The Use of Phytosociological Methods in Ecological Investigations: II. Practical Issues Involved in an Attempt to Apply the Braun-Blanquet System

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THE USE OF PHYTOSOCIOLOGICAL METHODS IN ECOLOGICAL INVESTIGATIONS

II. PRACTICAL ISSUES INVOLVED IN AN ATTEMPT TO APPLY THE BRAUN-BLANQUET SYSTEM

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(With three Figures in the Text)

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I. INTRODUCTION

The case for the Braun-Blanquet system presented in Part I is compounded of elements which are both good and bad, and grounds can readily be found for criticism. Indeed, it would be surprising if this were not the case in a scheme so ambitious. I am at present, however, more concerned that the criticism should be selective and that those points which are good should not be discredited with the bad. For this reason I wish first to emphasize those features which I believe to be of value.

The most important of these is simply the technique of distinguishing units which can be named. Whatever faults one may have to find with the criteria used by the Zürich-Montpellier school to delimit associations, each of their named associations does refer to a published series of lists; and inspection of this will immediately show exactly the sort of community that is meant. Such loose naming according to the dominant (Molinietum, Callunetum, Betuletum, Vaccinietum, etc.) as is prevalent in British literature is to be deprecated. Continental critics point out pertinently that, without having seen our vegetation, they cannot visualize what is meant; as all these species referred to above can dominate numbers of different communities. Certain vegetation types described in our

literature are, on the contrary, well characterized (e.g. the grassland communities on the Breckland, and the Chiltern beech woods; see Watt 1934, 1940). But these are given nicknames (Grasslands A, B, C, etc.) which, although useful for the particular local study, do not place them in relation to communities described elsewhere.

The named associations of the Zürich-Montpellier school are naturally not based on the description of one site, but are synthesized from the descriptions of many, thus ensuring that there is not an excessive multiplication of units. This has given rise to the technique of comparing and contrasting lists of stands in tables which is the second feature of value offered by the Braun-Blanquet system. For the tabulation permits one to see at a glance the range and type of floristic variation that may occur in one community, and in what characteristics it differs from those most nearly allied to it. This cannot be done from the synthetic lists giving constancy and average abundance which are common in current British literature.

Thirdly, the system draws attention to the differences in floristic composition and habitat between communities of the same successional grade at a particular moment. This does not detract from the importance of succession but merely emphasizes that it is possible and useful to look at vegetation in a different way. Plant sociology poses questions of the kind: communities A and B are different; what are the habitat factors which at this moment cause the difference and how do they operate? It is no answer to this question to say that A and B are stages in distinct series.

Detailed criticisms of the system will be reserved until Part IV, after consideration of the field data; but, as the more fundamental of them have a direct bearing on the discussion about methods which follow, it will be profitable to mention them briefly and in a preliminary way. They are:

(1) A lack of appreciation of the importance of the dominant and more common species, both in determining the structure of the community and in establishing relationships.

(2) The over-emphasis of fidelity as a characteristic of the Association and the assumption that the tolerance of species are concentric, which is a necessary condition, if associations defined by faithful species are to be classified in an hierarchy.

(3) The belief that associations can be classified in an hierarchy.

It will be realized that the apparent answers to all these questions can be biased by the type of site which is chosen for description and by the criteria used in sorting out lists on the tables. This will emerge from the discussion of the practical working out of the method with which we shall be concerned later.

The field study which will appear in Part III was designed to show how the more valuable features of the system could be used as a tool in ecological research. Uniform areas were to be chosen and described; the lists thus obtained were to be tabulated; and the results used to demonstrate whether vegetation units of the kind postulated by the plant sociologists could be distinguished, what criteria (dominance, constancy, fidelity, etc.) were most useful for distinguishing and characterizing these units and what size of unit seemed most real (i.e. 'the species' of plant sociology). In addition, data would be accumulated for a consideration of the various methods of classifying vegetation. At an early stage in field-work it nevertheless became clear that the system could be used as a research method without committing the worker to any particular system of classification (cf. Sjörs, 1946). Before embarking on a field study, it was necessary to consider

critically the techniques which were to be used. Basically the system consists of four stages:

(1) Choosing uniform areas of vegetation.

(2) Describing these areas (as explained in Part 1, pp. 236 sqq.).

(3) Tabulating the lists obtained and segregating from the tables lists which are sufficiently alike to be considered to belong to the same vegetation unit.

(4) Grouping these units according to their affinities.

Each of these steps requires that a certain judgement should be made, viz:

(1) What is a uniform area, and should all such areas in a region be described?

(2) What is the best method of description?

(3) What degree of similarity is required among lists in order that they may be attributed to the same unit?

(4) What criteria are most important in establishing affinities between units?

The next few sections will be devoted to a discussion of these problems.

II. THE UNIFORM AREA

To each of the questions suggested above there are two answers, the analytical and the empirical. The techniques of the Braun-Blanquet school undoubtedly belong to the second of these categories and are, as such, worthy of the most serious consideration; but, unfortunately, their exponents have thought it necessary to underpin them with fundamental assumptions which cannot be strictly maintained and to use mathematical concepts, such as that of 'minimal area' which will not stand up to close scrutiny. It is largely because of this, and of the excessive importance ascribed to fidelity, that the system has been discredited in this country; and, paradoxically, those arguments which were thought to establish it on sound foundations have drawn attention away from its other features which were incomparably more valuable.

A. *Statistical methods*

Goodall (1952) envisages a time when statistical techniques will be applied to all the processes in the distinction and classification of vegetation units. Such an ideal would involve, first, a statistical check on the uniformity of every stand followed by its statistical description, and, for the purpose of classification, objective methods for the measuring of relationships between the stands described. Both Clapham (1936) and Ashby (1948), however, consider that it is not profitable to apply statistical techniques to the description of vegetation for classification, and that their use in plant ecology should be at present confined to particular problems for which they are better fitted. It seems unlikely, in fact, that they will ever be extensively used for description and classification because of excessive time expenditure.

'Homogeneity' of the stand is unquestionably the basis of plant sociology. Of it Nordhagen (1928) writes with perfect justice: 'Mann kann füglich behaupten, dass es, wenn es in Natur keine homogen oder relativ homogen bewachsenen Areale gäbe, es auch keine Pflanzensoziologie gäbe.' Statistical treatments have so far done nothing except to establish arbitrary levels of homogeneity. For each species of a community there is a size of quadrat so small that the species will appear over-dispersed, and as the size of the quadrat is increased it will appear successively as normally dispersed and sometimes

as under-dispersed relative to the size of the quadrat (cf. Romell, 1925). If the quadrat size is chosen so large that all the species present are normally or under-dispersed, the vegetation can be considered homogeneous. But the numerical index obtained of the state of dispersion of the species is dependent on the size of the quadrat which is used for sampling. Dahl & Hadac (1949) have given the following definition of homogeneity: 'A plant species is said to be homogeneously distributed within a certain area if the probability to catch a plant species within a test area of a given size is the same in all parts of the area. A plant community is said to be homogeneous if the individuals of the plant species which we use for the characterization of the community are homogeneously distributed.' This definition depends on two ambiguous phrases, neither of which is fully defined by the authors, 'a test area of a given size' and 'the plant species which we use for the characterization of the community'. Nordhagen (1928) has given a review of these problems and has been forced to the arbitrary technique of using in his studies a quadrat size of 1 sq.m. in species-poor and 4 sq.m. in species-rich communities and thereafter deducing the degree of homogeneity from the frequency histograms obtained from ten samples in each stand. It would appear that no satisfactory definition of homogeneity has yet been given and that statistical techniques can only give us measures of the degrees of over- or under-dispersion of the various species of a community relative to a particular quadrat size or quadrat sizes, and with the same quadrat size relative to each other.

Thus two alternatives are open: to establish an arbitrary limit of this kind; or to fall back on an assessment of homogeneity by eye, 'die pflanzensoziologische Blick', as it is called. As this study is concerned primarily with the Braun-Blanquet system, where attention is focused not so much on the homogeneity of the vegetation as on the floristic uniformity, and as contemporary statistical techniques seem to offer no substantial improvement, I have decided to adopt the latter.

Without having recourse to mathematical treatments it is quite clear that homogeneity is a question of scale. An observer in an aeroplane has quite a different impression of the uniformity of a woodland from that of an ecologist analysing the ground flora with a metre quadrat; and a uniform habitat for the smaller soil organisms will be more restricted still. In fact, the more one examines vegetation, the more one is forced to the conclusion that absolute uniformity is an illusion.

B. *Mosaics*

Mosaics, of or in, different plant communities are often to be seen in the field. Watt (1947) has given a number of examples where the arrangement is due to the reaction of the dominant species. In other cases it may be imposed on the plants by an underlying mosaic of the physico-chemical factors of the habitat as, for example, in the vegetation of soil polygons (Warren Wilson, 1952; Lundquist, 1949). The practical problem for the sociologist is to decide whether to treat each element of the mosaic separately or to describe the complex as a whole. For, while it is undoubtedly true that, where the pattern depends on the reaction of the dominant, the various components of the mosaic are united by strong lateral ties, it may also be cogently argued that each element has a different micro-habitat, and that it should thus be described separately. For example, Grassland A on the Breckland, described by Watt (1947), shows a considerable degree of floristic and physiognomic uniformity; yet he has been able to split this up into a mosaic of four phases, each of which comprises a slightly different micro-habitat. Should

one treat the whole as a 'uniform' area for the purpose of sampling, or should one treat each element of the mosaic separately? The same question could be asked of all the communities quoted by Watt in this paper and about a very large number of other natural communities.

The answer seems to be that neither alternative is necessarily right or wrong; each case should be judged on its merits and different levels of abstraction may be appropriate for different ends. But in a floristic survey of a region some considered and consistent standpoint is desirable. The most practicable resolution of the problem seems to be as follows: if one element of a mosaic occurs in a very similar or identical form as a pure community independently of the other elements with which it is usually associated, it should be described separately; similarly, if one element associates with more than one other element to form different mosaics, it should again be treated as an independent entity. These criteria proved satisfactory during the Scottish field-work to be reported later. The following are some examples of the treatment accorded to certain communities which illustrate the application of these principles:

(1) High-altitude Nardetum. This community is, in fine structure, a mosaic of tufts of *Nardus stricta*** and spaces dominated usually by *Pleurozium schreberi* and containing the other species of the community, particularly *Carex bigelowii*. This has been treated as a single community because it fulfilled neither of the conditions outlined above. In this case it seems likely that the mosaic is caused by the death and regeneration of individuals of *Nardus stricta*.

(2) On the south-east spur of Ben Lawers between the altitudes of 2400 and 3100 ft. (722–945 m.) there is a development of small terraces comparable in their effect on the vegetation to those described from the Cairngorms by Watt (1947) and Metcalfe (1950). The communities of these terraces form a mosaic with one occupying the flat terrace, one the brow and one the angle between. The communities interdigitate with different partners according to the altitude, and all of them occupy considerable areas in a pure state elsewhere. They have accordingly been described as independent communities.

(3) The gorge of the Keltneyburn at the east margin of the area examined may illustrate how the problem could be tackled in complex communities. This gorge is typical of a number which occur in the district, for example, the Allt Odhar above Fortingall, and Acharn burn draining into the south side of Loch Tay. It cuts to a depth of as much as 200 ft. (61 m.) through a variety of schists and limestone. Its sides are covered with a mixed deciduous woodland containing *Quercus* sp†. *Betula pubescens*, *Fraxinus excelsior*, *Ulmus glabra*, *Corylus avellana*, *Acer pseudoplatanus*, *Sorbus aucuparia* and *Prunus padus*. This woodland grows on soils which show great variability in stability, depth and moisture content, and quite large trees are often found growing in cracks in bare rock. The ground flora varies independently of any variation in the composition of the tree layer, although of course it is dependent on the presence of some sort of cover for the maintenance of a moist, shaded micro-climate, for protection from excessive erosion and for the particular condition of at least the deeper soils. The various subordinate communities are as follows:

(a) Bryophyte communities of rock surfaces, which vary according to whether they

* Nomenclature of vascular plants follows that of Clapham, Tutin & Warburg (1952), and mosses of Richards and Wallace (1950); the authorities for nomenclature of liverworts are given in Appendix 1. Nomenclature of lichens is according to Watson (1953).

† The oaks are mainly attributable to *Quercus robur* or var. *intermedia* D. Don. *Q. petraea* seems to be rare.

are subject to periodical inundation, are permanently wet or are more or less dry (among other factors).

(*b*) Herbaceous communities which vary according to the stability or instability of the underlying soil, the chemical composition of the rock, the dip of the strata (whether parallel or normal to the angle of slope), and the degree of flushing by lateral streamlets.

(*c*) Epiphytic communities of ferns, bryophytes and lichens. (Most of these communities can be found occupying small, uniform areas.)

How could the sociological approach be applied to a situation such as this? The following seem to be the important points:

(1) A full description would take too long and would only be comparable with the full description of another such site; also this comparison would only be valuable if it could be made habitat by habitat.

(2) Any sample plot large enough to contain all the tree species would not be uniform in the ground layer, and would show considerable differences from any other sample plot because the two would be unlikely to contain the same micro-habitats in the herb and moss layers.

(3) The only possible treatment would seem, therefore, to be to describe the tree layer separately from the rest.

The following are two lists of the tree layer in sites in Keltneyburn to show that they are directly comparable (cover-abundance is assessed according to the scale of Braun-Blanquet):

Acer pseudo-platanus	1	—
Betula pubescens	2	1
Corylus avellana	2	4
Fraxinus excelsior	4	2
Sorbus aucuparia	2	1

(The area of the first sample was 900 sq.m., of the second 400 sq.m.) These descriptions should be supplemented by notes on the various vegetation units which occur in the ground layer and on the area covered by each. Clearly this is a more practicable proposition than listing all the species present in plots of 900 and 400 sq.m. respectively.

(4) Conversely, the uniform stands in the herbaceous and bryophyte communities should be described separately and notes made on the character of the tree layer. An example from Keltneyburn is that of a nitrophilous community dominated by *Mercurialis perennis* and *Allium ursinum* (see p. 251).

Details of the habitat of each of the listed sites are presented in Appendix 2. In standard Braun-Blanquet technique these are included at the top of the table.

The same treatment could be accorded to many of the herbaceous and bryophyte communities in Keltneyburn and would allow them to be compared directly with those in neighbouring gorges and with communities in other complexes. In this way similarities and differences may appear which might otherwise pass unnoticed. Such, in this case, are the similarities between the herbaceous flora of the more stable slopes and that of oak-ash woodland on brown earth soils, between the wetter facies and hill-side alder-wood flushes, and between the corticolous lichen communities and those on the extreme west of Scotland. The fact that the herb and moss communities are treated separately from the tree communities and that they are considered as static and not as part of a dynamic situation in which plant reaction and physical erosion play large parts, does not mean that the mutual bonds between the various layers are ignored, or that the influence of

dynamic factors is neglected. It means, merely, that for certain purposes it may be more convenient to abstract the tree layer from the community and consider it as a biotic factor of the habitat (a step which is perhaps little more arbitrary than to abstract all the animals), and to consider the various herbaceous and bryophytic communities as under close control by their habitat and describe them as such for comparison with other similar communities.

No. of sample plot	520025	520026	520027	520028
*Corylus avellana	×	–	–	–
Fraxinus excelsior	–	×	×	×
*Sorbus aucuparia	–	×	–	–
*Ulmus glabra	×	–	×	×
Rubus idaeus	–	–	2	–
Dryopteris filix-mas	6	4	5	6
Allium ursinum	8	5	6	6
Polygonatum verticillatum	1	–	–	–
Asperula odorata	–	4	–	–
Circaea intermedia	2	–	2	1
Chrysosplenium oppositifolium	2	–	–	–
Fraxinus excelsior (s)	2	–	–	–
Geranium robertianum	–	–	2	1
Geum urbanum	–	–	3	–
Mercurialis perennis	9	9	10	9
Oxalis acetosella	–	1	–	–
Urtica dioica	–	8	–	–
Brachythecium rutabulum	7	5	5	5
Dicranum scoparium	1	–	–	–
Eurhynchium praelongum	1	–	–	–
Mnium undulatum	–	5	–	1
Neckera complanata	1	–	–	–
Thuidium tamariscinum	2	2	2	1
Plagiochila asplenioides	1	–	1	–

* The presence of the foliage of trees directly over the sample plot is indicated by a ×. No attempt was made to assess the different contributions made to the shade by the different species. Constant species are in heavy type. Figures of cover-abundance are according to the scale of Domin; see below (p. 254).

But the views of Gams (1918) in his *Principienfragen der Vegetationsforschung* are relevant to this discussion. In this work he has given a comprehensive review of the problems of biocoenology, and has proposed a completely new system of nomenclature for the classificatory units within the biome on the grounds that the existing terms have become ambiguous through misuse. He draws a basic distinction between two kinds of unit, the ecological and the topographic.

In Gam's system the concrete ecological unit is the stand (*Bestand*), which occupies a uniform habitat. From the comparison of numerous stands within one floral or faunal district abstract ecological units can be built up, which are known as Synusiae. These may be of three grades, which are defined as follows:

'Synusia 1. Gesellschaften von Pflanzen oder Tieren, deren selbständige Komponenten derselben Lebensform und innerhalb desselben Distrikts derselben Art angehören.

'Synusia 2. Gesellschaften, deren selbständige Komponenten verschiedenen Arten derselben Lebensformenklasse und wesentlich derselben Aspecktfolge angehören.

'Synusia 3. Gesellschaften von Pflanzen oder Tieren, deren selbständige Komponenten verschiedenen Lebensformenklasse und Aspecktfolgen angehören, die aber durch feste

Korrelationen zu einer ökologischer Einheit auf einem einheitlichen Standort verbunden sind.' (The life-form system is one produced by Gam himself which includes both plants and animals: by 'selbständige', lianes, parasites and symbionts are excluded.)

He defines the concept of the synusia further: 'Zum Begriff der Synusie gehört, das ihre Komponenten eine ökologische Einheit bilden, die nicht ohne weiteres, innerhalb dessalben Distrikts, durch andere ersetzt werden kann. Eine solche Einheit muss aber nicht notwendigerweise für sich allein vorkommen, sondern kann mit andern zu einer topographischen Einheit verbunden sein.' He points out also that since a synusia of the second or third grade can only be recognized through the examination of as numerous as possible corresponding stands, its distinction is largely subjective; the entire species list is necessary and not merely a list of the dominant or most important species. These last views, with which I fully agree, are very similar to those of the Braun-Blanquet and other plant-sociological schools. The Association (*sensu* Braun-Blanquet) usually, but not always, corresponds with a synusia of the third grade.*

The concrete topographical unit is known as a *Siedlung*, and occupies a definite habitat with a lesser degree of uniformity from that of the synusia; it may consist of many synusiae of different grades or of fragments of synusiae. Here the habitat is more important for characterization than either the species list or the life-form. A unit of this kind corresponds roughly to the Association in the sense used by Clements, Tansley and many English-speaking authors; it applies to both seral and climax units. The abstract unit corresponding to the Siedlung is called by Gams the phytocoenose (or, where it concerns both plants and animals, the Biocoenose).

This distinction is valuable, for it recognizes that there is more than one level of uniformity in a complex community. But there is still doubt where the division should fall between a synusia of grade 3 and a phytocoenose. Gams gives the following example of a resolution of this problem; a wood is always considered as a phytocoenose (topographical unit), except when the correlations between the various synusiae which form it are so close that the field and ground layers can only occur under the particular tree layer concerned. He believes from extensive observation that this is very rarely the case; and as an example he cites *Asperula odorata* and *Allium ursinum*, thought characteristic of beech woods, but which grow under streamside woods of ash, alder and willow. This is sufficiently familiar to British ecologists, and in fact both these species occur in just this situation in the community which I have chosen to illustrate the same point. Similar considerations have influenced Lipmaa into believing that communities of similar life-form (Unions)† should be the basic units of phytosociology (Lipmaa, 1939); and although Tansley does not subscribe to this view, he and Adamson have suggested (Tansley & Adamson, 1926) that the synusiae of Gams may prove the most profitable tool in the study of chalk communities.

In the succeeding vegetation study I have chosen units which have a floristic uniformity at least as great as the synusiae of the third grade; this is a requirement which is more rigid than that required by many workers of the Braun-Blanquet school, many of whose 'associations' are phytocoenoses in the sense of Gams.

* Where synusia is used in the subsequent text it will be used in the sense of Gams, and not as synonymous with a layer of vegetation, as it is frequently misapplied (cf. Lipmaa, 1939, p. 144).

† See Part I, Appendix, for a survey of the various names proposed by different authors for phytosociological units.

III. DISCUSSION OF DESCRIPTIVE METHODS IN FIELD ECOLOGY

All schools of plant sociology are agreed that the abstract units should be built up by the description and comparison of as many uniform stands of vegetation as possible (cf. Gams, 1942, p. 203). It is important therefore to decide on an appropriate method of description and certain amendments may be necessary in the Braun-Blanquet method outlined in Part I.

Every stand has certain characteristics apart from any direct assessment of habit: the total species complement together with their respective densities, cover-values and dispersions; the structure of the vegetation, its periodicity, the presence or absence of seedlings, the vitality of the individual plants composing it—in fact, the total of the inter-relations between all the plants (and the associated animals) in the stand. A study of all these interrelations, if indeed it were practicable, would be a work of years, and the study of each item would require its own particular methods.

Thus if many stands are to be examined and described for classification, it is necessary to pick out those characteristics which are most relevant for the comparison and grouping of stands into associations. Of paramount importance is undoubtedly the list of all the species present in the stand; for classification according to floristics is based on the assumption that the species are a direct reflexion of the habitat of the stand. Next important is an estimate of the relative role which each species plays in the economy of the community. The percentage cover is frequently used as the most convenient single measure of this. Of these two the former requires adequate systematic knowledge; and, the more detailed the identification can be, the more useful is the description. In the search for exactitude in taxonomy the ecological description may lead incidentally to the recognition of ecotypes.

For an adequate technique of evaluating the quantity of each species there are three prerequisites: it should be applicable to any type of vegetation; it should be sufficiently accurate for the purpose for which it is required; and it should be rapid.

A. *Statistical methods*

Much literature has appeared in recent years on the application of statistical techniques to the description of vegetation, stemming from the early work of Jaccard, Romell, Kylin and Raunkaier. This has been reviewed recently by Ashby (1948) and by Goodall (1952). While agreeing with Goodall that it is possible that statistical methods could ideally be used both for determining the uniformity of each stand, and for obtaining an exact quantitative description of it when delimited, I believe with Braun-Blanquet (1932) and Gams (1918) that the possible loss in accuracy associated with subjective methods is amply compensated by the much greater rapidity with which surveys can be made and the much greater number which will consequently be available for comparison. If, how-ever, statistical methods can be devised which are both rapid and capable of universal application, they should certainly be used. Two other points should, perhaps, be borne in mind. First, in many communities the quantitative relations of the various species vary within wide limits in the course of a season. Statistical methods should naturally be used in examining this seasonal variation within one stand, but the effort of making exact quantitative descriptions of similar but different stands will be largely wasted unless these are made at exactly equivalent stages of the annual cycle. Secondly, the plant sociologist must be prepared to describe all types of community, and quantitative methods devised for relatively simple communities such as grassland or salt marsh may well prove

impossible to apply in, for example, the swamp carr around the Norfolk broads or ledges on mountain cliffs.

I conclude, therefore, that current statistical methods are inappropriate for this purpose, and that the plant sociologist should have recourse to the most accurate methods of estimation available to him. It should of course be realized that the results he obtains will be suitable only for qualitative comparison, and that any more rigid treatment is illegitimate. The proper province of plant sociological studies should be to describe vegetation and to discover and define problems for solution by more exact methods; in addition, they will often indicate what lines of future research will prove most fruitful.

B. *Methods of estimation*

The current British system for estimating the status of the various species in the stand by symbols (*d*, dominant; *a*, abundant; *c*, common, etc.), is unsatisfactory because it introduces sources of error both in the interpretation which different workers may put on these terms and in their visual estimation of abundance in the field (cf. Hope-Simpson, 1940). Symbols with an exact quantitative meaning can be used with more confidence. A cover of 90 %, for example, can be checked if necessary against a model, and the only discrepancy which will arise between different workers will be the accuracy with which they can estimate visually a cover of 90 %. But there is no common standard of 'commonness' or 'abundance'.

Various systems of this kind have been used. Four of the commonest are:

(1) The direct assessment of percentage cover, usually divided into ten classes (1, 0–10 %; 2, 10–20 %, etc.).

(2) Braun-Blanquet's scale.

(3) The Hult-Sernander scale.

(4) The Domin scale.

The first is used by Nordhagen. It is a good system on small areas, but its top classes are sometimes difficult to distinguish, and the bottom class makes too little distinction between species which have small cover value but which may differ considerably in abundance.

The Hult-Sernander scale (5, 100–50 % cover; 4, 50–25 %; 3, 25–12$\frac{1}{2}$ %; 2, $\frac{1}{8}$–$\frac{1}{16}$; 1, $<\frac{1}{16}$, is easy to apply, but the top class is too broad.

The remaining two scales deal with cover in the upper classes and abundance in the lower. The first of these, that used by Braun-Blanquet and by all followers of the Zürich-Montpellier school, has already been described, and the advantages of this compromise explained (Part I, p. 236). The last, that of Domin as quoted by Dahl and Hadac (1941), gives a more detailed description. It is perfectly practicable to apply, at least in simple communities, and for different workers to obtain the same results. In addition it may be converted directly into the Braun-Blanquet scale, if desired.

This scale is as follows:

	Domin	Braun-Blanquet
Cover about 100 %	10	5
Cover > 75 %	9	
Cover 50–75 %	8	4
Cover 33–50 %	7	3
Cover 25–33 %	6	
Abundant, cover about 20 %	5	2
Abundant, cover about 5 %	4	
Scattered, cover small	3	
Very scattered, cover small	2	1
Scarce, cover small	1	
Isolated, cover small	×	×

It may perhaps be said that an exact numerical value should be given to 3, 2 and 1, and this might indeed be an advantage; but in practice it seems relatively easy to distinguish three degrees of abundance. Furthermore, the type of conclusions which can be drawn later from these lists allows for a considerable margin of error in the descriptions.

Nordhagen has used a compromise between methods of measurement and estimation. He distributed evenly through the stand ten quadrats (of a fixed size for each type of community which he examined), and in each of these he estimated the percentage cover (in 10 % classes) of every species, thus gaining, in addition to a measure of the cover of each species in the community, some idea of their dispersion. But it is doubtful whether this method, which uses insufficient quadrats to give a statistically significant measure of dispersion, is worth the extra expenditure of time. In communities which regularly occupy a small area (e.g. communities of springs), Nordhagen has himself had to abandon this more elaborate system. The results, too, require much more space for representation.

Having considered these various methods, I decided therefore to use the scale of Domin, where it was practicable (I have, however, found it unnecessary to use the ×); and the scale of Braun-Blanquet where the other proved too difficult.

C. *Sociability*

Braun-Blanquet's index of sociability is merely a subjective estimate of dispersion,* and, although information on the dispersion of the species within the stand would form a valuable part of its detailed description, it has already been argued that it is necessary to forego this in order to obtain measurable results. Braun-Blanquet maintains (1932) that 'only a few plants have a predetermined unchangeable degree of aggregation of individuals and shoots (sociability) based on the manner of growth'. This is largely true, but the variation in any particular species can usually be inferred from the size of the stand and the index of cover-abundance. If there is any ambiguity, or if a particular species can grow in two distinct forms, the matter can be made clear by a note. For instance, in a sample plot of 4 sq.m. '*Eriophorum vaginatum* 4' could mean either one large tussock of *E. vaginatum* covering about 5 % of the area or a large number of single shoots also covering about 5 %.

The sociability scale used by Braun-Blanquet leaves much room for ambiguity. For instance, at what density does a species distributed uniformly over the stand cease being Soc. 1 and become Soc. 5? The distinction between 5 and 5 would lessen though not remove this difficulty, but it is in fact very rarely used.

I have therefore decided not to use the sociability scale, but have merely noted the features of aggregation whenever they were unusual or ambiguous.

D. *Vitality*

No satisfactory index of vitality has yet been proposed. The most exact would perhaps be the measure of growth, the unit leaf rate (Briggs, Kidd & West, 1920; Blackman & Rutter, 1948); but in addition to this the success of an individual in a community may depend on the presence and number of flowers, the number and fertility of seeds or, in the case of a plant with predominantly vegetative spread, the number and vigour of rhizomes, tillers, etc., produced. Stebbins (1950) has also pointed out that vegetative and reproductive capacity may vary independently. This is very clear in *Hedera helix* in

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* I.e. dispersion of either individuals or shoots—Braun-Blanquet's analysis mixes both up.

Denmark and in other countries on the continental margin of its distribution (Iverson, 1944).

For this reason I have not attempted to give an index of vitality, but have only noted the two easily recognizable extremes—very good and very poor. All other species may be assumed to lie in the range of average vitality—which is, admittedly, very wide. Any other treatment would claim more for superficial survey methods than they can hope to accomplish.

E. *Other criteria*

No attempt has been made to describe any other sociological features systematically, but any qualitative observation which was thought to have bearing on the status of the community was noted; in particular, questions of structure, presence or absence of seedlings, of the unusual abundance or scarcity of certain species within particular microhabitats within the 'uniform' stand.

F. *Summary*

Stands are described for a number of purposes: to describe the plant cover of a region, to build up named units for classification, and to form primary hypotheses about the causal factors differentiating them. For these purposes a large number of accurate descriptions is required. There are two temptations, on the one hand of concentrating on a few quasi-comprehensive descriptions and on the other of producing a very large number which are inaccurate or wholly superficial. Both these must be avoided, and this discussion indicates where the middle way may lie.

IV. An example of the field description of two stands

Superficial examination might convince an observer that no communities in the field are sufficiently alike to be tabulated together. Thus, in order to illustrate the field application of the Braun-Blanquet techniques (modified as indicated above), I had to find certain communities which were distributed fairly widely over the Breadalbane hills, and which were usually distinctly delimited in the field. Two communities dominated respectively by *Rhacomitrium lanuginosum* and *Carex bigelowii* and by *Nardus stricta* fulfilled those requirements. Both communites occur, often in juxtaposition, on flat or gently sloping areas between the altitudes of 1500 and 3900 ft. (762–1190 m.), this latter height being possibly not a true altitudinal limit, but dependent simply on the fact that in this area there is no topography suitable for their development above 3900 ft. (1190 m.). The two communities have definite physiognomies determined largely by their dominants, the former having a continuous moss layer of *Rhacomitrium lanuginosum* with shoots of *Carex bigelowii* evenly distributed throughout, and the latter being dominated by an even and dense stand of *Nardus stricta*. The line between them was usually found to be very sharp, again probably due to the reaction of the two dominants.

My choice of sampling site was influenced solely by this physiognomy. Moreover, as the communities in any one site were very uniform to the eye, it was rarely necessary to make any selection within them, and the first square metre was laid out anywhere near the centre of the stand. However, if any part could be seen to be different in kind from the rest (e.g. a small piece of protruding rock with species of *Stereocaulon* or *Grimmia*, or a hollow with *Rhytidiadelphus triquetrus* or *Silene acaulis*), such a part would be omitted

from the sample plot. Any local variation without change in dominance, or without the introduction of species thought to be 'foreign' to the community examined would, however, be included.

The following example is of a survey made in such a situation, showing how the field notes were organized. The method used is the standard technique of Braun-Blanquet (see Part I, pp. 236 sqq.) but using the Domin scale.

Copy of field notes

May 26   520035
Locality: spur below the summit of Ben   1 m.   Rhacomitrium languinosum   10
  Ghlas, M. R. 630397   Carex bigelowii   4
Altitude 3100 ft.   Agrostis canina   3
Aspect 0°   Galium hercynicum   2
Slope 0°   Dicranum fuscescens   2
Cover 1/10*   Cladonia uncialis   3
Height 2–3 cm.   C. alpicola   2
Microrelief: even slope, flat   Cetraria aculeata   1
                                                        C. islandica   2
Soil   Cladonia squamosa   1
0–2·5 cm., dark humus layer (blackish) with small   Polytrichum alpinum   1
  quantities of mineral matter   2 m.   Cerania vermicularis   2
2·5–6, greyish brown leached layer with humus   Ochrolechia tartarea *var.* frigida 1
  throughout, grading (6–8) into   4 m.   No addition
8–35, ochreous brown fine textured schisty sand

* The convention adopted in indicating cover is as follows: the upper layer (in this instance the herb layer) is given first, the lower layer or layers afterwards. Cover is estimated in 10% classes and the indices for different layers are separated by an oblique line.

Copy of field notes

May 26   520036
Locality and altitude: ditto   1 m.   Nardus stricta   10
Aspect 40°   Vaccinium myrtillus   4
Slope *c.* 2°   Galium hercynicum   3
Cover 10/?   Carex bigelowii   3
Height 10 cm.   Rumex acetosa   3
Soil   Cerania vermicularis   2
  3 cm., moss and stem base litter   Pleurozium schreberi   6
  0–0·5, black humus   Rhytidiadelphus squarrosus   3
  0·5–6/7, slate grey schist layer with stones of   Polytrichum *cf.* commune   3
    grey, very finely foliated schist and pieces   Rhacomitrium lanuginosum   2
    of quartz   Ptilidium ciliare   2
  6/7–10, dark brown humus layer   Festuca vivipara   4
  10–13, red-brown transition   Cladonia rangiferina   1
  10–17, brown schisty soil   C. uncialis   1
  17–36 plus, olive brown schisty soil full of   Cetraria *cf.* islandica   1
    schist detritus   2 m.   Rhytidiadelphus loreus   1
                                               4 m.   No addition
                                                        Many loose fragments of various lichens

Comparison between two described stands

This is a concise description in symbols of representative pieces of two plant communities and of an ecological situation, by inspection of which certain resemblances and differences in floristics and habitat conditions between the two stands can be detected. These are as follows:

(1) Species which are present in sample no. 520035 and absent in no. 520036 (index of cover-abundance in brackets):

Agrostis canina (3)   Cetraria aculeata (1)
Dicranum fuscescens (2)   Ochrolechia tartarea *var.* frigida (1), and
Cladonia alpicola (2)   Polytrichum alpinum (1)
C. squamosa (1)

S   Ecol. 43
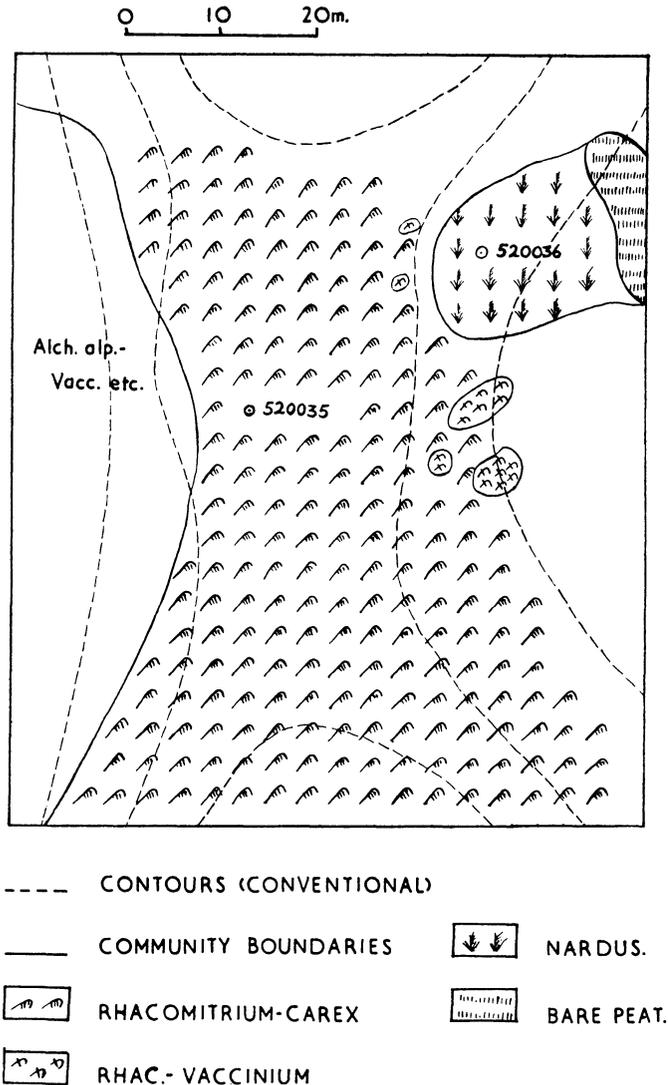
Fig. 1. Elaboration of field sketch.

(2) Species present in no. 520036 and absent in no. 520035:

Nardus stricta (10)
Vaccinium myrtillus (4)
Rumex acetosa (3)
Pleurozium schreberi (6)
Rhytidiadelphus squarrosus (3)

Polytrichum commune (3)
*Ptilidium ciliare (2)
Festuca vivipara (4)
Cladonia rangiferina (1), and
Rhytidiadelphus loreus (1)

In addition, *Rhacomitrium lanuginosum* was dominant in no. 520035 with an index of 10, whereas only scattered individuals (2) are present in no. 520036.

Differences in the observable environment include the small slope to the north-east and the podsolic profile of no. 520036 as against the level situation and immature profile

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* Authorities for names of liverworts are given in Appendix 1.

of no. 520035. The small slope to the leeward in such an exposed situation may, however, occasion very different conditions in the *Nardus* community during the winter.

From this comparison of only two contrasting samples certain very provisional hypotheses may be drawn on the nature of the factors which differentiate these two communities. Confirmation of these must come ultimately from quantitative and experimental data, but circumstantial evidence may be accumulated by the listing and inspection of a number of further examples of the same two communities in similar situations. In this way, also, it will become apparent which characters of the communities in question are as it were, systematic and which accidental (for example, *Cerania vermicularis*, which appears in no. 520036, is absent in all other comparable *Nardus* communities which I have listed in the region. In view of the fact that a number of unattached fragments of lichen were also found in this sample plot, it seems likely that *Cerania* was accidental and had become temporarily established from a fragment derived from a neighbouring community.)

V. Problems associated with the production of tables

The Geobotanical section of the 6th Botanical Congress made the following recommendations:

1. To use the term 'Sociation' for vegetation units characterized mainly by dominance in the different layers, in the sense of the Scandinavian plant ecologists.

2. To use the term 'Association' for vegetation units characterized mainly by characteristic ((i.e. faithful)) and differential species in the sense of the Zürich-Montpellier school of plant sociologists, or at least for units of the same order of sociological value; sub-associations and facies can, where necessary, be used for their subordinate units.

3. To unite sociations and associations into alliances in the sense of the Zürich-Montpellier plant sociologists, and the alliances into higher units.

Gams (1918) appears to adopt a position that is less dogmatic. He considers that the distinction of his synusiae is to a great degree subjective, and that the whole species list should be taken into account. He believes also that no general rules can be laid down for the grouping of synsiae, but that each case should be considered on its merits. (He thereby escapes from the over-simplification of natural phenomena to which many plant-sociologists seem prone.)

There is some doubt about the equivalence of the units distinguished by constancy and dominance on the one hand and by fidelity on the other. Braun-Blanquet believes that the Scandinavian sociations are equivalents to sub-association or facies in his system; Dahl & Hadac (1941) that sociations and associations are frequently units of the same rank. Without discussing this problem further at the moment, it is necessary to discover whether the most readily recognized communities in Breadalbane can be grouped into abstract units in this way; and, if so, what are the most valuable criteria for distinguishing and characterizing them. Because of this confusion in terminology and because it is not always possible at the beginning of an investigation to decide what the status of a unit may be, the term NODUM is being adopted to apply to abstract vegetation units of any category. It corresponds to the term TAXON in systematics. Where the status has been decided the appropriate term will be used (see Appendix to Part I).

Both the *Rhacomitrium-Carex bigelowii* and the *Nardus* noda described in the last chapter are clearly defined communities which can be found frequently at high altitudes

in the Breadalbane hills. Table 1* contains lists from eight such communities of *Nardus* distributed widely over the area surveyed; each list was made by the methods already described.

Table 1

No. of sample plot	520007	520034	520063	520093	520131	520163	520036	520114
Vaccinium myrtillus	–	6	–	–	–	4	4	2
Agrostis stolonifera	–	–	–	–	–	2	–	–
A. tenuis	2	–	–	2	2	4	–	–
Deschampsia flexuosa	–	–	1	–	3	1	–	2
Festuca ovina agg.	–	–	–	2	–	–	–	–
F. vivipara	–	4	–	–	2	2	4	2
Nardus stricta	9	8	9	9	9	9	10	8
Carex bigelowii	3	3	3	3	3	3	3	3
C. pilulifera	–	–	–	1	–	–	–	–
Trichophorum germanicum	–	–	–	–	1	–	–	–
Alchemilla alpina	–	–	–	–	1	–	–	–
Galium hercynicum	4	3	3	3	6	4	3	3
Potentilla aracta	–	–	–	–	–	1	–	–
Rumex acetosa	1	2	–	–	–	1	2	–
Dicranum fuscescens	–	–	3	–	–	–	–	–
D. scoparium	1	1	1	–	4	1	–	–
Plagiothecium undulatum	1	–	–	–	–	–	–	–
Pleurozium schreberi	5	4	2	2	5	7	6	1
Polytrichum alpinum	–	1	2	–	3	3	–	–
P. commune	2	–	–	–	–	3	–	6
P. formosum	–	–	–	3	–	–	–	–
Rhacomitrium lanuginosum	–	–	3	–	1	–	2	–
Rhytidiadelphus loreus	2	–	3	–	1	3	1	–
R. squarrosus	5	4	–	3	4	2	3	2
Anastrepta orcadensis	–	–	1	–	–	–	–	–
Orthocaulis floerkii	–	–	–	3	3	3	–	–
Ptilidium ciliare	2	–	1	–	3	3	3	–
Cerania vermicularis	–	–	–	–	–	–	2	–
Cetraria islandica	–	1	1	–	–	–	1	–
Cladonia gracilis	–	–	–	–	–	1	–	–
C. pyxidata *var.* chlorophaea	–	–	–	–	1	–	–	–
C. rangiferina	–	–	–	–	–	–	1	–
C. sylvatica	–	3	3	–	–	–	–	–
C. uncialis	–	1	–	–	–	–	1	–

It can easily be seen from this table that the stands listed have more characters in common than the dominance of *Nardus* for which they were chosen; and that the synusia could be defined quite adequately by the dominant species (*Nardus stricta*), and the constant species (*Galium hercynicum, Carex bigelowii, Pleurozium schreberi* and *Rhytidiadelphus squarrosus*). The dominant by itself would not be sufficient; for there are at least two other recognizable communities in the region with the same dominant. Furthermore, none of the species of this nodum shows any particular degree of fidelity to it; and so, if fidelity is to be used as a criterion, this well-marked community is likely to be ignored, or dubbed an impoverished form of a related community which has got a faithful species. It appears, therefore, that this nodum at least can be characterized admirably by the dominant and constant species. The same is true for the *Rhacomitrium-Carex bigelowii* nodum of which eleven lists are shown in Table 2; and this unit can be adequately defined

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* Species in all the tables have been arranged in groups in the following order: trees, shrubs, dwarf shrubs, Pteridophytes, grasses, members of the *Cyperaceae* and *Juncaceae*, other Monocotyledons, dicotyledonous herbs, mosses, liverworts and lichens. Within each group species are arranged in alphabetical order. This arrangement is easy to use, and at the same time shows at a glance which groups predominate in the community in question. It is the standard Nordhagen technique; that of Braun-Blanquet can be seen in Table 1 in Part I.

as a series of communities dominated by *Rhacomitrium lanuginosum*, in which *Carex bigelowii*, *Dicranum fuscescens*, *Polytrichum alpinum*, *Cetraria islandica* and *Cladonia uncialis* are constant. Again, none of the species of vascular plants present could be considered faithful to the synusia. I am not sufficiently conversant with the tolerances of all the bryophytes to say the same confidently of them, but it is true of the majority.

I have pointed out above, Part I, p. 238, that I have been unable to follow the methods used by members of the Braun-Blanquet school to distinguish associations by faithful species. Moreover, almost all the descriptive material which I have collected has emphasized the value of dominant and constant species for this purpose. I was, therefore, faced with the problem of finding methods to distinguish my noda according to these criteria. This difficulty was partially resolved by consideration of the methods of the Scandinavian

Table 2

No. of sample plot	520010	520011	520035	520064	520068	520076	520117	520162	520167	520194	520006	520193*
Empetrum hermaphroditum	2	—	—	—	4	1	—	—	—	—	—	—
Salix herbacea	—	—	—	—	—	—	3	—	—	—	—	—
Vaccinium myrtillus	5	3	—	—	4	3	3	3	3	4	4	—
V. vitis-idaea	—	1	—	—	2	2	2	—	1	—	—	—
Lycopodium selago	3	—	—	—	—	2	—	—	—	—	—	—
Agrostis canina	—	3	3	—	—	—	—	—	—	—	—	—
A. tenuis	1	—	—	—	2	3	—	—	—	—	—	—
Deschampsia flexuosa	5	—	—	—	—	—	3	—	—	—	7	—
Festuca ovina agg.	3	—	—	—	—	—	—	—	—	—	—	—
F. vivipara	—	—	—	3	3	4	2	3	1	2	2	1
Nardus stricta	1	—	—	—	—	·	—	—	—	—	—	—
Carex bigelowii	4	4	4	4	3	3	3	5	4	4	6	9
Luzula multiflora	—	—	—	—	—	—	—	—	1	—	—	—
L. spicata	—	—	—	—	—	1	2	—	—	—	—	—
Alchemilla alpina	—	—	—	—	—	3	1	—	—	—	2	—
Galium hercynicum	1	—	2	—	—	2	2	—	—	—	2	1
Dicranum fuscescens	1	1	2	2	2	—	3	1	4	3	3	3
D. scoparium	—	1	—	—	—	—	1	2	—	—	—	—
Oligotrichum hercynicum	1	3	—	—	—	—	—	—	—	—	—	—
Pleurozium schreberi	—	—	—	—	—	1	1	—	—	—	4	—
Pohlia ?annotina	—	1	—	—	—	—	—	—	—	—	—	—
Polytrichum alpinum	3	—	1	3	2	2	3	3	1	3	3	2
Rhacomitrium lanuginosum	9	7	10	10	9	9	10	10	10	10	6	9
Rhytidiadelphus loreus	—	—	1	—	—	—	—	—	—	—	1	—
?Aplozia sphaerocarpa	1	—	—	—	—	—	—	—	—	—	—	—
Diplophyllum albicans	1	—	—	—	1	1	—	—	—	—	—	—
Nardia scalaris	—	—	—	—	—	—	1	—	—	—	—	—
Lophozia ?ventricosa	—	—	—	—	—	—	1	—	—	—	—	—
Ptilidium ciliare	—	—	—	—	—	—	—	—	—	—	1	—
Alectoria nigricans	—	—	—	—	1	—	—	—	2	—	—	—
Cerania vermiculoris	—	1	1	2	—	2	—	2	2	2	—	—
Cetraria aculeata	—	—	—	1	—	1	3	2	2	—	1	1
Cetraria islandica	2	1	2	3	2	1	2	2	3	3	2	3
Cladonia alpicola	—	—	2	—	1	—	—	—	—	—	—	—
C. bellidiflora	1	—	—	1	—	1	1	—	—	—	—	2
C. coccifera	—	—	—	1	1	—	—	—	—	—	—	—
C. crispata	—	—	—	—	1	—	—	—	—	—	—	—
C. furcata	—	—	—	1	—	—	—	—	—	—	—	—
C. gracilis	—	—	—	1	—	—	2	1	2	—	1	2
C. pyxidata	1	—	—	—	1	—	—	—	—	—	—	—
Cladonia rangiferina	—	—	—	—	—	—	—	—	—	2	1	—
C. sylvatica	—	—	—	—	2	3	—	3	2	1	1	—
C. squamosa	—	1	1	1	—	—	—	—	1	—	—	1
C. uncialis	4	3	3	2	3	1	3	3	3	3	1	—
Coriscium viride	—	1	—	—	—	1	—	—	—	—	—	—
Icmadophila sp.	—	—	—	—	—	—	—	1	—	—	—	—
Ochrolechia tartarea frigida	—	—	—	1	—	1	—	2	—	1	—	—
Sphaerophorus globosus	—	—	—	—	—	2	—	1	—	—	—	—

* Sample plot no. 520193 is from a site which differs from the rest in the high cover of *Carex bigelowii* (9), but which probably can be attributed to the same unit.

authors, whose sociation is usually a more integrated and definite unit than the association of Braun-Blanquet; and by insistence on the condition (which I consider essential in a satisfactory unit) that the noda can be characterized in such a way that they can immediately and correctly be recognized by another phytosociologist.

The important question to decide is this: what degree of homogeneity is required in the basic unit? The lists of the *Nardus* nodum are not identical. What, then, is the justification for considering that the similarities are more important than the differences? This question is not altogether easy to answer. For the breadth of variation which is allowed to an abstract unit is to a certain extent under the subjective control of the individual phytosociologist, just as the monographer of a genus is the arbiter of whether a group of plants constitutes a species or a subspecies.

It is important, however, that the element of subjectivity should be reduced, and that the arguments I have employed in reaching my decisions should be explained as far as possible. Let us consider an example; why should not 520034, 520036, 520114 and 520163 be separated from the others on the grounds that *Vaccinium myrtillus* is present in all of them; or 520007, 520093, 520131 and 520163 because *Agrostis tenuis* is present; or 520093, 520131 and 520163 because of *Orthocaulis floerkii*? The reason that I have not subdivided this table further is that none of these species (or any other) is particularly associated with or complementary to any other; neither is the presence or absence of any one of them particularly correlated with any of the observed environmental factors, and it is thus impossible to draw any clear line. If *Agrostis tenuis*, for example, had appeared in every list in which *Vaccinium myrtillus* was present, or in every list from which it was absent, there would have been provisional grounds for dividing the table into two on this account. Such a course would also have been justifiable if the presence of *V. myrtillus* corresponded with a particular soil profile or with any other environmental factor.* The more cases of correlation or complementarity that can be found, the stronger are the grounds for separation.

To include all these lists in the same table is not, however, to claim that their ecology is identical or to deny that the presence or absence of, for example, *V. myrtillus* is of significance. It is probable that these differences are determined by the variation of some environmental factor and not by chance. But for the practical purpose of defining and classifying vegetation units it is necessary to set some limit to the process of analysis, in order to avoid the absurd situation in which each stand by nature of its peculiarities is considered a discrete unit. Such differences are a proper field for more exact and experimental investigations; the plant sociologist, however, makes the assumption, and by the nature of his data has to make the assumption, that discontinuities which are marked by the simultaneous appearance or disappearance of several species are of more significance than those which involve only one.

The lists of the *Rhacomitrium-Carex bigelowii* nodum also show considerable variation among themselves, but this cannot in most cases be related with any obvious environmental change. Notes made in the field on the micro-distribution of certain species are suggestive; for example, *Polytrichum alpinum* was often observed to be commoner in small depressions in the moss mat, and in no. 520076 *Vaccinium myrtillus* was found to be more abundant in pockets with deeper soil and more pronounced leaching; but in no instance was the evidence sufficient to subdivide the unit. No. 520193 differs from the

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* Experience of the behaviour of these species in related communities is extremely helpful here.

others in the large degree of cover (75–90 %) of *Carex bigelowii*, in the absence of *Cladonia uncialis*, in the fewer species present (11 compared with the average of 16·7 for the other stands), and in the fact that it was on peat from 10 to 30 cm. thick. It is impossible, without further examples, to say whether these differences are systematic. But this is an example of the type of observations which may be taken into account in subdividing a nodum.

Dahl & Hadac (1949) have pointed out pertinently that in most of the convincing sociations of the Scandinavian school (and also in many associations of the Zürich-Montpellier school) the number of species in presence class V is greater than that in presence class IV. They have produced theoretical reasons why this should be true, based on assumptions made about the dispersion of individuals in natural communities and minimal area.

Whether or not the premises of this work are sound, and at present they are certainly unproven, the fact that presence class V is greater than presence class IV is a measure of the homogeneity of the material. That this is the case can readily be seen by mixing two noda together. The results of this are shown below:

Presence class	V	IV	III	II	I
Nardus nodum	5	4	5	6	14
Rhac.–C. big. nodum*	6	2	5	11	24
Two noda together	1	7	3	12	36

* These figures are taken from the first ten lists on Table 3.

When all the communities described in the region, in all twenty-five ranging from woodland to snow-patch, were grouped together the curve obtained by plotting number of species against number of occurrences was a hollow logarithmic curve (cf. Williams, 1947; see Fig. 2, p. 264).

It has therefore proved convenient, in characterizing noda which are to serve as points of reference, to try and aim at a table where species with presence V are more numerous than those with presence IV. This has not always proved possible (e.g. in some communities of springs), but this seems to be due to paucity of material.

Now it has been seen that the field lists of certain communities may be built up into abstract noda, which have such a degree of internal integration that no rational grounds can be found for subdividing them further. These are ideal units, built up by a process of selection which is operative both in the field and in the process of tabulation; they are useful because their limits can be defined exactly, and they can consequently be used as points of reference. The techniques used here are related to those of the quantitative description of vegetation in much the same way as classical taxonomy is related to biometrics. Both are arts rather than sciences; but arts, nevertheless, which are very necessary to the success of the related sciences. It is for this reason that criticism directed at the subjectivity of plant-sociological techniques miss their mark. If an analytical, biometrical approach had been applied to the myriads of plant individuals, before they had been sorted by classical taxonomy, the result would have been a mass of indigestible data, but very few species. In the field of plant sociology the number of units distinguished and described by purely analytical techniques is negligible.

The use of constant species for the characterization of noda has been criticized on the two following grounds:

(1) True determinations of constancy can only be made on random samples, because any element of choice will influence the constancy figures obtained.

(2) The number of species constant to a particular community will depend on the area sampled in each stand.

Both of these comments are quite true, but they do not affect the sociological systems nearly as much as might be imagined. I shall deal with each of them in turn.

(1) If the analytically minded plant sociologist wants to discover what are the constants in a certain nodum, he chooses, let us say, ten communities which he considers to belong to that nodum; he lists all the species which occur in each of these ten communities; and
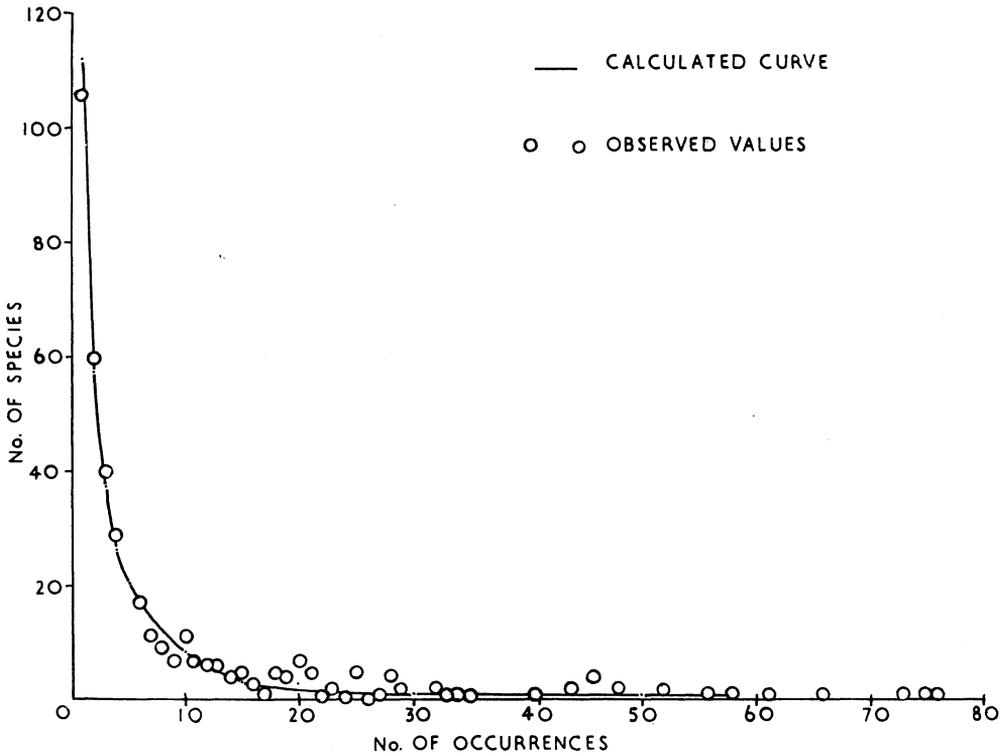

Fig. 2. For explanation, see Text.

he divides them into five classes according to their degree of presence, those occurring in more than 80 % of the stands being considered arbitrarily to be the constants. But he has already made a selection before he begins, and the result which he gets is a list of the species constant to communities, *which he thought belonged to this particular nodum before he began listing*; and this choice must be influenced by the superficial appearance of the community, i.e. dominance and physiognomy, rather than by its exact composition. Unless this is the result which he wishes to obtain this is an example of a false application of an analytical method. For, after examining all the communities in detail, he is in a better position to say whether they are similar to one another (and, therefore, suitable material for making determinations of constancy) than he was before he examined them. (It would, of course, be quite legitimate to use such a technique if it were desired to find out what species were constantly associated with some readily observed phenomenon, such as plants of *Calluna*.)

With their own techniques sociologists attempt to distinguish vegetation units by what

I am calling a 'process of progressive approximation'. Faced with the situation mentioned above, the orthodox, but critical, sociologist chooses the communities which he is going to sample by their more obvious features (as, indeed, he must); but he does not fall into the trap of considering that constancy figures derived directly from his first lists are more objective. Instead he inspects and compares the lists, rejects any which are clearly different from the rest, and determines constancy indices from those that remain.

Suppose, for instance, that a species X was present in nine lists out of the ten made. Is the sociologist justified in removing the one list from the table so that X may have a degree of presence of 100%? If he has any other reason for believing this community to be aberrant, he is; for these reasons:

(a) The table represents an ideal unit with great internal integration.

(b) The absence of X in the tenth community does not alter the fact that it was invariably present in the remaining nine.

(c) The absence of a species with such a regular record in similar communities is likely to mean some effective difference in the tenth community.

In fact, the significance of the table lies in the integration which is shown by the finished product and not in the various lists which have been excluded in the making of it. This will be discussed further in a future part of this publication.

(2) The number of constants obtained depends also on the size of the sample area used in each stand. Considerations of this kind have led to the formulation of the concept of 'Minimal area'. In Part I, I have explained that Braun-Blanquet recommends that the whole stand should be described; but that, if this is impracticable, an area at least as large as the 'minimal area' of the association should be described. What is the 'minimal area'?

If the number of species is plotted against area in a uniform community, the curve usually rises rapidly at first and then tends to flatten out (Braun-Blanquet, 1932; Romell, 1925); whether at large areas it tends towards an asymptote or continues rising slowly is not certain, because in practice the limits of the uniform community are frequently reached before this can be determined. This initial steep rise and subsequent flattening can be seen clearly in the results from eight of the sites already tabulated (Fig. 3).The Minimal Area of the association, that is, the area which for practical purposes is considered representative of the whole, has been variously defined as 'that area which contains 80% of the total number of species of the community', of the area corresponding to 'the point of inflection of the curve'. Both points are vague and arbitrary; the former cannot be defined unless the final part of the curve is known with accuracy, and the latter is vague because the point of inflexion of the curve can be altered by changing the co-ordinates of the graph (Pearsall, 1924). But in spite of this quite justified condemnation of the fundamental basis of 'minimal area' (cf. also Nordhagen, 1928), the concept is still used as an empirical tool in plant sociology and is still valuable. The reasons for this appear to be quite simple. If the sample area is not large enough the number of species which appear constant is nil or small, and it is consequently impossible to obtain a unit with the required degree of internal integration. If the sample area is increased greatly in size, the number of additional species obtained is few, and these are likely to play very little part in the economy of the community (they may, however, be sensitive indicator plants). It is best to describe the whole stand if possible; but in the course of tabulation it will become apparent what is the characteristic combination of species in the nodum, and samples which are too small will automatically be excluded because they do not reach this ideal.

A taxonomist will not describe a species as 'sometimes without flowers' because he sometimes collects a shoot that is too small to bear them.
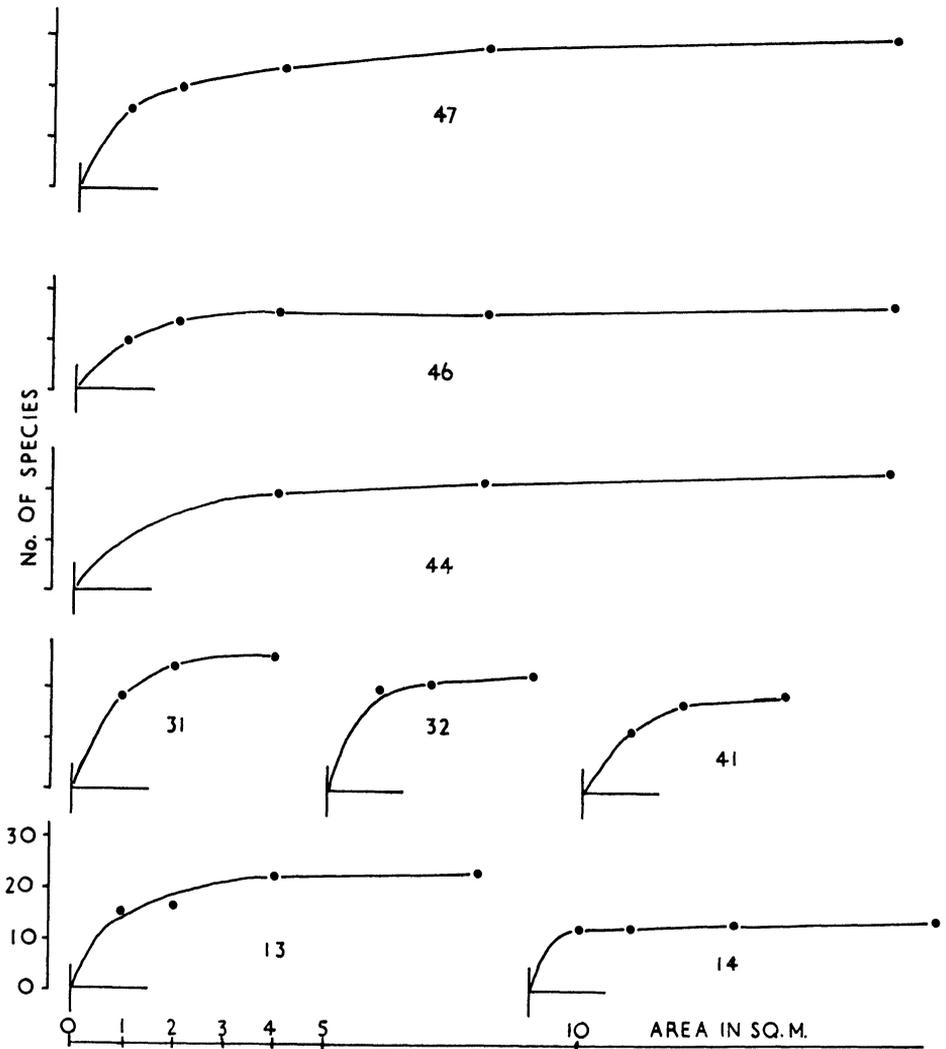

Fig. 3. 'Minimal area' curves.

Intermediates

I have therefore tried to build up noda which:

(1) have considerable internal integration as judged by their homogeneity, and

(2) occur frequently enough to provide the material for a Table, in which it is recommended that presence class V should be larger than presence class IV.

These can then be termed sociations, but when a number of noda have been established it is not possible to attribute to them all the vegetation of an area. This is because transitions occur in the field between stands of two noda, and because communities occur which are intermediate between them. Both these are eliminated by processes of selection used in the choice of the sample plots and in the building up of tables. The whole picture of

vegetational variation will only appear slowly as more and more descriptive material accumulates. The first noda to be distinguished are likely to be those that are most obvious to the eye and which occur frequently with but little variation. The safeguard of 'constancy' will, however, ensure that only genuine vegetation units will be distinguished in this way.

When a survey is begun, any uniform community which can be recognized in the field should be described. The boundaries between them will usually be found to be one of the following kinds:

(1 a) Quite sharp, as in the example I have given above of the *Nardus* and *Rhacomitrium-Carex bigelowii* communities, where it corresponded with the change of dominance, a fact which suggested that it is the very different growth forms of these two species which determined the floristics of the community. This hypothesis was supported by a search for intermediates, which proved to be exceedingly rare. Small clumps of *Nardus* could occasionally be found scattered in stands of the *Rhacomitrium-Carex bigelowii* nodum, but these, if consisting of more than one or two plants, had the structure and floristics of the *Nardus* nodum; conversely, at 3900 ft. (1190 m.) on the east ridge of Ben Lawers was found a patch of small plants of *Nardus*, dwarfed by exposure, and forming an open community, in the gaps of which grew *Rhacomitrium* and its associates. It appears that no intermediates between these two noda occur, as all such can be interpreted as mosaics rather than transitions. While it is possible that there is also a sharp discontinuity of external habitat factors separating them, it is probable, if so, that this line is made sharper by the fact that the change in dominance involves a large change in micro-habitat. To this 'incompatibility' may perhaps be ascribed the lack of intermediates.

(1 b) Sharp, due to the rapid alteration of effective habitat factors, e.g. at the border of a flushed area, or at the boundary between exposed rock surface and soil.

(2) Associated with a sharp change of this kind there may be a well-marked zonation of communities, as, for example, round the margin of a pond. If the intermediate communities in this zonation have either a structure or species which is different from those of the communities on either side of them, they should be described separately.

(3) Where the change in habitat factors is gradual and two 'incompatible' dominants are not involved, gradual ecotones between communities may occur. For example, although the *Nardus* and *Rhacomitrium-Carex bigelowii* synusiae have a sharp boundary when they adjoin each other, the *Nardus* synusia grades gradually through communities in which *Trichophorum germanicum* and *Sphagnum russowii* play a considerable part into communities of wet peat; and the *Rhacomitrium-Carex bigelowii* nodum into *Dicranum fuscescens* and *Juncus trifidus* communities, *Empetrum-Vaccinium* heaths, and by intimate mosaics into *Gymnomitrium concinnatum* communities of solifluction soils on extremely exposed crests. While noticing the existence of these ecotones, it is wise to leave their analysis until a frame of reference of well-marked communities has become available.

The pattern which should emerge from the procedure which I have explained is one of a number of well-characterized noda, round each of which can be grouped other communities varying slightly from it in response to changes in particular habitat factors, or even exactly intermediate between it and some other nodum. Such intermediates should only be raised to the rank of a nodum if they too not only have a definite structure and specific composition, but also occur frequently. It is the latter condition which they seldom seem to fulfil.

VI. Summary

The main conclusions of this discussion can be summarized as follows:

1. Absolute uniformity in vegetation or habitat does not exist, but it is possible to find various levels of relative uniformity, any of which may be selected according to the degree of exactitude required for particular research problems. One such level of uniformity has been chosen to exemplify the use of plant sociological techniques in a study of the vegetation of the Breadalbane district of Perthshire. (The field study and conclusions derived from it will appear in succeeding parts.)

2. By the description of numerous stands of 'uniform' vegetation, abstract points of reference (called noda above), can be established which coincide with frequently occurring and easily recognizable plant communities.

3. These points can be defined most exactly and most readily by the constant and the dominant species together. Neither the faithful species nor the dominant alone are suitable.

4. Not all the vegetation of a region can be attributed to these described noda; many communities may be intermediate; but the noda should be sufficiently numerous that all the vegetation can be described in terms of them.

The combination of the methods of various schools which I have adopted results from an attempt to rationalize and examine critically the technique of the Braun-Blanquet school. The application of this revised version to a field problem leads inevitably to a conception of the problems of vegetational classification, which diverges from Braun-Blanquet's. This will emerge in subsequent articles.

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APPENDIX 1

Authorities for nomenclature of hepatics

Anastrepta orcadensis (Lindb.) Schiffn.
Anthelia juratzkana (Limpr.) Trev.
Aplozia cordifolia (Hook.) Dum.
A. sphaerocarpa (Hook.) Dum.
Barbilophozia barbata (Schmid.) Lake.
B. lycopodioides (Wallr.) Lake.
Blepharostoma trichophyllum (L.) Dum.
Calypogeia trichomanis (L.) Cda.
Cephalozia ambigua Mass.
C. bicuspidata (L.) Dum.
Conocephalum conicum (L.) Dum.
Diplophyllum albicans (L.) Dum.
Gymnomitrium concinnatum (Lightf.) Cda.
G. coralloides N.
Lophozia alpestris (Schleich.) Evs.
L. ventricosa (Dicks.) Dum.
L. wenzelii (N.) St.

Moerckia blyttii (Moerck.) Brockm.
Mylia anomala (Hook.) Gray.
Nardia scalaris (Schrad.) Gray.
Odontoschisma elongatum (Lindb.) Evs.
Orthocaulis attenuatus (Mart.) Evs.
O.floerkii (W. & M.) Buch.
Pellia fabbroniana Raddi.
Plagiochila asplenioides (L.) Dum.
P. spinulosa (Dicks.) Dum.
Pleuroclada albescens (Hook.) Spr.
Porella cordeana (Hüb.) Evs.
Ptilidium ciliare (L.) N.
Saccobasis polita (N.) Buch.
Scapania irrigua (N.) Dum.
S. uliginosa (Sw.) Dum.
S. undulata (L.) Dum.

APPENDIX 2

Habitat data of sample plots

Sample plot no.	Map. ref. 27/	Alt. (ft.)	Aspect (deg.)	Slope (deg.)	Cover*	Height (cm.)	Area of plot (sq.m.)
520006a	567397	2700	0	5	10	10	4
520007	567397	2650	240	3	10	10–15	2
520010	667442	3000	325	2–3	—	—	4
520011	667442	3000	325	2–3	—	—	4
520025	768503	650	160	30	10	40/90	4
520026	768503	650	160	30	10	40/90	4
520027	768503	650	160	30	10	40/90	4
520028	768503	650	160	30	10	40/90	4
520034	632397	2900	80	20	10	15	2
520035	630397	3100	—	0	10	2–3	2
520036	630397	3100	40	2	10	10	2
520063	615424	3100	50	2–3	10	15–10	4
520064	615426	3100	50	2–3	10	2–5	4
520068	489334	2800	0	3–5	10	3–5	2
520076	562377	2990	310	5	10	2/5	16
520093	587397	2750	150	5	10	11/15	2
520114	652408	2350	100	5	10	15/20	2
520117	484336	2700	—	0	1–10	5/20	10
520131	645417	3275	200	2	9/5	—	4
520162	691495	3100	120	2	10/3	—	4
520163	691496	3100	120	2	10/7	—	4
520167	707508	2800	—	0	2/10	5/15	4
520193	687512	3200	130	3	9/10	5	4
520194	691510	3150	310	1–2	4/10	3/20	5