# SOME CONSIDERATIONS IN THE USE OF POINT QUADRATS FOR THE ANALYSIS OF VEGETATION 

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## Summary

The use of vertical pins or point quadrats in the analysis of vegetation, and the statistical treatment of results obtained with them, are discussed on the basis of data collected in different parts of Victoria. Results are expressed in terms of the proportion of the ground covered by each species ("percentage cover"), the average number of layers of foliage covering each point of ground ("cover repetition"), and the proportion of each species in the vegetation as a whole ("percentage of sward").

It is shown that pin diameter affects the results markedly, except those for percentage of sward. Percentage cover and cover repetition both tend to be over-estimated by pins.

Equal distribution of points over the area under study is advocated, rather than random distribution of individual points or groups of points. Where changes in the vegetation are the main subject of interest, successive observations should be made at the same points.

The use of transformations in the statistical treatment of the data is discussed. It is shown that the number of contacts of a pin with a given species can generally be fitted by a negative binomial distribution, if the number of points at which there is no contact be ignored.

Subjective factors may lead to consistent differences between observers recording the same vegetation by the point-quadrat method, but these differences are small compared with those occurring with many other ecological techniques.

## I. Introduction

For purposes of analysing vegetation, sample areas or quadrats varying widely in size have been used. The extreme limit of this variation is represented by the point quadrat, virtually without area. If a narrow rod or pin is passed vertically through the vegetation, the plants it touches are those vertically over a single point of ground, and recording these contacts at a large number of points can provide information as to the composition of the vegetation.

This method appears to have originated in New Zealand in 1925, and the first oblique reference to it was published by Cockayne in 1926. From 1927 onwards a number of papers appeared recording results obtained by its use (Levy 1927a, 1927b; Levy and Smith 1929; Levy and Davies 1929, 1930), but the first description was that of Du Rietz (1932). The following year, Levy (Levy and Madden 1933; Levy 1933) himself published a rather fuller description of the method; a frame supported on two legs contained 10 ver-

[^0]tical holes, 2 in. apart, through which hat pins could pass. The frame was placed at a number of points within the area under study; at first these points were spaced equally (Levy and Smith 1929), but later they were selected at random (Levy 1933; Levy and Madden 1933). In earlier work only a list of species touched by each pin in its descent was recorded, but later the number of contacts with each species was counted. This made possible the analysis of the results in four ways:
(1) "The percentage of ground covered by each species," i.e. the number of points per 100 examined at which contact was made with the species (called "percentage cover" below).
(2) "The percentage cover each species is contributing to the total area." This is the value under ( 1 ) divided by the sum of the values under (1) for all species and multiplied by the percentage of ground with any vertical cover.
(3) "The relative frequency of each species in the cover," i.e. the total number of contacts with the species per hundred points examined.
(4) "The percentage each species is contributing to the pasture sward," a value obtained by expressing that under (3) as a percentage of the sum of values under (3) for all species (called "percentage of sward" below).
A point-quadrat method modified from that described by Du Rietz was adopted by Lindquist (1932) for the analysis of the field layer in Swedish beech forests; he used 100 points equally spaced over a square-metre quadrat, the rods being 3.5 mm . in diameter; Böcher (1935), Julin (1948), and Arnborg $(1943,1949)$ later made use of the same technique. The method as described by Levy and Madden was recommended to British agrostologists by Davies (1931) and Fenton (1933, 1934). In subsequent years the method has been used extensively, particularly in America, for grassland investigations (Hanson 1934, 1950; Tinney, Aamodt, and Ahlgren 1937; Sell 1941; Ellison 1942; Drew 1944); in some cases, the pins were inclined at an angle of $45^{\circ}$ instead of vertical (Tinney, Aamodt, and Ahlgren 1937; Henson and Hein 1941; Hein and Henson 1942; Arny and Schmid 1942; Arny 1944; Rhoad and Carr 1945; Sprague and Myers 1945; Musser 1948; Leasure 1949). Point-quadrat methods have also been used in South Africa (West 1937), Finland (Charpentier 1940; Charpentier and Saarela 1941), Argentina (Burkart 1941), and Ceylon (Eden and Bond 1945; Bond 1947). In Australia they have been applied to the analysis of South Australian pasture vegetation (Crocker and Tiver 1946, 1948), and since 1945 in studies of the grasslands of the Victorian Alps (Fawcett and Turner, unpublished data).

Despite the considerable number of investigators who have made use of the point-quadrat method, remarkably little has been done to study the soundness of its bases and details of its application. Levy and Madden (1933) tested the method on cards distributed over an area of $14 \mathrm{sq} . \mathrm{ft}$., and obtained satisfactory agreement between analyses by their methods (1), (2), and (4) and the values derived from direct measurement. Lindquist (1932) tested the method on distributions of pieces of paper cut to three sizes- $50 \times 5 \mathrm{~mm}$.,
$20 \times 20 \mathrm{~mm}$., and $200 \times 200 \mathrm{~mm}$.--representing different types of foliage. These pieces were distributed without overlap over an area of 1 sq. m., with deliberate over-dispersion or under-dispersion. He found that the ground covered was consistently over-estimated, but much more with the smaller pieces than with the largest size, and more when the pieces were under- than over-dispersed. For the smallest pieces, when the true percentage cover was 37.5 per cent., the value obtained with over-dispersion was 45.82 per cent., and with under-dispersion 78.52 per cent.

The variance of data obtained by point quadrat analysis has been studied by Clarke, Campbell, and Campbell (1942), Drew (1944), Crocker and Tiver (1948), and Leasure (1949), but the statistical methods used were often inefficient or faulty, and the results inconsistent.

In view of the inadequacy of fundamental knowledge concerning a method of some popularity, with much to commend it from both theoretical and practical viewpoints, a detailed study of certain aspects of it was considered worth while. No comparisons with dry-matter analyses were made; it was considered that point-quadrat analysis should be judged on its own merits as an ecological technique, and that its value was independent of agreement with other ecological techniques which, from the ecological point of view, had no greater prima facie validity.

Of the methods of analysis proposed by Levy and Madden (1933), only "percentage cover" and "percentage of sward" were considered. The second method, "the percentage cover each species is contributing to the total area," seems to have little significance, and may even be misleading; it expresses nothing that is not better expressed by the percentage of bare ground on the one hand and the figures for "percentage of sward" on the other. Levy's third method ("relative frequency") gives a value largely dependent on that under (1); but if it is divided by (1) one obtains a figure without direct dependence upon (1), which estimates the average number of times the ground is covered by the species in question where it is present, and this quantity, termed "cover repetition," has been used in place of Levy's "relative frequency" in the present study.

Modifications of Levy's methods of analysis have been suggested by other writers. West (1937), Clarke, Campbell, and Campbell (1942), and Coupland (1950) recorded contact at ground level only, thus obtaining an estimate of basal area. Hanson and Whitman (1938) and Henson and Hein (1941) appear to have used a modified form of Levy's method (2). Tinney, Aamodt, and Ahlgren (1937) and Drew (1944) recorded only the first species with which contact was made at each point; this has the grave disadvantage that the percentage cover by lower-growing species is greatly underestimated, though it might be useful in estimating the degree of dominance by different species. Crocker and Tiver (1948) used a combination of Levy's methods (2) and (4), multiplying the figures for percentage of sward by the fraction of the ground covered by any sort of vegetation; this has the putative advantage of including the area of bare ground in the same analysis with the proportional composi-
tion of the "sward," but unless used with great care such a treatment of the data, involving a combination of quantities different in kind, is likely to lead to misapprehensions, and may cause real differences to be ignored.

In the present investigations, the data were treated, then, in three ways:
(a) "Percentage cover," corresponding with Levy's method (1);
(b) "Cover repetition"; the mean number of layers of foliage of a species covering the ground vertically; and
(c) "Percentage of sward," corresponding with Levy's method (4).
"Percentage cover" and "cover repetition" are concerned with individual species independently; between them, they contain the whole of the information the technique yields in respect of each species considered separately. The figures for "percentage of sward" express the relationships among the species, and though containing no more information than is available in "percentage cover" and "cover repetition" they enable relevant points to be grasped more readily; moreover, the variability of "percentage of sward" cannot be deduced from that for "percentage cover" and "cover repetition." To attempt to express the results of point-quadrat analysis by a single figure for each species, as is done for instance by Crocker and Tiver (1948), is to sacrifice much of the information one has been at such pains to collect.

In subsequent pages the three methods of treating point-quadrat data"percentage cover," "cover repetition," and "percentage of sward"-are considered seriatim, for the problems they involve are in the main distinct.

The observations on which this paper is based were collected in 1949 and 1950 in various parts of Victoria. The majority come from the Bogong High Plains, a plateau at 1700 m . in the north-east of Victoria, covered with alpine grassland, snow gum (Eucalyptus pauciflora Sieb.) occupying the more sheltered parts. Others were collected south-east of Melbourne, on the heaths east of Frankston and on sand dunes along the shores of Port Phillip Bay; yet others were obtained on waste ground in the northern Melbourne suburbs and at Blackwood in the Dividing Range, 45 miles north-west of Melbourne. Unless otherwise stated, all results were obtained with pins 4.08 mm . in diameter arranged in frames with places for 10 spaced at 8.9 cm .

## II. Estimation of Percentage Cover

In this use of point quadrats, the purpose is to estimate the proportion of ground covered vertically by the species in question. Only presence or absence of each species at each point is recorded, and the results are thus comparable with those for frequency obtained with larger quadrats. It is necessary to consider how the technique should be used to obtain the closest possible agreement of the estimate and the true proportion of ground covered, with a given limited amount of observational work. The most important factor that may be varied to attain this end is the distribution of the point quadrats, but the effects of size of pin and of personal characteristics of the observer were also studied.

## (a) Size of Pin

The projection on a horizontal surface of the foliage of most species forms an intricate mosaic; the dimensions of the elements of this mosaic are not greater than those of the leaves, and may be substantially less if many of the leaves are far from horizontal. In broad-leaved plants, the spaces between the projections of the leaves are usually much narrower than these projections


Fig.1.-Projection of part of tussock of Ammophila arenaria, showing areas over which contact would be made with the foliage by pins of the diameters stated; each zone is understood as including those with less dense shading.
themselves, for leaves of successive tiers are often arranged so that the lower ones tend to fill the spaces between those above. Under most plants, the ground not covered vertically by foliage is thus distributed in many small areas, at least one dimension of which is usually not more than a centimetre or two. These areas in sum may represent a large part of the whole; but the possibilities of systematic error in their measurement through faulty outlining are very considerable. Systematic errors of this sort occur when frequency of contact with a vertical pin is used as a method of measuring their area. Assuming that the vegetation is still and the pin moves vertically through it, the area
within a single open space in which the centre of the pin must fall if the pin is not to touch the foliage is less than the total area of the open space by an amount depending on the diameter of the pin. This effect is shown in Figure 1, which represents the projection on a horizontal plane of part of a tussock of Ammophila arenaria. The true projection occupies 51 per cent. of the area of the circle. A pin of 1.0 mm . diameter-which would hardly have adequate rigidity for practical use in most types of vegetation-would make contact with plants over 82 per cent. of the area, one of 2 mm . diameter over 96 per cent., and one of 3 mm . diameter over 99 per cent. of the area of the whole circle. Hence the frequency of contact with pins of finite diameter is bound to provide an excessive estimate of the proportion of ground covered by a species.

This source of error is accentuated if there is any relative movement of the projections of pin and foliage while the former is moving downwards. If this occurs, for instance through wind, by the time the pin has reached the ground, it is often in contact with a leaf or branch of which the position of rest does not lie on its direct path-through their relative displacement, this leaf or branch made contact with the pin during its downward movement, and remains in contact under slight strain. All such relative lateral movements of pin and foliage tend to increase the probability of contact between them above that to be expected on the basis of their projections on a horizontal plane while at rest.

As already mentioned, over-estimation of percentage cover by pins was demonstrated by Lindquist (1932), using cut paper. West (1937) surmised that "the comparatively thick points used in our extemporised apparatus would tend to magnify the Percentage (basal) Area," but most workers do not seem to have been aware of this possible source of error, and so far as I am aware no tests in vegetation of the effects of size of pin have hitherto been performed. Accordingly, a series of such trials was carried out, and some of the results are presented in Table 1. For comparison, observations were made with an apparatus consisting of a tube hung in gimbals with cross-wires at each end. Observations of the vegetation through this tube enabled one to determine whether the ground vertically beneath the centre line of the tube was bare, or was covered by some particular species, and such observations could be regarded as records obtained with a dimensionless optical point quadrat; these are the frequencies shown in the zero diameter column. All the data in this table were obtained from points distributed at random in quadrats 1 m . square. The significance of differences between frequencies obtained with the three types of point quadrat was determined by the $\chi^{2}$ test.

In Table 2, the frequencies of contact with the more abundant species (all those for which the mean exceeded 5 per cent.) in much larger areas of alpine pasture on the Bogong High Plains are given, as determined with pins of two sizes. The pins were used in frames, each holding 10, placed at each of 200 randomly selected points ( 100 for the narrower pins) in each of the two
areas. The significance indicated in the last column is based on a $t$ test using the variance between frame means after angular transformation (see below).

In all the data recorded in Table 1, the cross-wire apparatus gave a lower frequency of contact than the smaller pins, many of the differences being highly significant. The differences between the two types of pin were not so marked, though in three instances the narrower pin gave a significantly lower frequency. In the more extensive series of observations in Table 2, in all cases but one the narrower pin gave a lower frequency and in many the difference is highly significant.

Table 1
FREQUENCY (PER CENT.) OF CONTACT BETWEEN FOLIAGE AND PINS OF DIFFERENT DIAMETERS

| Locality | Species | No. of Points | Pin Diameter (mm.) |  |  | Significance ( $P$ ) for Difference in Pin Diameter |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  | 0 | 1.84 | 4.75 | $0-1.84 \mathrm{~mm}$. | $1.84-4.75 \mathrm{~mm}$. |
| Seaford | Ammophila arenaria | 200 | 39.0 | 66.5 | 71.0 | < 0.001 | $>0.05$ |
|  | Ammophila arenaria | 200 | 60.5 | 74.0 | 82.0 | 0.001-0.01 | $>0.05$ |
| Black |  |  |  |  |  |  |  |
| Rock | Ehrharta erecta | 200 | 74.5 | 87.0 | 93.5 | 0.001-0.01 | 0.01-0.05 |
| Sorrento | Lepidosperma concavam | 200 | 19.5 | 22.0 | 27.5 | $>0.05$ | $>0.05$ |
|  | Spinifex hirsutus | 200 | 35.0 | 48.5 | 61.0 | 0.001-0.01 | 0.01-0.05 |
| Carlton | Fumaria officinalis |  | 20.5 | 31.5 | 30.0 | 0.01-0.05 | $>0.05$ |
|  | Ehrharta longifora | 200 |  | 25.5 | 37.5 | $>0.05$ | 0.01-0.05 |
|  | No contact |  | 53.0 | 42.5 | 38.5 | 0.01-0.05 | > 0.05 |
|  | Lolium perenne | 200 | 65.0 | 85.5 | 82.5 | $<0.001$ | $>0.05$ |

Since the error in estimating percentage cover by the use of pins depends in part on the size distribution of gaps in the foliage, it will in general be greater for species with smaller leaves, as Lindquist (1932) concluded. This implies that a constant correction factor for pins of a given size is out of the question. Within a single species, environmental conditions affecting the size of leaves and the habit of the plant may cause the error in estimating percentage cover to vary, but these variations will in general be small, and a correction factor or curve could probably be used. At high values of percenage cover for microphyllous species, broad pins will, however, be an insensitive means of estimation, and there will be a range where the true percentage cover falls short of 100 yet all the pins make contact.

## (b) Distribution of Points

The next question to be considered is how points of observation should be distributed in the area of vegetation under study. In most work of this type, the pins have been spaced evenly along a frame, commonly containing 10 , and the frames have been located and oriented at random within the area. The desirability of placing the points in close groups, as against their distri-
bution as individual observations, must be considered, as also the wisdom of arranging these groups or individual observations at random.

Since, in most types of vegetation, the scale of the pattern presented-the average distance between individuals or groups of individuals of the same species-is considerably greater than the size of the frame used for placing the pins ( 1 m . or less in length), it seems probable, as suggested by Blackman (1935), that the probability of hitting a given species will vary less between

Table 2
FREQUENCY (PER CENT.) OF CONTACT BETWEEN FOLIAGE AND PINS OF different diameters, bogong high plains

|  | Species | $\begin{gathered} \text { Pin } \mathrm{Dia} \\ 2.05 \end{gathered}$ | $\frac{\mathrm{r}(\mathrm{~mm} .)}{4.08}$ | Significance ( $P$ ) for Difference in Pin Diameter |
| :---: | :---: | :---: | :---: | :---: |
| Plot A (298 sq. m.) | Carex hebes | 64.1 | 76.55 | $<0.001$ |
|  | Poa caespitosa | 5.7 | 8.15 | $>0.05$ |
|  | Rumex acetosella | 6.1 | 11.15 | 0.001-0.01 |
|  | Viola betonicifolia | 9.6 | 14.60 | 0.001-0.01 |
|  | No contact | 20.9 | 7.60 | < 0.001 |
| Plot $B$ ( 670 sq. m.) | Carex hebes | 57.1 | 70.20 | 0.001-0.01 |
|  | Poa caespitosa | 15.7 | 13.70 | $>0.05$ |
|  | Asperula gunnii | 5.0 | 6.45 | $>0.05$ |
|  | Viola betonicifolia | 4.5 | 6.60 | $>0.05$ |
|  | Microseris scapigera | 7.2 | 8.00 | $>0.05$ |
|  | No contact | 14.1 | 6.95 | $<0.001$ |

the different sections of one frame than between different positions of the frame. This is illustrated in Table 3, the data for which come from Plot $A$ of Table 2. The binomial distribution of frequencies in samples of 10 has been computed for the overall mean frequency of contact, and this has been compared with the actual frequencies observed in the groups of 10 provided by the 200 frame locations. It will be seen that the spread of values is much greater than would be expected on the assumption that the 10 pins in each frame represented random samples of a single population. With some of the scattered shrubs on this plot, the discrepancy would be even greater; for instance, Phebalium podocarpoides occurred in only two frames, but in these four and three pins respectively made contact with it; and Grevillea australis occurred in four frames only, in one of which seven pins touched it. Thus it is clear that the proportion of ground covered by each species differs from frame to frame, or in other words that the variation in percentage cover within the frame is less than that between frames.

A small part of the variation between frames may be ascribed to personal differences among observers, for the frames were recorded by three different teams, each consisting of three workers who observed in rotation. It is shown later that such personal differences are not altogether negligible, but they are much smaller than those recorded here between frames.

From this fact that the variation in percentage cover within the frames is less than that between frames, it may be deduced that a given number of points distributed individually over the plot would give a more precise estimate of mean percentage cover than the same number grouped in frames. Conversely, if the precision attained by use of 2000 points arranged in 200 randomly distributed frames is satisfactory, equal precision would be possible by use of a smaller number of individual points. Since the variance of the estimate of percentage cover obtained in this way would, after angular transformation (see below), be given by the expression $8100 / \pi^{2} n$, where $n$ is the number of points, one may readily calculate the number of individual points that, distributed at random, would give an estimate with the same variance as that observed for points arranged in frames. These results are given in Table 4, for the same area as figures in Table 3.

Table 3
FREQUENCY OF CONTACT WITH PINS IN 200 FRAMES OF 10 PINS, COMPARED WITH EXPECTATION ON A BINOMIAL DISTRIBUTION

| No. of Pins Making Contact | Number of Frames in which Stated Number of Pins made Contact With |  |  |  |  |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Carex hebes |  | Poa caespitosa |  | Rumex acetosella |  | Viola betonicifolia |  | Asperula gunnii |  |
|  | $\begin{aligned} & \text { "0 } \\ & \stackrel{\rightharpoonup}{0} \\ & 0 \\ & 0 \end{aligned}$ | $\begin{aligned} & \overrightarrow{\ddot{U}} \\ & \stackrel{\rightharpoonup}{0} \\ & \text { M. } \\ & \text {. } \end{aligned}$ | $\begin{aligned} & \text { Ju } \\ & \stackrel{\rightharpoonup}{0} \\ & 0 \\ & 0 \end{aligned}$ | $\begin{gathered} \text { "ّ̛ } \\ \stackrel{0}{0} \\ 0 \\ \text { Wi } \end{gathered}$ | $\begin{aligned} & \stackrel{\rightharpoonup}{D} \\ & \stackrel{4}{0} \\ & 0 \\ & 0 \end{aligned}$ |  | $\begin{aligned} & \text { D0 } \\ & \text { D } \\ & 0 \\ & 0 . \end{aligned}$ | $\begin{gathered} \widetilde{\rightharpoonup} \\ \stackrel{\rightharpoonup}{0} \\ 0 \\ \text { Ru } \end{gathered}$ | $\begin{aligned} & \text { D0 } \\ & \stackrel{0}{0} \\ & 0 \\ & 0 \end{aligned}$ | "00 |
| 0 | 0 | 0 | 115 | 85.5 | 95 | 56.0 | 60 | 42.2 | 176 | 142.2 |
| 1 | 3 | 0 | 41 | 75.8 | 43 | 69.3 | 56 | 71.2 | 6 | 49.3 |
| 2 | 3 | 0 | 22 | 30.3 | 31 | 38.6 | 42 | 53.8 | 6 | 7.7 |
| 3 | 3 | 0.4 | 14 | 7.2 | 16 | 12.7 | 28 | 24.1 | 4 | 0.7 |
| 4 | 3 | 2.5 | 4 | 1.1 | 11 | 2.8 |  | 7.1 | 4 | 0.1 |
| 5 | 14 | 9.4 | 4 | 0.1 | 2 | 0.5 |  | 1.4 | 3 | 0 |
| 6 | 25 | 25.5 | 0 | 0 | 1 | 0.1 | 3 | 0.2 | 1 | 0 |
| 7 | 35 | 47.7 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| 8 | 33 | 58.4 | 0 | 0 | 0 | 0 |  | 0 | 0 | 0 |
| 9 | 38 | 42.3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 10 | 43 | 13.8 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| $\chi^{2}$ |  |  |  |  |  | 39 |  |  |  |  |
| $n$ |  |  |  |  |  | 2 |  |  |  |  |
| $P$ |  |  |  |  |  | . 001 |  |  |  | 001 |

An alternative approach to the question of the relative efficiency of frames and individual points in estimating percentage cover may be illustrated with Grevillea australis. This plant occurred in four frames only of the 200 recorded on the plot, but in these four frames a total of 15 pins (out of 40 ) made contact with it. These results enable one to estimate the probability that a frame will include a record of Grevillea as 0.02 , and the probability, within such a frame, that any particular pin will make contact with it as 0.375 . Given these
probabilities, it is possible on binomial theory to compute the distribution of numbers of pins making contact in samples of 200 frames, and hence to determine the variance of these numbers, which is found to be 60.8. Now, for samples consisting of individual points distributed at random, the variance of the number of pins making contact with Grevillea will be $k p(1-p)$, where $k$ is the number of points, and $p$ the probability of contact (i.e. $0.02 \times 0.375=$ 0.0075 ). Thus the number of individual points required to give a variance of the estimate of percentage cover equal to that for 2000 points arranged in frames may readily be computed to be 490 . Admittedly, this treatment assumes that, within frames where the species occurs, the numbers of pins making contact with it are distributed binomially, and in other species this is known not to be true (see Table 3-data for Carex hebes); but the deviations from this assumption that have been observed have had the effect of increasing the range of variation, and their effect if taken into account in the calculations above would thus be to increase the variance of the estimate derived from frames, and hence to increase the relative precision of the estimate by individual points.

Table 4
No. OF INDIVIDUAL POINTS REQUIRED TO GIVE ESTIMATES OF PERCENTAGE COVER OF EQUAL PRECISION TO THOSE OBTAINED FROM 2000 POINTS IN FRAMES OF 10

| Carex hebes | 568 |  |
| :--- | :--- | :--- |
| Poa caespitosa | 902 |  |
|  | Rumex acetosella | 771 |
|  | Viola betonicifolia | 866 |

As a final test of the relative efficiency of sampling the vegetation by individual points and by frames, both methods were used on Plot $B$ of Table 2. In addition to the observations at 2000 points in frames, individual pins were distributed at random at 1000 points over the plot, and their contacts were recorded. The frames or points, as the case might be, were then randomly assorted into groups, each containing records from 100 pins, and the variance among the percentage cover estimates from these groups was computed after angular transformation. The results are shown in Table 5.

The variances do not differ significantly as between species, but the difference between the two methods is highly significant, and indicates that, taking all five species together, 670 individual points would be required to give a precision equal to that obtained with a sample of 2000 points in frames of 10 .

Apart from the relative value of individual points and groups of points such as are provided by the frames, the question must be asked whether the points or groups of points should be distributed at random, or whether some
restricted or regular arrangement is desirable. Let us suppose that the problem to be solved is whether the percentage cover by a given species is similar in two plots or not. Even if the true total area covered by the species in each plot could be determined accurately, without any observational error, these errorless estimates of the two means would not in themselves be enough to provide a basis for useful comparison of the two plots; without estimates of variability, such accurate data for percentage cover would be valueless. Besides the errors in estimation, which in the present case we have by hypothesis excluded, there is also the large variation in the composition of the vegetation from place to place in the plot. Though the percentage cover were greater in Plot $A$ than in Plot $B$, it might well happen that the relation would be reversed if the area of one of the plots were slightly increased or decreased to include a few more or a few less plants of the species in question. Clearly a difference which thus depended on the fortuitous location of the plot boundaries would be without any fundamental significance, and a criterion is needed to enable one safely to ignore such chance differences, and to identify those representing a real and consistent difference in the vegetation of the two plots. Thus a satisfactory distribution of points for observation will not only give unbiased estimates of the mean percentage cover within the plot, but will also give estimates of the variability of this value over the plot. At the same time, the sampling error of the percentage cover estimates should be minimal.

Table 5
VARIANCE OF PERCENTAGE COVER ESTIMATES FROM SAMPLES OF 100 POINTS (ANGULAR TRANSFORMATION)

|  | Species | 10 Frames Each <br> with 10 Points |
| :--- | :---: | :---: | 100 Individual Points | Carex hebes |
| :--- |
| Poa caespitosa |
| Viola betonicifolia |
| Asperula annnii |
| Microseris scapigera |

The importance of variation in percentage cover over an area has already been indicated by the smaller variability of points within frames than that between different frames (see Table 3 and accompanying text). That it also occurs on a larger scale, even where not immediately apparent to the eye, may be made clear by some data from another area (of $448 \mathrm{sq}$. m.) on the Bogong High Plains. In 1949 this land, originally selected for uniformity of vegetation, was divided into five strips of equal area, each of which was sampled by 20 frames each containing 10 pins. Some of the results are shown in Table 6. For each species, an analysis of variance was computed, after angular transformation (see below), and the variance ratios quoted are the ratios of the variance between strip means to that between frames within strips. Though
the differences in the less abundant species are not significant (both are shrubs, and hence the variance between frames is high), the differences in the proportion of bare ground almost reach significance, and those for the dominant, Poa caespitosa, are very highly significant.

Table 6
PERCENTAGE COVER BY CERTAIN SPECIES ON FIVE ADJACENT STRIPS OF LAND

|  | Poa <br> caespitosa | Hovea <br> longifolia | Phebalium <br> podocarpoides | Bare <br> Ground |
| :---: | :---: | :---: | :---: | :---: |
| 1 | 61.5 | 15.5 | 14.5 | 9.5 |
| 2 | 81.0 | 15.5 | 10.0 | 1.0 |
| 3 | 88.5 | 5.5 | 10.0 | 2.0 |
| 4 | 76.0 | 8.5 | 14.0 | 8.0 |
| 5 | 54.0 | 17.5 | 14.0 | 10.5 |
| Variance ratio, be- |  |  |  |  |
| tween strips/within |  |  |  |  |
| strips, after angular <br> transformation <br> $P$ | 47.81 | 1.69 | 0.34 | 2.29 |

The reasons in plant ecology for wishing to separate variance due to causes operating on different scales are not the same as the considerations involved in agricultural experimentation, where differences with location within an experimental area are undesirable complications, and are measured only incidentally in the course of attempts to restrict their influence on the experimental results. In the common "randomized block" type of design, the area is divided into a number of blocks, each further divided into as many plots as there are treatments, the treatments being allotted at random to the plots within each block. In this way it is possible to prevent differences between blocks affecting the comparisons between treatments, and only that smaller part of the variation in site factors which is operating within blocks will affect the treatment differences. The variance between blocks is eliminated with the loss of few degrees of freedom, and the bulk of the degrees of freedom among plots are retained for the study of the treatment differences.

In ecological studies of the differences in vegetation between areas, variation between blocks would be more relevant to the comparison than variation within blocks-because it includes all sources of variation within the area, and not merely those operating over short distances only. Hence any degrees of freedom for differences within blocks will be lost to the primary purpose of comparison of the main areas, and the greatest efficiency in this comparison will be reached if all degrees of freedom relate to comparisons between blocks - that is, if there are as many blocks as there are points of observation. ${ }^{*}$ Random distribution of replicate points within any area or sub-

[^1]area under consideration will mean that such points contribute no information about the variation of percentage cover over the area, but merely reduce the sampling error of the estimate. To take an extreme case, consider two areas in which half the surface is painted black and half white, but in the one each colour is in a compact block, while in the other the colours are distributed in a mosaic of minute alternating squares. Points placed at random will give on the average estimates of 50 per cent. black on both areas, and sample means will vary equally about this figure; from the sampling results, it will be impossible to distinguish between these two very diverse cases. If, however, the area is divided into small plots for sampling, and a few points are selected at random within each plot, the variance between plot means will be much greater in the first area than in the second (unless the plot size is as small as the mosaic squares of the latter), thus illustrating its greater uniformity. The variance between the means for replicate samples taken in the same way, plot by plot, will also be less than with random sampling.

The increase in precision through restricting the randomization of points for observation each within a separate small plot may be illustrated from a plan drawn by Davies (1945) showing the distribution of species in 1 sq. m. of a Molinietum in a Welsh bog. Seven per cent. of the area is bare peat, and this quantity would be estimated by randomly distributed samples of 100 points with a variance of 6.52 . If, however, the area is divided into decimetre squares, and sampled by groups of 100 points, one placed at random within each of these squares, the variance of the estimates so obtained is 5.63.

Taken as individual contributors to mean and variance, point observations under restricted randomization provide no more information about the distribution of species over the area than if randomized freely. It is only when the location of the points in the area and their relation to adjacent points is considered that this information emerges. But the variation among plots will often be non-homogeneous-the differences between adjacent plots will be less than between those more separated-and a question then arises as to what elements in the non-homogeneous variation are appropriate for use as estimates of error in comparisons between different areas. This question is too large to discuss here-it is hoped to deal with it in a subsequent paper.

If point samples need to be taken in each segment of an area, it would often be more convenient to take them at equal intervals along each dimension of the area-a practice analogous with that proposed for yield sampling in agriculture or forestry by Yates (1946)-than to place them at random within each plot. This has, however, the theoretical drawback that the sample may be biased and unrepresentative if the vegetation varies regularly over the area, with a period equal to a multiple or submultiple of the distance between points. This is perhaps rather a remote contingency, but unless there are serious difficulties in random sampling within each plot it would appear that this is slightly to be preferred. For most purposes, sampling error would be irrelevant, and information on it would not be available if one point only
were placed at random within each plot; if an estimate of sampling error were required it would be necessary to place at least two points at random within each plot.

A problem to which point-quadrat methods may often be applied is the determination of changes taking place in vegetation-for instance, the change in botanical composition of a pasture under grazing, the course of loss in vegetational cover under soil erosion, or the gradual deterioration in cover during a prolonged drought. For this purpose, assessment of the condition of the vegetation at any one time has no direct relevance, and the quantities whose estimation is required are the changes in percentage cover by each species from time to time, and the variations in those changes over the area studied. If successive random samples are taken, whether the randomization is free or restricted as suggested above, the error variance of the estimate of change will of course be double that for the mean of a single sample, and will be less if the randomization is restricted within plots than if it is free. Variation over the area in the changes will be superimposed upon this error variance if the area has been sampled by plots, and the distribution of the differences between successive observations on the same plot may be used to indicate the consistency of the changes over the area.

However, a much more powerful means than division into plots is available for reducing the error of estimates of changes, namely, to take successive observations at the same series of points. This will enable sampling errors to be excluded from the estimate of change, except for those arising from movement of the foliage and in so far as the points chosen are not completely representative of changes occurring in the area as a whole. The differences observed over a series of fixed points chosen by free or restricted randomization will give an unbiased estimate of the changes in the area as a whole during any one period. But changes over successive periods at a given point are likely to be correlated, and hence caution must be used if the observations are intended to show changes over several successive periods; estimates of these changes will not be independent, and if the estimate of increase in percentage bare ground (for instance) over the first period exceeds by chance the true mean for the whole area, then this deviation is likely to occur again in the second period. This difficulty may be overcome by using a different series of points for estimating the change over each period. For instance, if the practice advocated above of dividing the area into small plots within each of which a single point is selected be adopted, an observation would be made in Plot A at point 1 on the first occasion, points 1 and 2 on the second, and 2 and 3 on the third, and so forth. Thus the estimate of change at point 1 during the first period would be independent of that at point 2 during the second period -apart from the consistency of changes in the same plot, a point of interest that could be elucidated by analysis of variance-and the mean estimates of change over the whole area would likewise be independent in successive periods.

The great superiority of successive observations at fixed points (comparable with permanent quadrats) over successive series of independently ran-
domized points is shown by the results recorded in Table 7. These were obtained from another area in the Bogong High Plains, at the head of Pretty Valley. This area was 74 m . long, and on average 12 m . wide. In 1949, 100 frames of 10 points distributed at random were recorded, and in 1950200 similar frames; further observations were made on 121 frames placed at the same points (within the limits of measurement-say, 5 cm .) in each of the two years, these points being equally spaced at intervals of 1.83 m . across the plot and 3.30 m . along it. The variances quoted in the table are expressed on a basis comparable between the two methods-that is, for observations on one frame in each year. In all cases but one, the variance is much greater with randomly distributed points than with fixed points.

Table 7
CHANGES IN PERCENTAGE COVER AS ESTIMATED BY RANDOM POINT QUADRATS AND PERMANENT POINT QUADRATS

| Species | Permanent Point Quadrats |  |  | Random Point Quadrats |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | Mean, $1949$ | $\begin{gathered} \text { Mean, } \\ 1950 \end{gathered}$ | Variance of Differences | $\begin{gathered} \text { Mean, } \\ 1949 \end{gathered}$ | $\underbrace{}_{\substack{\text { Mean, } \\ 1950}}$ | Variance of Differences |
| Poa caespitosa ("fine grass") | 54.6 | 53.4 | 336.8 | 49.9 | 54.7 | 1456.1 |
| Poa caespitosa ("horny grass") | 12.0 | 15.3 | 169.8 | 15.4 | 14.0 | 871.5 |
| Leptorhynchus squamatus | 19.3 | 18.1 | 312.0 | 18.8 | 19.1 | 870.5 |
| Carex breviculmis | 18.3 | 18.5 | 346.1 | 20.7 | 15.6 | 406.5 |
| Ceimisia longifolia | 6.4 | 8.1 | 134.5 | 4.1 | 7.3 | 239.6 |
| Scleranthus biforus | 2.2 | 2.1 | 29.2 | 1.2 | 2.5 | 58.4 |
| Ranunculus lappaceus | 3.2 | 3.9 | 78.6 | 2.3 | 3.0 | 67.1 |
| Danthonia semiannularis | 3.9 | 3.1 | 82.6 | 3.9 | 4.2 | 143.2 |
| Bare ground | 3.2 | 2.4 | 31.0 | 2.1 | 3.5 | 208.4 |

## (c) Statistical Treatment of Results

In common with other variables in which a part is expressed as a proportion or percentage of the whole, estimates of percentage cover from samples will not be distributed normally about their mean with a variance independent of the mean. Their distribution, however, is such that, for large samples, the function

$$
\arcsin \sqrt{\frac{\text { percentage cover }}{100}}
$$

is distributed approximately normally, and (measured in degrees) has a variance $8100 / \pi^{2} n$ ( $n$ being the number of observations in the sample) independent of the value of the mean (Fisher and Yates 1938). The equalization of variances by this angular transformation is demonstrated by the results in Table 8. These observations were made with the cross-wires instrument already described, on
areas of 1 sq. decimetre. In each such area, 10 series of 100 observations were taken, and the variances of the percentage cover estimates so obtained were determined; for each species five or six areas were studied in which its abundance varied widely.

Table 8
VARIANCE OF PERCENTAGE COVER ESTIMATES DERIVED FROM RANDOM SAMPLES OF 100 POINTS

| Species |  | Area |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | A | B | C | D | E | $F$ |
| Leucopogon parviflorus at Seaford | Mean | 96.8 | 48.9 | 36.2 | 8.1 | 0.7 | - |
|  | Variance | 4.84 | 21.88 | 9.07 | 9.07 | 1.12 | - |
|  | Variance after transformation | 17.21 | 7.18 | 3.12 | 3.12 | 15.95 | - |
| Ehrharta longiflora at Carlton | Mean | 97.6 | 85.9 | 57.1 | 6.8 | 2.1 | - |
|  | Variance | 2.04 | 29.88 | 33.43 | 5.51 | 2.77 | - |
|  | Variance after transformation | 13.21 | 20.16 | 11.27 | 8.32 | 19.61 | - |
| Pteridium aquilinum at Blackwood | Mean | 99.2 | 83.5 | 46.2 | 37.2 | 2.5 | - |
|  | Variance | 0.84 | 13.39 | 40.62 | 68.62 | 1.83 | - |
|  | Variance after transformation | 14.93 | 8.25 | 17.64 | 25.03 | 7.18 | - |
| Hypochoeris radicata at Blackwood | Mean | 67.7 | 44.9 | 18.4 | 7.4 | 1.6 | 0.3 |
|  | Variance | 18.01 | 13.66 | 7.38 | 1.82 | 1.82 | 0.23 |
|  | Variance after transformation | 7.44 | 8.30 | 4.16 | 2.20 | 19.11 | 7.58 |

It will be seen that the variances, differing markedly with the mean in the original percentage data, become much more uniform within a species after angular transformation; in each of the four species, the differences among the transformed variances are non-significant, as judged by the Bartlett test. It is surprising that this uniformity does not extend to interspecific comparisons ( $x^{2}=9.09 ; n=3 ; P$ nearly equal to 0.03 ), as might be expected; the mean variances for Ehrharta longiflora and Pteridium aquilinum are moreover found to differ significantly from the variance ( 8.21 ) expected between percentages based on 100 observations after angular transformation. These discrepancies may perhaps be due to imperfect dimensionlessness of the point quadrat as determined by cross-wires and eye, or to movements of foliage in the wind affecting results with some species more than others.

This transformation is not always needed for work with percentage cover data. For direct comparison of means, as in Table 7 for instance, the means of large samples have a sampling variance whose distribution approaches normality, and provided the magnitude of the means under comparison does not differ widely the differences in their variance need not be a source of difficulty. Where, however, one wishes to include in the same treatment samples of which the means differed widely-if, for instance, one wished to
find whether grazing had the same effect on a given species irrespective of whether it was a major or minor constituent of the vegetation-transformation would be necessary in order to render the variances uniform.

## (d) The Personal Factor

The personal error in determining whether or not a pin touches a given species-that is, in estimating percentage cover-was tested by comparing results obtained by three experienced observers working on waste ground in Carlton. Each observer recorded contacts with the same pins in succession, the pins remaining in position and great care being taken to avoid disturbing the vegetation. To eliminate possible effects of such disturbance, the order in which the observers recorded was varied from pin to pin. In all, 300 points were recorded in this way. An analysis of variance was performed on the data for each species, its presence at a point being treated as unity, its absence as zero. The significant differences shown in Table 9 below are derived from the interaction term (observers $\times$ points) in these analyses of variance. Observers $B$ and $C$ agreed satisfactorily throughout, but observer $A$ exceeded their estimates significantly for two species, and fell below theirs for another.

Table 9
the personal factor in records of percentage cover

| Species | Percentage Cover as Estimated by Observer |  |  | Significant Between | Difference Observers |
| :---: | :---: | :---: | :---: | :---: | :---: |
|  | A | B | C |  |  |
| Lolium perenne | 65.3 | 61.7 | 66.3 |  | n.s. |
| Plantago lanceolata | 51.3 | 51.0 | 51.3 |  | n.s. |
| Bromus spp. | 30.7 | 23.3 | 25.0 |  | 4.3 |
| Cryptostemma calendulaceum | 20.3 | 23.3 | 23.0 |  | 2.4 |
| Romulea bulbocodium | 9.0 | 7.0 | 5.3 |  | 2.4 |
| Medicago arabica | 5.3 | 6.0 | 6.0 |  | n.s. |
| Medicago denticulata | 5.3 | 4.0 | 4.3 |  | n.s. |

Another series of observations was made without moving the frames, each observer placing the pins afresh before recording contacts, in order to test the possible extra source of personal error involved in guiding the pins through the holes in the frame. However, the movement of the pins introduced additional random variance, obscuring even the personal errors in observation noted above, and none of the differences between observers was significant.

Few investigators have studied observer differences in point quadrat work. Ellison (1942) found marked variation in estimates of percentage cover on one of the three areas he studied. The observations were made by using a frame in a fixed position, the pin being dropped afresh for each record, and the results obtained by the different observers for percentage cover by Buchlö̈ dactyloides (the only species recorded) ranged from 68 to 87 per cent.; it would seem from the results above that with observers well accustomed to the method considerably better agreement than this can be expected. It may be
mentioned that in the tests above the conditions of observation were more difficult than usual, on account of the need to avoid disturbing the vegetation, and this is more likely to have increased than diminished the variance between observers.

## III. Estimation of Cover Repetition

At a point where a species is present, its foliage may cover the ground once, or many times over. The average value of this quantity is here termed "cover repetition," and it is estimated by the number of times each pin hits the species while moving downward through the vegetation.*

> (a) Size of Pin

As in the estimation of percentage cover, so here the results are also affected by the diameter of pin used. All the considerations leading to an excessive estimate of percentage cover with a broad pin also tend to increase the number of times it comes into contact with the same species at any one point. Furthermore, if an upper leaf or branch is strained slightly out of its position of rest by the passage of the pin past it, this may affect the position of leaves or branches at a lower level and cause them to make contact where in their position of rest they would not have done so, or vice versa. This will tend to increase the variance of the number of contacts.

Table 10
COVER REPETITION BY FOLIAGE OF DIFFERENT SPECIES AS ESTIMATED BY PINS OF DIFFERENT DIAMETERS

| Locality | Species | Pin Diameter (mm.) |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | $\begin{aligned} & \text { 高 } \\ & \text { 竒 } \\ & 0.0 \\ & 0 \text { O } \end{aligned}$ |  |  |  |  |
| Seaford | Ammophila arenaria | 2.03 | 133 | 2.09 | 142 | $>0.05$ |
|  | Ammophila arenaria | 2.57 | 148 | 2.63 | 164 | $>0.05$ |
| Black Rock | Ehrharta erecta | 2.64 | 174 | 3.01 | 187 | 0.001-0.01 |
| Sorrento | Lepidosperma concavum | 1.20 | 44 | 1.20 | 55 | $>0.05$ |
|  | Spinifex hirsutus | 1.64 | 97 | 1.80 | 122 | $>0.05$ |
| Carlton | Fumaria officinalis | 1.89 | 63 | 2.42 | 60 | 0.01-0.05 |
|  | Ehrharta longiflora | 1.27 | 51 | 1.67 | 75 | 0.01-0.05 |
|  | Lolium perenne | 2.87 | 171 | 3.25 | 165 | $>0.05$ |

Tables 10 and 11 give results for cover repetition similar to those in Tables 1 and 2 for percentage cover. The significance of the differences shown in Table 10 was examined by the $\chi^{2}$ test applied to the original distribution of numbers of contacts per point; since the observations in Table 11 were made

[^2]by frames, the significance indicated in the last column is based on the weighted variance between frames, the weights being proportional to the number of pins in the frame making contact with the species in question (see below). It will be seen that in most cases the narrow pin gives a lower value for cover repetition than the broad pin, and that often this difference attains a high level of significance. It may be supposed that the cross-wire apparatus, had its use for this purpose been practicable, would have given still lower results.

Table 11
COVER REPETITION BY FOLIAGE OF DIFFERENT SPECIES ON BOGONG HIGH PLAINS, as estimated by pins of different diameters, arranged in frames of 10

|  | Species | Pin Diameter |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | 2.05 |  | 4.08 |  |  |
|  |  |  |  |  |  |  |
| Plot A | Carex hebes | 2.20 | 97 | 2.93 | 200 | 0.001-0.01 |
|  | Poa caespitosa | 1.68 | 56 | 2.53 | 86 | 0.001-0.01 |
|  | Asperula gunnii | 2.73 | 40 | 2.29 | 23 | $\xrightarrow{>} 0.05$ |
|  | Viola betonicifolia | 1.15 | 91 | 1.37 | 139 | 0.001-0.01 |
|  | Rumex acetosella | 1.41 | 59 | 1.58 | 106 | $>0.05$ |
| Plot B | Carex hebes | 2.58 | 94 | 3.32 | 196 | 0.01-0.05 |
|  | Poa caespitosa | 1.95 | 66 | 2.04 | 125 | >0.05 |
|  | Asperula gunnii | 3.45 | 24 | 2.94 | 49 | $>0.05$ |
|  | Viola betonicifolia | 1.15 | 31 | 1.47 | 78 | 0.01-0.05 |
|  | Microseris scapigera | 1.41 | 22 | 1.59 | 56 | $\xrightarrow{>} 0.05$ |

## (b) Distribution of Points

Where the foliage of individuals of a species does not overlap, the cover repetition will depend only on the habit of the plants and their height. Hence it is to be expected that, provided the areas sampled are large enough for few of the individuals present to be cut by the boundaries, the variability of cover repetition data should be small.

In the areas mentioned in connection with Tables 2 and 11, the variation in mean cover repetition between frames has been tested for a number of species, and has been found to be significantly greater than that within frames only* in Carex hebes, the dominant, as shown in Table 12; in other words, for this one species differences in cover repetition did in fact occur over the plot, but for other species they were negligible. In another plot on the Bogong High Plains-that at the head of Pretty Valley (see Table 7)-it is also true that the cover repetition by the dominant (Poa caespitosa var. "fine grass") varies significantly from frame to frame. This plant forms tussocks, and where the number of contacts exceeded 10 (which often occurred near the centre of

[^3]a tussock) counting was impracticable. It was therefore necessary to treat these data in two stages; first it was shown that the proportion of points at which the contacts exceeded 10, among those for which the species was recorded at all, varied significantly between frames, the variance being 1979 (with 116 degrees of freedom) after angular transformation, as compared with the theoretical value of 820.7 had there been no differences among the frames. Then differences were tested among the numbers of contacts in different frames for points with no more than 10 contacts, with the results in Table 13. Thus on both criteria Poa caespitosa showed significant variation in cover repetition within the plot.

Table 12
analysis of variance of cover repetition by carex hebes, bogong high plains (SQUARE ROOT TRANSFORMATION)

| Plot | $\begin{gathered} \text { Pin } \\ \text { Diameter } \\ (\mathrm{mm} .) \end{gathered}$ | Between Frames |  | Within Frames |  | $F$ | $P$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | Variance | D.F. | Variance | D.F. |  |  |
| A | 2.05 | 0.2201 | 96 | 0.1665 | 543 | 1.32 | 0.01-0.05 |
|  | $\{4.08$ | 0.4314 | 199 | 0.1991 | 1329 | 2.17 | $<0.001$ |
| B | 2.05 | 0.3694 | 93 | 0.1915 | 489 | 1.93 | $<0.001$ |
|  | $\{4.08$ | 0.6577 | 195 | 0.2487 | 1176 | 2.64 | < 0.001 |

A part of the additional variance between frames in cover repetition is associated with variation in percentage cover. In general the cover repetition at a given point is greater in frames where the species occurs at most points than where it occurs at few. This is illustrated for Carex hebes in Table 14. In each plot, the regression of cover repetition on percentage cover is highly significant.

Table 13
ANALYSIS OF VARIANCE OF NUMBERS OF CONTACTS PER POINT WITH POA CAESPITOSA FOR POINTS WHERE THIS NUMBER DID NOT EXCEED 10

|  | Degrees <br> of <br> Freedom | Sum <br> of <br> Squares | Mean <br> Square | $\boldsymbol{F}$ | $\boldsymbol{P}$ |
| :--- | :---: | :---: | :---: | :---: | :---: |
| Between frames | 116 | 835.7 | 7.20 | 1.60 | $<0.001$ |
| Within frames | 383 | 1719.9 | 4.49 |  |  |

This effect is not peculiar to the species or the area. It has also been demonstrated for Poa caespitosa on the other plot discussed. In Table 15, the number of points with more than 10 contacts and of those with fewer are compared for frames differing in percentage cover; a significant regression is shown. This relation is doubtless due to the extensive overlapping of the foliage of different individuals that occurs when the percentage cover is high.

When variation between frames in cover repetition associated with variations in percentage cover has been eliminated, the residual variance between frames for Carex hebes remains highly significant, indicating that there are additional sources of local variation independent of this factor. This is also clear on a larger scale from comparison of the data from the two plots in Table 14. For a given value of percentage cover, the mean cover repetition by Carex hebes is almost always greater in Plot B.

Table 14
COVER REPETITION BY CAREX HEBES IN RELATION TO PERCENTAGE COVER (4.08 MM. PINS)

| Percentage Cover | Plot $A$ |  | Plot B |  |
| :---: | :---: | :---: | :---: | :---: |
|  | Mean Cover Repetition | No. of Frames | Mean Cover Repetition | No. of <br> Frames |
| 100 | 3.21 | 43 | 4.10 | 27 |
| 90 | 2.91 | 38 | 3.51 | 36 |
| 80 | 3.06 | 32 | 3.14 | 35 |
| 70 | 2.70 | 35 | 3.07 | 24 |
| 60 | 2.43 | 24 | 2.98 | 22 |
| 50 | 2.90 | 16 | 2.86 | 16 |
| 40 | 3.00 | 3 | 2.56 | 21 |
| 30 | 2.11 | 3 | 2.43 | 7 |
| 20 | 1.67 | 3 | 1.80 | 5 |
| 10 | 3.33 | 3 | 1.33 | 3 |
| Regression mean square | - 7.43 |  | 55.72 |  |
| Error mean square | 0.83 |  | 1.06 |  |
| $F$ | 8.97 |  | 52.55 |  |
| $P$ | 0.001-0.01 |  | < 0.001 |  |
| $b$ | 0.0094 |  | 0.0231 |  |

The variation between frames in cover repetition which is demonstrated above is paralleled on a larger scale by variation between adjacent strips in a plot selected for homogeneity, already mentioned in relation to Table 6. In Table 16 it is shown that for the most abundant species, Poa caespitosa, the proportion of points with more than 10 contacts among all those where this species was recorded varied markedly from strip to strip.

No other species is very general on this plot, but in two the variance of cover repetition has been tested. An analysis of variance was performed after square-root transformation, and the variance between the means for the five strips was compared with the variance between frames within each strip (Table 17).

The conclusion to be drawn from the results presented above, for the more abundant species anyway and probably for all were the data sufficient to prove it, is that local differences in cover repetition occur even within vegetation selected for homogeneity, and that hence the same sampling practices as those recommended in respect of percentage cover will also be appropriate for estimating cover repetition. Points arranged in frames are likely to give
less efficient estimates for the more abundant species than points distributed individually. This question has been tested directly for Plot $B$ on the Bogong

Table 15
COVER REPETITION BY POA CAESPITOSA IN RELATION TO PERCENTAGE COVER

|  | Number of Points With |  |
| :---: | :---: | :---: |
| Percentage Cover | 10 or Fewer Contacts | More than 10 Contacts |
| 100 | 30 | 20 |
| 90 | 22 | 14 |
| 80 | 59 | 21 |
| 70 | 92 | 27 |
| 60 | 112 | 26 |
| 50 | 108 | 22 |
| 40 | 41 | 11 |
| 30 | 20 | 7 |
| 20 | 12 | 0 |
| 10 | 4 | 1 |
|  |  |  |
| Mean square for regression of percentage of points with more | 2921 |  |
| than l0 contacts on percentage cover | 473 |  |
| Error mean square | 6.17 |  |
| $F$ |  | $0.01-0.05$ |
| $P$ |  | 2.362 |

High Plains, already mentioned, results with a series of single points having been compared with those for points in frames. For a given number of points, the error variance was found to differ significantly only for the dominant, Carex hebes, for which 423 individual points would give as accurate an estimate of mean cover repetition as 2000 points in frames. This comparison is based on an equal distribution of pins making contact among the frames in

Table 16
COVER REPETITION BY POA CAESPITOSA ON ADJACENT STRIPS, BOGONG HIGH PLAINS

| Strip | Observed |  | Expected |  |
| :---: | :---: | :---: | :---: | :---: |
|  | 10 or Fewer Contacts | More than 10 Contacts | 10 or Fewer Contacts | More than 10 Contacts |
| 1 | 76 | 54 | 66 | 64 |
| 2 | 81 | 81 | 82 | 80 |
| 3 | 117 | 111 | 116 | 112 |
| 4 | 90 | 67 | 80 | 77 |
| 5 | 34 | 74 | 55 | 53 |
|  | $\chi^{2}=21.58$ | $n=4$ | $P<0.001$ |  |

which the species occurs. The fact that the variability of percentage cover causes variations in the number of points per frame for which cover repetition
data are available introduces a further complication into the estimation of mean cover repetition by the use of frames, and will tend to reduce their efficiency compared with that of individual points still further.

Table 17
VARIATION IN COVER REPETITION FOR TWO SPECIES ON ADJACENT STRIPS OF GROUND

| Strip | Cover Repetition |  |  |  |  |  | Hovea longifolia <br> No. of Frames | Phebalium podocarpoides <br> Cover Repetition | No. of Frames |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |

Thus for mean cover repetition, as for percentage cover, one may conclude that individual points are preferable to points arranged in frames, and that these points should be distributed not at random but in such a way as to ensure equal representation of all parts of the area covered. Whether or not

Table 18
CHANGES IN COVER REPETITION AS ESTIMATED BY RANDOM POINT QUADRATS AND PERMANENT POINT QUADRATS (SQUARE ROOT TRANSFORMATION)

| Species | Permanent Point Quadrats |  |  |  | Random Point Quadrats |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  |  |  |  |  |  |  |  |
| Poa caespitosa* <br> (var. "fine grass") | 1.791 | 1.764 | 0.563 | 115 | 1.868 | 1.787 | 0.812 | 554 |
| Poa caespitosa* <br> (var. "horny grass") | 1.721 | 1.753 | 0.270 | 44 | 1.596 | 1.737 | 0.814 | 141 |
| Leptorhynchus squamatus | 1.545 | 1.507 | 0.516 | 153 | 1.639 | 1.471 | 0.615 | 433 |
| Carex breviculmis | 1.358 | 1.240 | 0.215 | 85 | 1.345 | 1.304 | 0.341 | 511 |
| Celmisia longifolia | 1.393 | 1.471 | 0.532 | 62 | 1.476 | 1.504 | 0.579 | 175 |
| Scleranthus biflorus | 2.040 | 1.993 | 1.772 | 22 | 2.050 | 1.936 | 0.838 | 55 |
| Ranunculus lappaceus | 1.100 | 1.172 | 0.112 | 20 | 1.183 | 1.134 | 0.147 | 76 |
| Danthonia semiannularis | 1.432 | 1.650 | 0.656 | 28 | 1.536 | 1.539 | 0.873 | 121 |

[^4]equal weight should be given to all parts of the area is a question for ad hoc decision; for most purposes it will probably be preferable to give weights proportional to the percentage cover by the species in question-which simply means that all points at which the species is recorded are given equal weight.

Again, as with percentage cover, it is to be expected that changes in cover repetition can better be estimated by repeated observations at fixed points than by repeated sets of random observations. This has been tested on the data from Pretty Valley (Table 18).

To facilitate comparison between the two methods, the variances in Table 18 are in each case expressed in terms of observations at a single point on each occasion. For Poa caespitosa the mean number of contacts at points where they were counted must again be treated separately from the proportion of points where the number of contacts exceeded 10 and was not counted. The latter values are given in Table 19. The variances in Table 19 are éxpressed in terms of a single frame.

Table 19
CHANGES IN PROPORTION OF POINTS WHERE POA CAESPITOSA WAS RECORDED AT WHICH THE NUMBER OF CONTACTS EXCEEDED 10, AS ESTIMATED BY TWO METHODS (ANGULAR TRANSFORMATION)

|  |  | Mean, | Mean, | Variance of |  |
| :--- | :--- | ---: | ---: | :---: | ---: |
| Variety | Method | 1949 | 1950 | Differences | D.F. |
| "Fine grass" | Permanent point quadrats | 23.4 | 15.4 | 2841 | 116 |
|  | Random point quadrats | 26.8 | 16.1 | 3171 | 278 |
| "Horny grass" | Permanent point quadrats | 12.0 | 7.5 | 1484 | 90 |
|  | Random point quadrats | 18.8 | 10.8 | 2226 | 144 |

From Tables 18 and 19, it will be seen that the effect of permanent positions of observation, as compared with independent randomizations, on the precision of estimates of changes in cover repetition is considerably smaller than that for percentage cover (Table 7). The variances for "fine grass" in Table 19 do not differ significantly though those for "horny grass" do; in Table 18 the variances for seven of the eight species or varieties were less with permanent positions for observation-significantly so in three of the most abundant (both varieties of Poa caespitosa, and Carex breviculmis) - but in Scleranthus biflorus the difference was in the opposite direction, and also reached significance.

## (c) Distribution of Data for Cover Repetition and Their Statistical Treatment

If the number of contacts per pin followed consistently some mathematical law of distribution, the statistical treatment of such data could be put on a much sounder basis. Moreover, if this distribution were known, a complete count of the number of contacts might be unnecessary for some purposes, since the contribution of the larger classes to the total might be deduced from the frequency of the smaller classes. Some examples of the distributions found in practice are shown in Figure 2; all classes are expressed as percentages of all points where contact with the species was made, the large zero class being omitted. This is in accordance with the general principle adopted here of treating percentage cover and cover repetition as separate variables; it is clearly possible to conceive that two plots, one of which contained one plant
only of the species under study, the other a large number of plants scattered so that their foliage did not mingle, would have the same distribution of number of contacts per pin, except for the zero class, which would differ enormously.


Fig. 2.-Distribution of cover repetition data for four species.

Attempts have been made to fit various types of distribution to the numerous sets of data available. The Poisson series was first tested, and was found to fit only a few cases where the cover repetition was very small; this is in accordance with expectation, for on theoretical grounds the number of contacts should follow the Poisson series only when individuals are distributed at random and the chance of more than one contact with the same individual may be neglected. Contagious distributions seemed much more promisingthe distribution of projections on a horizontal plane of leaves borne on shoots spreading from a centre is clearly analogous with the situation envisaged by Neyman (1939) of larvae dispersing over a limited distance from a clump of eggs. Neyman pointed out that this implied that there was a limited area within which larvae found in any given sample area could have originated;
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Table 20
CONTAGIOUS distributions of neyman's type $A$ fitted to data for cover repetition

if the distribution within this larger area of the probability of origin of larvae found within the sample area were known, the distribution of total numbers of larvae in the sample area could be derived. Making three different assumptions regarding the distribution of the probability of origin of the larvae, he derived three types of distribution for numbers in the sample area. In spite of the artificiality of the underlying assumption, his Type $A$ distribution has in practice been found to fit adequately many groups of observational data, not only from entomology (Beall 1940), but also for the numbers of individual plants within small areas of natural vegetation (Archibald 1948). It was hoped that it would also fit the distribution of numbers of contacts in point quadrat data.

In Table 20 are shown some examples of contagious distributions of Neyman's Type A fitted to data for cover repetition. Where a satisfactory fit was not obtained by Neyman's method of moments, Shenton's (1949) maximum likelihood method was applied. It will be seen that, though several sets of data could be adequately fitted by this distribution, three could not.

A number of other distributions were tested, among them Neyman's Types $B$ and $C$, the double Poisson series of Thomas (1949), the negative binomial series, and the truncated log-normal distributions of Thompson (1950). None gave consistently more successful results than Neyman's Type A, and most were considerably worse.

It seemed likely that the difficulties in fitting might well arise from the fact already mentioned that, from the biological point of view, the distribution of numbers of contacts where the species is present at all should be independent of the size of the zero class. Accordingly, attempts were made to fit distributions to the data, treating the zero class as unknown; in other words, one could assume that the zero class of the observational data was made up of one part properly belonging to the distribution under test-perhaps that part falling within the outlines formed by joining the extreme branches of each individual-and another part unrelated to that distribution and depending on percentage cover. The number of points actually in the zero class was accordingly ignored, and arbitrary smaller numbers inserted, that giving the best fit with the distribution under study being found by trial and error. With the negative binomial distribution, a good fit was invariably obtained by this procedure. Some examples are shown in Table 21.

It has already been pointed out that there are species of plants, notably the tussock grasses, in which a complete count of contacts with a vertical pin is impracticable where the contacts are numerous. Even in species where a complete count is practicable, it may be undesirably laborious, and a method of estimating the mean cover repetition from the frequency of points with a few contacts only would be welcome for routine use where speed is more important than precision. Since it has been shown that, apart from the "contaminated" zero class, cover repetition data can be satisfactorily fitted by a negative binomial distribution, if such a distribution could be fitted taking into account only the first few classes an estimate could be obtained of the
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frequencies of the higher classes, and hence of the mean cover repetition. Unfortunately, a method of fitting a negative binomial distribution to data comprising a limited range of classes only has yet to be devised, and in the absence of such a method it is necessary to proceed empirically. It has been found that the frequencies in the lower classes bear a fairly constant relationship to the mean-not only in different sets of data for a single species, but also in different species.


Fig. 3.-Relation of mean cover repetition to proportion of pins with a single contact only.

In Figure 3, the mean cover repetition has been plotted against the proportion of points with only a single contact. The data for this diagram have been taken from 5500 records on 31 species in four types of vegetation-heath, mountain grassland, sand dunes, and waste land. It will be seen that the relationship is close-at least where the number of points with a single contact is large enough to give a reasonably satisfactory estimate of the proportion of such points. A curve such as that of Figure 3 could clearly be used to estimate the mean cover repetition if only points with a single contact had been counted; for higher values of cover repetition, however, the precision of
such an estimate would be low. The precision could be improved by taking, instead of the unit class only, the proportion falling into a number of the lower classes together. This has been done in Figure 4 for the points with from one to four contacts inclusive; it will be seen that the extreme error in the estimation of mean cover repetition from such a curve would be unlikely to exceed 10 per cent. Curves of this type would, then, provide a way out of the impasse presented by plants like Poa caespitosa where counting of the larger numbers of contacts is impracticable; it should be borne in mind, however, that the tussock habit of these plants, which prevents a direct measure of cover repetition, may also result in these species not obeying the same rule as those included in Figures 3 and 4. However, faute de mieux, it may sometimes be necessary to obtain estimates in this way of mean cover repetition, and of the mean number of contacts at points where they cannot well be counted. The procedure may be illustrated by a series of observations on the "ledge grass" variety of Poa caespitosa, for which the distribution was:

| Contacts | Points |
| :---: | :---: |
| 1 | 68 |
| 2 | 38 |
| 3 | 28 |
| 4 | 9 |
| 5 | 6 |
| 6 | 5 |
| 7 | 3 |
| Numerous, uncounted | 7 |

The proportion of points with from one to four contacts was 0.872 ; from the curve in Figure 4 this would correspond with a mean cover repetition of 2.63 -which in turn would indicate an average number of contacts of 12.3 for those points at which they had not been counted.

The facts that the observational data consist of integers, generally small, that their distribution is very skew, and that the variance is not independent of the mean suggest that the usual statistical techniques for normally distributed data would not be appropriate without modification. A transformation is required that can be applied to the data to render their distribution more nearly normal and equalize their variance, and hence to make it possible to use the usual tests of significance. Anscombe (1948) has proposed a hyperbolic sine transformation for the negative binomial distribution, but it seems doubtful whether that would be applicable where the zero class is ignored, as in the present case. For many types of skew data, it has empirically been found that square root transformations are satisfactory; they were likewise found to give reasonably good results with cover repetition data. As an example of the effect of this procedure, the results for Carex hebes on Plot $B$ (Table 14) may be cited. It has already been shown that the mean cover repetition for this plant differs for frames with different percentage cover. Accordingly, the variance between frame means has been computed separately for the frames with seven or more records for this species, and for those with six or fewer. The results are shown in Table 22. It will be seen that whereas
the difference in means was in the untransformed data accompanied by a difference in variance, after transformation the variances were almost identical.


Fig. 4.-Relation of mean cover repetition to proportion of pins with fewer than five contacts.

One further question in connection with the statistical treatment of data for cover repetition needs to be mentioned: when a mean is being computed for a plot of ground, should values from different parts of this plot be weighted in proportion to their area, or in proportion to the product of area and percentage cover? The latter seems the more logical procedure for most purposes, allowing each part of the plot where the species occurs to contribute equally to the mean, whereas the former procedure would give much greater weight to isolated individuals than to others forming a continuous cover. Accordingly, in this paper values from equal areas have been weighted in proportion to the percentage cover. For certain purposes, though-as, for instance, where one has reason to suspect a change in plant habit along a local gradient of climatic or edaphic factors-equal weighting of equal areas may be more appropriate.

## (d) The Personal Factor

Personal differences between observers might be expected to be more important in determining cover repetition than percentage cover-the scope for variation in counting contacts is greater than in determining whether or not contact has occurred.

Table 22
EFFECT OF SQUARE ROOT TRANSFORMATION ON VARIANCE OF COVER REPETITION FOR CAREX HEBES

| Variance Among Frames With |  |  |  |  |
| :--- | :---: | :---: | :---: | :---: |
|  | 1-6 Records | 7-10 Records | $F$ | $P$ |
| Untransformed data | 4.959 | 10.551 | 2.128 | $<0.001$ |
| Transformed data | 0.590 | 0.615 | 1.043 | $>0.05$ |

The data collected for Table 9 were examined in respect of cover repetition, only those points being taken into account at which the species was recorded by all three observers. The data were subjected to analysis of variance, after square root transformation (Table 23). Only in one species were significant differences between observers demonstrated. In view, however, of the much smaller number of observations than for percentage cover, it is hardly possible to draw conclusions as to the relative importance of personal variation in estimating these two characteristics.

Table 23
THE PERSONAL FACTOR IN ESTIMATING COVER REPETITION

| No. of <br> Soints | $\overbrace{A}$ | Mean Cover Repetition <br> as Estimated by Observer |  |  |  |  | B | Significance ( $P$ ) <br> of Differences <br> Among Observers |
| :--- | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Lolium perenne | 138 | 3.17 | 3.70 | 3.41 | $0.001-0.01$ |  |  |  |
| Plantago lanceolata | 136 | 2.24 | 2.40 | 2.39 | $>0.05$ |  |  |  |
| Bromus spp. | 48 | 2.15 | 2.04 | 2.15 | $>0.05$ |  |  |  |
| Cryptostemma calendulaceum | 57 | 1.88 | 2.18 | 2.14 | $>0.05$ |  |  |  |
| Romulea bulbocodium | 9 | 2.78 | 2.78 | 2.89 | $>0.05$ |  |  |  |
| Medicago arabica | 13 | 1.62 | 1.54 | 2.00 | $>0.05$ |  |  |  |
| Medicago denticulata | 7 | 2.00 | 2.29 | 2.43 | $>0.05$ |  |  |  |

## IV. Estimation of Percentage of Sward

The third type of measurement for which point quadrats may be used is a determination of the proportion each species forms of the total quantity of vegetation. This is often termed "percentage of sward," and is generally assessed in terms of dry weight. It has been claimed that point quadrats can provide a good estimate of this-that the number of contacts of pins with
one species as a proportion of the total number of contacts with all is closely related to the proportion of dry matter provided by this species (see Levy 1933; Levy and Madden 1933; Charpentier and Saarela 1941; Arny and Schmid 1942; Arny 1944; Eden and Bond 1945). With this question we shall not concern ourselves here, though it is plain that where herbaceous and woody plants grow together such a relationship cannot be expected to hold between them, and there is considerable evidence that even in a purely herbaceous community the relation is far from constant. Be this as it may, it would seem that this ratio of contacts with one species to contacts with all has some claim to be regarded, in its own right, as a measure of the part played by a species in the vegetation, irrespective of its relation to dry weight or any other measure; accordingly we shall proceed to discuss the derivation and treatment of data for "percentage of sward," defined as
$\frac{\text { (Percentage cover }) \times(\text { cover repetition }) \text { for one species }}{\text { The sum for all species of }(\text { percentage cover }) \times(\text { cover repetition })} \times 100$.
As estimated by the point quadrat method, this is of course equivalent to

$$
\frac{\text { Number of contacts with one species }}{\text { Number of contacts with all species }} \times 100
$$

Table 24
PERCENTAGE OF SWARD FORMED BY DIFFERENT SPECIES, AS ESTIMATED BY PINS OF DIFFERENT DIAMETERS

| Mean Percentage of Sward |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: |
| Plot | Species | 2.05 mm. Pin | 4.08 mm . Pin | $t$ | $P$ |
| A | Carex hebes | 71.00 | 69.80 | 0.48 | $>0.05$ |
|  | Poa caespitosa | 4.77 | 6.68 | 1.52 | $>0.05$ |
|  | Rumex acetosella | 4.16 | 5.26 | 1.15 | $>0.05$ |
|  | Viola betonicifolia | 5.47 | 6.13 | 0.84 | $>0.05$ |
| B | Carex hebes | 54.59 | 62.91 | 2.31 | 0.01-0.05 |
|  | Poa caespitosa | 11.28 | 7.49 | 1.99 | 0.01-0.05 |
|  | Asperula gunnii | 6.61 | 5.23 | 0.78 | $>0.05$ |
|  | Viola betonicifolia | 2.20 | 2.72 | 0.78 | $>0.05$ |
|  | Microseris scapigera | 3.90 | 3.31 | 0.51 | $>0.05$ |

## (a) Size of Pin

It is to be expected that the estimates of percentage of sward will be much less affected by pin size than either percentage cover or cover repetition. Since the variation in estimates of cover repetition with varying pin size tends to be greater for microphyllous than macrophyllous species, one would expect percentage of sward for the former to be slightly over-estimated, that for the latter underestimated, from the proportion of contacts with a coarse pin. That such effects may, however, usually be ignored is shown by Table 24, which presents the estimates of percentage of sward calculated from the same data as Tables 2 and 11. Only in two cases do the differences just reach significance, and it seems likely that these may well be the result of chance variation.

## (b) Distribution of Points

Since percentage cover and cover repetition had been shown to vary from point to point over an area, it was to be expected that the figures for percentage of sward would likewise vary. This is shown in Table 25, where the variances within and between frames are given for the data from Plot $B$ discussed above (those obtained with broad pins). The level of significance reached is so high that further demonstration is hardly necessary. These results imply, of course, that arrangement of points in frames leads to inefficient use of the observers' time-even more so than in estimating percentage cover. It may be computed from these data that the number of individual points giving estimates of equal precision to the means for 200 frames each with 10 points would range from 423 for Asperula gunnii to 704 for Poa caespitosa.

Table 25
ANALYSIS OF VARIANCE OF DATA FOR PERCENTAGE OF SWARD, BOGONG HIGH PLAINS

| Weighted Variance Weighted Variance <br> Between Frames <br> (D.F. 199) |  |  |  |  |
| :--- | :---: | :---: | :---: | :---: |
| Within Frames <br> Species | 28441 | 4125 | 6.89 | $<0.001$ |
| Carex hebes | 5134 | 1610 | 3.19 | $<0.001$ |
| Poa caespitosa | 6133 | 854 | 7.18 | $<0.001$ |
| Asperula gunnii | 1196 | 371 | 3.22 | $<0.001$ |
| Viola betonicifolia | 2444 | 562 | 4.35 | $<0.001$ |
| Microseris scapigera |  |  |  |  |

In addition to the variation in percentage of sward between frames, variation is also, as one might expect, found to occur between larger areas within apparently homogeneous vegetation. In the plot divided into strips already discussed in connection with Tables 6,16 , and 17 , an analysis of variance of the data for percentage of sward gave the results in Table 26. In deriving these percentages, at points where the contacts with the dominant "fine grass" variety of Poa caespitosa were too numerous to be counted they were taken as 10 , a figure derived for this variety by the procedure described on pp. 29-30. It will be seen that two of the four species show significantly greater variance between strips than within strips between frames.

Thus we come to the conclusion that for percentage of sward, as for percentage of cover and cover repetition, individual points are to be preferred to points arranged in frames, and they should be distributed over the area under study in such a way as to ensure equal representation of all parts of it; furthermore, records should be kept in a manner that will enable the data to be reassembled in different ways, so that the variation over the area may be studied.

The results already described for percentage cover and for cover repetition lead one to suppose that changes in percentage of sward, too, can be more accurately estimated from permanent point quadrats than from points distributed independently for each occasion of observation. This has been
tested on the data from Pretty Valley, Bogong High Plains, and the results are shown in Table 27. Records for Poa caespitosa of more than 10 contacts at a point have been treated in the way described on pp. 29-30. In all species but one the change is estimated more precisely by permanent point quadrats, and in the more abundant species the difference is very marked. It may, then, be concluded that, for determination of changes in the composition of the "sward," observational labour will be more economically used if the same points are used in successive years than if the points are distributed afresh at random in each year.

Table 26
VARIATION IN PERCENTAGE OF SWARD FORMED BY FOUR SPECIES ON ADJACENT STRIPS OF GROUND

| Species | 1 | 2 | $\underbrace{\text { trip }}_{3}$ | 4 | 5 |  |  | $F$ | $\boldsymbol{P}$ |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Hovea |  |  |  |  |  |  |  |  |  |
| longifolia | 12.2 | 8.3 | 2.0 | 4.0 | 10.6 | 2.51 | 0.88 | 2.85 | 0.01-0.05 |
| Poa |  |  |  |  |  |  |  |  |  |
| caespitosa <br> ("ledge grass") | 0.8 | 1.1 | 0.1 | 0.4 | 1.2 | 0.0308 | 0.0314 | 1.02 | > 0.20 |
| Phebalium podocarpoides | 9.5 | 6.0 | 7.4 | 10.0 | 14.2 | 1.13 | 1.72 | 1.52 | $>0.20$ |
| Carex |  |  |  |  |  |  |  |  |  |
| breviculmis | 1.1 | 0 | 0 | 0.6 | 0.3 | 0.0245 | 0.0095 | 2.58 | 0.01-0.05 |

## (c) Statistical Treatment of Results

Where for any purpose-for instance, forage studies-an estimate of the percentage composition of the total amount of vegetation over an area is required, it will clearly be necessary to use a weighted mean in combining data for percentage of sward from different parts of the area, the weights being proportional to the total quantity of vegetation. In practice, this means that the weights are proportional to the total number of contacts with all species within each portion of the area. This procedure has been used for all "percentage of sward" data in this paper, and variance estimates are weighted correspondingly. For certain purposes, however, it may be preferable to use weights proportional to areas rather than to total numbers of contacts.

As with results for percentage cover, those for percentage of sward will not have variance independent of their mean, but it may be expected that their sampling variance will be equalized by angular transformation. In Table

28 are shown the results of applying this transformation to the data already used in Table 26. The differences among the variances in different strips have been reduced by the transformation, but remain significant as judged by the

Table 27
CHANGES IN PERCENTAGE OF SWARD AS ESTIMATED BY RANDOM AND PERMANENT POINT QUADRATS

| Species | Permanent Point Quadrats |  |  | Random Point Quadrats |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  | $\begin{aligned} & \text { Mean, } \\ & 1949 \end{aligned}$ | $\begin{aligned} & \text { Mean, } \\ & 1950 \end{aligned}$ | Variance* | $\begin{gathered} \text { Mean, } \\ 1949 \end{gathered}$ | Mean, 1950 <br> 1950 | Variance* |
| Poa caespitosa <br> ( var. "fine grass") | 55.70 | 51.68 | 4.7183 | 51.24 | 54.80 | 13.5607 |
| Poa caespitosa (var. "horny grass") | 9.62 | 13.64 | 2.2559 | 14.34 | 10.93 | 8.3416 |
| Leptorhynchus squamatus | 10.09 | 10.04 | 1.0303 | 10.79 | 9.77 | 3.8896 |
| Carex breviculmis | 7.33 | 6.99 | 0.6672 | 7.77 | 6.34 | 0.9981 |
| Celmisia longifolia | 2.75 | 3.78 | 0.3915 | 2.07 | 3.97 | 0.8420 |
| Scleranthus biforus | 1.83 | 1.63 | 0.3547 | 1.02 | 2.20 | 0.6137 |
| Ranunculus lappaceus | 0.72 | 1.19 | 0.0923 | 0.62 | 0.89 | 0.0844 |
| Danthonia semiannularis | 1.80 | 2.15 | 0.5606 | 2.17 | 2.43 | 0.7161 |

* To facilitate comparison, the variance in each case is that of the difference between the means in 1949 and 1950 of samples of 100 frames ( 1000 points). The variance estimates for permanent point quadrats are based on 109 degrees of freedom, those for random point quadrats on 296 degrees of freedom.

Bartlett test. It has already been shown that variance between frames exceeds the sampling variance (that within frames), and it is clear that this additional component of the variance is not equalized by the transformation.

Table 28
WEIGHTED VARIANCE OF ESTIMATES OF PERCENTAGE OF SWARD, BEFORE AND AFTER ANGULAR TRANSFORMATION

| Strip | Untransformed | Transformed | Hovea longifolia |  |
| :---: | :---: | :---: | :---: | :---: |
|  | 12960 | 13476 | Untransformed | Transformed |
| 1 | 9770 | 11227 | 16487 | 15589 |
| 2 | 2020 | 4551 | 7455 | 7928 |
| 3 | 3240 | 5348 | 14938 | 14596 |
| 4 | 16050 | 17876 | 13789 | 12282 |
| 5 | 26.3 | 12.6 | 53892 | 35814 |
| $\chi^{2}$ | $<0.001$ | $0.01-0.05$ | 21.8 | 10.3 |
| $P$ |  |  | $<0.001$ | $0.01-0.05$ |

## (d) The Personal Factor

Idiosyncrasies of observers affect the results obtained for percentage of sward, as well as those for percentage cover and cover repetition. In Table 29 are presented the results for percentage of sward from the collection of
data already used for Tables 9 and 23. Records at 288 points (those at which all observers recorded contact with at least one species) were available for this purpose, and the results of the weighted analysis of variance are indicated in the last column of the table.

Table 29
PERSONAL FACTOR IN ESTIMATING PERCENTAGE OF SWARD

| Species | Percentage of Sward as Estimated by Observer |  |  | Significance ( $P$ ) of Differences Among Observers |
| :---: | :---: | :---: | :---: | :---: |
|  | A | $B$ | C |  |
| Lolium perenne | 41.1 | 45.6 | 43.7 | 0.001-0.01 |
| Plantago lanceolata | 26.0 | 25.2 | 25.6 | $>0.05$ |
| Bromus spp. | 13.5 | 9.2 | 10.6 | $<0.001$ |
| Cryptostemma calendulaceum | 8.7 | 10.2 | 10.0 | 0.01-0.05 |
| Romulea bulbocodium | 3.4 | 2.6 | 2.4 | 0.01-0.05 |
| Medicago arabica | 2.1 | 1.8 | 2.7 | 0.01-0.05 |
| Medicago denticulata | 2.4 | 1.7 | 2.4 | $>0.05$ |

In five of the seven species studied, the observers differed significantly in their estimates of percentage of sward. Except for Medicago arabica, however, the main contribution to this effect was from Observer $A$, and the differences between Observers $B$ and $C$ were much smaller-a result similar to that already mentioned in respect of percentage cover.

Crocker and Tiver (1948) failed to find significant differences between their three observers, using a method of calculation essentially similar to that for percentage of sward. It must be noted that the method used here provided a highly sensitive measure of personal differences, in view of the fact that each observer recorded at precisely the same points; though it is not explicitly stated, it would appear that in Crocker and Tiver's work different positions for the frames were used for each observer, which greatly reduced the sensitivity of their test.

It is clear, then, that the point-quadrat method is not quite as objective as has been claimed, and that personal differences cannot be ignored, though the differences demonstrated between observers are small compared with those commonly studied in vegetation.

## V. Discussion

The first conclusion that may be drawn from the results presented is that the pins used in point quadrat work should be as fine as is practicable, and that where data for percentage cover only are required an optical apparatus is preferable to a rigid pin, which must lead to over-estimation of percentage cover and cover repetition; figures for percentage of sward are much less sensitive to pin size. Where the principal interest centres in changes in the vegetation, the use of a thicker pin is probably less objectionable - changes recorded will be in the correct direction, though their magnitude will often not provide a measure of the true extent of the changes occurring. An optical method would, of course, be essential for use with the tree layer.

The use of oblique rather than vertical pins (see Introduction) would appear to be unobjectionable provided information only on percentage of sward is required, and an appropriate definition of this quantity is accepted. Since most plants include vertical and oblique, as well as horizontal, organs, the use of oblique pins certainly increases the number of contacts per point and hence the precision obtained with a given number of points, but information on percentage cover and cover repetition is lost. Incidentally, since the vertical component in the distribution of organs differs from species to species, it is to be expected that the figures for percentage of sward obtained by the two methods would not be identical; since, however, the definition of percentage of sward adopted for its estimation by vertical pins is arbitrary, and the quantity is intended merely as an index of the proportional composition of the vegetation, figures obtained with inclined pins have no less validity than those with vertical pins.

It is clear that a great deal of time and effort has been wasted in the past through the use of frames with 10 places for pins instead of individual placement of each pin. Blackman suggested the latter technique in 1935, but the only published work in which it has been used seems to be that of Eden and Bond (1945) and Bond (1947) in Ceylon. However, in assessing the advantages of individual points as against groups, it must not be forgotten that the time occupied in placing each pin at random is greater in the former, and the most economical procedure could be worked out precisely only if information were available both of the rates of work by the two methods and of their relative precision in the particular problem under investigation. Moreover, the scope for subconscious choice of placement is greater with individual points than with frames, and special care must be taken to avoid it. This difficulty could be eliminated by using frames in each of which only one point is recorded, the position of that point in the frame being determined at random.

Fresh random distributions of points on each occasion, when changes in the vegetation are the main subject of interest, are an extremely uneconomical procedure, and should be abandoned in favour of fixed positions for the points to be observed on each pair of successive occasions. The points should be marked, not by a pin or peg permanently placed there, which might affect the growth of the plants, but by measurement from pegs at some distance. With the exception of Arnborg (1943, 1949), previous investigators appear not to have recognized the advantages of performing successive observations at the same points.

The personal differences demonstrated between observers, although not large, show that it is desirable as far as possible to use the same observers throughout a series in which comparisons are to be made. If this is impracticable, supplementary comparisons of results obtained by the different observers on the same vegetation should be included, in order that the magnitude of the differences among them may at least be known, and perhaps corrected.

Several investigators who have used the point quadrat method have attempted to determine the number of points required to give a trustworthy analysis of the vegetation. This is not a question that can be answered in general terms. The answer not only will depend on the degree of precision required, but will vary from species to species (particularly as between more abundant and less abundant species), and will not be the same for determinations of percentage cover as for percentage of sward. The question can be answered only in relation to the particular problem and the particular type of vegetation involved.

As regards percentage cover, if points are distributed at random an answer may readily be given from first principles. The standard deviation of values obtained by use of $k$ points will be $\sqrt{\frac{p q}{k}}$ where $p$ is the percentage cover and $q$ its complement $(100-p)$. If, for instance, a standard error of 10 per cent. of the mean were considered satisfactory, this would be attained for a species occupying half the area with the use of 100 randomly distributed points; but for a species occupying only one-tenth of the area, 900 points would be necessary, and for one occupying one-hundredth, 9900 points.

For percentage cover if the points are not distributed at random, and for density of cover and percentage of sward in any circumstances, an answer cannot be given a priori to the question of how many points are required to give a specified degree of precision, but must be derived from observations directly on the vegetation concerned. In general, if the area under study be divided into small portions and two points placed at random be recorded within each portion, the variance between the points of a pair will indicate roughly the number of points required to produce results of a given precision. For observations on changes in vegetation in the course of time, without knowing how variable the changes in fact are it is impossible to obtain a firm figure for the number of points needed to estimate them with the accuracy required, and any estimate based on observations on a single occasion is bound to be no more than guesswork.

In general, if the same points are used for recording abundant and infrequent species, the relative precision of estimates obtained for the former will necessarily be greater than for the latter. While estimates of equal relative precision for the less abundant as for the more abundant species may be desirable, they will not usually be practicable, and a compromise will be necessary.

Although a critical approach to the point-quadrat method has been adopted, and attention has been drawn to some of the difficulties in applying it, the general conclusions that emerge are not adverse to the method. On the contrary, it remains one of the most trustworthy methods available to the ecologist, and one of the most nearly objective. With the improvements suggested here, one need be in no doubt that the method will in future serve ecology even better than it has done in the past.

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[^0]:    * Botany School, University of Melbourne.

[^1]:    * Moreover, this procedure ensures that equal weight is given to all parts of the area, whereas random distribution of points implies that weights given to different portions are themselves allowed to vary at random.

[^2]:    * The use of the cross-wire apparatus for determining this quantity is hardly practicable, for its use would necessitate moving each upper storey of foliage aside in order to get a clear view of the lower storeys.

[^3]:    * Apart from Asperula gunnii in one of the four series of observations.

[^4]:    * Points with not more than 10 contacts in either year.

