

STUDIES IN APPLIED ECOLOGY. I.

A STATISTICAL ANALYSIS OF REGENERATION FOLLOWING PROTECTION FROM GRAZING.

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(Plates ii-iii; one Text-figure.)

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Introduction.

Ecology is concerned with the interaction of organism and environment. The common approach to ecological problems is to regard the organism as the dependent and the environment as the independent variable; this approach has led to some understanding of the effect of environment upon plant and animal communities.

Some eighty-five per cent. of the area of New South Wales is under occupation. The effect on the vegetation of such changes in the habitat as man can make is therefore of great importance. In the United States the technique of the ecologist has profitably been applied to problems of land utilization; a similar opportunity to apply ecological technique exists here. The present paper initiates a series of studies in the effects of deliberate changes in the environment upon vegetation.

For some years the country surrounding Broken Hill, New South Wales, has been very badly eroded as a result of timber cutting and heavy grazing by rabbits, goats and stock (Morris, 1939). In an endeavour to protect their new buildings from sand-drift, the management of the Zinc Corporation at Broken Hill fenced, in June-August 1936, about 22 acres on the south-west side of their works. After a few months, during which there were good falls of rain, the protection of this area led to the appearance of many grasses and native shrubs, although it had previously been practically bare. The contrast between the fenced area (now known as the Albert Morris Park) and the surrounding country was so marked that Mr. Albert Morris, at whose suggestion the area had been fenced, found support for a proposal he had advocated for many years: to arrest sand-drift by fencing a wide area round the outskirts of the town. He believed that fencing, by the exclusion of stock and rabbits, would permit the regeneration of the natural plant-cover. With the financial help of the North Broken Hill and Broken Hill South Mining Companies, Mr. A. J. Keast, manager of the Zinc Corporation, fenced about 3.5 square miles of country. The enclosed area lies as a semi-circle of nine paddocks on the southern and western outskirts of the town. The fences are of iron posts and 1.5-inch rabbit-proof netting and were erected during the period from July 1937 to February 1938. In March 1939 an additional area was fenced at the expense of the Government of New South Wales.

The effect of fencing is most beneficial. Areas which previously were sparsely-populated sandy wastes are now occupied by a good cover of grasses and

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native shrubs. Consequently the amount of dust on windy days and the drifting of sand have been reduced. Residents on the outskirts of the town are no longer forced to abandon their homes.

The Albert Morris Park, which is the property of the Zinc Corporation, is irrigated and has been extensively planted with *Atriplex nummularium* and *Eucalyptus* spp., especially *E. camaldulensis*. The other fenced reserves, formerly used by the townspeople for grazing stock, have with one exception not been treated or planted in any way.

With the exception of the work carried out at Koonamore, South Australia, no ecological study has been made in Australian arid country of regeneration of vegetation protected from grazing. The Koonamore studies (Osborn, 1925; Osborn, Wood and Paltridge, 1931, 1932, 1935; Wood, 1936) deal mainly with the regeneration of individual species. In addition the rainfall records at Broken Hill and Koonamore during the period of enclosure are markedly different. Impoverishment of land by wind erosion following overstocking is serious in western New South Wales. Accordingly there is need to study the nature and rate of regeneration in this country. It is not sufficient to know merely that a cover of vegetation is re-established. One needs also to know the names of the more effective colonizing species, and the resistance of the colonizers to drought and competition. From such information as this it should be possible to recommend the propagation of certain species to combat wind erosion, and to foretell the results of fencing as a measure for the control of wind erosion in arid pastoral country.

DESCRIPTION OF THE VEGETATION.

Red sandy plains with scattered rock outcrops and a few sandhills compose the physiography of the reserves. The flora of the enclosed areas and the surrounding commons is predominantly herbaceous (Table i).

The country in the vicinity of Broken Hill is occupied on the plains by communities of *Atriplex* and *Kochia*, frequently admixed with grasses, and on the rocky hills by shrub communities of *Acacia aneura* (mulga) and *Eremophila* (Collins, 1923, 1924). For many miles outside the town the salt-bushes have been almost entirely eaten out, and most species are slow to regenerate. A few plants only of *Atriplex nummularium* (old man saltbush) and only local patches of mulga were recorded in the reserves. The fenced reserves have in all cases already reverted to mixed grassland, in which *Stipa variabilis* is the dominant (Plate iii, fig. 1). Small shrubs of *Cassia* spp., and bushes of *Bassia*, *Kochia* and *Atriplex* are scattered throughout the community. The ground cover is formed by *Schismus*, *Enneapogon*, prostrate species of *Eragrostis*, and by local patches of *Tetragonia* and species of *Zygophyllum* (Plate iii, fig. 2). *Lotus* and *Convolvulus* are notable ground creepers. Shrubs (up to 1-5 metres in height) of *Solanum Sturtianum* and *Sida virgata* occupy the low rocky hills.

In normal seasons the unfenced commons are sandy wastes with a scattered assemblage of weeds, most of them annuals. The time of the present survey (August 1939) was said to be the best season for 27 years. There was on the unfenced ground a fairly good cover of *Malva*, *Tetragonia*, and *Zygophyllum*, with interspersed bare patches varying in extent according to the amount of grazing. Grasses were present, sometimes in large numbers; but individually they were so poorly developed that they did not contribute to the physiognomic character of the community. *Argemone mexicana* and *Salsola Kali* form extensive local societies.

TABLE I.

List of species († = introduced species) recorded in a reconnaissance survey of the Reserves in August 1939. Many of these occur only very infrequently; those of frequent occurrence were recorded by quantitative methods (Table v).

In column 2, the duration of the life-cycles of the species is indicated for the Broken Hill District. A = Annual, B = Biennial, P = Perennial.

In column 3 the degree of palatability is indicated: u, unpalatable; nvp, not very palatable; sp, slightly palatable; mp, moderately palatable; p, palatable; p‡, palatable when young before spiny fruits occur; vp, very palatable; y, in young stages (e.g. p.y, sp.y).

The absence (—) or presence (x) of the species in the adjacent commons is recorded in column 4.

Species.	2	3	4 Occur- rence in Com- mons.	Species.	2	3	4 Occur- rence in Com- mons.
Gramineae							
<i>Aristida arenaria</i> Gaud. . .	P	nvp	—	<i>B. divaricata</i> F. Muell. . .	P	p‡	—
¹ † <i>Avena fatua</i> L.	A	p	—	<i>B. eriacantha</i> R. H. An- derson	P	p‡	—
<i>Chloris acicularis</i> Lindl. . .	P	p	—	<i>B. lanicuspis</i> F. Muell. . .	P	p‡	—
† <i>Cynodon dactylon</i> Richard	P	p	x	<i>B. obliquispis</i> R. H. Anderson	P	p‡	—
<i>Danthonia</i> sp., aff. <i>semi-</i> <i>annularis</i>	P	vp	x	<i>B. paradoxa</i> F. Muell. . .	P	p‡	—
<i>Enneapogon</i> sp.	P	vp	x	<i>B. patenticuspis</i> R. H. Anderson	P	p‡	—
† <i>Eragrostis Barrelieri</i> Daveau	A	mp	x	<i>B. sclerolaenoides</i> F. Muell.	A	p‡	—
<i>E. Dielsii</i> Pilger	P	p	x	<i>B. uniflora</i> F. Muell. . .	P	p‡	—
<i>E. setifolia</i> Nees	P	p	—	<i>Chenopodium carinatum</i> R. Br.	A	p	x
† <i>Hordeum leporinum</i> Link.	A	p.y	—	<i>C. murale</i> L.	A	mp	x
<i>Trisetum pumilum</i> Kunth.	A	mp	—	<i>Enchylaena tomentosa</i> R. Br.	P	mp	—
<i>Neurachne Mitchelliana</i> Nees	P	p	—	<i>Kochia appressa</i> Benth. . .	P	mp	—
† <i>Phalaris canariensis</i> L. . .	A	p	—	<i>K. aphylla</i> R. Br.	P	mp	—
† <i>Schismus barbatus</i> Thell. . .	A	mp	x	<i>K. brevifolia</i> R. Br. . . .	P	mp	—
<i>Stipa variabilis</i> Hughes . .	P	mp	x	<i>K. Georgei</i> Diels.	P	mp	—
¹ † <i>Triticum sativum</i> Lamarck	A	p	—	<i>K. pyramidata</i> Benth. . .	P	mp	—
Liliaceae				<i>K. sedifolia</i> F. Muell. . .	P	p	—
<i>Anguillaria dioica</i> R.Br.	P	nvp	—	<i>K. tomentosa</i> F. Muell. . .	P	mp	—
† <i>Asphodelus fistulosus</i> L. . .	P	nvp	—	<i>Rhagodia spinescens</i> R. Br.	P	p	—
Polygonaceae				<i>Salsola Kali</i> Linn.	A	sp.y	x
† <i>Emex australis</i> Steinheil . .	A	nvp	x	<i>S. Kali</i> var. <i>strobilifera</i> Benth.	A	sp.y	x
† <i>Rumex vesicarius</i> L.	A	u	—	Amarantaceae			
† <i>Polygonum aviculare</i> L. . . .	A	p	x	<i>Trichinium alopecuroideum</i> Lindl.	A	mp	—
Chenopodiaceae				<i>T. obovatum</i> Gaud.	P	mp	—
<i>Atriplex angulatum</i> Benth.	A	p	—	<i>T. spathulatum</i> R. Br. . . .	P	mp	—
<i>A. campanulatum</i> Benth.	A	p	—	Aizoaceae			
<i>A. conduplicatum</i> F. Muell.	A	p	—	<i>Tetragonia expansa</i> Murr.	A	p	x
<i>A. halimoides</i> Lindl.	A	p	—	Portulacaceae			
<i>A. Muelleri</i> Benth.	A	p	x	<i>Calandrinia pusilla</i> Lindl.	A	p	—
<i>A. nummularium</i> Lindl. . . .	P	p	—	<i>Portulaca oleracea</i> Linn. . .	A	p	x
<i>A. spongiosum</i> F. Muell. . . .	A	p	—	Caryophyllaceae			
<i>A. stipitatum</i> Benth.	P	p	x	<i>Polycarpaea corymbosa</i> Lam.	A	sp	—
<i>A. vesicarium</i> Heward	P	p	—	<i>Spergularia rubra</i> Camb.	A	sp	—
<i>Babbagia acroptera</i> F. Muell. & Tate	A	sp	—	Papaveraceae			
<i>Bassia brachyptera</i> R. H. Anderson	P	p‡	—	† <i>Argemone mexicana</i> L. . .	A	u	x
<i>B. convexula</i> R. H. An- derson	P	p‡	—				

¹ Occurs only in drains where fruit has been washed from the town.

† <i>Glaucium corniculatum</i> L.	A	—	—	Convolvulaceae			
Cruciferae				<i>Convolvulus erubescens</i> Sims	P	mp	×
<i>Blennodia lasiocarpa</i> F.				Boraginaceae			
Muell.	A	p	×	† <i>Echium plantagineum</i> L.	A	p	×
<i>B. trisecta</i> Benth.	P ?	p	×	† <i>Heliotropium asperrimum</i>			
† <i>Diplotaxis muralis</i> DC.	A	nvp	—	R.Br.	A	u	—
	or B			<i>Lappula concava</i> F. Muell.	A	sp	×
<i>Lepidium papillosum</i> F.				† <i>Lithospermum arvense</i> L. . .	A	sp	—
Muell.	A	p	×	Labiatae			
<i>Stenopetalum lineare</i> R. Br.	A	p	×	<i>Prostanthera striatiflora</i> F.			
† <i>Sisymbrium officinale</i> L.	A	mp	×	Muell.	P	sp	—
† <i>Rapistrum rugosum</i> All.	A	sp	×	Solanaceae			
Leguminosae				<i>Lycium ferocissimum</i> Miers.	P	u	—
<i>Acacia aneura</i> F. Muell.	P	p	—	² <i>Nicotiana glauca</i> Graham	P	u	—
<i>A. tetragonophylla</i> F. Muell.	P	sp	—	² <i>Solanum ellipticum</i> R. Br.	P	u	—
<i>A. Victoriae</i> F. Muell.	P	sp	—	² <i>S. opacum</i> L.	A	u	×
<i>Cassia artemisioides</i> Gaud.	P	mp	—	² <i>S. petrophilum</i> F. Muell. . .	P	u	—
<i>C. eremophila</i> Cunn.	P	mp	—	² <i>S. Sturtianum</i> F. Muell. . .	P	u	×
<i>C. eremophila</i> var. <i>platypoda</i>				Myoporaceae			
Benth.	P	mp	—	<i>Myoporum montanum</i> R. Br.	A	mp	×
<i>C. Sturtii</i> R. Br.	P	mp	—	<i>Eremophila serrulata</i> Druce	P	mp	—
<i>Clianthus Dampieri</i> A. Cunn.	A	p	—	Cucurbitaceae			
	or B			† <i>Cucumis myriocarpus</i>			
² <i>Lotus australis</i> var.				Naudin	A	nvp	×
<i>pubescens</i> Benth.	A	mp	×	† <i>Citrullus vulgaris</i> Schrad.	A	nvp	×
<i>Swainsona fissimontana</i>				Campanulaceae			
J. M. Black	A	sp ?	—	<i>Isotoma petraea</i> F. Muell. . .	P	nvp	—
<i>S. stipularis</i> F. Muell.	A	sp	—	<i>Wahlenbergia gracilis</i> DC.	P	mp	—
<i>Trigonella suavissima</i> Lindl.	A	p	—	Goodeniaceae			
† <i>Vicia sativa</i> L.	A	p	—	<i>Goodenia glauca</i> F. Muell. . .	P	sp	—
Geraniaceae				Compositae			
† <i>Erodium Botrys</i> Bertol.	A	p	—	<i>Angianthus Burkittii</i> J. M.			
<i>E. cygnorum</i> Nees	A	p	×	Black	A	sp	—
† <i>E. cicutarium</i> L'Hér.	A	p	—	<i>Brachycome ciliaris</i> Less.	A	mp	—
Zygophyllaceae				<i>B. pachyptera</i> Turcz.	A	mp	—
<i>Zygophyllum ammodendrum</i>				<i>Craspedia Chrysantha</i> Benth.	A	mp	—
F. Muell.	A	nvp	×	<i>Calotis cymbacantha</i> F.			
<i>Z. crenatum</i> F. Muell.	A	nvp	×	Muell.	A	mp	×
<i>Z. iodocarpum</i> F. Muell.	A	nvp	×	† <i>Carthamus lanatus</i> L.	A	mp	×
Euphorbiaceae				† <i>Centaurea melitensis</i> L. . . .	A	p.y	×
² <i>Euphorbia Drummondii</i>				<i>Cryptostemma calendulaceum</i>			
Boiss.	A	mp	×	R. Br.	A	sp	—
Sapindaceae				<i>Gnaphalodes uliginosum</i>			
<i>Dodonaea lobulata</i> F. Muell.	P	sp	—	A. Gray	A	sp	×
Malvaceae				<i>Helipterum albicans</i> DC. . . .	A	sp	—
<i>Abutilon</i> sp.	P		×	<i>H. corymbiflorum</i> Schlecht.	A	mp	—
<i>Hibiscus Sturtii</i> Hook.	P	sp	—	<i>H. floribundum</i> DC.	A	mp	—
† <i>Lavatera plebeia</i> Sims	A	sp	—	<i>H. microglossum</i> Tate	A	sp	×
† <i>Malva parviflora</i> L.	A	sp	×	<i>H. moschatum</i> Benth.	A	sp	—
<i>Sida corrugata</i> L.	P	sp	×	<i>H. polygalifolium</i> DC.	A	sp	—
	or B			<i>H. pygmaeum</i> Benth.	A	sp	—
<i>S. intricata</i> F. Muell.	P	nvp	×	<i>Inula graveolens</i> Desf.	A	sp	—
	or B			<i>Ixiolaena leptolepis</i> Benth.	P	mp	—
<i>S. virgata</i> Hook	P	nvp	—	<i>Podolepis canescens</i> A. Cunn.	A	sp	—
Asclepiadaceae				<i>Senecio brachyglossus</i> F.			
<i>Marsdenia australis</i> J. M.				Muell.	A	mp	—
Black	P	u	—	<i>S. Gregorii</i> F. Muell.	A	mp	—
				† <i>Sonchus oleraceus</i> L.	A	vp	×
				<i>Vittadinia australis</i> A. Rich.	P	sp	—

² Poisonous.

³ Poisonous to sheep.

QUANTITATIVE ANALYSIS.

It is clear from Plate ii, figures 1 and 2, that even in so short a time as two years, fencing the land has restored the vegetation. In order to follow in greater detail the history of recolonization a permanent quadrat of 50 square metres was laid out in one of the fenced reserves (regeneration reserve no. 4, enclosed in September 1937). The position and approximate size of every individual in this quadrat has been entered on a chart. Mrs. M. Morris, of the Zinc Corporation, who directs the regeneration work in the Albert Morris Park, has kindly undertaken to make records of the changes in this quadrat from time to time, in order to determine the effects of fluctuations of climate upon the population.

That there has been a change of vegetation following fencing is too evident to need analysis; but there are certain features of the change which can be disclosed only by the use of quantitative methods. Has, for instance, fencing increased the richness of the flora (number of species) or merely the density (number of individuals per unit area)? Is the change due to a profusion of annuals or to the spread of perennial plants? Is more ground covered with vegetation or is the vegetation merely taller? Can one obtain some precise way of measuring the rate of colonization? Is the permanent quadrat an adequate sample of the whole community, i.e. can conclusions drawn from the quadrat be extended to the whole area? What is the incidence of species with increase in area? In order to answer such questions as these it is necessary to study the dispersion of the various species in the community.

The basic assumption in describing vegetation from a sample area is that the environment and vegetation are uniform, i.e. that the species are as a whole randomly distributed. This randomness will not be apparent until a certain limiting area is reached; the size of this limiting area depends upon the coarseness of the mosaic of species which compose the community. The coarser the mosaic, i.e. the less frequently any species recurs in the community, the larger must any permanent quadrat be if it is to represent the whole. The ecologist is now supplied with statistical methods which enable him to test the assumption of randomness in communities and in species. The tests applied in the present study fall into two categories: (i) the relation between species and area, and (ii) the density and distribution of individual species in fenced and unfenced areas.

METHOD OF SAMPLING.—Before entering upon a statistical analysis of a plant community it is necessary to decide upon the shape and size of the samples to be taken.

(a) *Shape of sample areas.*—It has been customary to sample vegetation by means of square quadrats. In dense communities there is often difficulty in laying such quadrats on the ground; in the fenced areas at Broken Hill this difficulty would have been considerable. Accordingly in this work the vegetation was sampled by means of rectangular strips of 1.05 and 1.50 square metres. The sampling was carried out simply by laying a string seven or ten metres in length at random over the community, and counting all the plants within 15 centimetres on one side of this string. The use of rectangular strips in place of square quadrats has the additional advantage that the variance of samples from strips is less than that of samples from squares of the same area. A strip therefore yields more information

than a square. Clapham (1932) found that the estimated variance of species counts from square and rectangular plots was as follows:

Shape of plot	Estimated variance
Square metre quadrats	400.80
Strips 4m. \times 0.25m.	219.77

(b) *Size of sample strips.*—It has been shown experimentally (Ashby, 1935) that the relation between the chance of finding a randomly distributed species in a quadrat and the density of the species is not linear but logarithmic, and is expressed by the equation:

$$p = 1 - e^{-kx}$$

where p = the probability of occurrence of the species in a quadrat of size k , and x = the density in number of individuals per unit area. The variance of x increases rapidly for high values of p , so that a large quadrat laid a few times will not give such an accurate measure of density as a small quadrat laid many times. There is, moreover, a lower limit to the size of a quadrat: it must not be so small that the size of the plants becomes an appreciable fraction of the quadrat size. The size of the quadrat must lie within these two extremes. The simplest method of choosing the appropriate size is to find by preliminary trial an area such that few species occur with a frequency exceeding 80 per cent. Under these conditions (Ashby, 1935, p. 787) most species will have a frequency of 20 per cent. or less. This is the optimum condition for sampling a community. In the present instance it was found that a 1.50 metre sample (10m. \times 0.15m.) gave the distributions of species in the different communities shown in Table II. These distributions conform with the above requirements; this size was accordingly chosen. The sampling was carried out in two fenced reserves and in the two adjacent unfenced commons. The areas chosen were the west reserve (regeneration reserve no. 9) enclosed in December 1937, and the south reserve (racecourse extension to reserve no. 1) enclosed in February 1938. Fifty random samples were taken (i.e. 75 square metres) in the fenced west reserve and the adjacent unfenced common, forty samples (60 square metres) in the fenced south reserve, and 39 samples (58.5 square metres) in the unfenced south common.

TABLE II.
Number of species in frequency classes, using a sample area of 1.50 square metres (10m. \times 0.15m.).

Frequency Class.	0-20	21-40	41-60	61-80	81-100	Total
West reserve fenced	19	6	3	2	5	35
West common unfenced	19	2	4	2	3	30
South reserve fenced	23	6	3	0	3	35
South common unfenced	17	5	4	1	5	32

SPECIES-AREA CURVES.—It is inadmissible to draw conclusions from samples of the fenced and unfenced areas unless it can be shown that the distribution of species in the community is approximately at random. A test of random distribution in the fenced and unfenced areas was made from the species-area curves, obtained from counts of the number of species occurring in sample strips of different sizes. The larger samples are not composed from a random assortment of the smaller samples, as some workers have done (Arrhenius, 1921), for it has been pointed out (Blackman, 1935) that the method of grouping small samples to make large ones obscures any irregularity in the distribution of species.

Consequently the sampling was done by increasing the size of the original, e.g. 10m. \times 0.1m. \rightarrow 50m. \times 0.1m. \rightarrow 50m. \times 0.2m. \rightarrow 50m. \times 1m. \rightarrow 100m. \times 1m. \rightarrow 100m. \times 2m. The data are presented graphically in Figure 1. If the distribution of species is not distorted by local disturbances, but is due to chance, the relation between species and area should approximate to some exponential function, e.g.:

$$n = m \log a + b$$

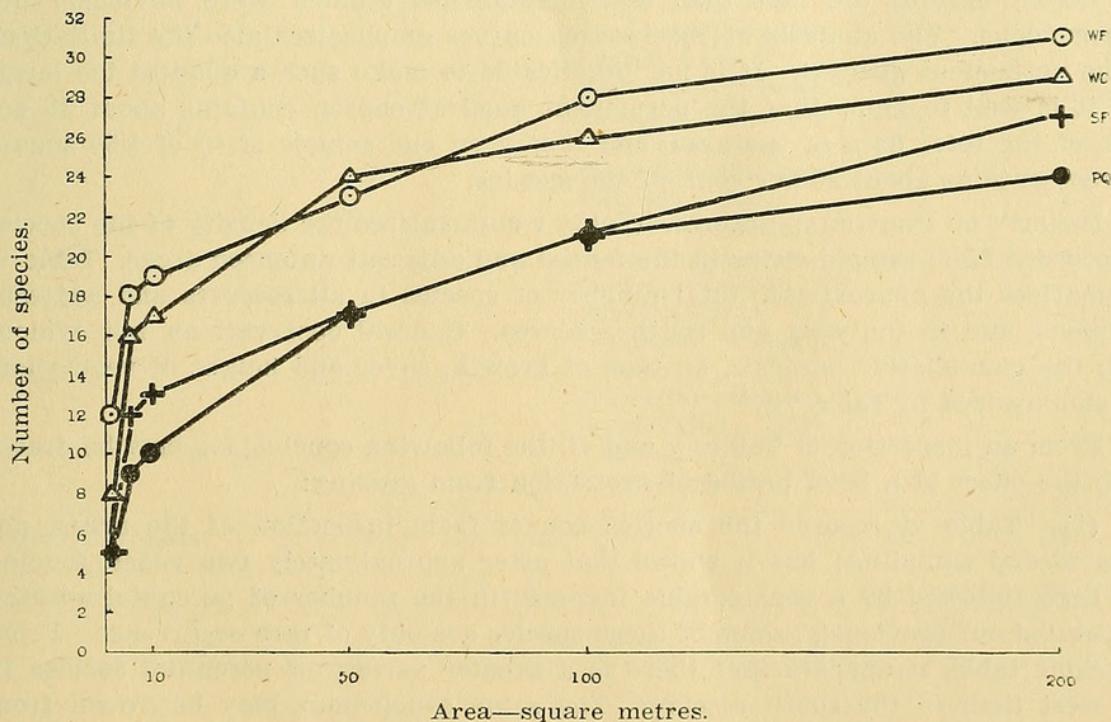
where n = number of species, a = area, b = number of species per unit area, and m is a constant which measures the floristic variety of the community.

An agreement between the observed data and values calculated from this equation would indicate that the community is homogeneous and uniformly distributed. It would then be justifiable to draw conclusions from the sample to the whole; although such a relation as this cannot be extrapolated to very high values of "a" because, as the area is increased, heterogeneity of the environment is bound to increase. The results of the comparison are presented in Table iii.

TABLE III.

Observed (obs.) and calculated (cal.) number of species for four sampled communities, using increasing sample areas.

Area of Sample (sq. m.)	Western Area				Southern Area		Permanent Quadrat			
	Unfenced		Fenced		Fenced		Fenced			
	Obs.	Cal.	Obs.	Cal.	Obs.	Cal.	Obs.	Cal.		
1	8	9.0	12	11.6	5	5.0	5	2.6		
5	16	15.0	18	17.4	12	10.9	9	8.9		
10	17	17.5	19	20.0	13	13.5	10	11.5		
50	24	23.6	23	26.0	17	19.5	17	17.7		
100	26	26.2	28	28.6	21	22.2	21	20.5		
200	29	28.7	31	31.1	27	24.8	24	23.1		



Text-figure 1.

Number of species plotted against area; ordinates number of species, abscissae area in square metres.

WF, West fenced; WC, West control (unfenced); SF, South fenced; PQ, Permanent quadrat (fenced).

From these figures it seems clear that there is no striking heterogeneity in the communities. On the assumption of random distribution a good agreement is obtained between calculated and observed values. It may safely be assumed therefore that a sample in one part of the community will be an adequate expression of the whole community.

An interesting feature of secondary importance appears from this test. It should be possible, since the equation fits the data fairly well, to predict the total number of species within a known area of each regeneration reserve. This has been done for three of the reserves on which one of us (I.M.P.) had made fairly complete lists of species. The agreement between the number of species found on the observed area (roughly estimated in acres) and the calculated number is shown in Table iv. The probability in favour of this agreement (calculated from a value of $\chi^2 = 1.012$) is over 60 per cent.

TABLE IV.

Observed number of species on three of the areas compared with the numbers calculated from the equation $n = m \log a + b$.

Situation	Approximate Area (acres)	Number of Species		
		Obs.	Cal.	Difference
West, unfenced	3	37	43.4	-6.4
West, fenced	8	50	50.4	-0.4
South, fenced	8	47	44.0	3.0

This assurance that the communities are homogeneous is a most important pre-requisite for detailed ecological research. A great many of the ecological analyses published in the literature are invalidated because this precaution was not taken, despite the fact that the communities studied were obviously not homogeneous. The analysis of species-area curves emphasizes also the limitations of the permanent quadrat. It is not practicable to make such a quadrat too large, and it is well to know that the permanent quadrat chosen contains about 35 per cent. of the total flora of the area, and that even one sample strip of 1.50 square metres contains about 20 per cent. of the species.

DENSITY OF INDIVIDUAL SPECIES.—Table v summarizes the density of the species as recorded from sample strips in the fenced and adjacent unfenced areas. Table vi summarizes the approximate total number of species in all reserves and adjacent commons, and in the west and south reserves. General observations, not evident from the quantitative analysis, on type of growth, cover and height of vegetation, are summarized in Table vii.

From an inspection of Tables v and vi, the following conclusions may be drawn as to the effect of a brief period of protection from grazing:

(i). Table vi records the species counts from inspection of the areas, not from formal sampling; but it shows that after approximately two years, fencing has been followed by a considerable increase in the number of perennial species. As pointed out previously, some of these species are only of rare occurrence. From the same table, it appears that there is a greater variety of perennial species in the west than in the south reserve. The same conclusions may be drawn from Table v, even though only one-third of the number of species is listed. The differential effect of fencing can be attributed only to a chance distribution of seed or to a slight variation in the environment. Table vi also shows that fencing, by

TABLE V.

Density of the species as recorded from sample strips in two fenced and adjacent unfenced areas. The results are expressed to the nearest whole number per 100 square metres, calculated from counts of the number of individuals on 75 m² (western areas), 60 m² (south fenced) and 58.5 m² (south unfenced). Figures printed in *italics* represent densities which are randomly distributed ($P > 0.05$).

Localities: W.F. = West fenced (reserve); W.C. = West control (unfenced); S.F. = South fenced (reserve); S.C. = South control (unfenced).

Perennial Species	Densities in various localities				Annual Species	Densities in various localities			
	W.F.	W.C.	S.F.	S.C.		W.F.	W.C.	S.F.	S.C.
<i>Stipa variabilis</i> ..	958	175	1112	1193	<i>Eragrostis Barrelieri</i> ..	2465	1540	390	625
<i>Eragrostis Dielsii</i> ..	51	60	577	468	<i>Schismus barbatus</i> ..	372	97	—	22
<i>Enneapogon</i> sp. ..	157	12	—	3	<i>Tetragonia expansa</i> ..	447	1011	218	786
<i>Danthonia</i> sp. ..	64	11	3	2	<i>Argemone mexicana</i> ..	23	205	20	20
<i>Sida intricata</i> ..	23	7	15	12	<i>Centaurea melitensis</i> ..	421	64	2	5
<i>S. corrugata</i> ..	132	22	15	87	<i>Salsola Kali</i> ..	130	1	15	5
<i>Convolvulus erubescens</i>	59	23	45	26	<i>Sonchus oleraceus</i> ..	8	7	2	14
<i>Cassia eremophila</i> ..	13	1	3	3	<i>Malva parviflora</i> ..	47	299	12	576
<i>Bassia uniflora</i> ..	31	—	—	—	<i>Lotus australis</i> ..	58	130	37	39
<i>B. patentiscuspis</i> ..	4	4	—	—	<i>Zygophyllum crenatum</i>	—	—	110	183
<i>Cassia artemisioides</i> ..	4	—	—	—	<i>Z. ammophilum</i> ..	—	—	73	22
<i>Atriplex stipitatum</i>	16	—	2	14	<i>Z. iodocarpum</i> ..	—	—	183	58
<i>Blennodia trisecta</i> ..	—	—	45	19	<i>Echium plantagineum</i>	—	—	13	15
<i>Cynodon Dactylon</i> ..	—	4	2	—	<i>Cucumis myriocarpus</i>	1	—	2	10
<i>Goodenia glauca</i> ..	4	—	—	—	<i>Citrullus vulgaris</i> ..	—	—	3	10
<i>Solanum Sturtianum</i> ..	7	—	—	—	<i>Sisymbrium officinale</i> ..	—	6	5	10
<i>Trichinium obovatum</i> ..	1	—	—	—	<i>Lepidium papillosum</i>	—	—	33	17
<i>Abutilon</i> sp. ..	1	—	—	2	<i>Erodium Botrys</i> ..	7	9	40	—
<i>Marsdenia australis</i> ..	1	—	—	—	<i>E. cynnorum</i> ..	—	—	5	—
					<i>E. cicutarium</i> ..	—	—	2	—
					<i>Calotis cymbacantha</i>	1	4	2	22
					<i>Chenopodium carinatum</i>	4	7	—	—
					<i>Lappula concava</i> ..	—	1	2	2
					<i>Euphorbia Drummondii</i>	4	3	—	—
					<i>Swainsona fissimontana</i>	4	—	—	—
					<i>Clanthus Dampieri</i> ..	7	—	—	—
					<i>Gnaphalodes uliginosum</i>	—	3	—	—
					<i>Calandrinia pusilla</i> ..	—	—	2	—
					<i>Atriplex spongiosum</i> ..	—	—	3	—
					<i>Blennodia lasiocarpa</i>	—	—	3	2
					<i>Carthamus lanatus</i> ..	1	1	—	—
					<i>Rumex vesicarius</i> ..	1	—	—	—
					<i>Helipterum microglossum</i> ..	—	3	—	—
					<i>Trigonella suavissima</i>	—	—	—	1
					<i>Cryptostemma calendulacea</i> ..	—	1	—	—
					<i>Trisetum pumilum</i> ..	—	1	—	—
Total number species	17	10	10	11		18	20	25	21
Total number individuals	1526	319	1819	1829		4001	3393	1176	2444

Grand Totals

	W.F.	W.C.	S.F.	S.C.
Species	35	30	35	32
Individuals	5527	3712	2995	4273

TABLE VI.

Approximate total number of annual and perennial species in all the reserves and adjacent commons, and in the west and south reserves. Data obtained from reconnaissance surveys.

						Number of Species		
						Perennial	Annual	Total
All reserves	}	Compiled from				65	78	143
All adjacent commons		Table I				12	35	47
West reserve						43	53	96
South reserve						30	48	78

TABLE VII.

Comparison of features of the vegetation in the reserves and adjacent grazed commons.

	Fenced Reserves.	Unfenced Commons
Height of vegetation	About 60 cm.	Ground flora 10 cm. with irregularly scattered weeds up to 30 cm.
Cover	In most of the reserves the perennial vegetation forms a fairly continuous cover.	Considerable areas of bare ground.
Grasses	(i) Mature plants. (ii) Flourishing. (iii) Firmly rooted. (iv) <i>Stipa</i> tufts up to 75 cm. (See Pl. iii, figs. 1, 3.)	(i) No well-developed plants. (ii) Dying off in young and early-mature stages. (iii) Often partially uprooted by grazing stock. (iv) Prostrate. (See Pl. iii, fig. 4.)
Weeds (undesirable species)	(i) Mostly small plants and seedlings. (ii) <i>Malva</i> : limited in occurrence by competition with <i>Stipa</i> tufts.	(i) Mostly mature. (ii) <i>Malva</i> : extensive spreading colonies, overrunning grasses.
Sand-binders	<i>Sida intricata</i> and <i>S. corrugata</i> occur as mature spreading plants holding extensive mounds of sand.	<i>Sida</i> spp. not evident as sand-binders. Occur mostly as seedlings.

protecting seed, has increased the variety of annual species, but obviously this is of much less significance.

(ii). Fencing has a marked effect on the mean density of individuals per unit area. In the west reserve, which has been fenced for twenty months, protection has greatly increased the number of individual perennial plants. In the south reserve, which has been fenced for 18 months, there has been no change. Another notable feature is that the total number of perennial plants in the west reserve is about 15 per cent. lower than that in the south reserve. These differences are mainly due to differential conditions of the two areas before fencing. The western area was much more heavily grazed than the southern area because it was near several dairies. In addition there were, on the west reserve, a large number of tracks and bare areas on which the top soil was worn and washed away. On the other hand, the south reserve formerly used to be the old racecourse which was not open to grazing until a few years ago. It is also situated to the windward of and immediately adjacent to the oldest block in the regeneration reserve, and therefore it had an initial advantage with regard to availability of seed. These

differential environmental conditions are reflected in the physiognomy of the vegetation of the two reserves. The south reserve appears to be adequately covered while in the west reserve there are many bare patches. In the south reserve the individual plants are better developed, e.g. the percentage of mature *Stipa* plants in the south is 56 compared with 40 in the west. Thus, although it has actually been enclosed for a shorter period, the south reserve is far ahead of the west from the point of view of succession. The same conditions with regard to differential grazing still applied on the unfenced commons at the time of the survey. The west common was heavily grazed and was characterized by large areas of bare ground, whereas the south common was fairly well covered. These differences are strikingly reflected in the mean density of perennials in the two commons. Marked differences between the density of perennials in the south fenced and unfenced areas are not to be expected because of the light grazing. The main difference between the perennial flora in these areas is in the height of the grasses (see Pl. ii, fig. 1). Thus the effect of protection from grazing on the perennial flora is determined by the condition of the land before fencing. Fencing may increase the number of individuals in bare areas or it may merely improve the growth of individuals already present.

The effect of fencing on the annual flora is of much less importance, partly because of the limited period during which annuals are effective sand-binders and partly because their numbers vary considerably with the seasons. However, the results are interesting. Both areas in the south have relatively few annuals because of competition with perennials. This is very marked in the south reserve where the perennial grasses are so well developed that there is little space open to annual invaders. The west reserve and common have a much larger annual population because of their extensive bare areas; the west reserve has the larger mean density of annuals because of protection.

(iii). Protection from grazing affects the density of individual species in general by decreasing the number of so-called weeds or undesirable species, and by increasing the number of perennials, particularly of palatable species. In the elucidation of Table v the following suggestions are made as to the effect of fencing on the more important species:

Perennial Species.

Grasses.

(a). *Stipa variabilis**: In the west area, protection has markedly increased the density, but there is no significant difference in the south. This may be explained by differential grazing as discussed above, and also by the fact that the position of the south reserve is such that the prevailing westerly winds carry fruits directly on to the unfenced common. The west unfenced area is not so favourably situated.

(b). *Eragrostis Dielsii*: This species appears to be independent of grazing. It has a prostrate habit of growth and is therefore grazed mainly by sheep, whereas this area is grazed mainly by cattle. The greater density of *Stipa* and *Eragrostis Dielsii* in the south is probably due to the fact that the south reserve is to the windward of the oldest reserve.

(c). *Enneapogon* and *Danthonia*: Protection has increased the density only in the west. These species are very palatable and were almost eaten out. They do not seed abundantly, and *Danthonia* spp. often have a low percentage germina-

* This grass is believed to be the same as that discussed by Osborn, Wood, and Paltridge (1931). The nomenclature of this species is still under revision.

tion. The differential establishment is probably due to availability of seed; when seed is available, there is every reason to suppose that these grasses will become established in the south reserve.

Erect shrubs or undershrubs.

(a). *Sida corrugata* and *S. intricata*: These species appear to be independent of grazing. The high densities obtained in the west reserve for *S. corrugata* were due mainly to seedlings.

(b). *Bassia uniflora*: Palatable when young; fencing increases numbers in west reserve.

(c). *Cassia eremophila*: A marked increase in the fenced western reserve, where it added a distinctive character to the community. *Cassia* spp. were plentiful before grazing. At Koonamore, *Cassia eremophila* was recorded as regenerating rapidly after rains.

(d). *Atriplex stipitatum*: According to Wood (1936) this is the least palatable of the perennial species of *Atriplex* owing to a bitter principle which it contains. Its relative high density in the south common is an indication of the light grazing in this locality, and also of the relative abundance of grasses. At Koonamore, this species was noted for its free-seeding, ready germination and rapid regeneration; it is therefore significant that at Broken Hill it was the first of the perennial saltbushes to reappear in considerable numbers.

Creepers.

(a). *Convolvulus erubescens*: In both areas fencing has increased the density. This species is palatable in mixed grazing.

Annual Species.

As with all annuals, density per unit area is dependent on a complex of factors such as availability of seed and space and on ability to withstand competition. Since the south and west areas are separated by several miles, the available seed may vary in the two areas, and, as has already been mentioned, the proportion of bare ground for colonization is much greater in the west than in the south reserve. In addition, the following points explain some of the differences in distribution of annuals:

Grasses.

(a). *Eragrostis Barrelieri*: This species is eaten, but it is probably only moderately palatable. Although it is a free-seeding grass, its density is increased by fencing only when competition is not severe. The highest densities are in the western section where there is least competition.

(b). *Schismus barbatus*: Probably a fairly palatable species. Its behaviour is much the same as *Eragrostis Barrelieri*, except that it is not so widespread. Its absence from the south regeneration reserve may be attributed to competition or to absence of seed.

Prostrate spreading herbs.

(a). *Tetragonia expansa*: Said to be good fodder, but at the time of the survey did not appear to be eaten by stock, probably because of the relative abundance of more palatable species. In both cases fencing, by increasing competition, decreases the density.

(b). *Zygophyllum* spp.: Eaten by stock, but said to be not very palatable. Absence from southern area probably correlated with inefficient seed dispersal (succulent fruits). Fencing has increased only *Z. ammophilum* and *Z. iodocarpum*

and, although no information is available, this rather suggests that these two species may be more palatable.

(c). *Clanthus Dampieri*: (May be a biennial in good seasons.) A very palatable species, which had disappeared from this area more than 30 years ago. Its fruits are known to be highly resistant and long lived; germination must have been from very old seed. Protection will therefore increase this species.

(d). *Lotus australis*: Reports differ, but it is said to be a poisonous plant containing hydrocyanic acid; it may be only undesirable in certain combinations of feed. Fencing decreases the density in the west reserve by competition. In the southern area in this particular season, there is competition both inside and outside the fences. Apparently this species is unable to endure much competition, even in the absence of a vigorous growth of grasses (see also *Argemone*, *Centaurea*, *Salsola*).

Herbs or undershrubs, usually erect.

(a). *Malva parviflora*: This is usually an erect plant, but at Broken Hill at the time of the survey it was diffuse and spreading. It is either unpalatable or only slightly palatable and in both reserves its density has been markedly decreased by competition.

(b). *Argemone mexicana*: Very unpalatable and on the whole undesirable, although it has been recorded as effectively retaining wind-blown sand.

(c). *Centaurea melitensis*: Palatable only in young stages and regarded as a pest.

(d). *Salsola Kali*: Fairly good fodder when young and camels eat it even when dry. It is an effective sand-retainer during the spring season, but its habit of piling against fences makes it undesirable. *Argemone* reacts in the same way as *Lotus*. Both are unable to stand competition; their highest density is in the unfenced western common where there is least competition. On the other hand, *Centaurea* and *Salsola* are at first increased by protection (west reserve), but are crowded out when competition is more severe (south reserve). The fact that *Salsola*, *Centaurea*, *Lotus* and *Argemone* have approximately the same densities in the south fenced and unfenced areas indicates that these particular species are kept in control equally well by competition with grasses (fenced area) or with robust spreading types such as *Malva* and *Tetragonia* (unfenced area). This effect is not apparent under heavy grazing or in bad seasons; both factors decrease mean density of cover and consequently competition.

DISTRIBUTION OF INDIVIDUAL SPECIES.—The distribution of individual species in the areas examined must be either random, or over- or under-dispersed. If distribution is random it is possible to estimate accurately changes in density over wide areas by rapid sampling methods, for the relation between the chance of finding 0, 1, 2, n plants in a sample strip and the mean density of the species is given by the terms of a Poisson distribution:

$$\frac{1}{e^{kx}} \left(1, kx, \frac{(kx)^2}{2!}, \dots, \frac{(kx)^n}{n!} \right)$$

where k is the area of the strip as a fraction of the unit area, and x is the mean number of individuals per unit area. Agreement with the hypothesis of random dispersion may be tested by the application of the χ^2 function. If there is random dispersion the ecologist (and the agrostologist) has a most valuable tool for studying changes in plant populations (Svedberg, 1922; Blackman, 1935; Clapham, 1936; Ashby, 1936). In the few instances previously studied it has been found that many species are not randomly distributed, but are over-dispersed (i.e.

aggregated) so that proximity to another member of the same species is the more favourable site for colonization. This aggregation is due to one or more of three causes: the stage of colonization of the species, its mode of reproduction, or soil heterogeneity. Under intense competition, on the other hand, species may be over-dispersed, so that the more favourable sites are those removed from other individuals. A knowledge of the type of dispersal of a species enables the ecologist to draw conclusions as to its manner and rate of colonization in relation to the environment. When the densities set out in Table v were recorded from the sample strips, information was obtained as to the number of strips with 0, 1, 2, etc. individuals of each species. From these data it is possible to determine how many of the species are randomly distributed, and how many show aggregation or over-dispersion. The data are too extensive to reproduce in full, but in column 3 of Table ix the agreements with Poisson distributions are recorded for all random species as probabilities from the table of χ^2 . It may be assumed that departure from randomness is not significant unless the values of P (the probability) are less than 0.05. A few examples showing the degree of agreement with Poisson distributions are given in Table viii.

TABLE VIII.

Observed and calculated number of throws of sample strip containing 0, 1, 2, individuals. Total 100 throws. Calculations expressed to the nearest whole number.

Species	Locality	—	0	1	2	3	4	5	6
<i>Enneapogon</i> sp. P=0.70	W.C.	obs.	84	14	2				
		cal.	83	15	2				
<i>Schismus barbatus</i> P=0.60	S.C.	obs.	72	23	5				
		cal.	72	24	4				
<i>Sida corrugata</i> P=0.55	W.F.	obs.	26	30	30	8	4	0	2
		cal.	24	34	24	11	5	1	1
<i>Sida intricata</i> P=0.45	W.F.	obs.	76	22	2				
		cal.	77	20	3				
<i>Sida intricata</i> P=0.01	S.F.	obs.	90	5	3	2			
		cal.	84	14	1.2	0.8			
<i>Danthonia</i> sp. P=0.01	W.F.	obs.	46	32	12	4	0	6	
		cal.	38	37	18	6	1		

It will be observed that agreement among the first four species is tolerably good, and among the last two it is poor. From these data were calculated the probabilities of agreement with the hypothesis of random distribution. These are given with the complete list of species in Tables ix and x. In Table ix it should first of all be observed that in 24 cases departure from the assumption of random distribution (Poisson distribution) is not significant. In these cases the number of *empty* sample strips may be taken as a basis for the calculation of density. Thus, in order to discover any change in the density of *Sida corrugata* in the western reserve it would be unnecessary to count the number of individuals; it would suffice to lay the sample strip randomly over the area and to find the percentage

of strips in which *Sida* does not occur.* Other workers (Blackman, 1935; Clapham, 1936, dealing with data from Steiger, 1930) find that in grassland relatively few species are randomly distributed. It is therefore of some ecological interest to find so many instances of random distribution in what is essentially a grassland community. Singh and Das (1938, 1939) find that most weeds in arable land are randomly distributed. They worked on weeds which colonized land during a short fallow; and it may be that in the present work, as in theirs, the high proportion of randomly distributed species is a symptom of an early stage of colonization, and would disappear as the community became consolidated. Further evidence in favour of this view is given below.

Where distribution is random it should be practicable to replace the laborious counting of plants by the rapid method of percentage absence. This is demonstrated in Table ix by comparing the actual counts of individuals in the several areas with the density calculated (a) from the whole of the appropriate Poisson distribution, and (b) from the percentage of empty strips alone. For practical purposes it is the agreement between observed density and density calculated from the percentage absence which matters. This agreement is tested by means of the χ^2 distribution. It will be seen that the agreement for all species with a value of $P > 0.05$ is good. The densities of species which have values of $P < 0.05$ bear, of course, no simple relation to their percentage absence in sample strips.

The data summarized in Table ix contain another noteworthy feature. The same species may be randomly distributed in one area and aggregated in another. *Convolvulus*, for instance, occurs randomly in unfenced areas, and is aggregated in the fenced areas. Other species (*Malva*, *Lotus*) are randomly distributed in one area only, and aggregated in the rest. It is therefore inadmissible to consider the distribution of any species as random "by nature". From a comparison of Tables v and ix, a cause for this inconsistency may be suggested: namely, that normality of distribution seems to disappear with increasing density. The possibility of this has already been mentioned. Table xi, which is composed from the data of Tables v, ix and x, illustrates this point. This table contains the distributions (random or non-random) of all observations of density greater than 5 per 100 square metres, according to three density classes. It is clear from the table that species are randomly distributed only at moderate densities, and that all observations of densities exceeding one individual per square metre (with the exception of *Sida corrugata*) are non-random. This suggestion is supported by the fact that randomness among perennials is about twice as common in the west, which is more sparsely populated (1,845 individuals) than in the south (3,648 individuals).

* Thus the observed density of *Sida* in the west fenced reserve was 99 individuals in 75 square metres. Of 100 throws of the sample strip of 1.50 square metres, 26 were free from *Sida*. Therefore we may say that $e^{-kx} = 26$, $kx = 1.35$, $x = 96.45$.

TABLE IX.

Comparison of calculated and observed densities of randomly distributed species.

Cal. (a) is calculated value from Poisson distribution; Cal. (b) is calculated value from the number of empty sample strips.

Localities: W.F. = West fenced (reserve); W.C. = West control (unfenced); S.F. = South fenced (reserve); S.C. = South control (unfenced).

Species.	Locality	P	% Absence	Density (plants per plot)			Obs. - Cal. (b)
				Observed	Cal. (a)	Cal. (b)	
<i>Convolvulus erubescens</i>	W.C.*	0.99	82	17.0	15.0	16.50	0.50
<i>Convolvulus erubescens</i>	S.C.	0.85	67	15.0	14.8	15.62	-0.62
<i>Lotus australis</i> ..	W.F.*	0.99	54	43.0	43.0	43.50	-0.50
<i>Enneapogon</i> sp. ..	W.C.	0.70	84	9.0	9.0	8.75	0.25
<i>Schismus barbatus</i>	S.C.	0.60	72	13.0	12.9	12.87	0.13
<i>Sida corrugata</i> ..	S.F.	0.99	80	9.0	8.8	8.76	0.24
" " ..	W.C.*	0.07	80	16.0	14.2	15.75	0.25
" " ..	W.F.*	0.55	26	99.0	100.0	96.45	2.55
<i>Sida intricata</i> ..	S.C.	0.05	84	7.0	7.4	6.61	0.39
" " ..	W.C.*	0.40	92	5.0	5.7	5.47	-0.47
" " ..	W.F.*	0.45	76	17.0	18.6	18.00	-1.00
<i>Danthonia</i> sp. ..	W.C.	0.25	86	8.0	7.0	7.50	0.50
<i>Atriplex stipitatum</i>	S.C.	0.70	82	8.0	8.2	7.76	0.24
<i>Sonchus oleraceus</i> ..	S.C.	0.99	82	8.0	7.8	7.76	0.24
" " ..	W.F.	0.30	90	6.0	5.0	5.25	0.75
" " ..	W.C.	0.30	90	5.0	5.0	5.25	-0.25
<i>Erodium Botrys</i> ..	W.F.*	0.05	92	7.0	7.1	5.70	1.30
<i>Salsola Kali</i> ..	S.F.	0.06	77	9.0	9.2	10.41	-1.41
<i>Malva parviflora</i>	S.F.	0.25	88	7.0	5.6	5.12	1.88
<i>Blennodia trisecta</i>	S.C.	0.15	79	11.0	10.2	9.36	1.64
<i>Argemone mexicana</i>	W.F.	0.40	74	17.0	17.2	15.00	2.00
<i>Eragrostis Dielsii</i>	W.F.*	0.60	62	38.0	34.2	34.28	3.72
" " ..	W.C.*	0.30	62	45.0	41.5	34.28	10.72
<i>Zygophyllum iodicarpum</i> ..	S.C.	0.35	46	34.0	32.4	30.42	3.58

* Sample strip 1.05 m²; elsewhere 1.50 m².

$$\chi^2 \text{ for } n=24-1 : 6.269. \quad P > 0.99$$

TABLE X.

Distribution of species according to their density classes. Figures are percentages of the whole number of observations, excluding all those observations with densities less than five individuals per 100 square metres.

Classes of density (100 m ²)	Random distribution			Non-random distribution		
	Perennials	Annuals	Total	Perennials	Annuals	Total
0-50	10.6	9.4	20.0	10.6	27.1	37.7
51-100	2.4	1.2	3.5	3.5	4.7	8.2
Greater than 100 ..	1.2	0	1.2	8.2	21.2	29.4

TABLE XI.

Comparison of Calculated and Observed Densities of Non-randomly distributed Species.

Species.	Locality.	Observed.	Calculated.	Obs. — Cal.
<i>Eragrostis Barrelieri</i>	S.F.	234.0	90.00	144.00
" "	W.C.	1155.0	252.00	903.00
" "	W.F.	1849.0	382.00	1457.00
<i>Eragrostis Dielsii</i>	S.C.	274.0	87.80	186.20
<i>Enneapogon</i> sp.	W.F.	118.0	90.75	27.25
<i>Malva parviflora</i>	S.C.	337.0	89.68	247.32
" "	W.C.	224.0	69.23	154.77
" "	W.F.	35.0	15.50	19.50
<i>Schismus barbatus</i>	W.C.	73.0	64.13	8.87
" "	W.F.	279.0	46.43	232.57
<i>Stipa variabilis</i>	W.C.	131.0	96.75	34.25
" "	W.F.	718.0	326.63	391.37
<i>Tetragonia expansa</i>	S.F.	131.0	29.20	101.80
" "	W.C.	758.0	228.75	529.25
" "	W.F.	335.0	114.75	220.25
<i>Zygophyllum crenatum</i>	S.C.	66.0	60.84	5.16
" "	S.F.	107.0	76.08	30.92
<i>Zygophyllum iodocarpum</i>	S.F.	110.0	32.04	77.96
<i>Zygophyllum ammophilum</i>	S.C.	13.0	10.12	2.88
" "	S.F.	44.0	11.70	32.30
<i>Salsola Kali</i>	S.C.	9.0	7.80	1.20
" "	W.F.	97.0	32.10	64.90
<i>Sida corrugata</i>	S.C.	51.0	30.40	20.60
<i>Sida intricata</i>	S.F.	9.0	4.38	4.62
<i>Lotus australis</i>	W.C.	97.0	85.00	12.00
" "	S.F.	22.0	12.80	9.20
" "	S.C.	23.0	19.10	3.90
<i>Centaurea melitensis</i>	W.F.	316.0	178.50	137.50
" "	W.C.	48.0	34.20	13.80
<i>Argemone mexicana</i>	W.C.	154.0	44.25	109.75
" "	S.F.	12.0	8.82	3.18
" "	S.C.	11.0	9.36	1.64
<i>Danthonia</i> sp.	W.F.	48.0	39.00	9.00
<i>Convolvulus erubescens</i>	S.F.	27.0	15.60	11.40
" "	W.F.	44.0	23.57	20.43
<i>Bassia lanicuspis</i>	W.F.	23.0	18.00	5.00
<i>Blennodia trisecta</i>	S.F.	27.0	11.60	15.40
<i>Lepidium papillosum</i>	S.C.	10.0	7.80	2.20
" "	S.F.	20.0	9.60	10.40
<i>Erodium Botrys</i>	S.F.	24.0	7.60	16.40
" "	W.C.	5.0	5.70	-0.70
<i>Echium plantagineum</i>	S.C.	9.0	7.41	1.59
" "	S.F.	8.0	6.40	1.60
<i>Atriplex stipitatum</i>	W.F.	12.0	4.55	7.45
<i>Cassia eremophila</i>	W.F.	10.0	8.50	1.50
<i>Calotis cymbacantha</i>	S.C.	13.0	8.58	4.42
<i>Clanthus Dampieri</i>	W.F.	7.0	3.99	3.01
<i>Cucumis myriocarpus</i>	S.C.	6.0	4.29	1.71
<i>Citrullus vulgaris</i>	S.C.	6.0	3.12	2.88
<i>Sisymbrium officinale</i>	S.C.	6.0	3.12	2.88
" "	W.C.	5.0	3.99	1.01
<i>Chenopodium carinatum</i>	W.C.	5.0	3.00	2.00

DISCUSSION AND CONCLUSIONS.

At this stage we may revert to the questions asked on page 127.

(i). Has fencing increased the richness of the flora? From Table vi it appears that there is a greater variety of both annuals and perennials on the reserves than on the commons exposed to grazing; but reference to the statistical data in Table v indicates that these increases are at present in rare and not in common species. The striking differences in Plate ii are *not* accountable to an increase in floristic variety. Subsequent sampling may provide more reliable evidence on this point.

(ii). Has fencing increased the density of individual species? The change in density (Table v) is not commensurate with the obvious increase in plant cover shown in Plate ii. Despite the contrast between fenced and unfenced areas in the south, fencing has scarcely changed the number of perennials and it has actually halved the number of annuals. In the west, which was fenced earlier in the summer and which had been initially more heavily grazed, the perennials are increased nearly fourfold, although the annuals are only slightly changed. The decrease in annuals in the south reserve is probably due to the intense competition of such perennials as *Stipa* (cf. Pl. iii, figs. 1 and 4).

(iii). Is the change due to a profusion of annuals or to the spread of perennials? From the floristic list summarized in Table vi and from the data in Table v it appears that fencing has increased perennials relatively more than annuals, both in respect of species number and density of individuals. The effect of fencing upon annuals clearly depends upon the number and size of perennials present. If this conclusion is supported by subsequent sampling it will be important, for it will mean that fencing gives promise of a permanent improvement of the vegetative cover under these conditions.

(iv). Is more ground covered with vegetation, or is the vegetation merely taller? Some increase in mean area covered has occurred in the fenced areas but most of the visible differences between fenced and unfenced areas is due to the greater luxuriance of plants protected from grazing.

(v). Can one obtain some precise way of measuring the rate of colonization? In the 24 instances where individuals are randomly distributed it will be possible to measure accurately and quickly changes in density, due to season, grazing, competition, etc., by the random laying of sample strips and the determination of density from percentage absences (Table viii). Moreover, it is easy to obtain a variance for these determinations. The rate of colonization of non-random species can be followed with some precision by direct observations of density from sample strips laid repeatedly over the community, and from observations on the permanent quadrat.

(vi). Is the permanent quadrat an adequate sample of the community? The data assembled in Tables iii and iv show that the communities are homogeneous, and that the permanent quadrat, although it contains less than 40 per cent. of the total number of species, is large enough to manifest the homogeneity of the community.

(vii). What is the incidence of species with increasing area? The incidence of species follows the equation $n = 1.87 \log a + b$, where b is the mean number of species per unit area, and n is the number of species on area a . It is, however, inadmissible to extrapolate far from the data, although, as is shown in Table iv, a fair estimate may be made of the number of species to be expected on areas as large as 8 acres.

It is instructive to compare the data reported in this paper with those from similar investigations in other regions. Steiger (1930) published values for the abundance of species in high and low prairie. His data have been analysed by Clapham (1936). The degree of non-randomness is judged by the value of the ratio of the variance in the Poisson distribution to the mean. In a perfect Poisson distribution this value is unity. If it exceeds unity there is aggregation among the plants. Clapham shows that most of the randomly distributed species occur in "low prairie" where the ground is open, while in "high prairie" where the grasses form a dense turf, most species are aggregated. Just as *Eragrostis Dielsii* at Broken Hill is randomly distributed in medium densities and aggregated at high densities (Table v) so in Nebraska *Eragrostis pectinacea* is almost random in low prairie and is aggregated in high prairie.

Protection from grazing for a short period has had a beneficial effect on the vegetation at Broken Hill. The study was made during a very good season, and the conclusions advanced above must be examined with this in mind. Before fencing can confidently be recommended to restore vegetative cover, four important questions must be answered:

(i). Will a response to fencing, similar to that in the Broken Hill area, be obtained on other plant communities, e.g. on mulga scrub, stony plains, sand hills, etc.?

(ii). Should the fencing exclude rabbits, or merely be stock-proof?

(iii). What rainfall is required to restore vegetation in a fenced area?

(iv.) Is fencing beneficial only when there is an assured supply of seed nearby?

All these questions must remain unanswered until more work is done, but it is instructive to compare the results of fencing at Broken Hill with those at Koonamore. In the reserve at Koonamore there was a fluctuating population of annuals and short-lived perennials. After twelve years, fencing had not restored the perennial flora. This contrast to the promising results at Broken Hill may be attributed to three handicaps at Koonamore: subnormal rainfall, grazing by rabbits, and the eroded condition of the land before fencing. At Koonamore the mean annual rainfall between the time of fencing and the last observations (1925-1935) has been only 70 per cent. of the mean (8.12") for the last 27 years, whereas the mean at Broken Hill (9.31") was exceeded in 1937 and 1939; also there has been a deficiency of effective rainfalls at Koonamore, while in the 33 months ending September 1939 there were at Broken Hill 18 months with rainfalls exceeding 0.3". At Koonamore many species increased in numbers after the few effective rains, and of these a high percentage of those species unpalatable to rabbits (e.g. *Atriplex vesicarium* and *A. stipitatum*) survived the subsequent droughts. But the rabbit-proof fencing at Koonamore did not exclude rabbits, and they reached plague numbers in some seasons; under these conditions fencing which excluded stock was not effective in restoring the vegetation. Finally, the reserve at Koonamore was more heavily grazed before enclosure than the commons at Broken Hill, and erosion was so serious that in places the subsoil was exposed. The consequent destruction of seed bed and shortage of seed contribute doubtless to the contrasting results from the two areas; but the very contrast serves to emphasize that it would be premature to draw conclusions as to the effect of fencing either from Koonamore or from Broken Hill. Data from both these areas indicate that the pioneers on bare sand are annuals (in contrast to the perennials on sand dunes by the sea), and that perennials become established only after this preliminary colonization. At Broken Hill *Zygophyllum* spp., *Tetragonia*, and

Clanthus appear to be the best annual sand-binders. Of the perennials *Bassia* spp. are important as nurseries for other seed and *Sida intricata* and *Stipa* retain sand.

SUMMARY.

A comparative study has been made at Broken Hill of the vegetation of reserves protected from grazing and of the adjacent unfenced grazed commons.

The quantitative analysis includes observations on (i) the relation between species and area and (ii) the density and distribution of individual species in fenced and unfenced areas.

An analysis of species-area curves, obtained from sample strips of different sizes, showed that the communities studied were homogeneous, and that the species as a whole were randomly distributed.

The density and distribution of individual species was determined by sample strips 10m. \times 0.15m., since most of the species recorded in these samples were found to have a frequency of 20 per cent. or less.

In 24 cases out of 75, it was found that there was no significant difference between the observed density and the density calculated from terms of the appropriate Poisson series.

In the cases of non-random distribution where the χ^2 test indicated that there was significant departure from Poisson distribution (random distribution), the calculated densities differed significantly from the observed densities.

It was found that the same species may be randomly distributed in one area and aggregated in another; normality of distribution disappears with increasing density.

The data indicate that protection from grazing during a period of less than two years has been (i) to increase markedly the growth of the individuals present before fencing. The increase in the height of *Stipa* is mainly responsible for the visible differences between fenced and unfenced sections in lightly grazed areas (south reserve); (ii) to increase the density of perennial individuals in heavily grazed areas (west reserve); (iii) to decrease the density of three of the most undesirable species, viz. *Malva*, *Lotus* and *Argemone*, which apparently cannot withstand competition; (iv) to reduce in good seasons the mean density of annuals by competition with robust perennials (south reserve); (v) to increase the variety of perennial and annual species.

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DESCRIPTION OF PLATES II-III.

Plate ii.

Fig. 1.—The south regeneration reserve and the adjoining common. Except for the track along the dividing fence, the common is well covered (left middle ground); *Stipa variabilis* dominant in the fenced area.

Fig. 2.—Western reserve and common. *Stipa variabilis* not so well developed as in figure 1; cattle grazing on common (right background).

Plate iii.

Fig. 1.—*Stipa variabilis* in south reserve, average height 0.75 metre.

Fig. 2.—Reserve No. 4. *Stipa variabilis*, *Salsola Kali* and ground cover of *Tetragonia expansa*.

Fig. 3.—*Stipa variabilis* and *Eragrostis Barrelieri* (centre) inside reserve (cf. fig. 4).

Fig. 4.—Prostrate and heavily grazed tufts of *Stipa variabilis* in west common. *Tetragonia expansa* in right background. Metre rule.



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