding an
overall square pattern (Fig 4.1). About 95% of the water delivered
by the pump fell onto a plot of 4 m x 4 m.

The fine spray produced by these nozzles compensated for the high rate of delivery (60 mm of 'rainfall' per h) so that run-off was minimal. A curtain was used to eliminate spray drift in windy conditions.

It was necessary to cart water from rainwater tanks at Waukaringa, 30 km away, this being the nearest source of sufficiently pure water. Tests by the South Australian Dept of Agriculture showed this water to contain < 200 mg/l dissolved salts, most of which were Ca^{++} and HCO_3^-. The equivalent of 50 mm of rainfall was applied to each plot in two 'falls' separated by 24 h. If rain had fallen at Koonamore head station, 5 km to the north, within 48 h before my arrival at the sites, the quantity of artificial rainfall was reduced if necessary to give a total fall of 50 mm. Care was taken not to walk on any plot before irrigation lest compaction of the soil occur and infiltration characteristics be altered. Thus all sampling, except for initial soil samples taken from the edges of the plots, was made after irrigation.

4.13 Vegetation

4.131 Germination and establishment in the field

Total density of *Stipa* and *Schismus* was used as the vegetation variable for the cross-fence comparisons. It was sampled 6 weeks after irrigation. Biomass estimation was not used because errors would have been so high as to mask subtle differences. Vegetation sampling for the phenological study is described in section 5.21.

4.132 Seeds in the soil

The number of viable seeds per unit area of the soil is a very
useful measure of the size of a plant population. The fact
that many species have seeds which are extremely long-lived
when buried (Roberts and Feast 1973) has important consequences.
The first is that for any species, especially for those whose
seed longevity : plant longevity ratio is high (e.g. ephemerals),
abundance of seeds in the soil should be considered in conjunction
with above-ground production in measuring the success of the
species in a given locality Major and Pyott (1966). In a stand
where there is little relation between composition of vegetation
as measured by abundance of plants and as measured by densities
of viable seeds in the soil, the real nature of the vegetation would
be misinterpreted by sampling the former alone. Olmstead and
Curtis (1947) and Livingston and Alessio (1968) found that species
apparently rare or absent in some 'seral' and 'climax' stands
were in fact well represented by viable seeds (and vice-versa).

Various approaches to estimation of this parameter have
been used. The crudest technique is to count emerging seedlings
in the field (Pyatin 1970). An alternative is to attempt to
germinate the seeds in a topsoil sample by incubating subsamples
under a range of simulated field conditions (Johnston et al 1969;
Howard and Ashton 1967). This technique always results in
underestimation by failing to take account of dormancy factors
and unknown germination conditions.

Ideally, seeds should be separated from the soil by one of several available sieving and/or flotation techniques (Robinson and Kust 1972; Barbour and Lange 1967; Malone 1967), identified, and tested for viability by the tetrazolium chloride method (Colbry et al 1961; Malone 1967). This approach was tried but found to be too expensive in time. Many soil seed species from Koonamore (especially grasses) were very small and very difficult to identify.

Instead I used the soil incubation method, from each plot 4 topsoil samples (each 240 cm^2 x 2 cm) were taken and gently homogenised. Half of each sample was spread in a 30 x 15 x 2 cm plastic tray and the two subsamples separately incubated in a 'winter' (light, 20°C / dark, 10° C; day length = 10 h) and a 'summer' (light, 30°C / dark, 20°C; day length = 15 h) regime. Soil moisture was kept at about field capacity until germination rate had reached a plateau. Evaluation of germination of a seed was not made until it had produced a seedling large enough to determine whether the essential parts were present and undamaged, by the criteria of Colbry et al (1960). Total germinations of *Stipa* and *Schismus* were recorded for the cross-fence study. Germinations of other species were recorded also for the phenological study (chapter 5).

4.133 Cover

Total vegetative cover was measured to estimate shading of the soil for interpretation of the temperature measurements (section 4.146). It was determined from percent intercept in 1 cm units along 10 lines per plot, each 1 m long.

4.14 Soils

4.140 Introduction

The list of variables used by different workers to test effects
of stocking on soils is virtually endless. I chose a relatively
small number of variables to represent some key soil features.
Four variables were measured in the laboratory from the same
samples, taken from the upper 2 cm of the soil 24 h after
irrigation (*initial*), to allow tests of correlation. These were
moisture retention, total phosphorus (P), total sulphur (S) and
conductivity. The additional variables, unconfined compressive
strength, temperature, soil moisture, bulk density and depth of
limestone were sampled independently in the field.

4.141 Moisture retention

All of the *initial* upper 2 cm soil samples were dried at room
temperature (20° to 25°C) for one week, weighed, dried to
constant weight at 105°C, and reweighed. Gravimetric water
content (ω) was expressed as loss in weight in % of oven dry
soil weight (Rose 1966). This was used as an indirect measure
of the water holding capacity and hence the clay, and to a
lesser extent the organic matter, content of the soil.

4.142 Phosphorus and sulphur

Total P and S were used as a measure of the soil nutrient status.
Availability indices of N and P were considered but not used
for several reasons.

First, the procedures for their determination are extremely tedious, the outcomes are sensitive to slight variations in technique, and their interpretation is controversial, (Bremner 1965; Olsen and Dean 1965). In addition, not only do availability indices tend to be highly correlated with total element levels but also N tends to be determined largely by P in Australian soils (Charley and Cowling 1968; Prescott 1938). Total P and S (ppm) were determined by the rapid but accurate technique of X-ray fluorescence spectrography (Norrish and Hutton 1964; Norrish and Chappell 1967).

4.143 Conductivity

Low arid shrubland soils are often highly saline, and the distribution of salts in a community can influence strongly the distribution of plants (Charley and McGarity 1964). Osborn and Wood (1923) had reported total soluble salt contents of between 0.1 and 0.2% in the upper 20 cm of the medium textured saltbush soils at Koonamore. Such levels are sufficient to "restrict yields of many crops" (Richards 1954). I estimated salinity by determination of specific conductivity (mmho/cm) of a 1:5 soil suspension at $25^{\circ}C$ (Piper 1942).

4.144 Soil moisture

Soil moisture was sampled 24 h (*initial*) and 6 weeks (*final*) after irrigation. Four profiles were taken from each plot. The uppermost sample of a profile was a plug 6.5 cm in diameter by 2 cm in depth; thereafter cores were taken with a 5.5 cm diameter auger in 8.5 cm depth increments.

At the loam site profiles could be taken only to the limestone layer (ca 20cm) but at the sand site profiles were 50 cm deep. Gravimetric water content was determined as in section 4.141.

4.145 Compaction

In order to estimate compaction of surface soil, various methods of determining bulk density were tried. The soil lacked sufficient cohesion to be sampled with precision by any fixed volume corer, thus ruling out rapid (and extensive) sampling. A small number of samples was taken on a few plots by a slower excavation method.

A pocket penetrometer was used to estimate unconfined compressive strength (kg/cm^2) of the surface soil, as described by Davidson (1965). To minimise variance due to soil moisture content all plots were sampled on a single day when the soil was very dry. Forty random points were sampled on each plot.

4.146 Temperature

Soil and air temperatures were measured at the loam sites for both the cross-fence study and the phenological study. Air temperature was recorded continuously by a Casella thermograph in a Stevenson screen 1 m above the ground. Soil temperatures were recorded continuously with the apparatus described by Rogers (1971). In view of the heterogeneity of the soil surface and the small number of sensors available, comparisons of temperature between different surface conditions, accompanied by comparisons of surface types seemed the most useful approach.

Thermistors were placed at a depth of 1 cm under 3 surfaces viz:
shaded by vegetative cover, unshaded with lichen crust present,
and unshaded with lichen crust absent. Considerable technical
difficulty was experienced with the equipment, mainly through
thermistor corrosion and temperature induced drift in recorder
output. The latter was corrected by calibration.

4.147 Depth of limestone

At the loam site, depth of sdl overlying the limestone layer was
sampled to test for difference in erosional loss of topsoil
between KVR and S. Lake. It was assumed that in the undisturbed
situation the limestone horizon was at a constant depth below
the surface.

4.2   Results

Cross-fence comparisons were made at each site for each variable
except temperature by means of t tests (Table 4.1). The data
for all months were pooled to increase the power of the t test.
It was assumed that season dependent variables (e.g. vegetation
and soil moisture) behaved according to the same season-
dependent function in KVR as in S. Lake.

Cross-fence differences in density of *Stipa* and *Schismus*
were similar to the biomass differences observed in the initial
study (chapter 3). Furthermore, density of seeds in the soil
(estimated from the 'summer' incubation data, in which germination
was higher for both species) differed in parallel with density
of plants, reinforcing the view that there were permanent

population differences in these species between KVR and S. Lake.
The seed populations were much larger than the plant populations.
There were significant differences in cover, the means being
higher in KVR at both sites. Of the soil variables, moisture
retention, P, S, conductivity, *initial* moisture content (2 to
10 cm) and depth of limestone had higher means in KVR. The loam
soil surface was 4 cm lower in S. Lake than in KVR. The means
of bulk density and unconfined compressive strength were higher
in S. Lake. *Final* moisture content (2 to 10 cm) showed no
cross-fence trend. In general differences were larger and more
often significant at the sand site.

Correlation between plot means of most variables was
examined by means of linear regression (Table 4.2; Fig 4.2). In
the case of *Stipa* (density) and *Schismus* (density) only the plots
representing the growth period from April to October (see chapter
5) were used in these tests. There was strong positive inter-
action among soil moisture (except *final*) and chemical variables.
This group correlated positively with *Stipa* (density) and
negatively with *Schismus* (seeds). *Stipa* (seeds) and *Schismus*
(density) were not statistically active, probably because of high
variance. An unknown component of these correlations may have
been due to the cross-fence differences. Dividing the data by
site and soil as in chapter 3 would have resulted in ridiculously
small samples (n ≤ 9) and this was not done.

Monthly means of maximum and minimum daily air and soil
temperatures together with results of tests for differences between
them are presented in Table 4.3.

Daily rainfall at Koonamore head station is plotted in Fig 4.3.
The total rainfall for the 12 months from 1 Feb 1973 (487 mm) was
exceptionally high compared to the mean for all years of 200 mm.

4.3   Discussion

4.30   Introduction

It is difficult to separate mechanisms of change wrought by
stocking upon a whole complex of soil and vegetation variables
from interactions between them. Perhaps this is why few have
attempted such a study. Ellison (1960) in reviewing grazing
effects upon plant succession cited 250 references on herbivore-
plant effects but less than 50 on the effects on soils and
microclimate. However, the more recent ecosystem approach
(Lewis 1969) is changing this situation.

4.31   Soil chemistry and texture

The results of the present study suggest that protection from
grazing has enriched the chemical composition (albeit slightly)
of the surface soil. There is some controversy in the literature
about the effects of grazing on soil fertility in semi-arid to
arid systems. Kleiner and Harper (1972) and Charley and
Cowling (1968)reported a general decrease. On the other hand
Johnston et al (1971), Smoliak et al (1972) and Langlands and
Bennett (1973) found either little change or an increase,
especially in organic matter and 'available' N and P, and
especially at heavy stocking rates. Trumble and Woodroffe
(1954) made a similar claim without supporting data.

The occurrence of the latter situation is perhaps best explained by Langlands and Bennett (1973) who suggest that in a dry period plant litter and animal wastes high in 'available' nutrients temporarily accumulate on the soil surface. Thus the timing of sampling may be crucial.

In the long term, erosional loss of the topsoil would have less serious consequences at the semi-arid sites of the latter studies (excepting Trumble and Woodroffe 1954) than in arid systems like Koonamore where nutrients are concentrated in the top few cm of the soil (Charley and Cowling 1968). Because of the more arid climate and poor parent material (Pre-cambrian shales and tillites) of the saltbush soils at Koonamore (Carrodus et al 1965) replacement of nutrients by weathering of the siliceous fraction would be much slower than at the more humid sites with richer parent material studied by Johnston et al (1971) and Smoliak et al (1972).

At KVR the cross-fence differences in moisture retention, which is influenced by clay and organic matter content, suggest that textural differences have arisen in the topsoils. Although organic matter was not sampled, it was obviously more abundant in KVR, especially in the lichen crust. Differences in clay content, if present, may have arisen by faster dispersion of the clay in S. Lake than in KVR under the influence of trampling and rainfall impact (Rose 1966, section 4.3), and consequently accelerated erosion of this fraction. In KVR this process would have gradually slowed following protection and the resultant build-up of plant and lichen cover.

4.32 Hydrology

The lower *initial* moisture content (2 to 10 cm) in S. Lake than in KVR at the sand site probably resulted from reduced infiltration in S. Lake through soil compaction and sealing of the surface by the dispersed clay fraction. Langlands and Bennett (1973) and many others have reported this effect. During irrigation there was considerable run-off from the S. Lake plots but virtually none from the KVR plots. Run-off in KVR would have been reduced also by interception of 'rainfall' by the more abundant plant cover there. The lack of difference in *initial* water content at the loam site was probably due to the 4 cm difference in soil depth over the relatively impervious lime- stone layer. In KVR the greater capacity of the soil to absorb water would have been masked in terms of gravimetric water content by its greater depth and hence volume available for water storage. Thus in KVR the rooting zone and the total quantity of water available to plant growth was greater.

Final soil water contents did not differ, presumably because of the overriding effect of high evapotranspiration. This also suggests a lack of textural difference in the subsurface soils between the two areas.

4.33 Temperature

The temperature of bare soil was significantly more extreme (higher maxima, lower minima) that that of shaded soil,which was in turn more extreme than air temperature (Table 4.3).

There was no difference between crusted and uncrusted soil. Because of the significant differences in plant cover, S. Lake must have been more extreme in temperatures than KVR. The implications of these results for survival of seedlings are discussed in section 5.3.

4.34 Differences between sites

Many variables showed greater cross-fence differences on the sand site than on the loam site. The only exception was bulk density, which is expected because susceptibility of soil to compaction increases with fineness of texture. This accentuation of cross-fence differences on the sand site probably arose from the fact that it is 4.5 km from the only water point in S. Lake whereas the loam site is 6.0 km distant (Fig 2.1). Because of the 'piosphere' effect on sheep behaviour in the arid zone (Lange 1969) the stocking pressure in S. Lake at the sand site would have been greater than at the loam site. Sheep rarely range more than 5 km from a water point in the arid zone (Osborn et al 1932).

4.35 Interactions between vegetation and soils

Cross-fence differences in *Stipa* and *Schismus* (density and seeds) were large i.e. 2 to 4 fold. Relating these differences to stocking pressure and separating direct animal - plant effects from animal - soil - plant interactions is difficult. KVR is generally more favourable to plant growth, mainly in soil nutrients, but the actual differences observed in soil variables were small.

Thus it seems necessary to explore the possibilities of direct grazing effects.

Stipa is a highly preferred[†] species in various situations (Jessup 1951; Leigh and Mulham 1966[*]). Thus one may argue that by being eaten first and by being less resistant to damage *Stipa* is replaced by less preferred or more resistant species (Heady 1965) such as the spiny *Bassia* spp. But the tiny and delicate *Schismus* does not appear to be a plant that is competitively vigorous or resistant to damage. One may argue that it benefits from lack of competition in S. Lake. However, no correlation was detected in the original harvest biomass data from chapter 3 between *Stipa* and *Schismus* nor between *Schismus* and total biomass. On the other hand *Schismus* was very strongly negatively associated with all lichen species. This was obvious also in the field. A lichen crust is a tough mat of living tissue which may prevent seeds not specially adapted from penetrating the surface and reaching a level where dessication during germination is less likely. When shed, the seed of *Stipa* remains within the lemma. The awn of the lemma rotates in a corkscrew action to drive the seed into the soil. This process is further aided by the sharp callus and backward pointing hairs on the lemma (Fig 4.4a). On the other hand the seed of *Schismus* is small (1-2 mm), round and smooth (Fig 4.4b), and could penetrate the soil only by falling onto a loose surface or into a crack.

[†] Definition of Heady (1965).

[*] Leigh and Mulham use the name *S. variabilis* Hughes. There has been dispute for many decades as to whether *S. variabilis* and *S. nitida* are synonyms. Forms attributable to each mingle and intergrade at Koonamore.

Ioannou (unpublished thesis) found that mallee *Eucalyptus* seeds, if dropped on bare soil, germinated readily but did so on encrusted soil only if they fall into cracks. These seeds were very similar in size and shape to *Schismus* seeds. *Salsola,* like *Schismus* showed a strong negative correlation with lichens in the 1971 harvest data. Evans and Young (1972) showed that seeds of *Salsola* lying on the surface had a very low probability of germination. Sheldon (1974) shows clearly the important role of seed morphology in relation to soil surface morphology in determining whether or not a seed will germinate.

A further possibility is that chemical exudates from the lichens may influence other plants; for example, Pyatt (1967) showed that lichen extracts inhibited germination and growth of some grass seeds. Other physical and chemical roles of cryptogamic crusts have been suggested in the literature but little detail is known about their influence on surface soil properties.

4.4   Conclusions

Fifty years of exclosure of KVR from sheep grazing has led to a permanent increase in the population size of *Stipa nitida* and a permanent decrease in *Schismus barbatus*, as measured by biomass, plant density and numbers of viable seeds in the soil. Soil properties have also changed, principally in two ways. The surface in KVR has been stabilised by redevelopment of a lichen crust and increase in vegetative cover thus reducing soil erosion.

Also, total phosphorus and sulphur in the topsoil have increased and bulk density has decreased, suggesting a net build-up of organic matter in KVR. No major changes in soil texture have occurred, except in the upper 2 cm.

The observed soil changes seem too slight to explain the large changes in vegetation composition. It is suggested that removal of selective grazing of *Stipa* by sheep in KVR has led to its increase there. On the other hand, *Schismus* appears to have been suppressed by some property of the regenerated lichen crust. This property may be physical resistance to seed penetration. There is an obvious need for much more work on the role of arid zone lichen crusts in determining physical and chemical properties of surface soils.

Fig 4.1a   The equipment used to transport and pump water
           to the irrigation plots.   In the foreground
           is the kangaroo-proof fence.

Fig 4.1b   Irrigation in progress on the KVR loam-site
           plot, December 1973.   The mature grass is *Stipa*.
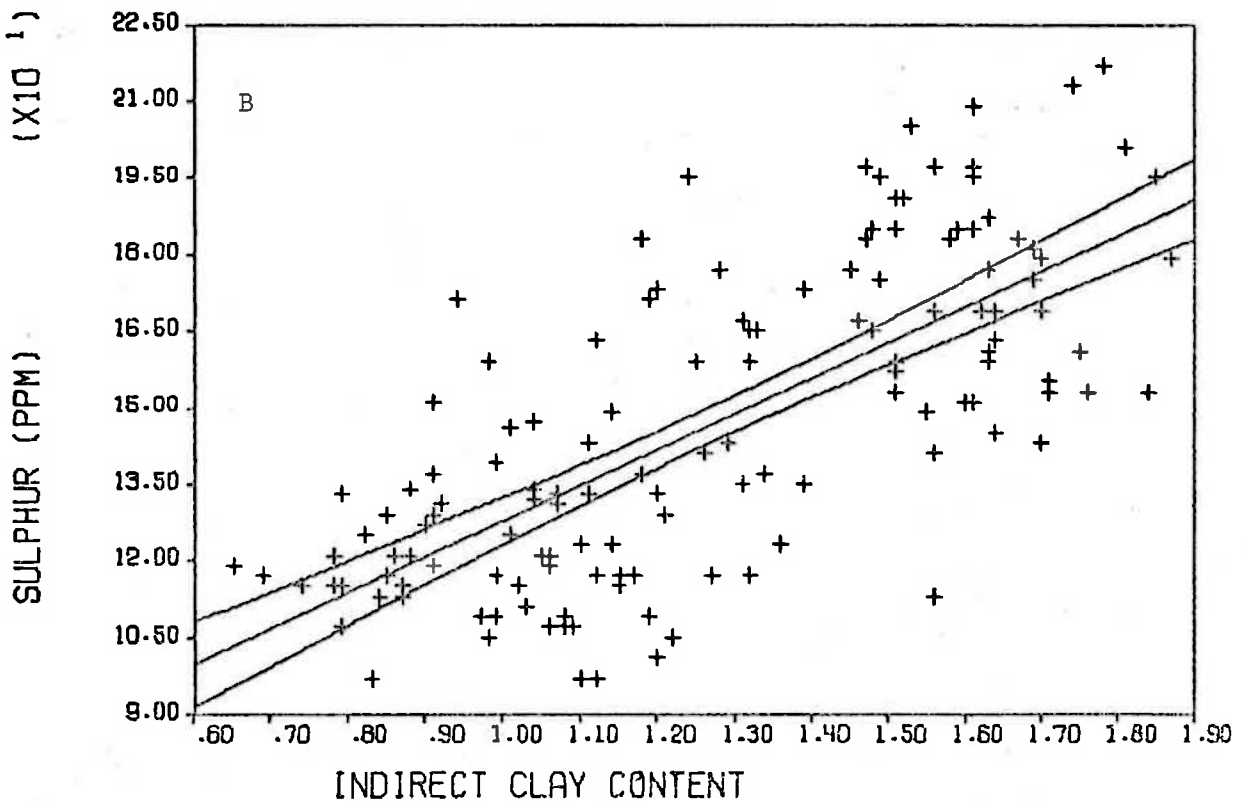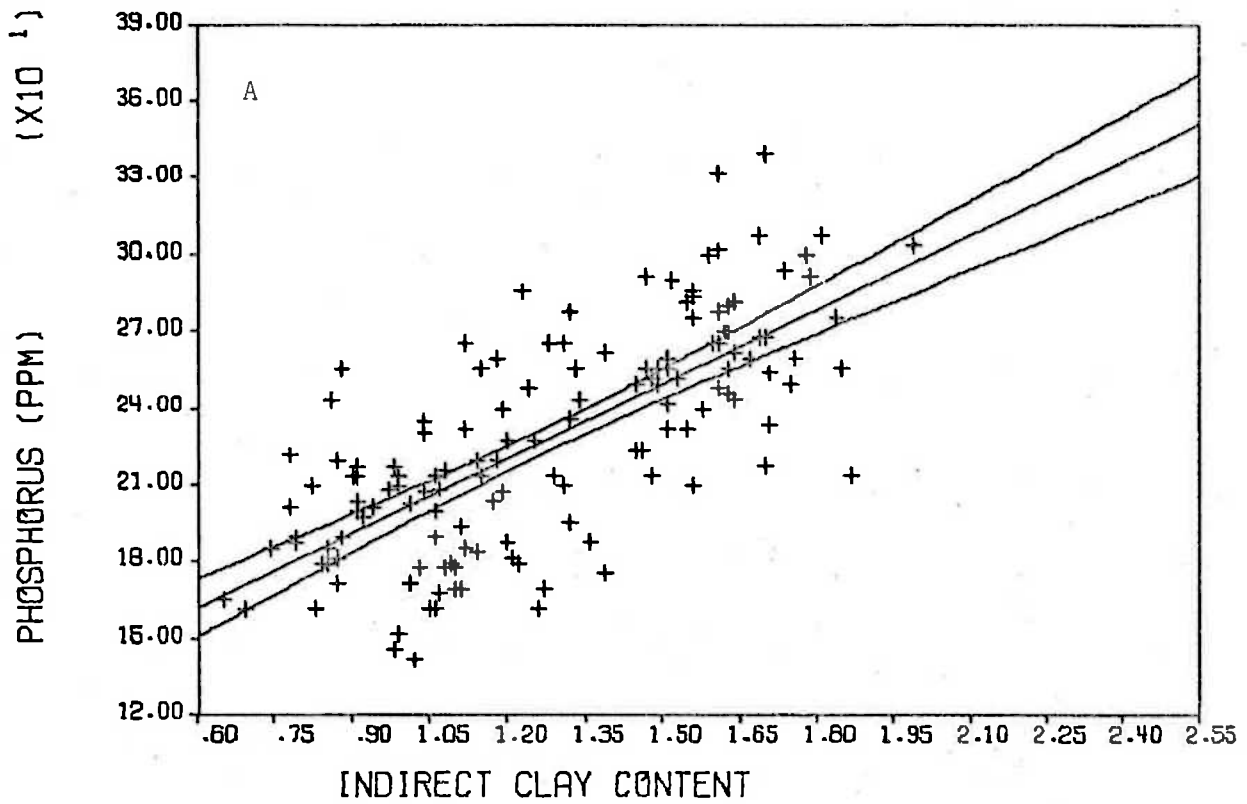
Fig 4.2   Linear regressions of (a) total phosphorus and (b)
           total sulphur on indirect clay content (moisture
           retention), from the irrigated small plots. All
           three variables were measured on each of the 144
           topsoil (0-2 cm) samples taken from KVR and S. Lake
           at the sand and loam sites in 1973-4. 95% confidence
           limits are shown about the lines.
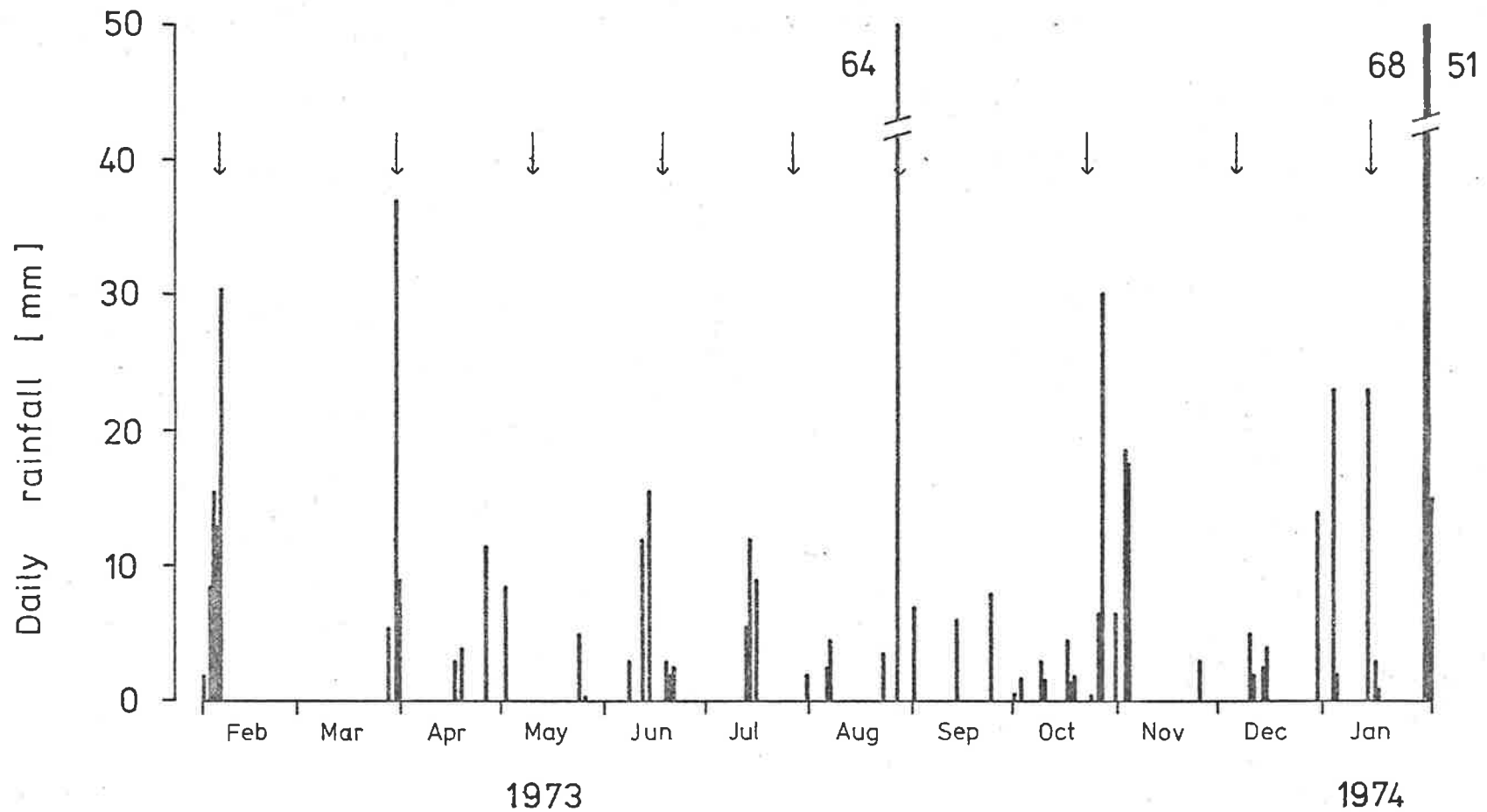
Fig 4.3   Daily rainfall over the period of irrigations, 1973-4. Vertical arrows
show times of irrigation, when 50 mm of 'rainfall' were applied to
each of the plots, except as indicated in section 4.12.

b.

2·5mm

a.

5mm
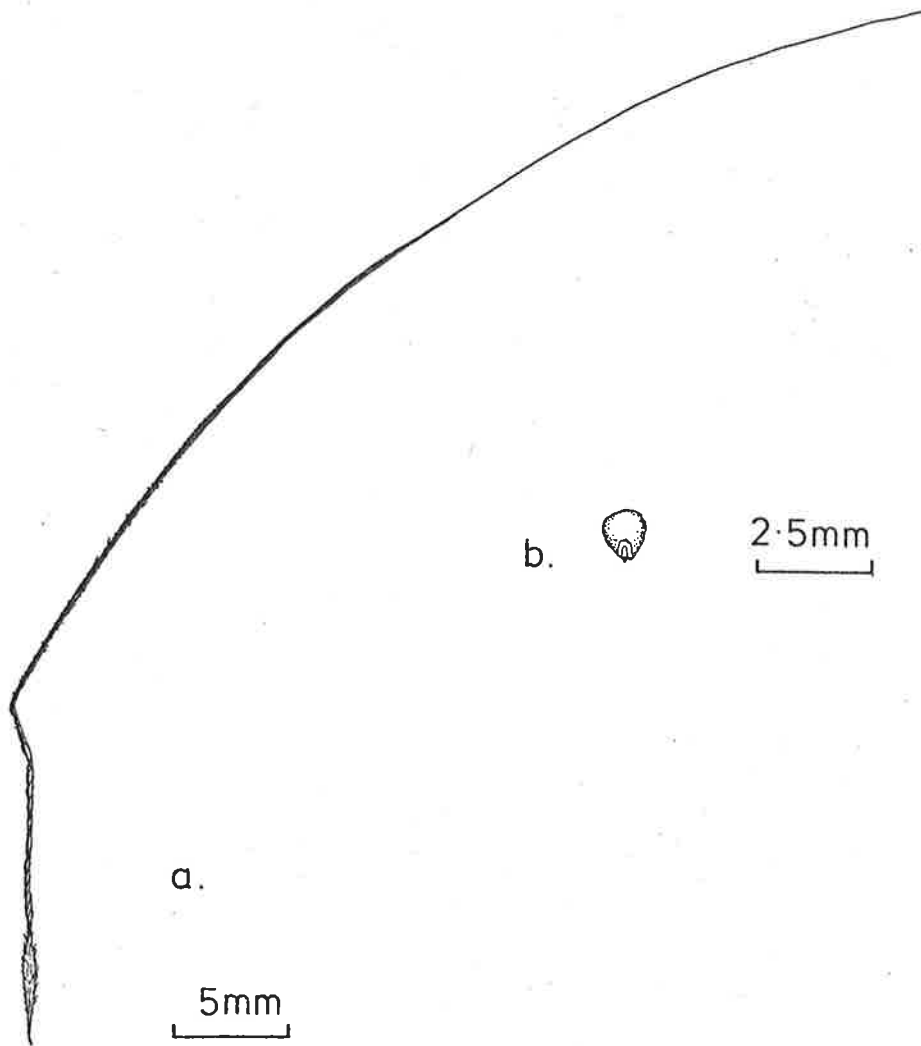
Fig 4.4   Seeds of *Stipa nitida* (a) and *Schismus barbatus*
           (b).   Only the lemma of *Stipa,* which is persistent
           and encloses the seed, is visible.

Variable	Loam Site				Sand Site			
	KVR	S. Lake	t test t	t test prob	KVR	S. Lake	t test t	t test prob
Stipa : density/m^2	39 (24)	18 (25)	5.09	3	10 (13)	5 (6)	3.05	2
seeds /m^2	320 (412)	83 (200)	2.67	2	179 (755)	103 (118)	1.39	
Schismus : density/m^2	6 (9)	28 (46)	3.96	3	8 (16)	23 (29)	3.80	2
seeds/m^2	270 (547)	560 (632)	1.83		1220 (1640)	2450 (2000)	2.33	1
Cover (%)	20 (17)	13 (10)	3.25	3	27 (14)	16 (16)	4.34	3
Moisture retention (% w/w)	1.57 (.18)	1.54 (.24)	.697		1.07 (.16)	.96 (.15)	3.10	2
Total P (ppm)	270 (30)	260 (27)	1.80		232 (50)	195 (25)	5.51	3
Total S (ppm)	196 (33)	176 (28)	4.33	3	137 (20)	123 (16)	4.47	3
Conductivity (mmho/cm)	.462 (.114)	.581 (.581)	1.28		.330 (.083)	.285 (.063)	2.02	1
Soil moisture, *initial*, 2-10cm (%)	10.7 (2.0)	10.7 (2.1)	.11		8.3 (1.6)	7.5 (1.3)	2.32	1
Soil moisture, *final*, 2-10cm (%)	5.1 (2.8)	5.6 (2.8)	.82		4.4 (2.5)	4.1 (2.1)	.47	
Penetrometer (kg/cm^2)	4.0 (4.9)	5.7 (5.4)	4.42	3	2.2 (1.2)	2.9 (2.7)	3.83	3
Bulk density	1.23(.12)	1.40 (.19)	2.15	1	1.35 (.16)	1.41 (.12)	.84	
Depth of limestone (cm)	15.4 (3.8)	11.4 (1.8)	6.27	3				

Table 4.1   Small scale cross-fence comparisons of ephemeral plants and soils on irrigated plots. Entries are of the form mean (standard deviation). Probability scores are as in Table 3.2.

Variable	1	2	3	4	5	6	7	8	9	10	11	12
1. *Stipa*: density				-2		3	3	3	3			
2. seeds	.022											
3. *Schismus*: density	.08	1.72			-1							
4. seeds	.009	.045	.0001			-3	-3	-3	-3	-2		
5. Cover	.54	.53	1.02	4.24								-1
6. Moisture retention	49.8	128	.70	2190	7.78		3	3	3	3		2
7. Total P	.365	1.61	.18	20.3	.018	.0071		3	3	2		
8. Total S	.490	1.76	.23	23.3	.024	.0085	.90		3	2		1
9. Conductivity	142	126	21.8	7.61	1.64	2.67	264	274		2		
10. Soil moisture, *initial*	1.89	22.8	1.57	259	.57	3.75	.024	.030	11.6			
11. Soil moisture, *final*	.93	17.5	2.08	130	.291	1.24	.001	.012	6.90	.266		1
12. Penetrometer	1.99	.619	4.46	46.6	2.26	.091	8.32	7.24	.033	.412	.318	

Table 4.2   Linear regressions between soil and vegetation variables, using plot means. The lower half of the table contains the absolute value of b (from y = a+bx). The upper half contains probability scores as in Table 3.2. Probability scores, where significant, carry the sign of b.

Month	Maximum temperatures				Minimum temperatures			
	Air	Shaded	Crust	No crust	Air	Shaded	Crust	No crust
Feb: 8th-28th	32.8(3.8)				19.1(3.0)			
Mar: all	31.5(6.6)				14.3(4.6)			
Apr: all	25.1(4.4)				11.5(3.9)			
May: 8th-31st	21.9(3.5)		20.8(5.1)	24.6(5.6)	6.3(5.0)		4.8(3.4)	5.5(4.7)
Jun: all	14.5(2.9)		15.6(3.1)	17.2(2.4)	5.1(4.6)		3.9(4.4)	3.2(5.6)
Jul: all	17.3(2.2)	19.1(2.5)	19.0(2.1)	19.7(2.7)	5.0(4.3)	3.0(2.4)	1.6(3.7)	1.3(4.1)
Aug: 1st-26th	18.2(3.3)	17.8(3.1)	22.8(5.0)	22.0(5.7)	4.4(4.5)	-0.1(3.0)	-1.3(4.8)	-1.2(4.5)
Sep: 5th-30th	23.4(4.5)	22.5(4.1)	32.0(6.3)	33.2(6.5)	7.1(3.9)	2.2(3.6)	3.3(3.8)	2.8(4.0)
Oct: 1st- 6th :22nd-31st	26.1(6.1)	29.3(6.1)	36.5(11.4)	37.3(11.1)	11.6(4.4)	7.3(5.9)	8.0(5.1)	7.1(5.1)
Nov: 1st-25th	29.3(6.3)	35.2(10.9)	41.2(11.2)	37.4(8.5)	12.6(3.6)	8.7(4.0)	9.7(4.1)	8.2(3.6)
Dec: 2nd-31st	32.7(5.1)	34.3(7.0)	40.2(8.3)	39.3(6.3)	15.6(4.6)	12.2(4.0)	13.0(3.5)	12.4(4.0)
Jan: all	31.7(4.7)	30.8(8.5)	35.8(11.0)	35.4(10.5)	20.6(3.3)	13.4(2.8)	15.1(2.4)	13.7(2.2)
Feb: 1st-20th	29.1(4.1)				15.9(3.8)			

Table 4.3a   Monthly mean maximum and minimum temperatures of air (1 m) and soil (1 cm deep) at KVR, 1973-4.
Entries are of the form mean (standard deviation). A blank entry means no data were taken.
Incomplete records are indicated by inclusive dates.

		1	2	3	4	5	6	7	8
1. Air : max			3		3		ns	
2. min				3		3		3
3. Shaded : max	3.91				ns		3	
4. min		5.25				ns		ns
5. Crust : max	6.36		.41				3	
6. min		6.42		1.06				ns
7. No crust: max	1.53		4.75		4.56			
8. min		6.17		.60		.51		

Table 4.3b   Results of *t* tests for comparisons between mean temperatures for July to January inclusive. The lower half of the table contains *t* values; the upper half probability ratings as in Table 3.3. Non significance ($P > 0.05$) is indicated by 'ns'.

5.   Seasonal trends in germination and growth of ephemerals

5.0   Introduction

The notion that arid zone ephemeral floras may be divided into
distinct 'winter' and 'summer' components has arisen from studies
in a number of regions e.g. the Mojave Desert in North America
(Beatley 1974), the Murchison Region of Western Australia
(Mott 1972), and the Riverine Plain in New South Wales (Williams
1970). A corollary to this notion is the idea that given
adequate soil moisture, strictly seasonal factors (usually
temperature) control the germination and growth of these species.
Beatley (1974) suggests that the term 'annual' is as applicable
to these short-lived desert plants as it is to their counterparts
from more humid regions. Conversely the term 'ephemeral' is
said not to apply to such plants.

However, there is no reason that a plant should not be
both ephemeral, in the sense that it is short-lived and
irregularly present because of unreliable rainfall, and annual
in the sense that it is limited by seasonal factors. The short-
lived plants at Koonamore were investigated to determine whether
they were annual or ephemeral or both.

5.1   Methods

Watered field plots were initiated nine times over one year from
February 1973 under the assumption that natural rainfall would
be too irregular for the purpose of this study. The procedure is
described in detail in section 4.1.

However, rains were exceptionally regular in 1973, and live plants of most species were generally present on the plots before irrigation. Thus to determine germination and establishment response *final* density counts (6 weeks after irrigation) were compared with *initial* counts (24 h after irrigation). Biomass estimation was not used because errors would have been so high as to mask subtle changes. *Initial* and *final* soil water contents were sampled (section 4.144) and air and soil temperatures were monitored continuously (section 4.146). Topsoil samples were incubated in two temperature regimes (section 4.132) to determine seed densities in the soil and to investigate temperature dependence of rate and total numbers of germination.

5.2   Results

5.21   Field germination and establishment

The field-plot data showed continuous variation between species in seasonal trends of germination and establishment (Table 5.1). *Enneapogon* germinated strongly in February, grew rapidly, flowered and fruited in April-May and lay dormant through winter. The following spring and summer the dormant plants resumed growth and fresh germinations occurred. *Salsola* and *Boerhavia* were similar, although the latter died out completely in winter. Several species (*Stipa, Schismus, Bassia sclerolaenoides, Tetragonia, Calotis, Crassula*) were able to germinate and establish throughout the period from late summer to mid-winter. All of these fruited in spring, and all except *Stipa* and *Bassia* died out at the onset of summer.

Stenopetalum was the nearest to being a strictly winter species, completing its entire life cycle in the period May-October. *Bassia sclerolaenoides* produced a very dense crop of seedlings in February, which continuously thinned itself over the next 12 months. By mid-winter new seedlings were distinguishable from the original crop and were recorded separately (Table 5.1), showing that germination and establishment were still occurring despite the overall decline in numbers. A similar germination and establishment occurred in January 1974. In summary, although a few species were restricted to summer or winter in germination and growth, the majority were capable of germinating and establishing in summer, autumn and winter. Of these latter, the majority completed their life cycles in spring but a few continued to grow through summer.

5.22 Laboratory germinations

Laboratory incubation of topsoil (0-2 cm) samples resulted in successful germination of nearly all species observed in the field (Table 5.2). The estimated mean numbers of germinable seeds per unit area was generally much higher than the density of live plants in the field (e.g. *Stipa* and *Schismus*, Table 4.1). In all species germination was more rapid in the 'summer' regime, commencing about 5 days earlier. This was true even in those species for which total germination was higher in the 'winter' regime (e.g. *Bassia sclerolaenoides,* Fig 5.2). For all species in both regimes germination was nearing a plateau after 14 days, and essentially complete after 20 days.

5.23 Air and soil temperatures

In order to illustrate seasonal and other influences on soil
and air temperatures, daily maxima and minima over 3 periods
have been plotted (Figs 5.3, 5.4 and 5.5). Influence of temperature
on germination and establishment of seedlings is discussed in
section 5.3.

In mid-winter (Fig 5.3) maximum temperatures were moderate,
with soil maxima slightly higher than air maxima. Soil minima were
as much as 8° C lower than air minima, and frequently fell below
0° C. Shade reduced the range and variation of soil temperatures.
A fall of rain disrupted this general pattern. The preceding build-
up of cloud caused air and soil temperatures to converge, probably
by reducing net radiation falling on the soil (10-11 July).
During the rainfall period soil minima rose sharply (13 July)
presumably because of the high thermal capacity of the warmer rain.
Immediately afterwards, all temperatures fell sharply. This was
partly because of evaporative cooling and partly because of the
strong, cold southerly winds which usually follow a winter rainfall
in the region (14-18 July). Over this latter period, soil temp-
eratures rapidly became more extreme than air temperatures.

In summer (Fig 5.4) soil maxima were very high during clear
sunny weather (e.g. 15-25 November), often over 50° C and up to 30° C
above air temperatures. As in winter, shade moderated soil
temperatures to values intermediate between unshaded soil temp-
eratures and air temperatures. In summer (Fig 5.4) the moderating
and cooling influence of a fall of rain followed a similar pattern
to that in winter. However, the evaporative cooling effect on

soil temperatures lasted only 5 days, as was shown by the sudden increase in the gap between soil and air maxima after 8th November. Mason (1959) also found that evaporative cooling in soils after summer rain was short-lived. Temperatures in December 1973 and January 1974 were very atypical. There were regular and heavy rainfalls throughout those months, the total gauging at Koonamore head station being 230 mm. The sky was mostly heavily overcast between falls, and maximum soil temperatures were greatly reduced (Fig 5.5).

Two further points are illustrated by Fig 5.5. The irrigation of 4-5 December had a typical moderating influence on soil temperatures but none at all on air temperatures. In other words, the irrigated plot was a small oasis in an ocean of hot dry air. Under such circumstances, evapotranspiration is higher than would occur following natural rainfall. This is one of the chief problems in simulating rainfall by irrigation (Slatyer 1967, p 54). The other feature illustrated by Fig 5.5 is the sharp rise in minimum temperatures on 21 December, followed by a sharp drop in all temperatures on 22-23 December, apparently signifying a heavy fall of rain. However no rainfall was recorded at Koonamore head station, 5 km away. This illustrates the localised nature of summer thunderstorms and the need to take care in extrapolating rain gaugings over relatively small distances.

Similar relationships to those at Koonamore between air and soil (shaded and unshaded) temperatures in arid regions have been observed by numerous authors (Specht 1956; Herbel et al 1970;

Rogers 1971; Mott 1972; Evans and Young 1972).

5.24 Soil moisture

Although it was intended to consider principally the influence
of temperature and other periodic phenomena on possible seasonal
patterns in germination, establishment and growth of short-lived
plants at KVR, the effects of soil moisture cannot be ignored.
The possibility of predicting change in soil water content from
initial values on a daily basis was considered. Two approaches
to modelling soil moisture are possible, namely the water balance
and the energy balance approaches(Slatyer 1967, chapter 2). The
water balance approach is based on solving the equation.

$$P - O - U - E + \Delta W = 0 \qquad (5.1)$$

where ΔW is the change in soil water storage for the period and
depth under study, and P, O, U and E are precipitation, run-off,
deep drainage and evapotranspiration respectively (all expressed
in linear units e.g. mm). The energy balance approach requires
solution of the equation

$$R_n + H + \ell E + G + aA = 0 \qquad (5.2)$$

where R_n is the net radiation reaching the vegetated surface, and
H, ℓE, G and aA are heat dissipated by sensible exchange with
the atmosphere, latent exchange with the atmosphere, sensible
exchange with soil and vegetation, and chemical conversions due
to photosynthesis respectively (all expressed in calorific units).

The principal problem in evaluation of Equation 5.1 is
to determine the relationship between potential and actual

evapotranspiration, which is highly dependent upon local site parameters (Slatyer 1968). Similarly, to evaluate Equation 5.2, the relationship between temperature - and water vapour - gradients and local site factors must be known (Slatyer 1967, p 58). In heterogeneous arid systems, such as the KVR plots of the present study, detailed measurements of these local site parameters is necessary to obtain meaningful averages (Specht 1959; Slatyer 1967, p 59). Such measurements were beyond the scope of the present study. Instead, *final* soil water contents, although only an approximation to the conditions during the critical first 14 days (section 5.22) following 'rainfall', were used as an indication of those conditions. They showed a clear seasonal trend and correlated negatively with temperatures (Fig 5.6). The relationship between *final* soil water contents and germination, establishment and growth of short-lived plants at KVR are discussed in section 5.3.

5.3   Discussion

There was continuous variation between species in response to season at KVR, and distinct 'summer' and 'winter' floras could not be defined. This finding contrasts with conclusions of other workers such as Mott (1972) and Beatley (1974), although the difference may be in the systems studied rather than in interpret-ation of data. In the semi-arid mallee districts of southeastern Australia, Holland (1968) found that all 'field layer' plants (including annuals) germinated in winter and matured in the following spring and early summer i.e. they were 'winter' annuals according to most definitions.

No evidence of 'summer' annuals was found by him. This is not unexpected since summer rainfall is insignificant in the mallee region.

The results of the present study reveal a need to differentiate germination and establishment from growth in discussing seasonal trends in short-lived species. Some species germinating in February 1973 matured within 6 weeks (e.g. *Enneapogon, Euphorbia*) while others did not do so for 6 months or more (e.g. *Stipa, Bassia*).

Many of the species studied were 'ephemeral' in the sense of being opportunistic; that is, they germinated and established at both high and low temperatures (laboratory and field). However, there were some species which did not germinate and establish in midsummer and others which did not succeed in mid-winter. Even the most opportunistic species had reduced germination and establishment rates at those times. Some possible reasons for this are examined.

After a winter rainfall the chief hazard for a seedling is stress from low temperature. In the wake of winter rainfall at KVR soil minima soon plunge to freezing values (section 5.23). Levitt (1956) showed that plants were most susceptible to freezing temperatures when highly hydrated. A newly germinated seedling must be highly susceptible to damage by freezing because of its state of hydration, its small bulk and the proximity of its essential parts to the soil surface where temperatures are most extreme. The sudden drop in germination and establishment of all species in the July - August period (Table 5.1) probably resulted from the very low August soil minima, which averaged less than

0° C (Table 4.3).

High temperatures also can be fatal to plants. The range
45 - 55° C in hydrated tissue is fatal to most higher plants
(Levitt 1956). Values within this range were frequently recorded
1 cm below the soil surface, especially in November (Fig 5.4),
although not within 10 days of rainfall or irrigation. It is
difficult to separate heat stress from drought stress, especially
since both derive from similar conditions. The more rapid
germination of all species at higher temperatures (Fig 5.2; section
5.22) partly offsets the disadvantage of rapid onset of drought
and heat stress in summer. However, the fact that soil moisture
was very low after December 1973 and January 1974 (Fig 5.4) even though
rainfall was exceptionally high in those months (Fig 4.3) suggests
that drought would normally prevent most species from establishing
in mid-summer, irrespective of direct temperature stress effects.
In the case of *Stipa* (one of the species which continued to grow
after shedding seed in October) even the survival of established
plants was affected by low soil moisture in the summer 1973-4
(Fig 5.6).

Many species which established successfully in the field
late in summer 1973 failed to do so early in the following summer
(Table 5.1) despite heavy follow-up rains (Fig 4.3). Some
possible reasons for this are examined.

Lack of seedling input may result from lack of germinable
seeds. Availability of germinable seeds depends upon production
in previous growth periods, viability, dormancy (whether intrinsic
or induced), loss by predation, and longevity (Roberts 1970;
Sarukhan 1974). Any one of these factors may become limiting in

such a way as to enforce seasonal variation in seedling input.
Some authors have failed to satisfactorily explain periodicity in
seedling input by not taking all factors into account. Evans &
Young (1972) and Janssen (1973) attributed periodicity to intrins-
ic dormancy of newly set seeds and assumed, but did not state,
that significant germination events exhausted soil seed reserves.
Mott (1972) also attributed periodicity to dormancy, but his
comprehensive approach makes his conclusion credible. Sarukhan's
(1974) outstanding study of three Ranunculus species reveals
remarkable differences between species in the way in which the
factors interact to determine seed availability. On the one hand
R. bulbosus produced large quantities of seed which turned over
rapidly by germination and death, and on the other, R. repens
produced few seeds which turned over very slowly. R. acris was
intermediate in its strategy.

Hence 'a priori' assumptions about the importance of any of
the factors in a given species should not be made. In the present
study I avoided the difficulty of measuring all factors in all
species by sampling availability of germinable seeds directly. At
no stage during the year of study were germinable seeds of any
species lacking in the soil (Fig 5.1).

An alternative explanation is that rapid growth response
by previously established plants after rain or irrigation may have
offered severe competition to new seedlings, either by increasing
evapotranspiration, or by competing for nutrients. This last
hypothesis is supported by the model of nutrient cycling proposed
by Charley (1972) for the same ecosystem. He suggests that after
a protracted rainfall period, almost all of the small pool of
labile mineral reserves becomes tied up in the vegetation biomass.
Any plant establishing at the end of such a period would be faced
with severe nutrient stress, and would come under severe
competition from the previously established vegetation.

Sarukhan and Harper (1973) found that in pasture the greatest
risk to an individual came during periods of rapid growth.

Fig 4.1b, a photograph taken in December 1973, shows a dense crop
of mature and apparently dead *Stipa* which nevertheless sprouted
vigorously in response to rainfall and irrigation. In February
1973 there were no pre-existing plants to offer such competition
because 1972 had been a year of drought. Thus although there
is not conclusive evidence to support this explanation, it appears
that competition from established plants may have prevented
establishment in the second summer of species which had
succeeded in the first.

5.4   Conclusions

There was continuous variation between short-lived species at KVR in
germination response to season, and distinct 'summer' and
'winter' floras could not be defined. There was considerable
variation between species in relationships between time of
germination and time of maturity. Some species matured in 6 weeks;
others did so only after 6 months. Almost all species were
ephemeral in the sense that they were both short-lived and oppor-
tunistic by virtue of their ability to germinate and establish in
most seasons. Almost all could also be described as annual in
the sense that they matured at a particular time of the year
(usually spring to early summer). Not all species died after
maturity, the exceptions being *Stipa, Bassia* spp and *Enneapogon*
spp. Irrespective of other considerations, it appeared that all
species were restricted in germination and establishment in mid-
winter by sub-freezing temperatures, and in mid-summer by drought
(and possibly high temperature) stress.
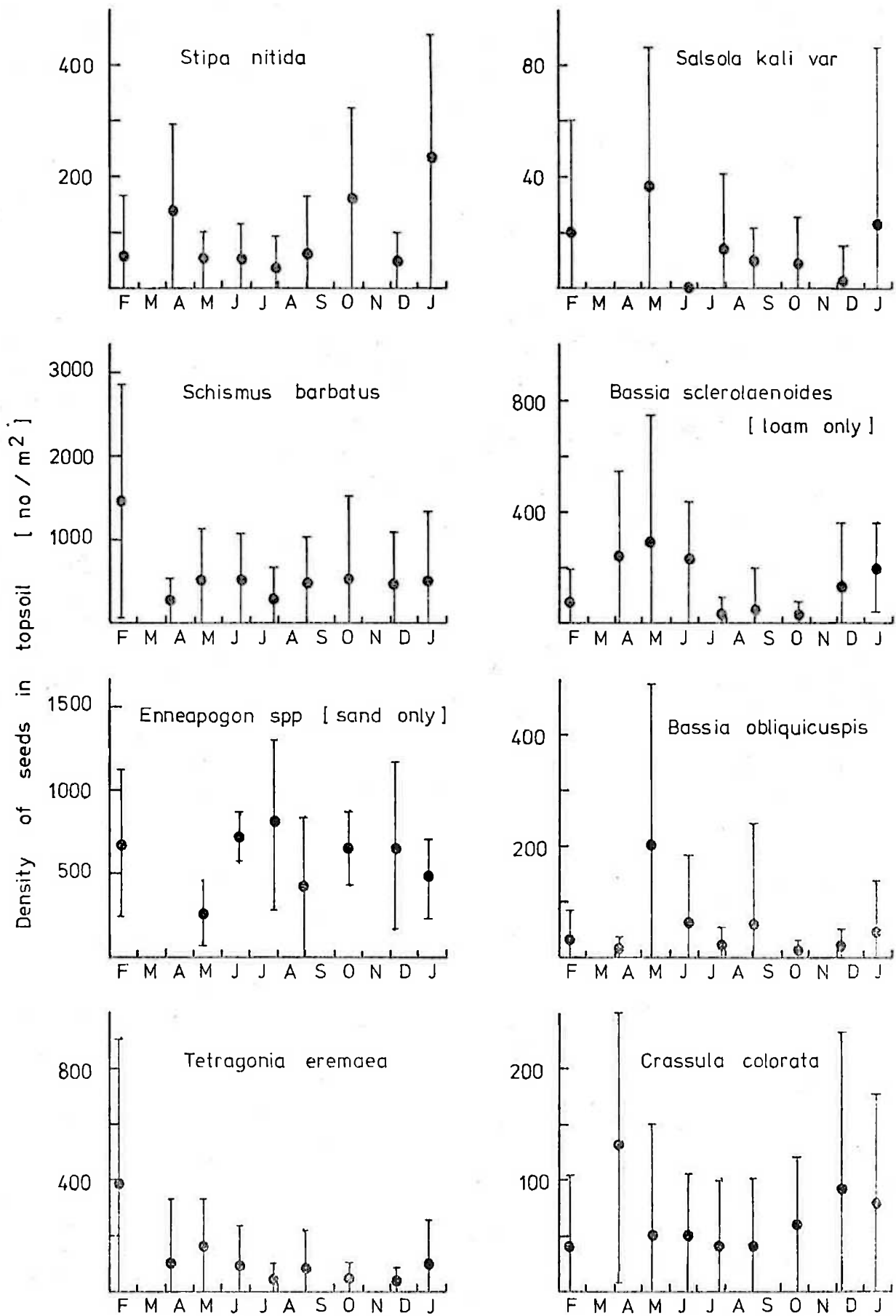
Fig 5.1   Seasonal trends of germinable seeds of ephemerals
           in the topsoil (0-2 cm) at KVR, 1973-4, showing
           means for all plots (●) with standard deviations (I).
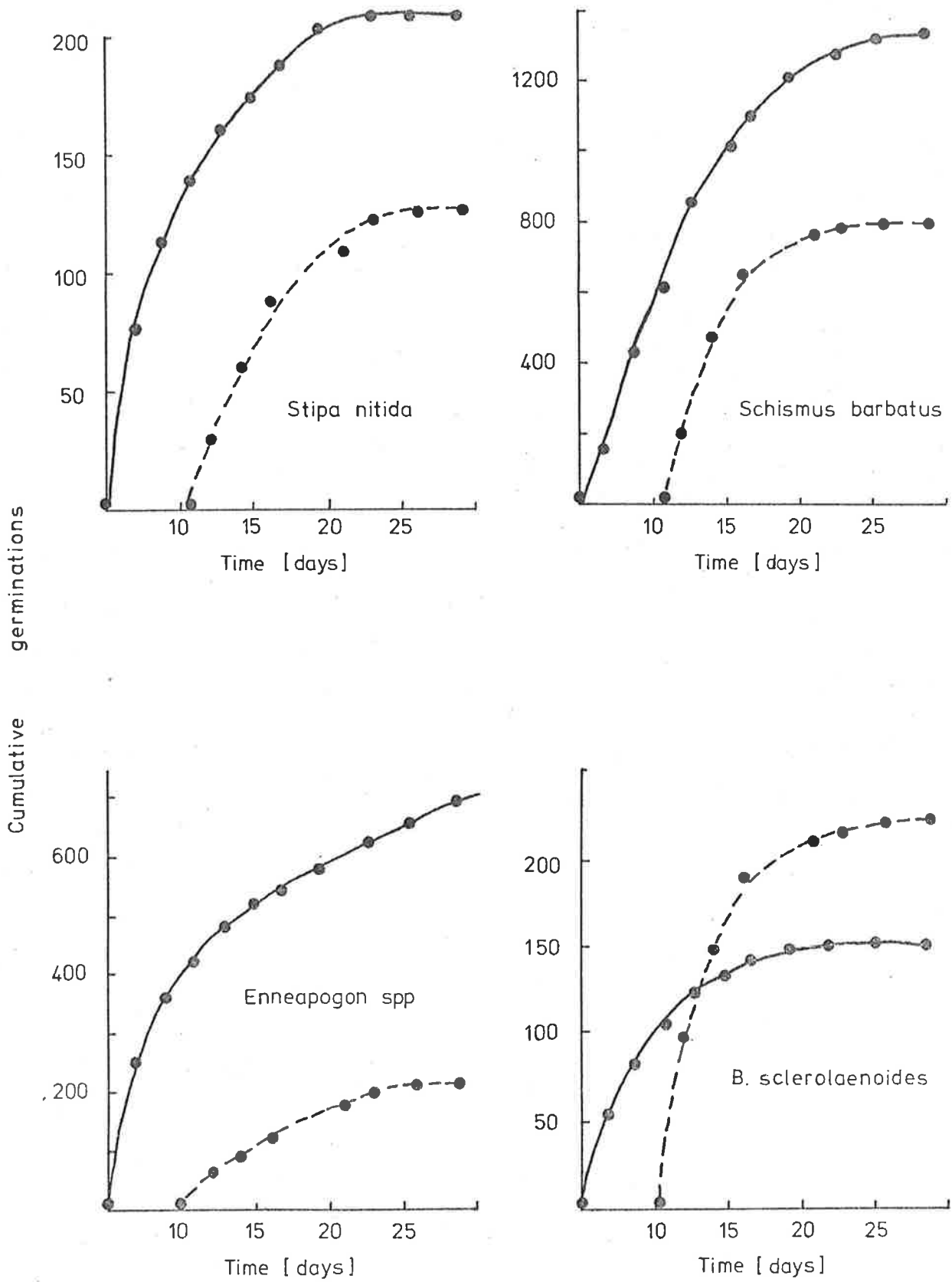
Fig 5.2   Cumulative germinations of ephemeral seeds in topsoil
          samples in the laboratory. The continuous line
          represents the 'summer' regime; the broken line,
          the 'winter' regime. See section 4.132 for further
          details.
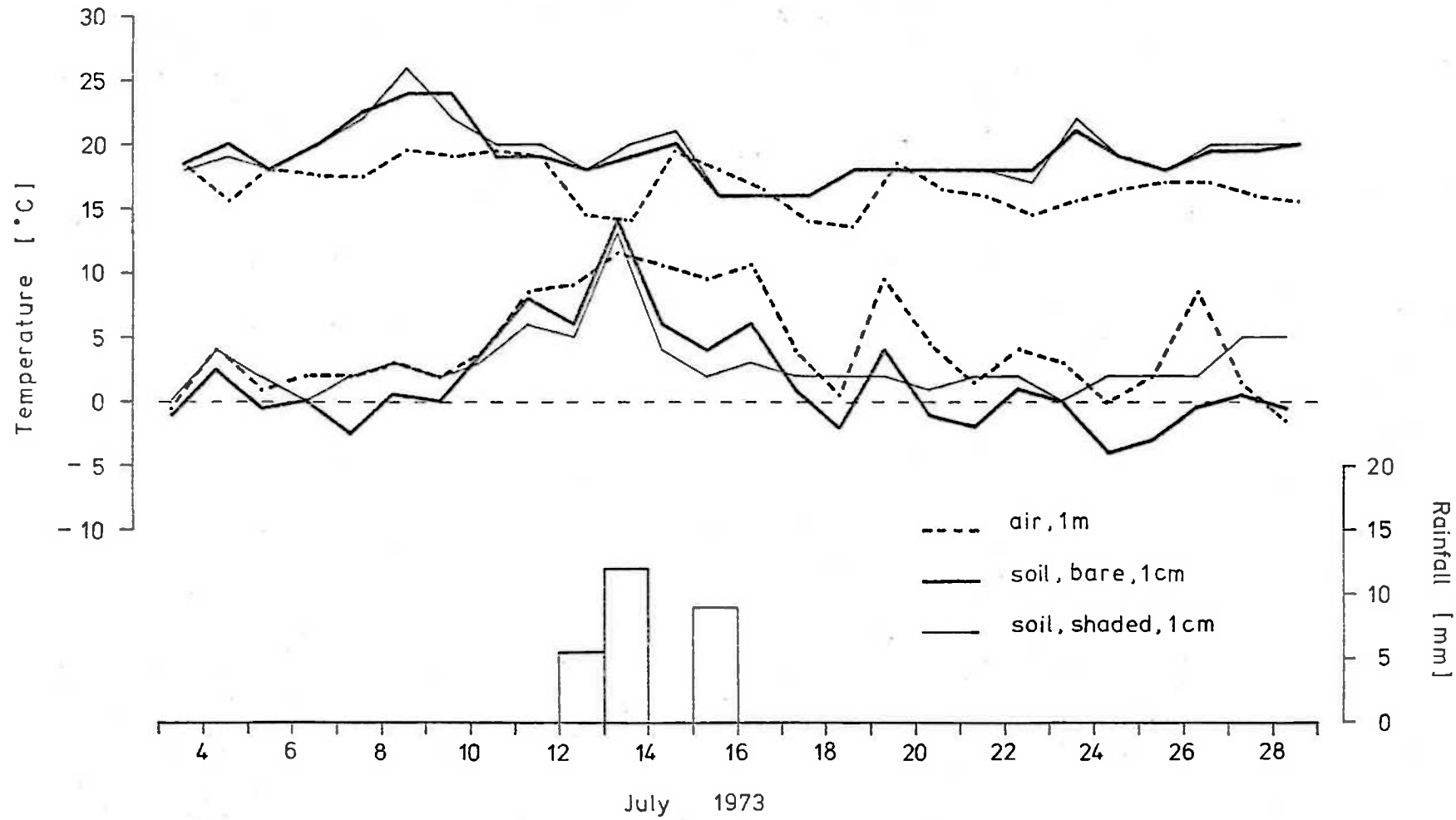
Fig 5.3   Daily air and soil temperatures at KVR, July 1973.   Upper lines show maxima;   lower lines show minima.
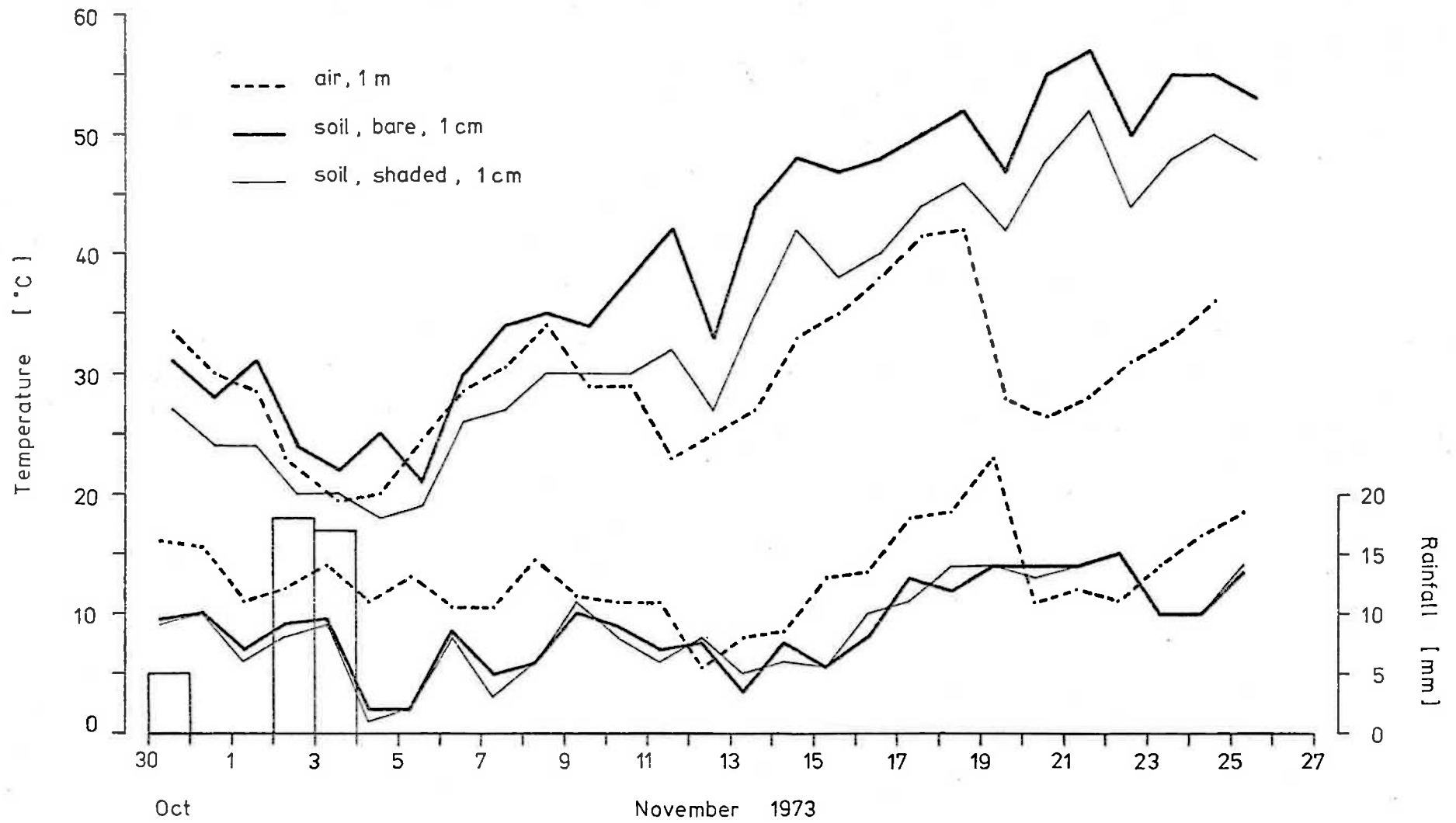
Fig 5.4   Daily air and soil temperatures at KVR, November 1973.   Upper lines show maxima; lower lines show minima.
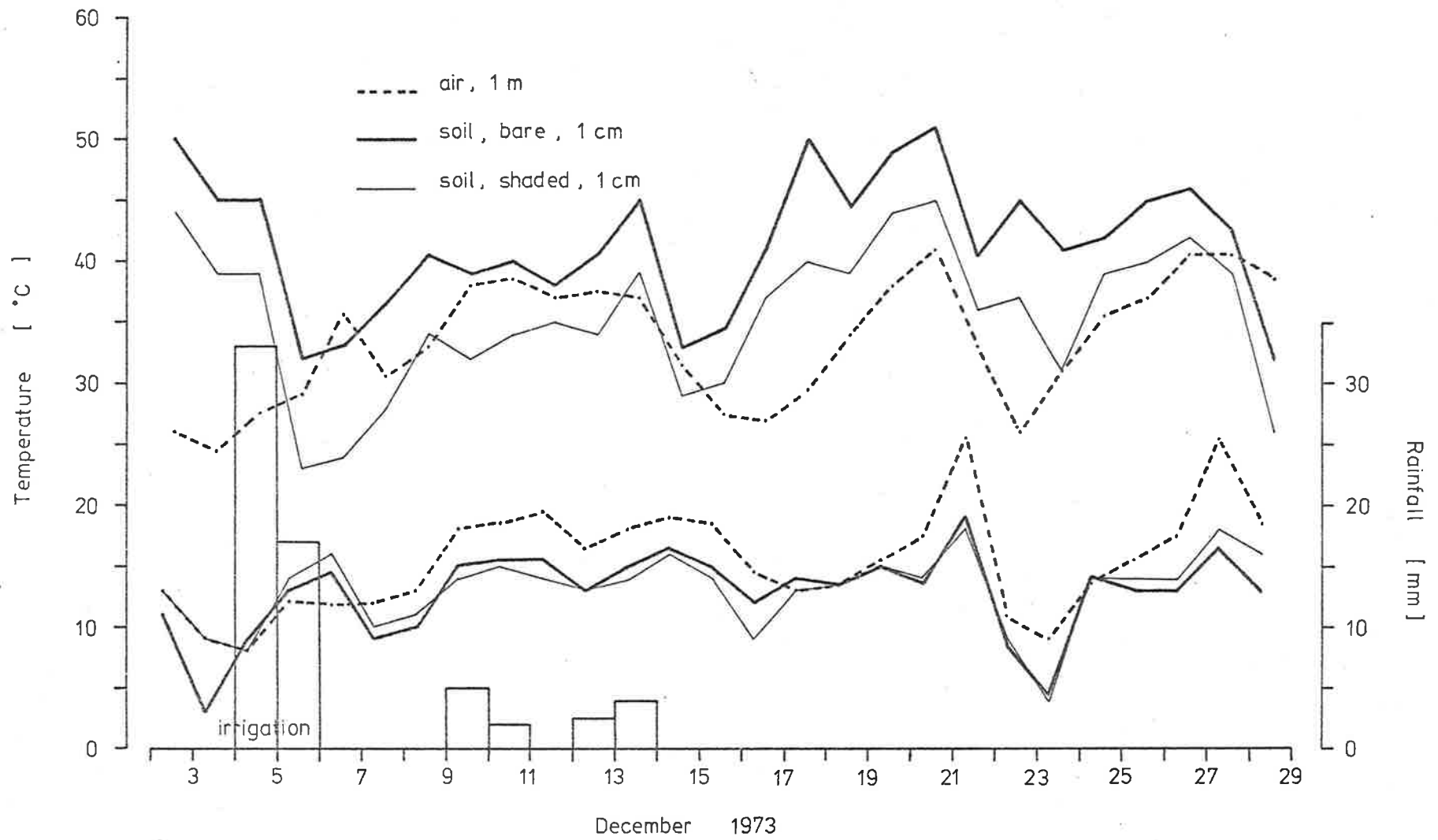
Fig 5.5   Daily air and soil temperatures at KVR, December 1973.   Upper lines show maxima;
lower lines show minima.
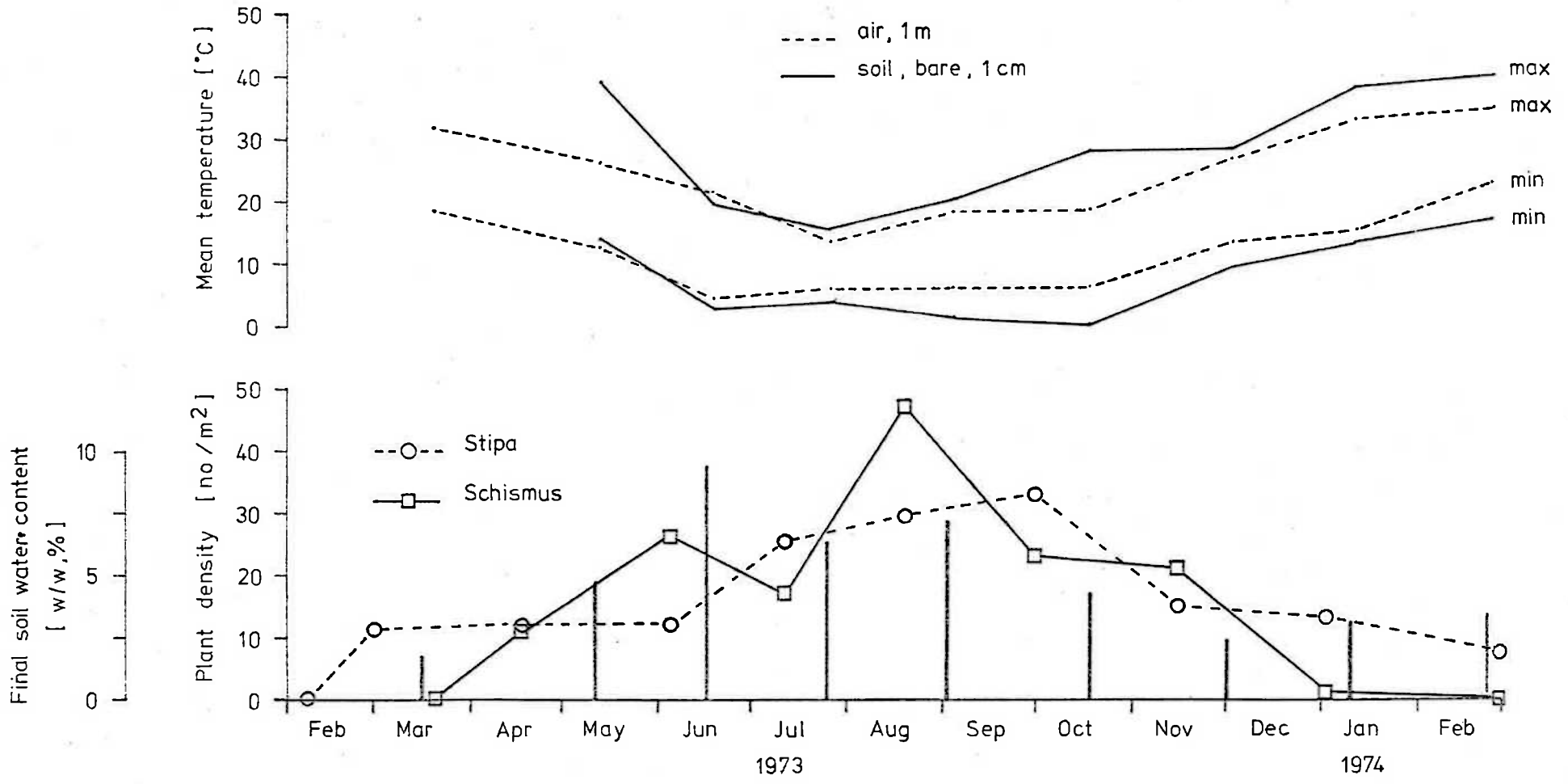
Fig 5.6   Monthly means of temperature, ephemeral plant density and *final* soil water contents at KVR, 1973-4.

	Feb	Apr	May	Jun	Jul	Sep	Oct	Dec	Jan
Enneapogon spp.	++++	--..	....	....	.. .	....	.. .	+. .	++ .
Boerhavia diffusa	++ +	....	.-.		.	+.	...	..	..
Euphorbia drummondii	++++	+...	....	....	.. .	....	+. -	.. -	.
Salsola kali var.	++++	..++	....	....	....	-...	....	....	-...
Bassia paradoxa	++ +	....	....	....	.-..	....	....	....	....
Stipa nitida	++++	++..	....	.+..	....	....	.-..	....	.+.+
Schismus barbatus		++++	++..	+.++	..++	-.-.	-.-.	. ..	. .
Tetragonia eremaea	+	++..	+.+.	..+.	....	---.	...		
Calotis hispidula		++ .	.+..	++.	.-..	-- .	.-..		
Crassula colorata		+ +	....	+++.	+...	...			
Bassia sclerolaenoides	++++	.+..	.--.	..--	..-.	-...	-.-.	-...	-..-
Bassia seedlings				++	. -				+
Stenopetalum lineare			++++	++++	...	..-	...		

Table 5.1   Seasonal trends in germination and establishment of ephemerals, 1973-4. Column headings show the month of irrigation ; response to irrigation was determined 6 weeks later. Each of the four plots (S. Lake, sand; KVR, sand; S. Lake, loam ; KVR, loam) is represented by a separate subcolumn per column. A stop indicates the presence of a species (alive) on a plot 6 weeks after irrigation. A significant change in density is indicated by the sign of the change.

	Summer	Winter
Enneapogon spp.	706	214
Boerhavia diffusa	9	-
Euphorbia drummondii	23	-
Salsola kali var.	19	42
Bassia paradoxa	16	21
Stipa nitida	212	125
Schismus barbatus	1321	782
Tetragonia eremaea	275	299
Calotis hispidula	119	74
Crassula colorata	148	46
Bassia sclerolaenoides	149	221
Bassia obliquicuspis	111	146
Stenopetalum lineare	2	-

Table 5.2   Total germinations over 28 days of seeds in topsoil
             samples (0-2cm) incubated in 'summer' and 'winter'
             laboratory regimes, as described in section 4.132.
             Ranking of species matches Table 5.1.

6.   Dynamics of shrub and tree populations

6.0   Introduction

KVR was originally designed to yield information on the autecology

of individual species as well as on the regeneration of an

overgrazed vegetation (Osborn 1927). However, because of

variation in rainfall and slow rates of change in the vegetation,

several decades elapsed before useful autecological data could be

obtained. Recently Crisp and Lange (1975) successfully used the

KVR records to analyse long term changes in *Acacia burkittii*

populations in relation to grazing and protection.

The KVR records consist principally of charts of permanent

quadrats and photographs repeatedly taken at fixed points. Both

are illustrated by Osborn et al (1935). Previously only the

quadrat charts have been used as a source of quantitative data

Hall et al (1964). However, in 1970 the majority (81%) of the 2350

KVR records consisted of photographs, a source of untapped data

with considerable potential. Furthermore, the photopoint records

all   were   more continuous than the quadrat chart records, all

of which contained gaps of several years.

Thus at the beginning of my Ph. D. studies I made an

investigation with the aim of exploring the potential of the KVR

records, especially the photographs. Three of the most important

Australian arid zone perennials were selected for studies in

population dynamics viz: saltbush (*Atriplex vesicaria*), bluebush

(*Kochia sedifolia*) and mulga *(Acacia aneura)*. At the same time

Noble (1975) used the photopoint records to investigate growth

in relation to climate of saltbush and *Stipa*.

6.1   Saltbush *(Atriplex vesicaria)*

6.10   Introduction

To make a demographic study of a population it is necessary to
follow the fates of individuals from first appearance to death.
Thus it is not surprising that most of the few examples of such
studies on plants concern short-lived herbs (Harper 1967;
Williams 1970b; Tamm 1972; Sarukhan and Harper 1973; Treshow
and Harper 1974). Hett and Loucks (1968, 1971) made demographic
studies of some species of trees but considered only seedlings.
Henry and Swan (1974) and Yarranton and Yarranton (1975) recon-
structed the histories of tree populations over long periods by
determining maximum age of live and dead plants. Unfortunately
this procedure does not account for plants which have decayed
since death.

The KVR records provided a unique opportunity for investigating
the demography of the relatively long-lived perennial, saltbush.
On one of the permanent quadrats ('10A', 10 m x 10 m in size) all
saltbushes had been mapped annually for 36 years. These data were
analysed to determine the age and survivorship characteristics of
saltbush.

6.11   Methods

Quadrat 10A had been charted annually over the period 1926 - 62
except for three gaps of less than 3 years. On each chart the
position and vertical canopy projection of all saltbushes except
very small seedlings had been plotted.

Because of turnover in personnel making the recordings and the small size of seedlings, inconsistency in the charting of these plants must be expected. In order to eliminate 'noise' due to spurious recordings and misidentifications I considered only plants which were charted for at least two successive years. Thus the lowest age class consisted of plants between 1 and 2 years old (and possibly some older ones). Plants which were defoliated had been recorded as present but dead thus allowing age at death to be determined. Rarely, a 'dead' plant put on new foliage after 1 - 2 years, according to the next recorder, in which case I rectified the previous diagnosis and continued the record for that plant. Care was taken not to confuse such 'revitalised' plants with new seedlings appearing under old dead plants. If there was any doubt as to whether an older plant had resprouted or a new one had germinated beneath it, I eliminated 'both' plants from the life table. Thus the fates of 146 plants germinating between 1936 - 1962 were followed until 1962. At that time about one third of them were still alive.

6.12   Data analysis and results

Individual cohorts of seedlings were too small to be used separately for calculation of survivorship curves, as was done by Williams (1970b). The largest cohort of 1 - 2 year - olds comprised 15 individuals. Instead a composite survivorship curve was constructed. A further problem arose from the fact that most cohorts of seedlings originating after 1932 contained individuals which were still alive in 1962.

In order to include these cohorts in calculating the survivorship curve without introducing bias by considering only the plants in them which died at a known (and therefore young) age, the following procedure was used.

Suppose G_x is the gross number of seedlings known to have reached age x. To calculate probability of survival from x to $x+1$ the number of plants (I_x) whose maximum age was indeterminate beyond x must be subtracted from G_x. Hence, the probability P_{x+1} of survival from x to $x+1$ is calculated by

$$P_{x+1} = G_{x+1} / (G_x - I_x) \qquad (6.1)$$

In other words, this procedure makes use of plants of indeterminate maximum age up to the time beyond which their survival becomes unknown, thereby reducing error associated with the curve in the younger age classes.

Survivorship was plotted linearly (Fig 6.1) and logarithmically (Fig 6.2) against age. Probability of survival also was plotted against age (Fig 6.2).

6.13 Discussion

The model most commonly used to describe decay of plant populations is the negative exponential model (Harper 1967) which assumes that the probability of mortality $(1 - P_x)$ is constant throughout the life span i.e. mortality is independent of age. Hett (1971) and others have proposed that for trees probability of mortality decreases with age because of density - dependent thinning.

Crisp and Lange (1975) found that in the tall shrub *Acacia burkittii*, decay was exponential for the first eight years, after which mortality was reduced almost to zero.

Of these models the negative exponential one most nearly describes survivorship of saltbush, particularly in the age range of 2 to 30 years, when probability of survival was more or less constant with mean value of 0.94 (Fig 6.2). Under this model the half life of saltbushes is 11 years. At 30 years the mortality rate increased dramatically (Fig 6.2), but this may not represent a departure from the negative exponential model. All the ten saltbushes which lived to more than 30 years died in the period 1959 - 61, a time of exceptionally low rainfall. Precipitation did not exceed 110 mm, or half the mean, in any of those years. This drought was probably sufficient to prematurely kill shrubs already weakened by old age.

There is evidence to suggest that mortality of saltbush seedlings is higher than predicted by the negative exponential model. The survival from the first age class (0.82) was much lower than the mean (0.94), and lower even than the value 0.88 ($=0.94^2$) expected if this is considered to be a two-year class (see section 6.11). It must be assumed that many very young seedlings were overlooked and not recorded. In addition, I specifically excluded plants surviving less than 1 year from the analysis (section 6.11).

In conclusion then, it is proposed that once *Atriplex vesicaria* is established at 2 years of age, mortality becomes

independent of age, in accordance with the negative exponential

model of population decay. The half life of saltbush at KVR

is 11 years.

6.2 Bluebush *(Kochia sedifolia)*

6.20 Introduction

It was not possible to make a full demographic study of bluebush

on KVR simply because only one seedling had been recorded in

45 years of observations. However I obtained some very useful

information on the decay of populations of mature plants present

at the time of fencing of the reserve. Photographs were used

as a source of data because very few bluebushes occurred on

the permanent quadrats. A preliminary investigation revealed

that bluebush canopies were so discrete that a large number of

shrubs could be consistently identified in successive photo-

graphs from two fixed photopoints. In addition an old quadrat

in an adjacent paddock which had been charted from 1926 - 30 and

then abandoned was relocated in 1972 and charted to determine

changes in a bluebush (and saltbush) population under sheep

grazing.

6.21 Methods and results

6.211 Photopoint data from KVR

Two photopoint series were used to obtain bluebush survivorship

data viz: PP 12[†] and the photopoint[*] at the northeast corner of

quadrat[+] 40A. Two other photopoint series, PP 11 and PP 3 showed

bluebush populations but ephemeral growth obscured the shrubs

in these so often as to make repeated indentification of

individuals very difficult. From the negatives of PP 12 and PP 40A,

enlargements (20 cm x 25 cm) with transparent overlays were made.

Fig 6.3 shows PP 12 in 1932 and 1972. Individuals were numbered

on the overlays and their fates followed in the photo series until

1972. A few problems were created by variation in camera position

and some poor quality negatives, but comparisons of relative

distributions of shrubs allowed most of these to be resolved. Any

shrub whose history was in reasonable doubt was eliminated from

the records. In the foreground of PP 12 defoliated shrubs and

dead stumps were also monitored.

Mortality of bluebush was very low over the period of

observations (Fig 6.4). In PP 12, 56 shrubs (86%) survived from

1931 - 72, and in PP 40A, 109 shrubs (92%) survived from 1926 - 72.

Decline of $\log_e$ of number of shrubs is linear in both cases (Fig 6.4),

suggesting that it is consistent with the negative exponential

model of population decay. If mortality is independent of age

then a population will decline exponentially with time no matter

what its initial age structure (Harper 1967). In the case of the

bluebush populations the initial age structures were, of course,

unknown.

[†] PP is used to abbreviate photopoint

[*] Hereafter referred to as PP 40A

[+] Hereafter referred to as Q 40A

The estimated half lives are 300 years and 150 years for PP 40A
and PP 12 respectively. Two seedlings germinated and survived
in PP 12 between 1931 and 1972.

In the first PP 12 photograph 55 of the foreground blue-
bushes (76%) were defoliated, many being reduced to mere stumps.
In the foreground of PP 11 in 1931 a similar proportion (70%)
of the population was defoliated. Since none of these subsequently
sprouted, it is assumed they were dead. All of the PP 12 stumps
decayed in the following decades, but since very few of the living
shrubs died in that time, the proportion of dead plants in the
population had fallen to 2 out of 14 or 14%. This considerable
decline in relative proportion of dead plants suggests that
bluebush mortality rate was very much higher under grazing prior
to the fencing of KVR than afterwards.

6.212 Quadrat data from Mustering Paddock no. 3

Q 40A in KVR and Q 40B in the adjacent Mustering Paddock no. 3
had been set up in 1925 as a matched pair a few metres apart so
as to compare changes in bluebush stands under protection with
stands under continued grazing. In 1925 these stands had had
very different histories. Whereas KVR had been heavily overgrazed
in the vicinity of Q 40A and contained only a few surviving
bluebushes, the paddock outside had been grazed little and
contained a mixed stand of saltbush and bluebush. Since 1925
Mustering Paddock no. 3 has been grazed intermittently, and only
heavily for spells of a few days per year (section 2.11).

Q 40B was charted from 1926 - 30 and then abandoned. In
1972 I relocated and charted it. Substantial changes in com-
position of the shrub stand on this plot had taken place over
1930 - 72 (Table 6.1). Only 20% of the bluebushes had survived
this period, and one seedling had germinated and survived. It
was difficult to tell whether any of the 1972 saltbushes were
survivors of the 1930 population; none are expected according
to the findings of section 6.1. However, the number of saltbush
on the quadrat had increased 3 fold, reversing completely the
ratio of saltbush : bluebush. The total number of shrubs (of
both species) on the plot was unchanged.

6.22 Discussion

Bluebushes which survived the overgrazing on KVR prior to 1925
were very long-lived. Their numbers apparently decreased
exponentially with half lives estimated to be 300 years and 150
years at each site studied (Fig 6.4). The large variation
between these estimates is not surprising since they were based
on a very short time period relative to the rate of population
decline. An analagous situation would be to attempt to estimate
half life of saltbush from two years' observations.

Under grazing by sheep, longevity of bluebush was much
lower. This was indicated by the decline in proportions of
dead plants in bluebush populations on KVR after the fencing of
the reserve. It was also shown by the high mortality rate on
Q 40B, an intermittently grazed area adjacent to PP 12 and Q 40A
(Table 6.1).

Over 1931 - 72, 76% of the Q40B population died whereas in the KVR populations only 12% died.

Seedling input to the bluebush populations in KVR (3) was negligible over 40 years. It is possible that the lack of seedlings in KVR resulted from permanent changes in the soil as a result of the overgrazing prior to 1925. *Atriplex vesicaria* has not invaded the Q 40A area from the adjacent paddock where it occurs in a dense stand, although it did invade the Q 10A area 1 km to the north (Hall et al 1964). On the other hand bluebush seedling input on Q 40B (1) has also been negligible, although saltbush has freely regenerated on the same area. Lay (1972) also found that seedling input to bluebush populations was very rare. Given the great longevity of bluebush, a very low rate of seedling input to undisturbed populations would be sufficient to ensure continuity of those populations. But in the grazed situation it appears that the greatly increased mortality alone would be sufficient to cause bluebush to be gradually eliminated from the landscape. In the lightly grazed Mustering Paddock no. 3 replacement of the bluebush with saltbush in equal numbers has masked this process because the density of shrubs has not changed, thereby giving the vegetation a 'well preserved' appearance.

6.3   Mulga *(Acacia aneura)*

6.30   Introduction

Mulga is probably the most widespread tree in arid Australia (Nix and Austin 1973).

Because of this and its economic importance as a drought fodder

reserve (Everist 1969; Gartner and Anson 1966) it has been the

subject of much research. Whereas in some regions regeneration

of disturbed mulga populations can be prolific (Everist 1949),

in most places its decline in both ungrazed and grazed situations

has caused much concern (Condon 1949; Lange 1966; Lay 1972;

Cunningham and Walker 1973). At Koonamore Hall et al (1964) have

echoed the latter view. There is an obvious need for more

information on the dynamics of mulga populations in different

regions.

6.31 Age determination[†]

From 47 years of size measurements of 9 young mulgas growing on

the KVR fire quadrats, linear relationships between height (H),

canopy diameter (D) and age (A) were obtained. A single index of

size (I) was calculated by summing H and D. The relationship between

A and I was linear and highly significant (Fig 6.5). From the fire-

quadrat-mulgas and 19 other juveniles located in KVR the relation-

ship between I and stem girth (G), measured just above the root

buttress, was determined. It was linear and highly significant

(Fig 6.6). Thus the relationship between A and G was determined

algebraically:

$$A = 4.39 + 1.20 \; G \qquad\qquad (6.2)$$

[†] The procedures used were identical to those employed by
Crisp and Lange (1975), and are briefly outlined here.

By general application of this relationship the age of any mulga could be predicted from a measurement of girth, although the confidence limits of predictions were unknown. It is probable that rate of girth increase decreases with senescence and varies with site, but the extent of such variation is unknown.

6.32   Age structure and spatial distribution

To determine age structure of mulga on KVR the nearest 160 trees to a central point in the southern half of the reserve were located and sampled for G. A problem in measurement was created by some trees which had branched at a low height and had subsequently split to the base. If all main stems were present, girth was measured by summing the outer portions of the individual stem circumferences, thus omitting the gaps. If this was not possible because of missing or fallen stems, no measurement was taken.

Fig 6.7 shows the age structure of the sample. This diagram reveals that input to the mulga population was drastically reduced from about 100 years ago. Crisp and Lange (1975) observed the same effect in *Acacia burkittii* populations, and attributed it to the introduction of sheep and rabbits to the district between 1865 and 1880. The cut-off in mulga reproduction was apparently less sharp than was the case for *A. burkittii*. This is probably an artifact, resulting from greater error in measurement of G in mulga due to the variation in its stem growth habit. Furthermore, mulga occurs in a wider range of habitats than *A. burkittii* and may vary more in growth rate. Age structure of mulga populations grazed continuously by sheep and rabbits was not sampled, but no seedlings have been observed in paddocks adjacent to KVR.

Input to the mulga populations on KVR did not resume until 1965 - 70.
The lack of regeneration of mulga on KVR was attributed by Hall
et al (1964) to rabbit grazing. The burst of regeneration since
1970, when rabbits were eradicated from the reserve, supports
this view. This seedling input was also a result of heavy summer
rainfalls between 1970 and 1975.

It was observed in the field that mulga usually occurred
in small well-defined stands (5 - 30 trees), generally on deep dunes
and in silty depressions. It was observed also that trees within
stands tended to be of uniform size. Analysis of variance of G
over 11 stands (not including seedlings) revealed that variance
between stands was significantly greater than variance between
trees (Table 6.2), supporting the second observation. This
disjunction between stands may be a result of variation in
favorability of sites and hence of maximum size attained. It may
also mean that the stands are even aged. In support of the second
hypothesis, it was observed that mulga seedlings were themselves
clustered and were associated with stands of dead trees. They did
not occur in living stands where they were apparently suppressed
by competition.

Preece (1971a) showed that heavy summer rains followed by
heavy winter rains are required before mulga will successfully set
seed. Summer rains are also required for germination of mulga
(Hall et al 1964; Preece 1971b). Because the probability of heavy
summer rainfall at Koonamore is low (Hall et al 1964) it is
expected that mulga germination events would be widely spaced.

Thus, a stand of mulga seedlings, once established, may grow to such a size before the next germination event that establishment of more seedlings within the stand is suppressed, resulting in a uniform age structure. Germination events are apparently not sufficiently widely spaced to cause significant disjunction (ignoring the historical grazing influence) in the overall age structure of a large mulga population (Fig 6.7).

6.33 Survivorship

Survivorship of mulga was investigated by using photopoint records, as described for bluebush (section 6.211). In order to obtain sufficient data, it was necessary to combine observations from 7 photopoints. A curve showing survival of mature mulga over 50 years was constructed (Fig 6.8). A surprising feature of this curve is the great increase in mortality after 1955. A possible explanation lies in the nature of the sample used in calculation of the curve. Table 6.3 gives details of the stands used in the photopoint sample. It can be seen that individual stands (e.g. Q 300; Q 200; PP 12 and PP 40A) have tended to die out over a short period or not at all (e.g. Q 6-80; PP 3). This observation is consistent with the idea that mortality in mulga is low until maximum age (250 to 300 years - Fig 6.7) is approached, as in *Acacia burkittii* and humans. Thus whole stands, being even aged, would tend to die out quickly. More than half of the particular sample used is comprised of two stands (Q 200; PP 12 and PP 40A) both of which commenced to die out after 1955.

In 1974 the remaining mulgas on Q 200 were obviously senescent and nearing death. In contrast, the trees on Q 6-80, although very large, appear to be very healthy, and have apparently not yet reached maximum age. Hence the decline of the total mulga population on KVR is probably more slow than is indicated by Fig 6.8. Significant numbers of the original trees should persist for another 100 years (see Fig 6.7).
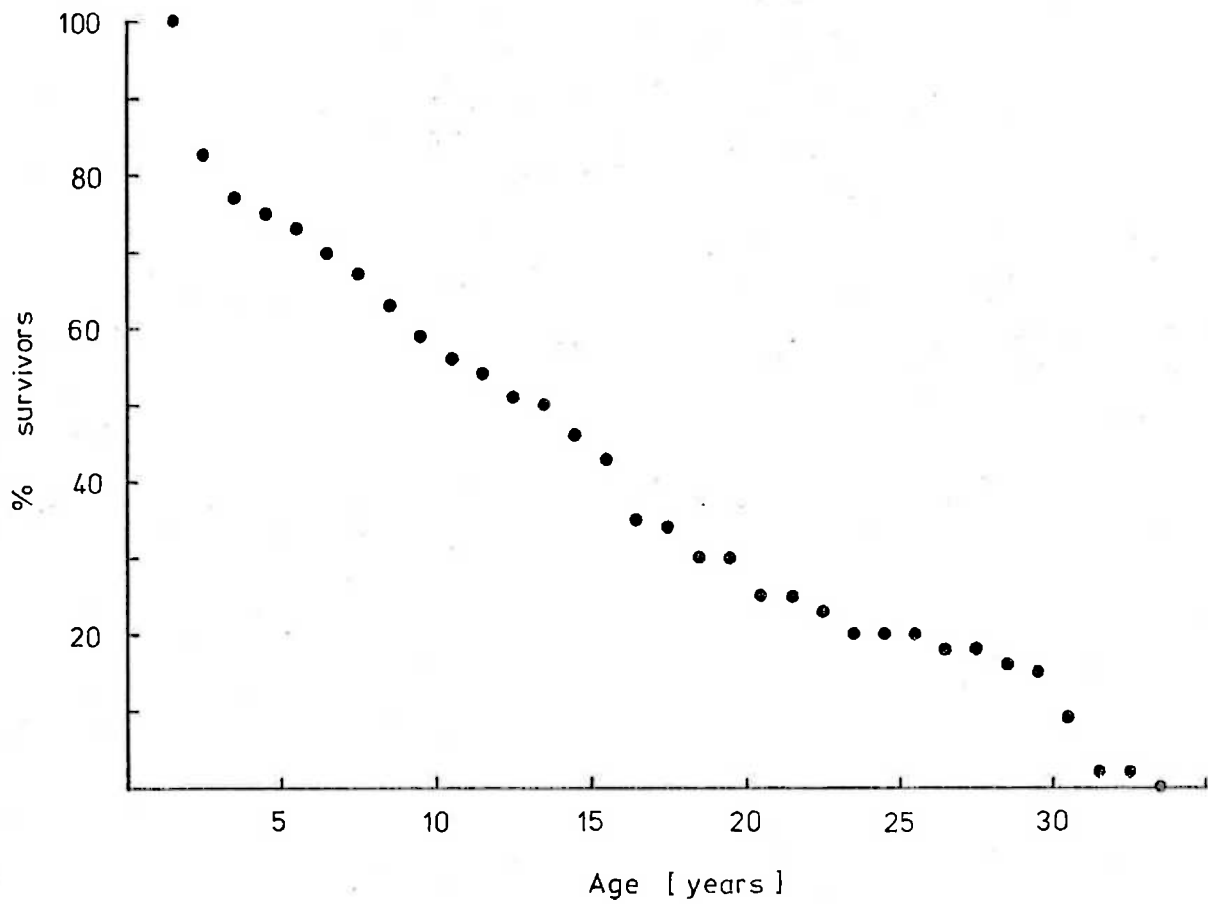
Fig 6.1   Survival of saltbush plants on Q10A (KVR), plotted
           linearly against age.
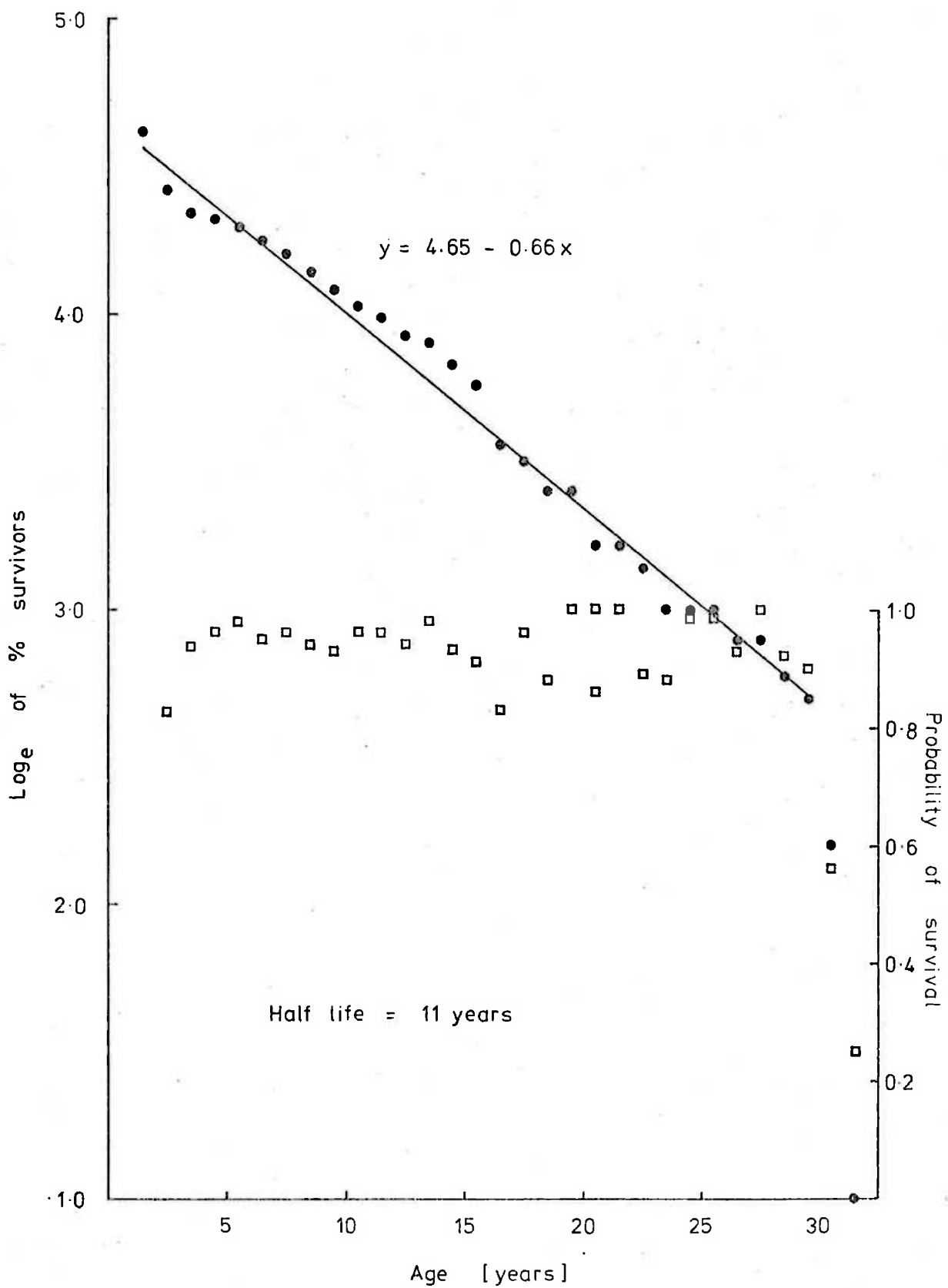
Fig 6.2   Log$_e$ of survival of saltbush plants, and probability
of survival, plotted against age.

A

B

Fig 6.3   PP12 on KVR in 1932 (A) and 1972 (B), showing
           the bluebush populations which survived over-
           grazing between 1900 and 1925. The tree in
           the middle-ground, and the dead ones behind it,
           are mulga.
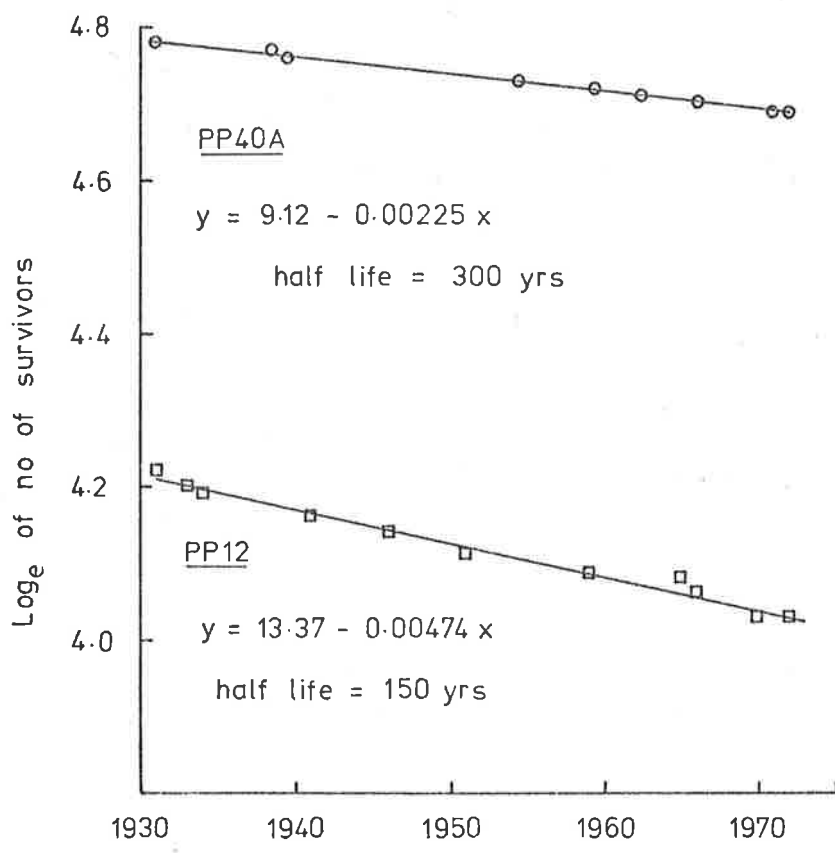
Fig 6.4 Log_e of survival of bluebush plants in two
KVR populations, 1931-72.
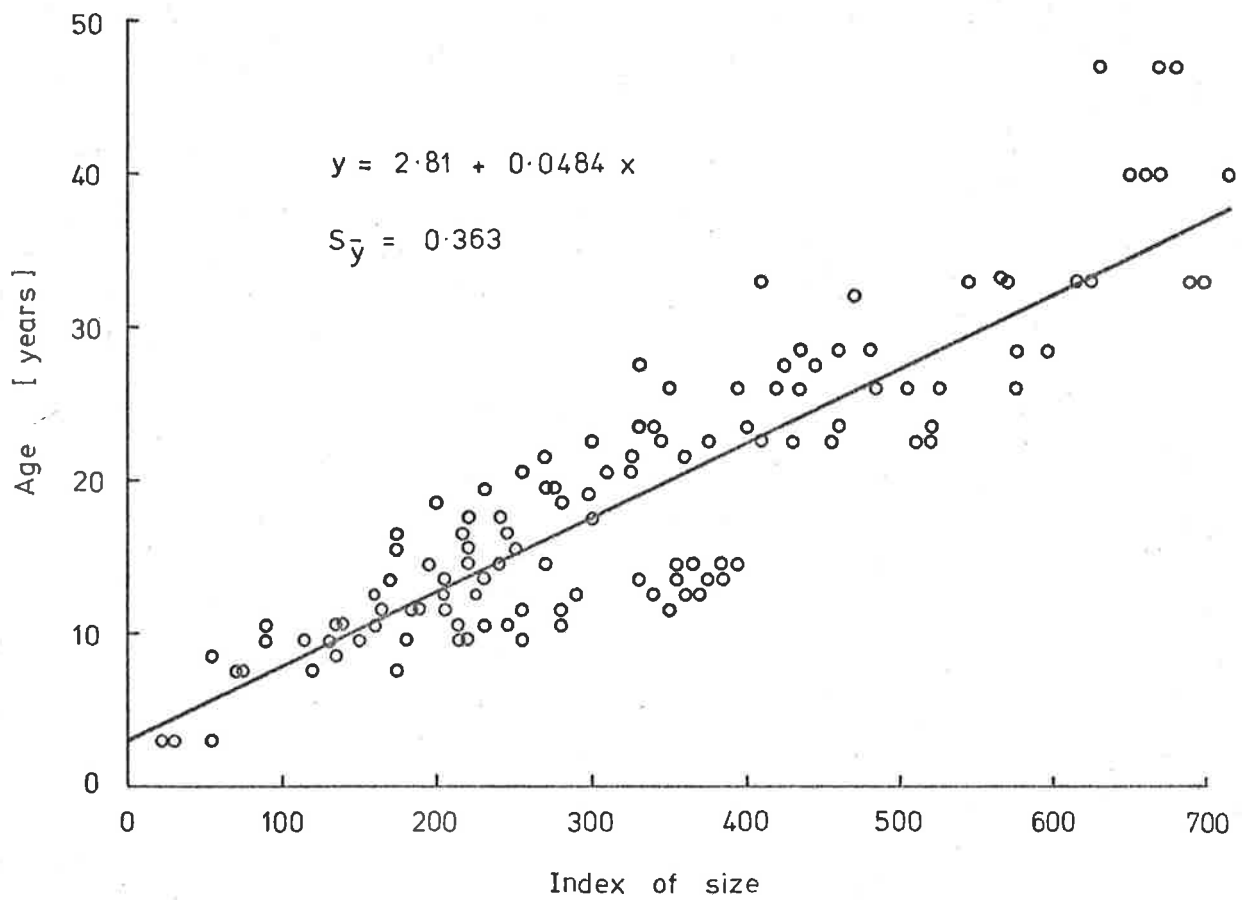
Fig 6.5   Relationship between age and index of size of mulga plants
           on the KVR fire quadrats. $S_{\bar{y}}$ is the standard error of the
           estimate of $\bar{y}$.
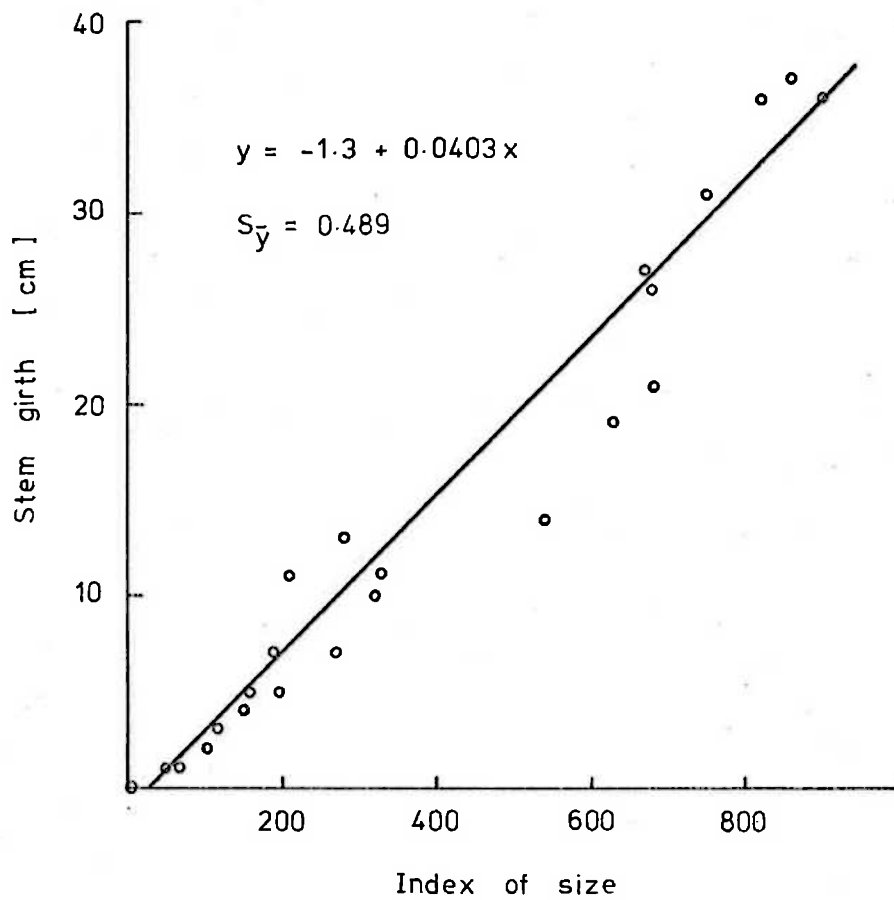
Fig 6.6   Relationship between stem girth and index of size
of mulga plants on KVR. $S_{\bar{y}}$ is the standard error
of the estimate of $\bar{y}$.
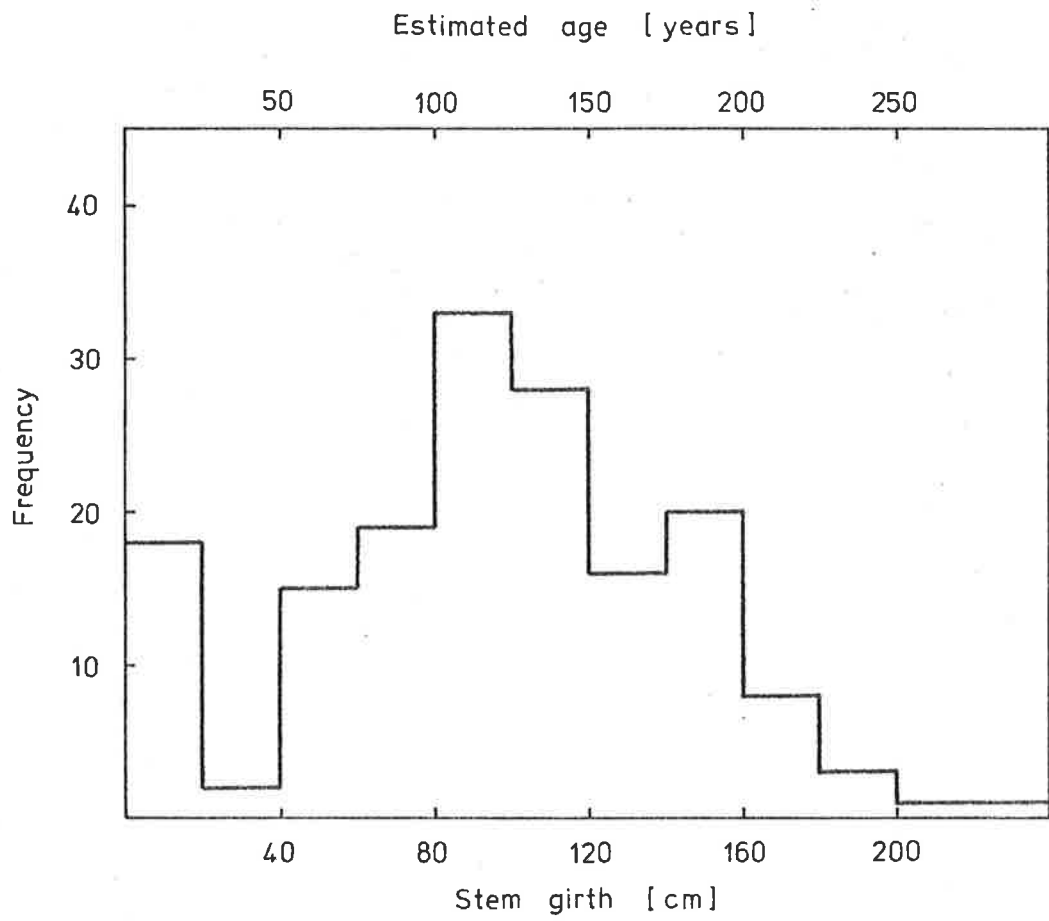
Fig 6.7   Age structure of a mulga population in southern KVR.
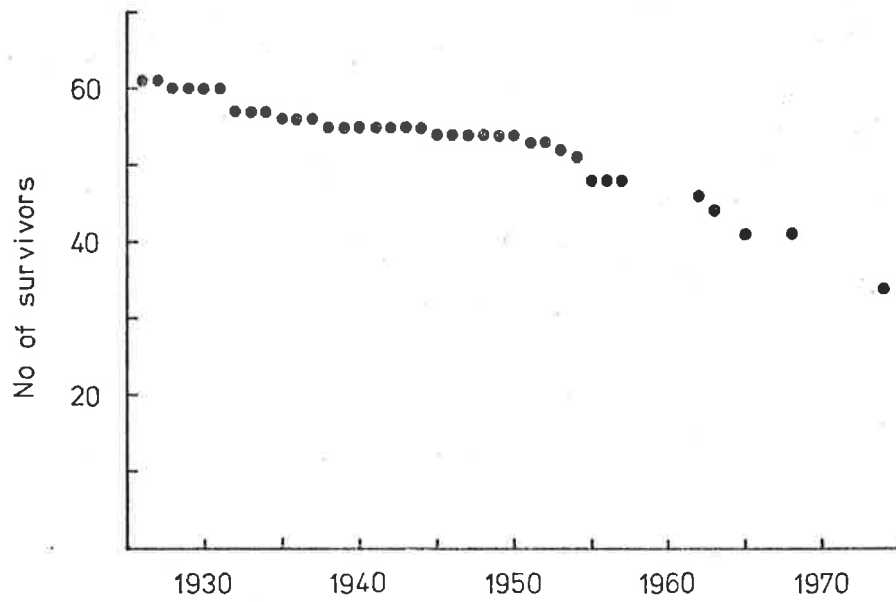
Fig 6.8   Survival of mulga plants in several photopoints
           and permanent quadrats on KVR, 1926-74.

Bluebush

Shrubs surviving 1930 - 72	7
Shrubs not surviving 1930 - 72	27
% survival	20 %
New shrubs, surviving 1972	1

Saltbush

Shrubs surviving 1930 - 72 (assumed)	0
Shrubs not surviving 1930 - 72	13
New (assumed) shrubs, surviving 1972	38

Change in composition

	1930	1972
No. of saltbush	13	38
No. of bluebush	34	8
Total no. of shrubs	47	46
Bluebush as % of total	72%	17%

Table 6.1   Changes in numbers of saltbush and bluebush
on Q40B over 1930 - 72.

Source of Variation	Sums of squares	Degrees of freedom	Mean squares
Between stands	59040	10	5904
Residual	100400	98	1025
Total (between trees)	159500	108	--

Result : F = 5.76 , P < 0.001

Table 6.2   Analysis of variance of girth (G) of mulga
on KVR, comparing variance between stands
with variance between trees.

Site	Original population, 1925	Survivors, 1974 (%)		Period of deaths
Q200	26	17	(65)	1965 - 1974
Q300	7	0	(0)	1927 - 1937
Q6-80	10	8	(80)	—
PP12 and PP40A	9	2	(22)	mostly 1955 - 1965
PP3	6	4	(67)	—
Other	3	3		—

Table 6.3   Details of mulga stands used in derivation of
Fig 6.8, and numbers and times of mortalities
within those stands.

7.   Discussion

7.0   Introduction

Two roles were envisaged for the KVR investigation, according to its
original aims (see chapter 1). First, it was to contribute to
management of the vegetation resource of the pastoral industry,
principally by allowing determination of the long term effects of
grazing on this resource, and especially of overgrazing. In
addition it was to be a study with wider and more academic
implications - a source of information on the basic biology of
arid zone vegetation and the nature of long term change within it.
In this chapter the success of KVR in playing these roles is
evaluated, and in the light of this, the future of KVR is discussed.

7.1   KVR and the pastoral industry

7.11 Fifty years of vegetation change : conclusions from the
present study.

7.111 Low shrubs

In 1925 the low shrub cover in S. Lake, including the site of KVR,
had been virtually destroyed by overgrazing. Since the fencing
of KVR, the two species of *Atriplex* have gradually invaded it from
the only available seed source, Mustering Paddock no. 3, in the
east. Hall et al (1964) documented this process. Now saltbush
is conspicuous over much of the reserve, but the process of
regeneration is not complete. This is most clearly indicated by
the gradient in saltbush abundance across KVR (Fig 3.6). A useful

scale of comparison of saltbush densities is the set of 6 'stages'
devised by Jessup (1951) to encompass the entire range of density
of *Atriplex vesicaria* in the 'Northwest' of South Australia. The
overall density of saltbush on KVR (1060 plants/ha) is low on
Jessup's scale, at stage 4. In the northeast corner of KVR,
nearest to the original seed source, the density (9050 plants/ha)
is high, corresponding to stage 1, whereas in the southwest
corner saltbush is virtually absent (stage 6). The shrubs
Atriplex stipitata and *Kochia georgei* show similar gradients across
KVR (Fig 3.6). In S. Lake, all these shrubs are virtually absent,
an indication that recolonisation of that area has been prevented
by continued grazing, albeit at lower rates. On the other hand,
saltbush has increased in density under intermittent grazing in
Mustering Paddock no. 3, at the expense of bluebush (section 6.212).
In the area around Southern Cross Bore, which was subjected to
destructive overgrazing in 1926 (section 2.11), not only has there
been no recolonisation by the original saltbush, but also a more
severe form of degradation has resulted from continued stocking of
that area. For a radius of ca 1 km around the water point the
vegetation consists almost entirely of the inedible perennials
Nitraria schoberi, Zygophyllum aurantiacum and the poisonous
Peganum harmala.

The very long lived bluebush has not recolonised KVR. Not
even a significant crop of seedlings has been produced. Those
plants which survived the heavy grazing before 1925 showed very low
mortality on KVR (12%) since that time. On the other hand mortality
was quite high (80%) in the adjacent intermittently grazed

Mustering Paddock no. 3, resulting in a gradual replacement of bluebush by saltbush. In conclusion, it appears that bluebush populations decline at KVR even under the lightest stocking pressure.

7.112 Ephemerals

There are few data concerning the abundance of ephemerals on KVR in 1925, or at any time until 1971. The 1 m^2 quadrats charted from 1926 - 31 were far too small to provide meaningful averages. Early descriptions established that *Stipa* and *Bassia patenticuspis*[†] were the principal species at the time of fencing of the reserve. The results of the 1971 harvests (section 3.2) suggest that while *Stipa* has retained its dominant status, *Bassia* has declined in relative abundance in KVR. The single example of early quantitative work on ephemerals was cross-fence comparisons of density of *Stipa* (Osborn et al 1931). Density was sampled with 31 matched pairs of 1 m^2 quadrats at fixed points on either side of each of the 4 KVR fence-lines. Osborn et al found that in a year of growth, *Stipa* density was maximum in August. This correlates well with my findings (Fig 5.6). Thus in August 1971 I relocated the old sampling sites along the 2 KVR/S. Lake fences and sampled *Stipa* density (Table 7.1). Statistical tests of comparison were not possible because Osborn et al (1931) presented only total counts, and their detailed data could not be found.

[†] As there was no mention at all of *B. obliquicuspis* in the early records, it is probable that it was confused with *B. patenticuspis*.

However it is clear that from 1928 - 30 to 1971 *Stipa* density on

KVR had changed little, although an increase might have been

expected. The lack of apparent increase of *Stipa* certainly can

not be ascribed to lack of rainfall in the growing season of

1971 (Table 7.1). In S. Lake *Stipa* density had decreased from 1928

to 1971. The 1930 sample is not directly comparable with the

others because grazing occurred in S. Lake in that year. Thus it

appears that the present cross-fence differential between KVR and

S. Lake in *Stipa* abundance may have arisen by reduction of the

S. Lake population under continued grazing from 1928 - 1971, rather

than by significant increase in the KVR population under protection

from grazing. Although compositional differences have developed

in the ephemeral flora of KVR (relative to S. Lake) after 50 years

of protection from grazing, the total productivity remains the

same as in S. Lake (Tables 3.2 and 3.3). Although competition

from shrubs in KVR must be higher, the ratio of ephemeral biomass:

shrub biomass (20 : 1) in 1971 indicates that such competition is

probably not limiting.

7.113 Tall shrubs and trees

After 35 years, Hall et al (1964) reported that input to the

populations of all but 3 of the 11 species of tall shrubs and trees was

negligible at least until 1954. Since that time all species have

produced significant quantities of seedlings which have survived.

This upsurge in regeneration could be ascribed to various causes,

for example the reduction in rabbit populations by myxomatosis in

the mid 1950s ; and two sequences of very high rainfall in the

1950s and 1970s It is possible also that the soil in KVR did not

become a suitable seed bed until 30 years had elapsed. In the
continuously grazed areas, input to the populations of all species
remains negligible. It appears that under continued grazing by
sheep and rabbits, most of these species will be eliminated from
the landscape.

7.114 Soils and lichen crust

Apart from verbal descriptions, there has been little indication
of the state of the soils on KVR until 1972. Early photographs
show a complete lack of a lichen crust and numerous scalded[†] areas
on the loam soils (Fig 6.3). Fifty years of exclosure have led to
a slight differential between KVR and S. Lake in soil fertility,
partly through build-up of organic matter and development of a
lichen crust in KVR, and partly because of continuing erosion
in S. Lake (section 4.4). Nevertheless, scalded areas are still
a conspicuous sight on the loam soils of KVR. They carry no lichen
crust or vegetation of any kind. A sample taken in the northwest
corner of KVR in 1972 showed that scalds had a mean diameter of
2.1 m, and occupied 14% of the loam soil area. Such scalds are not
a feature of shrublands on Koonamore which have not had a history
of overgrazing.

Rogers (1974) also observed the scalded areas on KVR. He
argued that development of a shrub cover was a necessary prerequisite
to redevelopment of a crust, and that lichen crusts could not of

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[†] A scald is a deflated surface which is compacted to such a
degree that it is nearly impervious to water. More complete
descriptions are given by Beadle (1948) and Hutton and North-
cote (1957).

themselves stabilise an actively eroding surface. This argument is contradicted by the fact that there is a well developed crust over most of southern KVR, where a shrub cover has never re-established (excluding the southeast corner). It is not at all clear from the available evidence as to whether development of a crust is a necessary prerequisite to development of vegetative cover, or vice-versa, or whether both processes are simultaneous.

7.115 Conclusions

The present study has revealed that although the traditional observations made on KVR alone have shown much about the regeneration of overgrazed vegetation, comparisons of areas with different grazing histories have shown a great deal more about the nature of vegetation change in relation to grazing. For example, the present differences in vegetation and soils between KVR and S. Lake are due not only to change in KVR (e.g. invasion of saltbush; regeneration of lichen crust) but also to change in S. Lake (e.g. continued soil erosion; decline of the *Stipa* population) despite a reduced stocking rate in that paddock. Near to Southern Cross Bore, where stocking was sustained at a higher rate than in S. Lake adjacent to KVR, the vegetation declined to such a degree that only inedible and poisonous plants inhabited the area. Finally, in Mustering Paddock no. 3, the bluebush population declined much more rapidly over 50 years than in KVR, despite the fact that it was only intermittently grazed.

7.12   Comparisons with other studies

Chenopod shrublands directly comparable with those at Koonamore
are distributed through the southern and central arid zone of
South Australia, and the far southwest of New South Wales (see
section 4.02).   Several studies of vegetation change under
grazing in this ecosystem have been made.

There is a fairly general consensus that under all but
the lightest stocking pressure, the dominant low shrubs decline
in abundance.   Osborn et al (1932) found that in the more heavily
grazed areas nearest to water points, saltbush was killed out,
but further away where the stocking pressure was lighter these
shrubs were either unaffected or even slightly improved in vigour.
Barker and Lange (1969) showed that under moderate stocking
pressure near to water points bluebush was gradually replaced by
other species, and that this effect tended to attenuate with
distance from water points.   Barker and Lange (1970) described very
similar trends in saltbush populations.   In the most arid part
of this ecosystem, Lay (1972) reported that both saltbush and
bluebush declined under even the most conservative stocking regimes.
There are a few descriptions of permanent destruction of chenopod
shrublands over short periods under heavy stocking (Ratcliffe 1936;
Knowles and Condon 1951; Lay 1972).   None of these studies have
produced results inconsistent with those from KVR.   However, in
complete contrast, Trumble and Woodroffe (1954) found that under
very heavy stocking, bluebush stands apparently increased in vigour,
 by comparison with stands which were lightly stocked or unstocked.

Furthermore, heavy crops of seedlings, which survived, were
produced in a wet year. This trend was attributed to increased
rate of turnover of the limited nutrient pool in the system, and
it was assisted also by extremely good rains in one year (1946).
These findings are not necessarily inconsistent with the general
concensus. If the study had extended over a period of more
that 10 years, it would probably have been observed that
accelerated erosion under heavy grazing would have eventually
robbed the system of its small pool of labile nutrients. Once
reduced to such a state, this ecosystem has little chance of
regenerating of its own accord (Charley and Cowling 1968).

Similar conclusions have been drawn from comparable low
arid shrublands elsewhere; that is, ecosystems in which low shrubs
are the only perennial ground cover. Holmgren and Hutchings
(1972) consider the North American salt desert shrublands to be
directly comparable with Australian low arid shrublands. Under
light to moderate grazing in the salt desert shrublands, preferred
shrubs are eliminated and replaced by non preferred shrubs. Under
heavy grazing, all shrubs are eliminated, and replaced by annuals
which are ineffective in preventing severe soil erosion.

7.13 Implications for the pastoral industry

The elimination of trees and tall shrubs under grazing in the
ecosystem studied must be a cause of concern. Not only are
these plants valuable from an aesthetic point of view, but they
are also important in providing shelter for livestock from the

intense arid zone solar radiation. There appears to be no ready
solution to this problem. The results of the KVR study suggest
that decades of exclosure from all introduced herbivores may be
necessary to allow successful reestablishment of trees in an
overgrazed vegetation, which is not a feasible proposition in
a grazed system. However, rabbit control may do much to alleviate
the problem.

Of greater concern is the result of removal of the perennial
shrub cover from this system. Since comparisons are inevitably
drawn between the present ecosystem and that of the Riverine
Plain in New South Wales, and since the latter has been studied
in considerable detail, I shall commence this discussion by
reference to it. The original chenopod shrubs of the Riverine
Plain have been mostly eliminated by sheep grazing, and replaced
by a vegetation consisting of annual and perennial herbs (Williams
1968a). This vegetation has apparently come to equilibrium with
grazing maintained at the original (moderate) rate (Williams
1968a, 1969), while maintaining a satisfactory level of animal
production (Leigh et al 1968). Hence these authors argue that
there is no need to alter the present management system. To seal
this argument, Williams suggests that it would take drastic
manipulations to alter the secondary vegetation, and that obviously
no amount of protection will bring back the eliminated saltbush and
other chenopods.

However, there is reason to believe that the same conclusions
do not apply to the KVR ecosystem. The Riverine Plain differs
from KVR in having a higher rainfall (the mean is ca 360 mm) and

heavier-textured soils. Whereas the secondary vegetation under grazing in that area has a significant perennial component, capable of protecting the soil against erosion, the secondary vegetation of the KVR system consists of ephemerals alone. With the lichen crust and chenopod shrubs gone, there is no protection against erosion during dry periods (Marshall 1973). Loss of even the top few cm of soil from this system results in a serious loss of labile nutrients, and hence serious loss of productivity (Charley and Cowling 1968). The resulting vegetation, although probably stable under grazing, would be unlikely to maintain a satisfactory level of animal production.

Assuming then that the perennial chenopod shrubs are essential to the maintenance of sustained animal production in the KVR system, the value of exclosure as a tool for regenerating a destroyed shrub cover must be assessed. In fact it appears to be a very poor tool. Even in the presence of a seed source, natural regeneration of the saltbush on KVR is far from complete after 50 years, and regeneration of bluebush has not occurred at all. Since this slow recovery is apparently largely due to severe soil damage (section 7.114), mechanical treatment, fertilisation and probably seeding would all be necessary for a satisfactory rate of regeneration. Avoidance of expensive treatments such as these seems to be highly desirable, and the only way to do this is to maintain the original shrubland (if it still exists). Much more research is needed on the question of what management systems will maintain both the vegetation and animal productivity.

7.2   KVR as a study in long term vegetation change

7.21 Approaches to the study of long term change

There has been a variety of approaches to the study of long term change in vegetation (Knapp 1974b). Two categories of approach, direct and indirect, can be recognised. Whereas direct studies involve repeated observations of vegetation over long periods, all indirect studies are based on extrapolation from short term investigations.

A common form of the indirect approach involves comparisons of vegetation on areas which are identical except in having different (but known) ages e.g. on morains and other sediments of recessing glaciers. In a similar way inferences may be drawn from relics of earlier vegetation. A third approach is to make inferences from age structures of stands of trees or shrubs (section 6.32). Finally, there is the use of profiles of plant macrofossils, pollen and spores; this is reviewed by Tüxen (1974). This last approach is of little use in studying arid zone vegetation. The chief disadvantages of the indirect methods are that dating is often imprecise, and that the influence of unmeasured variables e.g. climatic fluctuation can be unknown or overlooked.

The direct approaches are potentially more accurate than the indirect because they involve direct observation of change. However, the value of a particular method depends upon the number and type of variables measured, and the frequency of sampling.

With frequent sampling, the value of such an investigation increases considerably with time as longer term trends become separable from shorter term fluctuations. As the KVR investigation has shown, the amount of time required to obtain meaningful averages of some variables and to discern long term trends in the arid zone can be considerable.

7.22 Problems in the direct approach

Problems in the direct approach are discussed with particular reference to KVR. All arise from the fundamental nature of the approach, that is from the very fact that long time periods are involved.

The principal problem is to ensure continuity over long periods. For this to occur requires the continuous involvement of people with direct interest in the investigation. The presence of one of the founders of KVR (J.G. Wood) as head of the Botany Department, Adelaide University over 35 years was directly responsible for the long history of KVR. After his death in 1959 interest in KVR inevitably declined (Fig 1.1). To maintain enthusiasm for such a project over long periods when data accumulates slowly is difficult. Such loss of enthusiasm can be avoided only by carrying out long term investigations in institutions in which there is an active program of directly related short term studies. Apart from KVR, a good example of such a successful association is the Jornada Experimental Range in North America (Herbel et al 1970).

Even if continuity of the investigation is maintained, its
value may be seriously impaired by variations in sampling which
may effectively truncate a sequence of measurements. This may
arise either from lack of consistency in technique, or from
abandonment of a series of observations which have yielded no
apparent results. Abandonment is short-sighted, for many of
the KVR observation series yielded useful results only after
30 years. An example of the consequences of short-sighted
alteration of an observation series on KVR comes from the quadrat
Q 10A. About a quarter of the area of this plot was originally
scalded, as described in section 7.114. In 1955, after 30 years,
this area was still scalded, and carried no vegetation. The
investigators of that time decided to test the hypothesis that
a litter coverage would alter the soil conditions of the scald,
providing a suitable seed bed. Branches and other litter were
placed on the area, and spectacular germinations of many species
resulted. However, as a consequence of this action, the question
of whether such an area left to itself will ever regenerate, and if
so how this will relate to the dynamics of the vegetation on its
edges, can never be answered from Q 10A. Furthermore, resultant
changes to adjacent areas of the quadrat were so great as to cause
truncation of the demographic study of saltbush (section 6.1) and
disruption of Noble's (1975) growth studies. A much better action
would have been to set up a new quadrat on an adjacent scald for
experimentation, and to have used the Q 10A scald as a control.

The final problem in direct investigations is vulnerability
to catastrophic events, such as wildlife, whose probability is

significantly increased over long periods. Although such an event
may irreversibly alter the original conditions of the investigation,
it could be used to advantage, by altering the investigation to
one into the effect of a catastrophic event upon a vegetation of
known history.

7.23 KVR in relation to other long term studies

Only direct approach studies will be considered in this section.
The majority of direct approach studies have involved only one or
a few repetitions of sampling, with gaps of many years between
observations. There are so many examples of these, that some from
semi-arid and arid pastoral regions will suffice for the present
discussion e.g. Shreve (1929); Voigt (1951); Glendening (1952);
Robertson (1954); Branson and Lomasson (1958); Phillips (1963);
Buffington and Herbel (1965); Johnston et al (1971); Heath (1971);
Robertson (1971); Turner (1971); Smoliak et al (1972); Lay (1972);
Lang (1973). Studies which have been both comprehensive in
scope and regular in sampling (i.e. annual or nearly so) are rare.
Some examples are Adamson (1935), Trumble and Woodroffe (1954),
Williams (1969) and Holmgren and Hutchings (1972). Each of
these involved frequent sampling, but over much shorter periods
than KVR. One of the most notable long term investigations is
that of Watt (1957, 1960, 1962) in Breckland, United Kingdom. This
study involved a large number of small quadrats, charted annually
from 1936, in areas grazed by rabbits and protected from them.

Only the investigations at the Jornada Experimental Range in
New Mexico, U.S.A. seem comparable in scope, length and frequency
of sampling with those at Koonamore. Apart from a series of
4 surveys at widely spaced intervals (Buffington and Herbel 1965),
the main long term studies at Jornada were made on small quadrats
between 1915 and 1968 (Wright 1972). Both KVR and Jornada have
produced data sufficiently comprehensive to be usable in
detailed computer simulations of their respective ecosystems
(Herbel et al 1970; Noble 1975). The Jornada investigation
appears to have differed from KVR mainly by lacking comprehensive
photograph series. In conclusion, KVR by virtue of its length,
scope, depth and frequency of sampling appears to be a unique study
in vegetation dynamics.

7.4   The future of KVR

From the preceding discussion it is clear that the KVR investigation
must be continued. The present investigation has amply demonstrated
the potential of KVR to provide information on vegetation change
which is otherwise very difficult, if not impossible, to obtain.
This information relates to regeneration of overgrazed vegetation,
other changes in grazed vegetation, population dynamics, growth
in relation to climate, and so on. By the very fact of its great
length, the value of KVR must increase with time (section 7.21).
It is also essential that KVR be continued in its original form,
not necessarily because the original design was good, but rather
because of the overriding need for consistency (section 7.22) and
because regeneration of the overgrazed vegetation is not yet complete
(section 7.11). It is also highly desirable that certain observations

which were abandoned be resumed, especially on Q 10B and Q 40B (see section 6.2).

Interest in KVR has recently been revived within the Botany Department, University of Adelaide. Various actions to ensure the continuity of the investigation have been initiated. These include refencing the reserve, suppressing the rabbits, duplicating the records, and so on. An important new development has been the taking of all photographs in stereo, and some in colour, since 1972. However, the long term continuity of the investigation will depend upon people having a direct research interest in it. There is plenty of scope for short term experimental work based upon the results already obtained from KVR, as has been done at Jornada. One of the most interesting (and important) questions which might be pursued concerns the role of the lichen crust and its contribution to the nutrition and stability of the system. Other important questions are how scalds regenerate (if they do at all); how bluebush regenerates, and why it has not done so on KVR; and whether lack of a seed source is the only reason that saltbush has not invaded S. Lake following the reduction of grazing pressure there. There is plenty of opportunity to expand KVR into an investigation of far greater significance even than at present, if only the challenge is accepted.

Time of Sampling	North fence		West fence		Rain-fall (mm)
	KVR	S. Lake	KVR	S. Lake	
Aug 1928	23.9	17.2	15.6	15.6	62
Aug 1930	25.8	8.7	16.8	5.2	41
Aug 1971	29.1	9.0	14.3	5.6	260

Table 7.1   Cross-fence comparisons of *Stipa* density in
              1928, 1930 and 1971. Density is expressed
              as no. of plants/m^2 (including seedlings
              and dead plants). Rainfall is for the
              growth season, February - July inclusive.

Appendix 1

List of taxa recorded on Koonamore and in KVR.   This Appendix
lists all taxa collected by myself on Koonamore over 1971 - 1974.
Voucher specimens are lodged in the State Herbarium of South
Australia (AD) and in my personal herbarium.   Identifications
were verified by the staff of AD.   Nomenclature follows Black
(1948 - 1965) and Eichler (1965) except where more recent revisions
are available.   Uncertain identifications are marked by asterisks.

In addition, the taxa have been recorded in the following
categories :

   1.   Taxa not recorded by Carrodus et al (1965) -
          'new records'.

   2.   Taxa recorded in KVR - 'KVR'

   3.   Taxa recorded in the adjacent comparable parts
          of S. Lake - 'S. Lake'.

	New Records	KVR	S. Lake
AIZOACEAE			
Disphyma australe (Ait.) N.E. Brown	+		
Tetragonia eremaea Ostenf.		+	+
AMARANTHACEAE			
Amaranthus grandiflorus (Black) Black		+	
Ptilotus exaltatus Nees	+	+	
P. obovatus (Gaudich.) FvM.			
P. polystachyus (Gaudich.) FvM.			
APIACEAE			
Daucus glochidiatus (Labill.) Fisch., Mey. & Ave-Lall.		+	
Hydrocotyle trachycarpa FvM.			

	New Records	KVR	S.Lake

ASCLEPIADACEAE

Leichardtia australis R.Br.   · · · KVR: +
Sarcostemma australe R.Br.

ASTERACEAE

	New Records	KVR	S.Lake
Actinobole uliginosum (A. Gray) Eichler		+	+
Angianthus burkittii (Benth.) Black		+	
A. pusillus (Benth.) Benth.	+	+	+
A. tomentosus Wendl.	+	+	+
Aster subulatus Michx.	+		
Athrixia athrixioides (Sond. & FvM. ex Sond.) Druce	+		
Brachyscome ciliaris (Labill.) Less.	+	+	+
B. ciliaris var. *brachyglossa* Gauba	+	+	
B. ciliaris var. *lanuginosa* (Steetz) Benth.	+	+	
B. lineariloba (DC.) Druce	+	+	+
Calotis cymbacantha FvM.		+	
C. hispidula (FvM.) FvM.		+	+
C. multicaulis (Turcz.) Druce	+	+	
Carthamus lanatus L.			+
Centaurea melitensis L.	+	+	+
Centipeda cunninghamii (DC.) A.Br. & Aschers	+		
Cirsium vulgare (Savi) Ten.	+		
Conyza bonariensis (L.) Cronquist	+		
Craspedia pleiocephala FvM.		+	
Cratystylis conocephala (FvM.) Moore	+	+	
Elachanthus pusillus FvM.	+		
Erodiophyllum elderi FvM.		+	+
Gnaphalium involucratum Forst.f.	+	+	+
G. luteo-album L.		+	+
Gnephosis foliata (Sonder) Eichler	+	+	
G. skirrophora (Sond. & FvM. ex Sond.) Benth.	+		
Helichrysum bracteatum (Vent.) Andrews	+	+	
H. semifertile FvM.	+		
Helipterum floribundum DC.		+	
H. microglossum (FvM.) Tate	+		
H. moschatum (A. Cunn. ex DC.) Benth.		+	+
H. polygalifolium DC.	+		
H. pygmaeum (DC.) Benth.	+	+	+
H. strictum (Lindl.) Benth.			
Hypochoeris glabra L.	+		+
Isoetopsis graminifolium Turcz			
Ixiolaena leptolepis (DC.) Benth.			
I. tomentosa Sond.	+	+	
Lactuca serriola L.	+		
Microseris scapigera (Sol. ex A. Cunn.) Schultz-Bip.	+		
Minuria cunninghamii (DC.) Benth.		+	
M. leptophylla DC.	+	+	
Olearia pimeleoides (DC.) Benth.			
Onopordum acaulon L.	+	+	+

	New Records	KVR	S. Lake
ASTERACEAE (Cont.)			
Pentzia incana[†] Kuntze	+	+	
Podocoma nana Ewart & White		+	
Pterocaulon sphacelatum (Labill.) Benth. & Hook.			
Reichardia tingitana (L.) Roth.	+	+	+
Senecio glossanthus (Sond.) Belcher	+	+	+
S. aff. lautus Forst. f.ex Willd.	+	+	
S. magnificus FvM.		+	+
S. quadridentatus Labill.			
S. runcinifolius J.H. Willis	+		
Sigesbeckia orientalis L.	+		
Sonchus asper spp. *nymanii* (Tin. & Guss.) Hegi	+	+	+
S. oleraceus L.		+	+
Vittadinia scabra DC.		+	+
V. triloba (Gaudich.) DC		+	+
Xanthium spinosum L.			+
BORAGINACEAE			
Buglosoides arvense (L.) Johnson	+		
Echium lycopsis L.		+	+
Heliotropium curassavicum L.	+		
H. europaeum L.		+	
H. supinum L.	+		
Omphalolappula concava (FvM.) Brand		+	+
Plagiobothrys plurisepaleus (FvM.) Johnston		+	+
BRASSICACEAE			
Alyssum linifolium Steph. ex Willd.	+	+	+
Arabidella trisecta (FvM.) Schulz		+	+
Brassica tournefortii Gouan.	+	+	+
Carrichtera annua (L.) DC.		+	+
Diplotaxis tenuifolia (L.) DC			
Geococcus pusillus Drumm. ex Harv.		+	+
Harmsiodoxa blennodioides (FvM.) Schulz		+	+
Lepidium fasciculatum Thell.	+		+
L. hyssopifolium Desv.	+		
L. papillosum FvM.	+	+	
L. rotundum (Desv.) DC.	+		
Sisimbrium erysimoides Desf.	+	+	+
S. irio L.	+		
Stenopetalum lineare R.Br. ex DC.		+	+
CAESALPINIACEAE			
Cassia artemesioides Gaudich. ex DC.			
C. nemophila Cunn. ex Vogel		+	
C. nemophila var. *coriacea* (Benth.) Symon		+	
C. nemophila var. *platypoda* (R.Br.) Benth.		+	

[†] 'Karroo bush' from South Africa, deliberately introduced to KVR (Ratcliffe 1936).

	New Records	KVR	S. Lake

CAMPANULACEAE

	New Records	KVR	S. Lake
Isotoma petraea FvM.	+		
Wahlenbergia communis Carolin	+	+	
W. gracilenta Lothian	+	+	+
W. sieberi A.DC.			+

CARYOPHYLLACEAE

	New Records	KVR	S. Lake
Herniaria hirsuta L.	+		+
Scleranthus pungens R.Br.	+		
Spergularia bocconii (Scheele) Aschers & Graebn.	+		
S. marina (L). Griesb.	+		
S. rubra (L). J. & C. Presl.	+		
Stellaria media (L.) Vill.	+		

CASUARINACEAE

	New Records	KVR	S. Lake
Casuarina cristata Miq.		+	+

CHENOPODIACEAE

	New Records	KVR	S. Lake
Arthrocnemum arbuscula (R.Br.) Moq.	+		
A. halocnemoides var. *pterygospermum* Black			
Atriplex acutibracta Anderson	+	+	
A. angulata Benth.		+	+
A. eardleyae Aellen			+
A. eichleri Aellen			+
A. inflata Fvm.			
A. limbata Benth.	+	+	
A. lindleyi Moq.			
A. spongiosa FvM.		+	+
A. stipitata Benth.		+	+
A. vesicaria Heward ex Benth.		+	+
Babbagia acroptera FvM. & Tate		+	+
Bassia biflora (R.Br.) FvM.	+		
B. brachyptera (FvM.) Anderson		+	+
B. diacantha (Nees) FvM.		+	+
B. divaricata (R.Br.) FvM.		+	+
B. lanicuspis (FvM.) FvM.		+	
B. limbata Black			
B. obliquicuspis Anderson		+	+
B. paradoxa (R.Br.) FvM.		+	+
B. patenticuspis Anderson		+	+
B. quinquecuspis var. *villosa* (Benth.) Black	+		
B. sclerolaenoides (FvM.) FvM.		+	+
B. uniflora (R.Br.) FvM.	+	+	+
B. ventricosa Black			
Chenopodium cristatum (FvM.) FvM.		+	+
C. desertorum (Black) Black	+		+
C. murale L.	+		
C. pumilio R.Br.			
C. ulicinum Gandoger	+	+	+
Dysphania plantaginella FvM.	+		

CHENOPODIACEAE (Cont.)

	New Records	KVR	S. Lake
D. simulans FvM. & Tate ex Tate	+		
Enchylaena tomentosa R.Br.		+	+
Kochia astrotricha Johnson		+	+
K. brevifolia R.Br.			+
K. ciliata FvM.			+
K. erioclada (Benth.) Gauba		+	+
K. excavata Black		+	+
K. georgei Diels		+	+
K. integra P.G. Wilson	+	+	+
K. pyramidata Benth.		+	+
K. sedifolia FvM.		+	+
K. tomentosa FvM.			+
Malacocera tricornis (Benth.) Anderson	+		
Pachycornia tenuis (Benth.) Black			
Rhagodia gaudichaudiana Moq.		+	+
R. nutans R.Br.	+		
R. nutans var. *oxycarpa* Gauba	+		+
R. parabolica R.Br.	+	+	+
R. spinescens var. *deltophylla* FvM.		+	+
Salsola kali L.			
S. kali var. *strobilifera* Benth.	+	+	+

CONVOLVULACEAE

	New Records	KVR	S. Lake
Convolvulus erubescens Sims		+	+
Cressa cretica L.	+		

CRASSULACEAE

	New Records	KVR	S. Lake
Crassula colorata (Nees) Ostenf.		+	+
C. sieberiana (Schultes) Druce		+	+

CUCURBITACEAE

	New Records	KVR	S. Lake
Citrullus lanatus (Thunb.) Mansf.		+	+
Cucumis myriocarpus Naud.		+	+

CYPERACEAE

	New Records	KVR	S. Lake
Carex pumila Thunb.	+		
Scirpus antarcticus L.	+		

EUPHORBIACEAE

	New Records	KVR	S. Lake
Euphorbia australis Boiss.	+		
E. drummondii Boiss.		+	+
E. eremophila A. Cunn. ex Hook.			
Glochidion rigens (FvM.) Eichler			

FABACEAE

	New Records	KVR	S. Lake
Clianthus formosus (G. Don) Ford & Vickery		+	+
Glycine clandestina Wendl.	+		
Lotus cruentus Court		+	+
Medicago polymorpha var. *vulgaris* (Benth.) Shinners	+		+

	New Records	KVR	S. Lake
FABACEAE (Cont.)			
M. praecox DC.	+		
M. truncata Gaertn.	+		
Psoralea patens Lindl.			
Swainsona fissimontana Black	+		
S. flavicarinata Black	+		
S. phacoides Benth.			+
S. stipularis FvM.	+		
Templetonia egena (FvM.) Benth.		+	+
Trigonella suavissima Lindl.		+	
FRANKENIACEAE			
Frankenia connata Sprague	+		
F. cupularis Summerh.	+		
F. orthotricha (Black) Black	+		
F. pauciflora DC.	+		
GENTIANACEAE			
Centaurium spicatum (L.) Fritsch	+	+	
GERANIACEAE			
Erodium aureum Carolin	+	+	
E. cicutarium (L.) L'Hér.ex Ait.	+	+	
E. crinitum Carolin		+	+
E. cygnorum Nees	+		
E. cygnorum ssp. *glandulosum* Carolin		+	+
GOODENIACEAE			
Goodenia cycloptera R.Br.	+		
G. pinnatifida Schlechtd.	+		
G. subintegra FvM. ex Tate		+	
Scaevola spinescens R.Br.	+	+	
HALORAGACEAE			
Haloragis aspera Lindl.	+		
Myriophyllum verrucosum Lindl.	+		
LAMIACEAE			
Marrubium vulgare L.	+		+
Prostanthera striatiflora FvM.			
Teucrium racemosum R.Br.		+	
LILACEAE			
Arthropodium minus R.Br.	+		
Asphodelus fistulosus L.			+
Bulbinopsis semibarbata (R.Br.) Borzi	+	+	
Thysanotus baueri R.Br.	+	+	

	New Records	KVR	S. Lake
LORANTHACEAE			
Amyema linophylla (Fenzl) Tiegh.	+		
A. maidenii (Blakely) Barlow			
A. pendula (Sieb. ex Spreng.) Tiegh.			
A. preissii (Miq.) Tiegh.		+	+
Lysiana exocarpi ssp. *diamantinensis* (Black) Barlow		+	+
MALVACEAE			
Abutilon fraseri Hook.		+	
A. leucopetalum (FvM.) FvM. ex Benth.	+	+	
A. otocarpum FvM.	+	+	
Lavatera plebeia Sims			
* *Lawrencia glomerata* Hook.	+		
Malva parviflora L.	+	+	
Malvastrum spicatum (L.) A. Gray			
Sida corrugata Lindl.		+	+
S. intricata FvM.			
S. petophila FvM.			
S. virgata Hook.	+	+	
MARSILIACEAE			
Marsilea drummondii A.Br.			
MIMOSACEAE			
Acacia aneura FvM. ex Benth.		+	+
A. burkittii FvM. ex Benth.		+	+
A. carnei Maiden			+
A. colletioides Benth.	+	+	+
A. kempeana FvM.	+	+	
A. oswaldii FvM.		+	+
A. tetragonophylla FvM.			
A. victoriae Benth.			
MYOPORACEAE			
Eremophila alternifolia R.Br.			
E. freelingii FvM.			
E. glabra Ostenf.	+		
E. longifolia (R.Br.) FvM.		+	+
E. oppositifolia R. Br.			
E. scoparia (R.Br.) FvM.		+	+
E. serrulata (A.Cunn. ex A. DC.) Druce			
E. sturtii R.Br.		+	+
Myoporum platycarpum R.Br.		+	+
MYRTACEAE			
Eucalyptus camaldulensis var. *obtusa* Blakely			
E. socialis FvM. ex Miq.		+	+

	New Records	KVR	S. Lake
NYCTAGINACEAE			
Boerhavia diffusa L.		+	+
OXALIDACEAE			
Oxalis corniculata L.		+	
PAPAVERACEAE			
Glaucium corniculatum (L.) Rudolph	+		
PITTOSPORACEAE			
Pittosporum phylliraeoides DC.		+	+
PIMELEACEAE			
Pimelea continua Black	+		
POACEAE			
Agrostis avenacea Gmelin	+		
Aristida browniana Henr.	+		
A. contorta FvM.	+		
Avena fatua L.	+		
Bromus arenarius Labill.	+	+	
B. rubens L.	+	+	
Chloris acicularis Lindl.	+	+	+
Cymbopogon exaltatus (R.Br.) Domin			
Dactyloctenium radulans (R.Br.) Beauv.		+	+
Danthonia caespitosa Gaudich	+	+	+
Digitaria brownii (R. & S.) Hughes	+		
Enneapogon avenaceus (Lindl.)C.E. Hubbard		+	+
E. caerulescens (Gaud.) N.T. Burbidge	+	+	+
E. cylindricus N.T. Burbidge		+	+
E. polyphyllus (Domin) N.T. Burbidge		+	+
Eragrostis cilianensis (All.) Link ex Vign.-Lut.	+		
E. dielsii Pilger		+	+
E. falcata (Gaudich.) Benth	+		+
Hordeum leporinum Link	+	+	+
Lophochloa pumila (Desf.) Bor.		+	
Panicum effusum R.Br.	+	+	+
Paspalidium constrictum (Domin) Hubbard	+	+	
Schismus barbatus (L.) Thell.		+	+
Stipa drummondii Steud	+		
S. elegantissima Labill.	+		
S. eremophila Reader	+	+	+
S. falcata Hughes	+		
S. falcata var. *minor* Black	+		
S. nitida Summerhayes & Hubbard		+	+
S. platychaeta Hughes		+	+
S. variabilis Hughes	+		
Tragus australianus S.T. Blake		+	+
Triraphis mollis R.Br.		+	
Triodia sp.			

	New Records	KVR	S. Lake
POLYGONACEAE			
Muehlenbeckia cunninghamii (Meisn.) FvM.			
Polygonum plebeium R.Br.	+		
Rumex brownii Campd.	+		
R. crystallinus Lange	+		
R. vesicarius L.		+	
POLYPODIACEAE			
Cheilanthes distans (R.Br.) Mett.			
C. lasiophylla Pichi-Sermolli			
PORTULACACEAE			
Calandrinia eremaea Ewart		+	
PROTEACEAE			
Grevillea nematophylla FvM.	+		
Hakea leucoptera R.Br.			+
RANUNCULACEAE			
Ranunculus pumilio R.Br. ex DC.	+		
RESEDACEAE			
Reseda luteola L.			
RUBIACEAE			
Galium gaudichaudii DC.	+		
G. tenerum Schleicher ex Gaudin	+		
SANTALACEAE			
Exocarpos aphyllus R.Br.		+	+
Santalum acuminatum (R.Br.) A.DC.		+	+
S. lanceolatum R.Br.		+	+
SAPINDACEAE			
Dodonaea attenuata A. Cunn.		+	+
D. lobulata FvM.			
D. microzyga FvM.			
Heterodendrum oleaefolium Desf.		+	+
SOLANACEAE			
Datura leichardtii FvM. ex Benth.	+		
Lycium australe FvM.		+	+
L. ferocissimum Miers	+		+
Nicotiana glauca Grah.		+	+
N. goodspeedii Wheeler		+	+
N. velutina Wheeler	+	+	
*Solanum coactiliferum Black	+	+	
S. ellipticum R.Br.			

	New Records	KVR	S. Lake
SOLANACEAE (Cont.)			
S. esuriale Lindl.	+		
S. nigrum L.		+	+
S. simile FvM.	+		
URTICACEAE			
Parietaria debilis var. australis (Nees.) Black			
VERBENACEAE			
Verbena supina L.			
ZYGOPHYLLACEAE			
Nitraria schoberi L.		+	+
Peganum harmala L.			
Tribulus terrestris L.		+	+
Zygophyllum ammophilum FvM.		+	+
Z. aurantiacum (Lindl.) FvM.		+	+
Z. aurantiacum var. *eremaeum* (Diels) Eichler	+	+	+
Z. billardieri DC.		+	
Z. crenatum FvM.			
Z. iodocarpum FvM.		+	+
Z. ovatum Ewart & White		+	+
Z. prismatothecum FvM.		+	+
Z. sp. †	+		

† Undescribed species (Eichler, pers. comm.).

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