QUANTITATIVE PLANT ECOLOGY

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PREFACE

CHANGE from a qualitative to a quantitative approach is characteristic of the development of any branch of science. As some understanding is achieved of the broader aspects of phenomena, interest naturally turns to the finer detail of structure or behaviour, in which the observable differences are smaller and can only be appreciated in terms of measurement. It is not surprising that a quantitative outlook has been attained earlier in most branches of physical science than in biological science. Perhaps the greatest single difference in methodology between the physical and biological sciences is that in the former it is generally possible to isolate one variable at a time for study, whereas in the latter this is rarely possible. Thus, in the physical sciences broad outlines of phenomena are more readily seen from a relatively simple programme of qualitative investigation, and the way cleared for the more exact quantitative approach. In biology not only is it rarely possible to isolate variables for study, but the subjects of investigation are themselves commonly so complex that they are difficult to measure. In some branches of biology, therefore, attainment of the quantitative stage is perhaps little more than an ideal unlikely to be achieved in the near future. Other branches are more tractable, notably plant physiology, where many 'unwanted' variables can at least be minimized by use of controlled environments and clonal material, and investigation is now very largely in the quantitative stage. Plant ecology is at present in a transitional stage, and great advances can be expected from the quantitative techniques now being developed.

The general impossibility of controlling 'unwanted' variables in biology leads to a much greater degree of error variability in measurement than in the physical sciences. In the physical sciences differences among replicate measurements are generally attributable to deficiencies of technique, whereas in biological observations differences may be due not only to these deficiencies, but also, and commonly to a much greater extent, to fluctuation in variables not under investigation and assumed to be constant. Put another way, it is very much more difficult to obtain truly replicate samples in biological measurements than in physical measurements. If measurements are made in two or more contexts with the object of determining if there is any difference in the variable measured, the means may be different but the ranges of individual measurements may overlap. Thus the problem arises whether an observed difference is significant or not, i.e. whether it reflects any real difference between the two groups sampled, or is due to chance. In the physical sciences the immediate reaction is to improve the technique to obtain more accurate measurements, when either the means remain different but the ranges no longer overlap, indicating real difference, or the means converge with ranges still overlapping, suggesting that there is no real difference. In biology, however, there is often little scope for improvement of technique, and the biologist is therefore forced to turn for help in judging significance of difference to the techniques of statistical analysis. These are based on probability theory and permit determination of the probability of observed differences arising by chance in different samples of the same population. Thus arises the apparent paradox that while the physical sciences make much greater use of a quantitative approach than the biological sciences, they are much less dependent on the techniques of statistical analysis for the interpretation of their quantitative data.

There is at the present time a growing awareness among ecologists of the need to place their science on a more exact basis. The impetus given by the pioneers of ecology, which led to rapid advances in the first three or four decades of this century, is dying down and it is clear that the emphasis is changing from extensive work on vegetation to intensive work on selected aspects. If this is to go forward, more exact techniques of examination are necessary. The need for improved technique is made the more urgent on the one hand by the rapid depletion of natural vegetation, the only source of data on many of the more fundamental aspects of ecology, and on the other hand by the realization that advances in many branches of agriculture and forestry depend upon answers to ecological questions.

Although aware of the value of the quantitative approach and of the valuable tools available in the techniques of statistical analysis, many ecologists, faced with the rapidly expanding literature on quantitative methods in ecology, are reluctant to adopt a fully quantitative approach. This reluctance is, perhaps, reinforced by the apparent disregard of practical ecological problems in some theoretical studies. There is a need, therefore, for an assessment of the practical potentialities of various methods and techniques. I have attempted to make such an assessment in this book, and it is hoped that an ecologist faced with a particular problem in the field will find here guidance on the most profitable means of obtaining and handling his data, as well as a broad survey of the quantitative approach to plant ecology.

Chapter 1 is concerned with the different methods of describing vegetation in quantitative terms. Chapter 2 follows closely on the first, and deals with the positioning and number of samples to be used and with the comparison of the results of different sets of observations.

In Chapter 3 a hypothesis is developed of the significance, in relation to determining factors, of pattern, i.e. departure from randomness of distribution of individuals within the plant community. This leads to consideration of the techniques of detection and analysis of pattern. Chapter 4, on association between species, considers pattern from another aspect, the relationship between the patterns of different species.

Chapter 5 deals with correlation between vegetation and the level of environmental factors, the type of data on which most conclusions on the main factors determining the distribution of plants have been based.

Chapter 6 is concerned with the delineation of plant communities and assessment of difference between vegetation stands. This inevitably leads to consideration of the classification of vegetation, whether it is possible and if so, how it may be placed on an objective basis.

Chapter 7 is to some extent speculative. Believing that the quantitative approach has its own distinctive contribution to make to ecological theory, as well as putting existing practices on a sounder basis, I have devoted the greater part of this final chapter to consideration of this theme.

The appendices include brief discussions of the handling of meteorological data and of the area occupied by species, topics which do not fit conveniently into the main text, and a few tables of functions which are not readily available.

I have assumed that the reader, if he intends to make serious use of quantitative methods, will have access to Fisher and Yates' 'Statistical Tables for Biological, Agricultural and Medical Research' or to some other source of the commoner statistical tables, and to one or other of the elementary textbooks of statistical methods for biologists such as Mather's 'Statistical Analysis in Biology' or Snedecor's 'Statistical Methods Applied to Experiments in

Agriculture and Biology'. At the same time I have not hesitated to illustrate and discuss procedures at length where experience suggests that the biologist who is not very mathematically minded has difficulty in grasping them. By contrast I have given no examples of computation at all for more complicated statistical procedures, but have merely outlined their principles, believing that in such cases the biologist should take advice from a competent statistician, at least until he has had very considerable experience of statistical methods.

The reference list is strictly a list of references cited and makes no attempt at completeness. At the same time I believe that it includes the majority of references on methodology which are of current practical value rather than historical interest. The literature pertaining to the subject matter of Chapters 1 to 4 and Chapter 6 has been listed fairly completely by Goodall (1952a).

The quantitative ecologist is very dependent upon sound statistical advice. It therefore gives me great pleasure to express here my especial thanks to Professor M. S. Bartlett, of the University of Manchester, who has given freely of his time to advise me on statistical methods on various occasions since I first became interested in quantitative ecology. He has very generously read the whole of this book in manuscript, except Chapter 7, and corrected a number of mis-statements and ambiguities.

To Professor P. W. Richards I am indebted for his constant encouragement during the writing of the book and for reading parts in manuscript and making a number of suggestions for improvement. I am grateful to Mr. R. I. J. Tully, of the Library of the University College of North Wales, for help in obtaining literature from other libraries, and to Dr. A. D. Q. Agnew, Dr. K. A. Kershaw and Dr. W. S. Lacey for allowing me to quote data prior to their publication.

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P. Greig-Smith

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April, 1957

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CHAPTER I

QUANTITATIVE DESCRIPTION OF VEGETATION

MANY ecological data take the form of description of vegetation with or without concurrent recording of factors of the environment. Such data have formed the main basis of most ecological theory and concepts and are likely to continue to do so. It is essential, therefore, to place the description of vegetation on as sound a basis as possible. Two methods of community description have, with only minor modifications, predominated in the past. The first involves the making of a complete list of the species present in a community with the assignment of 'frequency symbols' or numerical ratings by inspection. This developed from the subjective assessment of species as rare, occasional, common, etc. in floras and represents an essentially similar process applied to a much smaller and more closely defined area. The second method derives from the work of Raunkiaer (1909, see Raunkiaer, 1934), and depends on the recording of presence or absence of species in small samples of the community under investigation. The sampling unit is a square, or less commonly a rectangle or a circle, of defined area, which may be placed either at random or in some regular manner. The results are expressed as the *percentage frequency*, i.e. the percentage of samples in which each species has been found. The species may be grouped for convenience of comparison into a number of frequency classes, with the limits of the classes forming either an arithmetic or a geometric series. The five classes 0–20 per cent, 20–40 per cent, 40–60 per cent, 60–80 per cent, and 80–100 per cent have commonly been used. This procedure is sometimes referred to as *valence analysis*.

These two methods have been widely used and it is important to consider their validity and limitations. The species list with frequency symbols or ratings is so well established that its value is too rarely questioned. The surprising feature is the degree of consistency of results obtained by experienced field workers. Several attempts have been made to assess the importance of the personal factor in deciding the rating assigned. Hope-Simpson (1940) has shown that one observer may give markedly different assessments on different occasions, particularly at different seasons. Smith (1944) investigated personal error affecting the simpler technique of visual assessment of percentage cover of total vegetation in plots. He showed that individual observers out of a group of eight deviated in their assessments from the group mean by as much as 25 per cent. There was little evidence of any tendency to give consistently lower or higher values than the mean. There is little doubt that similar results would be obtained if the assignments of frequency symbols by a number of observers for the same sample area were compared. Indeed, in view of the complex of factors affecting assignment of a symbol, considered below, the discrepancy might well be greater. A further source of personal error lies in the mental state of the observer. Every ecologist with some experience of frequency estimation is aware that rare and inconspicuous species tend to be rated lower when the observer is tired than when he is fresh and fully alert. Conversely, familiarity with a vegetation type and the species involved tends to produce higher ratings.

The difficulties introduced by personal factors are perhaps less important to an independent worker than to teams of workers. Once he is sufficiently experienced to attain reasonable consistency in repeated assessments of the same vegetation his ratings are likely to give a fairly reliable comparison between different communities. It is still impossible to attach any absolute value to his results. Moreover, results of different workers cannot be compared except in very broad terms, unless ratings for at least one and preferably several communities in common are available for the several observers. This drawback is so serious that, in general, frequency symbols should be used as the sole description of a community only when lack of time prevents the use of any more exact measure.

The difficulties of comparison of the results of several workers are more obvious in co-operative work. Unfortunately it is often in such work, e.g. in broad-scale surveys of the vegetation of large areas, that a rapid method of description is required. The errors introduced by personal factors can, however, be considerably reduced by careful standardization on the same vegetation between members of a team before the work is started and at intervals during its course.

There is a more serious objection to the use of frequency symbols. Several factors influence the observer in his assignment of a frequency symbol. Those uppermost in the minds of most observers are probably *density* or number of plant units per unit area and *cover* or percentage of the total area covered by the aerial parts of plants of a species, rather than true *frequency*, which is itself a complex character (see below). It is, however, difficult to avoid being influenced by the differing growth forms of different species and by the varying pattern of distribution of the individuals of different species on the ground, two factors greatly affecting the relative conspicuousness of different species. Even if density and cover alone are taken into consideration, an ideal probably impossible to attain, an attempt is being made to assess on one scale two largely independent variables. The problem is made clear by inspecting a weedy lawn, which includes at one extreme grasses, such as *Poa annua*, which have a high density of shoots but relatively low cover value per shoot, and at the other rosette weeds such as *Plantago* spp., each shoot of which covers a relatively large amount of ground. Cover and density each represent only one aspect among several of the contribution made by a species to the community. With practice in one vegetation type an observer can establish for himself an arbitrary scale of relative importance attached to cover and density but this relationship can scarcely be standardized and cannot readily be communicated to others. Moreover it has to be established afresh for communities of different physiognomy.

The confusion between cover and density is unavoidable. Other sources of error may with experience be reduced, though not eliminated. Species vary in conspicuousness and it is difficult to avoid overrating conspicuous species and underrating inconspicuous ones. Even the same species may vary greatly in conspicuousness between flowering and non-flowering states, e.g. *Deschampsia flexuosa* growing in comparatively small quantity amongst *Eriophorum vaginatum* gives a distinctive appearance to the community when flowering but is picked out only with difficulty when purely vegetative. Seasonal variation in assessment by the same observer on the same community, other than for annual species, results mainly from this variation in conspicuousness between different states. A further complication is introduced by the varying patterns that individuals of different species may form within the community. Individuals may be distributed more or less randomly through the community or they may be markedly aggregated into groups more or less clearly separated by areas in which the species is lacking or sparse. A high degree of aggregation may be indicated by rating the species as 'locally abundant', 'locally frequent', etc. When the aggregation is less marked overrating is liable to occur through increased conspicuousness of a species whose individuals are found in groups. The nature of these spatial patterns is of great importance to an understanding of community structure and is discussed in detail in a later chapter.

The use of frequency symbols has been treated at some length because their nature is often not fully understood, and because the method is commonly regarded as an elementary and straightforward one not needing any detailed consideration. It is evident, however, once its basis is examined, that care and experience are necessary before results of value can be obtained and that at its best the method is subject to considerable error. It is more satisfactory in description and comparison of communities of similar and uniform physiognomy than in those including diverse growth forms.

Frequency symbols raise a further point of importance: the highest category normally used is 'dominant'. This term is rather an unfortunate one, but probably too well established to be replaced. In practice it generally represents nothing more than the highest grade of density plus cover in the vegetation under examination. Many ecologists accept to a greater or lesser extent an organismal view of the plant community and tend to confuse this use of the term 'dominant' with the concept of dominance as a degree of influence exerted over other species of the community (by a variety of competition and stimulant effects). It is clear that some degree of such controlling influence has often been attached to species figuring as 'dominant' in species lists, without any evidence other than their having been assigned the highest frequency rating. A species may be dominant in both senses in a community but is not necessarily so. Moreover, the existence of dominance in the second sense is not universally accepted. It would certainly lead to clarity if another term could be substituted for 'dominant' as a frequency symbol. The dominant species of a community might then be defined as that species which exerts the greatest influence on other species of the community and is least influenced by them. The determination of the dominant species of a community in this restricted sense would involve prolonged investigations in most, if not all, communities, including autecological studies of all the more important species. It would probably be least difficult in forest with a single species only in the canopy layer. A third sense for 'dominant' is occasionally found in ecological literature, viz. to describe any individual tree of the canopy in forest whose crown is more than half exposed to full illumination. It is widely used in this sense by foresters together with the complementary term 'predominant' (better, 'emergent') for individuals rising above the continuous canopy. Richards *et al.* (1940) suggested that 'dominant (ecol.)' should be used for the species with the highest frequency rating where there is any doubt about the meaning intended.

The percentage frequency method is more conveniently considered after discussion of the various quantitative measures of vegetation. There are many such measures and it will be necessary to consider in detail only the more important. They fall into two categories, those in which the figure obtained is independent, within the limits of observational error, of the method used to determine it, and those in which it is dependent on the mode of sampling and has meaning only when coupled with a statement of the method used. Of the former, which may be described as *absolute measures*, the more important are density, cover and the various measures of yield. Of the *non-absolute measures* the only one of importance is frequency.

Density is the measure of number per unit area. The objects enumerated may be either whole plants or portions of a plant, depending on the morphology of the species involved. Thus individuals of trees or annual herbs are usually clearly distinguishable but definition of an individual in many perennial herbs is difficult or impossible, e.g. many rhizomatous and rosette-forming species. Even if individuals are recognizable they may not be the most useful unit owing to their wide range of size, e.g. tussocking grasses in which tillers are more appropriate units. The term *mean area*, introduced by Kylin (1926) and defined as the reciprocal of density, is sometimes useful. Density is readily determined by direct counts in suitable sample areas. Density is inversely related to the mean distance between individuals and attention has recently been paid to the possibility of using a measure of this distance to estimate density, to avoid the necessity of laying out sample areas (see Cottam and Curtis, 1956). Unfortunately the determination of the mean distance is complicated by the spatial arrangement of individuals. The difficulties involved will be discussed in Chapter 2.

Cover is defined as the proportion of ground occupied by perpendicular projection on to it of the aerial parts of individuals of the species under consideration. Its nature is perhaps most clearly brought out by noting that if a community on level ground composed of one species only were illuminated vertically the proportion of ground in shadow would represent the cover of the species. Cover is usually expressed as a percentage, and it should be noted that the total cover for all species in a community may exceed 100 per cent and normally does so in all except open communities. This follows from the overlying or underlying of a part of one individual by parts of one or more others of different species, obvious in any closed community.

Cover may be either estimated or measured. Estimations are subject to the personal errors already discussed in relation to frequency symbols, though easier to make since they involve a single characteristic only. Various techniques have been devised to assist in estimation of cover. The literature has recently been reviewed by Brown (1954). Measurement of cover may be made by the point quadrat method, which depends on recording the presence or absence of a species vertically above a number of points in the community being described. The percentage of points above which the species is present represents the percentage cover. The theoretical basis of this method is simple. If a sample area has a finite but small size it may be completely covered by the projection of the aerial parts of individuals of a species under consideration, incompletely covered or not covered at all. As the size of the sample area is reduced it becomes more likely that it is either completely covered or not covered at all, until, when it is infinitely small, i.e. a point, it is always either completely covered or not covered. As long as the sample area is finite the whole area under examination may be considered as consisting of a large but finite number of such sample areas, each falling into one of the categories completely covered, partially covered and not covered. As the sample area decreases in size the proportion of the total number of sample areas which are either partially or completely covered approaches more nearly to the value of the species cover. At the limit, when the sample area becomes a point, the proportion which is covered of the infinitely large total number of sample areas equals the cover of the species. The points actually examined in an investigation, if properly selected, are an unbiased sample of the infinitely large number of possible points and give an estimate of the true value of cover, the accuracy of which can be increased to any desired degree of precision by increasing the sample size.

In practice the sample size used cannot, of course, be a true point. Some form of optical apparatus with a cross wire gives the nearest approach to a point, but is scarcely practical for any extensive work and sampling is usually by means of long pins which are lowered through the vegetation, contacts made with the various species being recorded. The use of a pin of finite diameter will give a value of cover greater than the true value because plants will be touched that would not make contact with the axis of the pin. The magnitude of this effect is frequently not realized. It is demonstrated by the data in TABLE 1 and by FIGURE 1, both taken from Goodall (1952b), who gives a critical discussion of the point-quadrat method. The values given in the table for pin diameter 0 were obtained by an apparatus of cross wires.

Basal area, as generally understood, is a measure somewhat similar to cover, being the proportion of ground surface occupied by a species. (The term has also been used instead of cover, e.g. West, 1937.) It is of particular value in dealing with species of tussock form. Its estimation and measurement involve similar considerations to those of cover. In measurement presence of basal parts of the plant at the sampling point is substituted for presence of aerial parts.

An alternative method of measuring cover is to record total length of interception made by plants of a species on line transects.

TABLE 1

FREQUENCY (PER CENT) OF CONTACT BETWEEN FOLIAGE AND PINS OF DIFFERENT DIAMETERS (from Goodall, 1952b, by courtesy of *Aust. J. Sci. Res.*)

Locality	Species	No. of points	Pin diameter (mm)			Significance (P) for difference in pin diameter	
			0	1·84	4·75	0–1·84 mm	1·84–4·75 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 concavum*	200	13·5	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*	200	20·5	31·5	30·0	0·01–0·05	> 0·05
	Ehrharta longiflora		24·5	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

The proportion of the total length of the transect intercepted by a species gives a measure of the cover of that species. This method has an evident advantage in speed of working and in eliminating the exaggeration introduced by using a point of finite size, but involves some approximation in that an individual plant must be assumed to have a definite boundary within which it has 100 per cent cover. It is thus well adapted to measurement of basal area, and of cover of densely tussocking species, where this condition is nearly true, but of little use for vegetation where species are intermingled with one another. It is also appropriate to the measurement of the canopy of trees and shrubs, a feature sometimes of importance and not necessarily equivalent to their cover. How nearly cover and canopy correspond depends on the proportion of gaps in the leaf mosaic.

Measures of *yield* call for little specific comment. They are determinations of quantity of material produced per unit area and are made in a similar way to density determinations, the harvest of the relevant material being substituted for a count of plant units. An

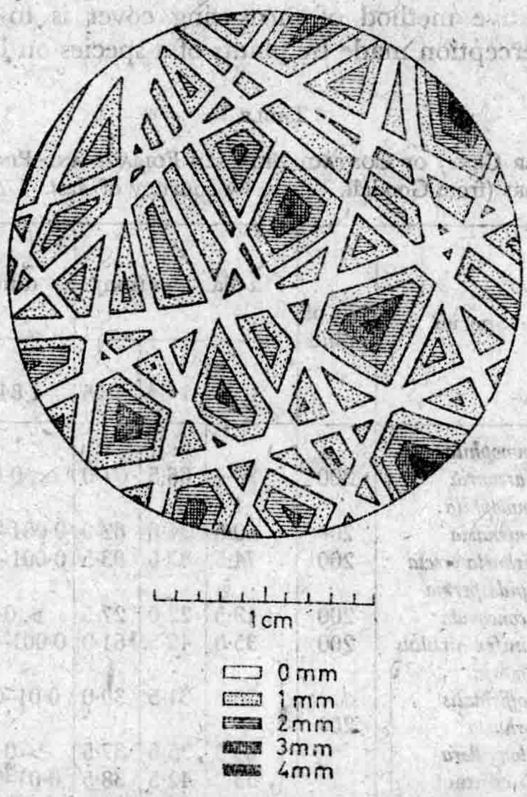

FIGURE 1. Projection of part of tussock of *Ammophila arenaria*, showing areas over which contact would be made with the foliage by pins of the diameters stated; each zone is understood as including those with less dense shading (from Goodall, 1952b, by courtesy of *Aust. J. Sci. Res.*)

indirect estimate of bulk of shoot material can be readily obtained in some types of grassland by a modification of the point-quadrat method. If the total number of hits made on each species is recorded instead of only their presence or absence at each sampling point, it has been found empirically that the proportions of hits on the different species correspond closely to the weight of shoot material. The validity of interpreting the proportions of hits in this way clearly depends on the species having similar growth form. Where it can be applied it is particularly valuable because it permits of an estimate of yield without destroying the vegetation, so that observations can be repeated on subsequent occasions without allowance having to be made for interference. Yield determinations have, naturally, been widely used in applied botany, e.g. dry weight in pasture assessment, volume of timber in forestry. Relatively much less use has been made of them in ecology, though they are valuable in such problems as the study of humus or mineral nutrient turnover, where it is important to know the rate of addition of plant material to the soil.

The measures so far considered are straightforward in conception, though they may present difficulties in determination. *Frequency* is usually the easiest of the quantitative measures to determine, but its meaning in biological terms is not so clear-cut. Frequency of a species, determined by a particular size of sample area, is the chance of finding the species within the sample area in any one trial. It is determined by examining a series of sample areas placed at random within the vegetation being described and recording the species present in each sample area. The number of samples in which a species occurs, expressed as a proportion or percentage of the total, is an estimate of the chance of its occurring in any one sample, i.e. the frequency. The accuracy of the estimate can be increased to any desired extent by increasing the number of samples. It is evident from the definition that a frequency value has meaning only in relation to the particular size and shape of sampling area used. Increase in size of sampling area will necessarily result in an increase in the chance of a species occurring in any particular sample.

The ease of determination of frequency, in comparison with density and cover, has weighed heavily with ecologists. Frequency has one disadvantage in that a value for one particular position on a transect line or a grid cannot be obtained by the normal method of random throws. A small quadrat in which a count of density is made, or a frame of, say, ten or twenty pins for cover determination may be placed in a definite position on a line or grid. The resulting value, though subject to a relatively large sample error, can be localized in relation to the frame of reference provided by the line or grid. Areas within which frequency is determined by random throws must be relatively larger, and the value obtained, though subject to proportionately less sample error than single determinations of density or cover, cannot be so precisely localized. Correlation with habitat factors which vary over small areas is thus made more difficult to detect. The difficulty may be largely overcome by using