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Miscellaneous ecological notes

VARIOUS AUTHORS

INVESTIGATION INTO THE SIGNIFICANCE OF PLANT DISPERSION IN ASSESSING PASTURE CONDITION

The description of pasture condition in terms of percent cover and species composition is undesirable as these measures are not the sole criteria. It has been found, for example, at the Rietvlei Agricultural Research Station, near Pretoria, that heavily fertilized mown veld has a lower basal cover than unfertilized grazed veld, yet produces more than three times the amount of herbage than the unfertilized veld. The ultimate aim of pasture management is the maintenance of a healthy sward and it is possible that the measurement of the uniformity of plant cover may be of value in establishing an objective concept of pasture condition. It is intended, in this Note, to discuss various aspects of plant dispersion and their use in interpreting certain phenomena. In this paper the nature of the non-randomness is termed 'overdispersed' or 'contagious' when individuals tend to be clumped together and 'underdispersed' or 'regular' when individuals are evenly scattered. It is stressed that the terms overdispersed and underdispersed refer to the distribution curves of data and not to the pattern of plant individuals on the ground.

For the purpose of this investigation the Bruce Levy point quadrat (Levy & Madden, 1933) was used. Three bridges were made with 20 points each spaced at 1 cm, 2 cm and 5 cm intervals. The bridges, referred to in this paper as quadrats, were laid either 100 or 200 times at random in each experimental plot, all of which were smaller than one hectare. A 't' test showed that sufficient samples had been taken to ensure an accuracy of 10 percent of the mean number of strikes per bridge at $p=0{,}05$. In one analysis a bridge with 30 points at 5 cm intervals was used.

Random distributions may be described by the Binomial distribution, or by the Normal and Poisson approximations to that distribution. When the frequency curves of plants occurring in quadrats are compared with any one of these curves (depending on the nature of the sample), it is noticed that there is often a considerable discrepancy between the observed and calculated values. Clapham (1936) and Blackman (1942) compared frequency distributions of species occurring in quadrats with the Poisson distribution and they found that many of the species were not randomly dispersed. They expressed this deviation from the expected distribution by comparing the observed variance of the samples with the expected variance. Neyman (1939) and Thomas (1949) expressed the principle of contagious distribution in generalized forms of the Poisson distribution. The various frequency distributions are described below.

The Binomial distribution

The frequencies of 0, 1, 2, ... successes (strikes) in N sets are given in terms of the binomial expansion of $N(p+q)^n$ where N is the number of quadrats, p the probability of an event occurring, q the probability of the event not occurring and n the number of trials (points per quadrat). An easy method of calculating the successive terms in a binomial expansion is by using the relationship:—

$$\log(\text{probability of x plants occurring in any 1 quadrat}) = \log n! - \log(n-x)! - \log x! + (n-x)\log q + x\log p.$$

In the Binomial distribution the mean is np and the variance npq.

The Poisson distribution

This distribution is given by the series

$$\text{probability of x plants occurring in any 1 quadrat} = \frac{m^x e^{-m}}{x!}$$

where m is the mean number of plants per quadrat. In the Poisson distribution the mean is equal to the variance. When m is very small the distribution is an approximation to a Binomial distribution.

The Neyman contagion

This distribution is a generalization of the Poisson distribution and is given by:

$$p\,(x=0) = e^{-m_1(1-e^{-m_2})} \text{ and subsequent terms by}$$

$$p\,(x=k+1) = \frac{m_1 m_2 e^{-m_2}}{k+1} \sum_{t=0}^{k} \frac{m_2^t}{t!}\, p\,(x=k-t)$$

where the parameters m_1 and m_2 are proportional to the mean number of groups per quadrat and mean number of individuals per group respectively (Neyman, 1939). The parameters can be estimated from the first and second moments of the distribution as

$$m_2 = (\mu_2-\mu_1)/\mu_1 \text{ and } m_1 = \mu_1/m_2$$

When m_2 becomes very small and m_1m_2 is finite the distribution approaches the Poisson where $\mu_2/\mu_1 = 1$.

The Thomas distribution

This distribution is given by

$$p\,(k=0) = e^{-m} \text{ and subsequent terms by}$$

$$p(k) = \sum_{r=1}^{k} \frac{m^r e^{-m}}{r!} \frac{(r\lambda)^{k-r} e^{-r\lambda}}{(k-r)!}$$

The parameters m and $1+\lambda$ are the mean number of groups per quadrat and mean number of individuals per group respectively and are obtained from the first and second moments of the distribution where

$$\mu_1 = m(1+\lambda) \text{ and } \mu_2 = m(1+3\lambda+\lambda^2)$$

As λ becomes very small the distribution approaches the Poisson (Thomas, 1949).

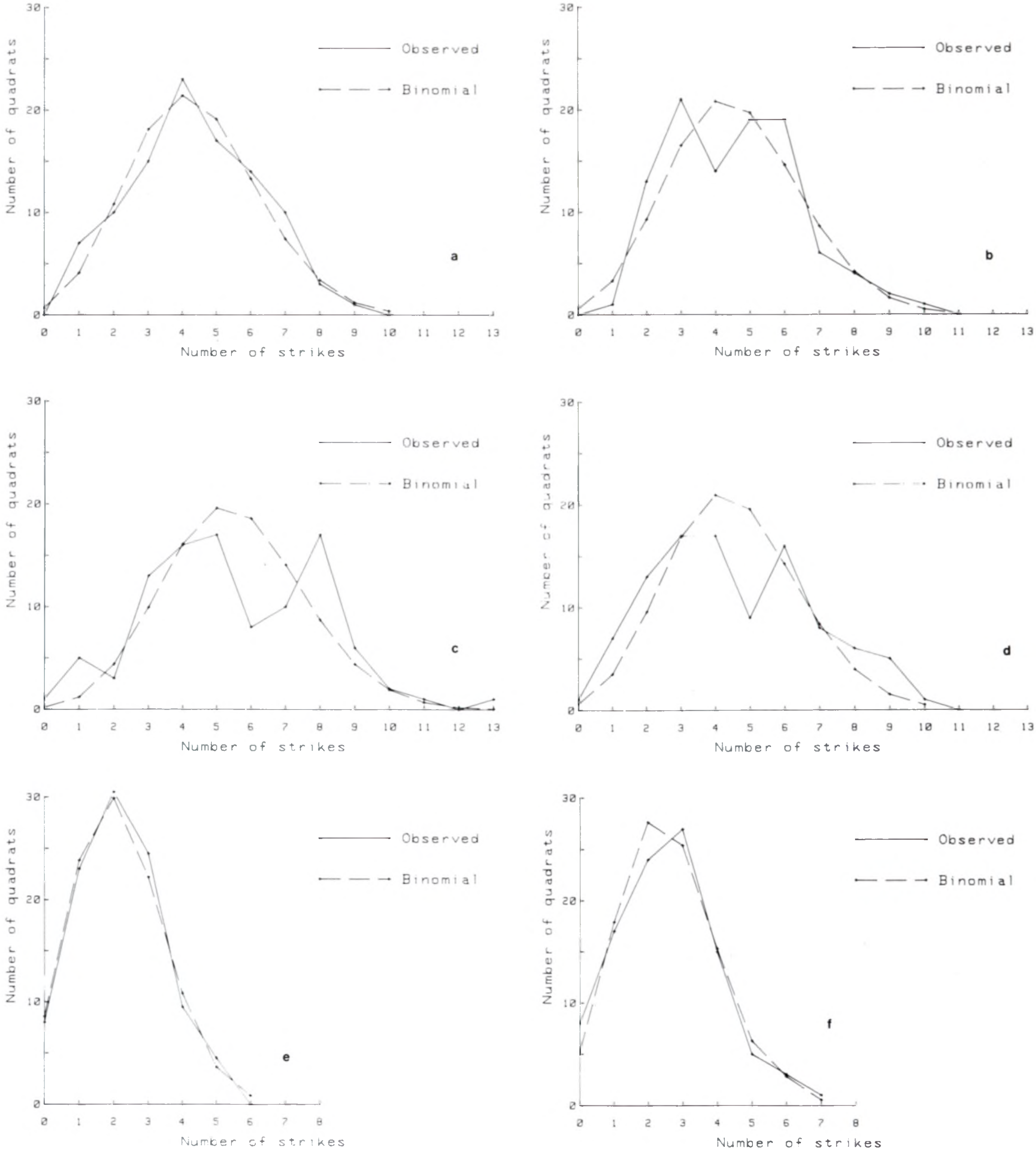

FIG. 1.—Frequency distributions of all plants compared with the expected Binomial distribution in a, plot 1; b, plot 2; c, plot 3; and d, plot 4 with 20 points per quadrat at 5 cm espacement and 100 quadrats; e, plot 1; and f, plot 3 with 10 points per quadrat at 10 cm espacement and 100 quadrats.

The frequency distribution of all plants occurring in plot 1 is given in Fig. 1a. The general appearance of the veld is that it is uniform and in excellent condition. The hay cuts from this heavily fertilized plot are more than three times those from unfertilized veld. The veld initially was a *Themeda triandra, Hyparrhenia hirta, Trachypogon spicatus* type but, as a result of the treatment, changed to *Setaria nigrirostris, S. perennis* and *Eragrostis chloromelas,* with relics of *Themeda triandra* and *Hyparrhenia hirta.* An examination of the figure will show that the fit of the observed values to the expected Binomial curve is very close ($P\chi^2$ = 0,8–0,9). The V/npq ratio (1,0104) is almost unity, signifying that the observed and expected parameters show close agreement. In plot 2, in which the treatment is the same as for plot 1, except that it is limed, the distribution also does not differ significantly from the expected values (Fig. 1b) although the fit is not quite as good. The V/npq ratio is 0,9985. Plots 3 and 4 were recently fertilized and grazed and from Figs 1c and 1d it is seen that the distributions of observed data points are distinctly bimodal and differ significantly from the expected Binomial distributions. From veld observations it was evident that vegetation changes were occurring in these plots. The initial effect of the fertilizer is that certain climax species are driven out and are replaced by others lower in the succession, and it is during this period that the productivity and vigour of certain species is profoundly affected. The bimodality of the distributions indicates that one is sampling a heterogeneous population, consisting of areas of low cover and others of high cover. The Neyman and Thomas distributions are built on premises that (a) the individuals in a cluster are randomly dispersed and (b) the clusters in a population are randomly dispersed. Because of the close agreement between the observed and expected values obtained by Archibald (1948, 1950), Barnes & Stanbury (1951) and in this paper, it may be accepted that these premises are valid. The bimodal curves, which cannot be adequately described by the Neyman and Thomas series, may therefore be explained as follows: the clusters of species which react unfavourably to high fertilizer dressings die out leaving bare areas while those species, normally randomly dispersed, which have responded to the fertilizer are showing increased vigour and a subsequent increase in number and size and are becoming contagiously dispersed. For example, it has been observed that tussocks of *Themeda triandra* and *Hyparrhenia hirta* die out and only after their death and the dissemination of their litter is the space which was occupied by those tussocks colonized by other species.

Corby (pers. comm.) showed that the further apart the points are the closer the distribution of species approached the Poisson values. Tidmarsh & Havenga (1955) showed experimentally that when the individuals of a population are dispersed at random, the distance between the points must exceed the average diameter of the individual to obtain a close fit to the expected Binomial distribution. The data for Fig. 1a-d were obtained from points spaced at 5 cm intervals. The distributions for plots 1 and 3 have been repeated in Figs 1e and 1f to show the effect of point espacement. The points of the 5 cm bridge were numbered from 1 to 20, and by recording each strike against the point number it was later, by taking alternate points, possible to examine and compare the distributions for the two espacements. The data presented in Fig. 2 are from a plot which has been moderately grazed by sheep and cattle subsequent to an accidental fire. Prior to the fire the veld had been leniently treated and used mainly as a source of hay. A comparison of the figures given for the 5 cm and 10 cm espacements in Fig. 1 shows that in plot 1 the closer fit to the expected values is obtained when the points are spaced at 10 cm, while the non-random distribution given for 5 cm points in camp 3 becomes random when the points are spaced 10 cm apart. In Fig 2a it is seen that the distribution changes from a highly contagious one for points at 1 cm to a somewhat doubtful distribution for points at 2 cm to a random dispersion with points at 5 cm. In the distributions for the 1 cm espacement (Fig. 2b) there is close agreement between the observed values and the Neyman contagion, as one would expect. It is of interest to note that in the distributions for the 2 cm espacement (Fig. 2c), the Poisson values do not differ significantly from the observed values, whereas the Binomial series does not describe the distribution adequately. Because the Poisson distribution is an approximation of the Binomial when the probability of an event occurring is small, it is felt that in this case the Poisson values should be discarded and that it should be accepted that the plants are contagiously dispersed for that particular espacement. The total number of strikes for the three espacements show a fairly close agreement, being 619, 610 and 587 for the 1 cm, 2 cm and 5 cm espacements respectively. A 't' test showed that the differences between these figures were not significant. It is the writer's contention that a cover made up of evenly dispersed small individuals is more desirable than one of large individuals and correspondingly large bare areas between the individuals, which causes the soil to be more erodable. It is probable that the competition for light and water is less when the dispersion of the plants is uniform. Where clusters are present, those individuals on the periphery of the clusters receive the greater light and water benefits.

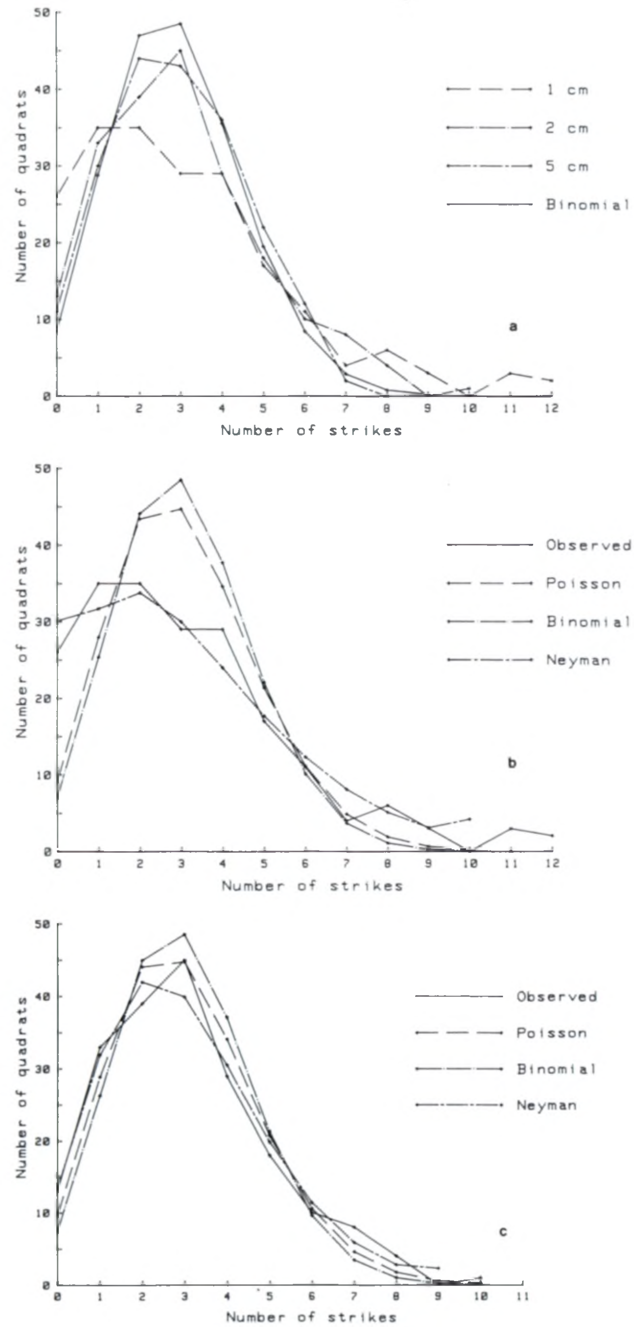

FIG. 2.—a, Comparison of frequency distributions of plants occurring in 200 quadrats, each with 20 variously spaced points, with the expected Binomial curve for 5 cm espacement; b, comparison of the Binomial, Poisson and Neyman series with the actual distribution of plants occurring in 200 quadrats each with 20 points spaced 1 cm apart; and c, of 200 quadrats each with 20 points spaced 2 cm apart.

Blackman (1935, 1942), Pidgeon & Ashby (1940), Archibald (1948, 1950) and Clapham (1936) have all

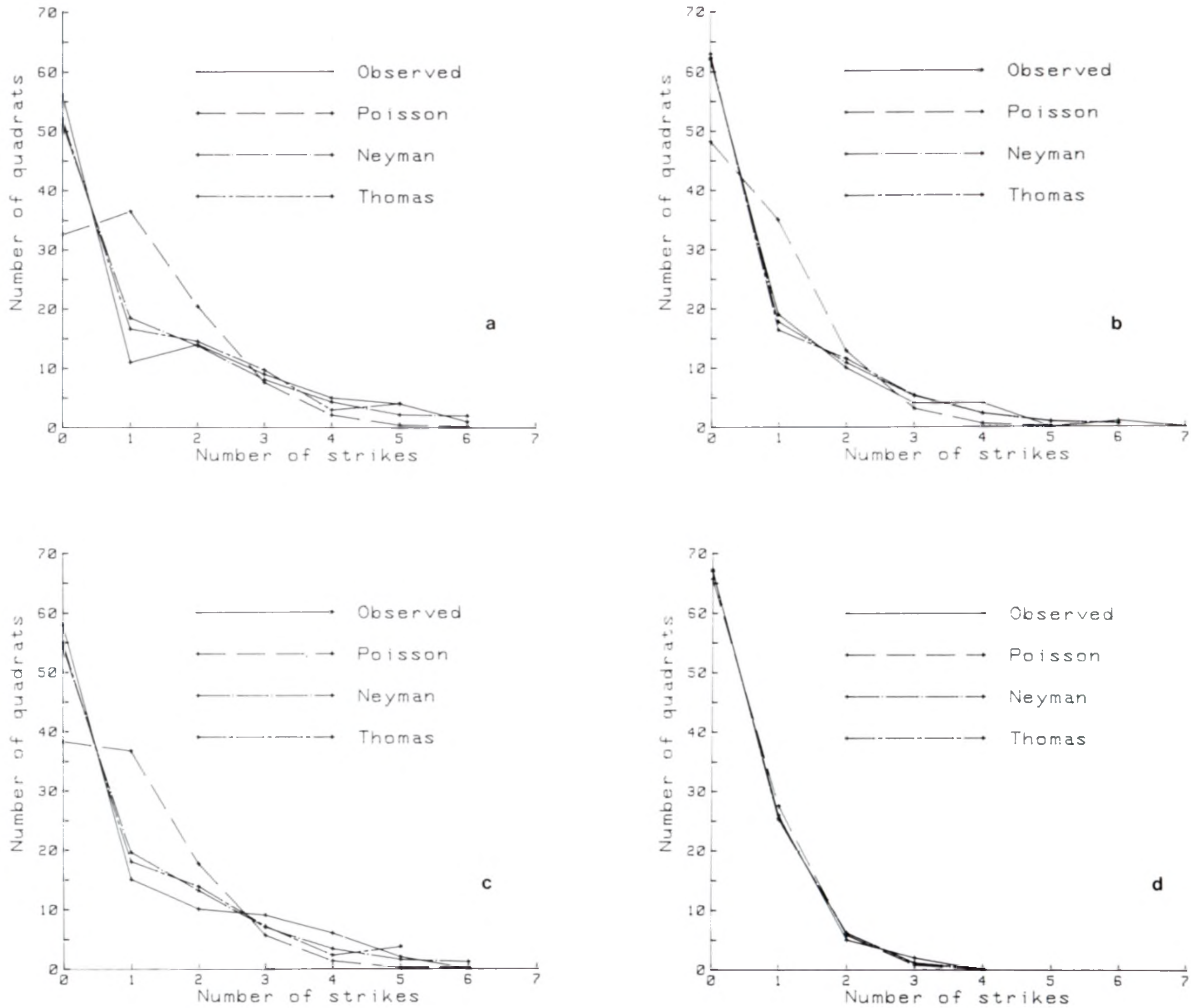

FIG. 3.—Frequency distributions of individual species from plot 5 compared with the poisson, Neyman and Thomas distributions from 100 30-point quadrats with points spaced 5 cm apart; a, *Trachypogon spicatus*; b, *Schyzachyrium sanguineum*; c, *Tristachya leucothrix*; and d, *Eragrostis capensis*.

shown that numbers of species in a plant community are not randomly dispersed and that the more abundant a species is, the greater is the degree of aggregation present. Ashby (1948) maintains that it is possible that species, without a biological predisposition to overdispersion, are randomly dispersed when they first occupy an area. Barnes & Stanbury (1951) found that as the vegetation developed, through spreading of 'islands' the distribution becomes highly contagious. If it is accepted that initial colonization is random and that the randomly distributed species later become contagiously distributed, it is reasonable to suppose that subsequent development of the vegetation will take place in, what may be termed as a series of waves of randomness, contagion and a subsequent randomness as the species is replaced. This process would continue until some state of equilibrium is reached where the climax species are contagiously dispersed while the pioneer relics are randomly distributed. Should the succession be driven back, then the reverse process would take place with the pioneer species tending towards contagion and ultimately the climax species would be randomly dispersed. From a series of analyses made at the Rietvlei Research Station, there is evidence which supports the argument propounded above.

Fig. 3 gives four frequency distributions from plot 5 which is rotationally grazed. From observations, this plot may be regarded as climax grassland and is in good 'health'. A bridge with 30 points spaced at 5 cm intervals was laid 100 times at random in the camp. The V/npq ratio is 0,9525 and χ^2 probability lies between 0,8 and 0,9. It will be noted that the distributions for *Trachypogon spicatus, Schizachyrium sangiuneum* and *Tristachya leucothrix* show a closer agreement to the Neyman and Thomas series than to the Poisson distribution. (When the probability of a plant being struck is very small (i.e. when np is small) then the Poisson series may be used to describe the distribution, however, when np becomes larger it is better to use the Binomial distribution). *Eragrostis capensis,* a relic pioneer is distributed at random, as are many other rare species such as *Brachiaria serrata* and *Eragrostis racemosa* (not plotted). The data for the four species given in Fig. 4 are from plot 3. It will be remembered that the distribution of all individuals in this plot was not random for points spaced at 5 cm intervals (Fig. 1c). *Heteropogon contortus* and *Setaria perennis* may be regarded as species near the climax stage and are overdispersed. *E. capensis* and *E. racemosa* have distributions approaching randomness but are, however, also overdispersed. These

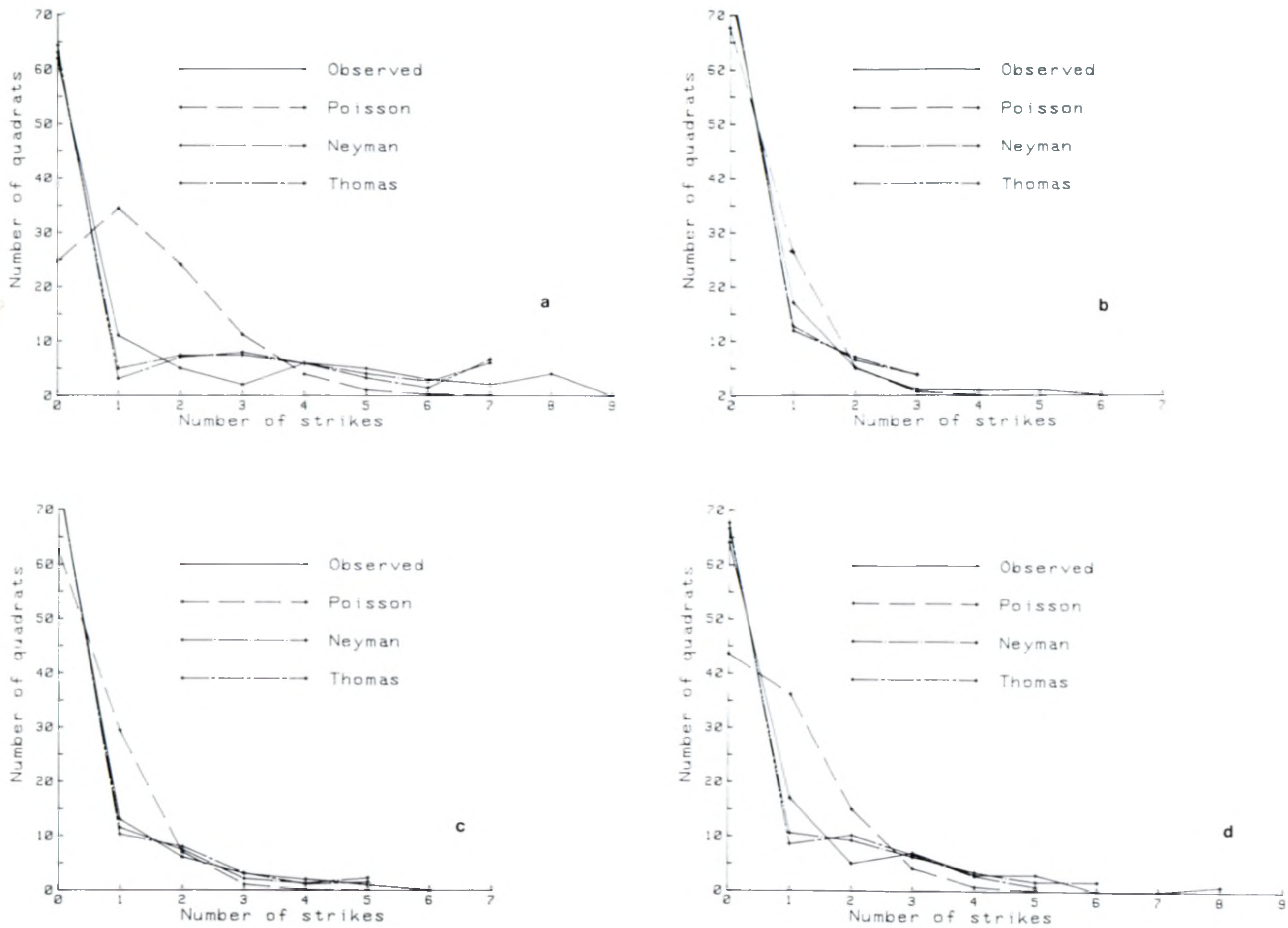

FIG. 4.—Frequency distributions of individual species from plot 3 compared with the Poisson, Neyman and Thomas distributions from 100 30-point quadrats with points 5 cm apart; a, *Setaria perennis*; b, *Eragrostis capensis*; c, *Eragrostis racemosa*; and d, *Heteropogon contortus*.

data suggest that both climax and pioneer species are contagiously dispersed. It has been shown by the writer that some species in which the frequency distribution cannot adequately be described by the Neyman or Thomas series, a better fit can be obtained if the points are moved further apart. It is quite possible that *Setaria perennis* and *Heteropogon contortus* would give a better fit to the contagious series if the points were moved apart. However, with the bridge used for these analysis, it was not possible to use 10 points at 10 cm intervals as there would be too few points to give an adequate representation of the dispersion. It is nevertheless obvious that the distribution is not random for these two species. From Figs 3 & 4 it appears as if the dispersion of the species can make a considerable contribution to the interpretation of botanical analyses, and the assessment of the condition of the sward. In plot 5, in which all plants are randomly dispersed, it is noticed that certain climax grasses such as *Schizachyrium sanguineum, Tristachya leucothrix* and *Themeda triandra* are not randomly distributed, whereas grasses near the pioneer stage such as *Eragrostis capensis, Brachiaria serrata* and *Eragrostis racemosa* are randomly distributed. The distributions for these last two grasses are not given, but the data indicate that they are randomly dispersed. In plot 3, in which the distribution of all plants is not random, it is found that both climax species and pioneer species are overdispersed.

This paper may be regarded as a preliminary report of certain points which came to notice during routine botanical analyses of grazing experiments on the Rietvlei Agricultural Research Station. It is felt that a deeper insight into the mathematical distribution of species and of individuals will throw light on the mechanism of vegetation changes and the direction in which these changes are proceeding. It is possible that the following points will indicate stability: (a) the frequency distribution of all plants is random when the points are closely spaced, the criterion of spacement being determined by the average size of the plant and the density of the cover; (b) the climax species are contagiously and the pioneer species randomly dispersed. When these conditions are not fulfilled, then there are indications that vegetation changes are occurring and a concept of the magnitude of these changes may be obtained by comparing the observed parameters of the population with theoretical parameters.

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