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THE USE OF PHYTOSOCIOLOGICAL METHODS IN ECOLOGICAL INVESTIGATIONS

I. THE BRAUN-BLANQUET SYSTEM

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(*With one Figure in the Text*)

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I. Introduction

During the past forty years or more much of the attention of continental plant ecologists has been devoted to devising and systematizing methods for the description and classification of plant communities. So impressive is the body of material collected that schemes have been proposed to establish rules for the correct description and nomenclature of vegetation units comparable for those in effect for taxonomic species, genera, families etc. (Barkman, 1950; Du Rietz, 1930, 1936).

British ecologists have so far stood by and let the stream flow past. Their attitude has been one of critical disinterest, because the data were collected in a way that did not meet with their approval and the whole method was based on doubtful premises; they were prepared to let it go its own way and judge by its results. But the movement has proceeded with an unforeseen momentum, and the time is clearly overdue for a critical assessment of this attitude. For the divergence of opinion between the two schools has now grown so wide that it has become detrimental to the cause of ecology. Continental phytosociologists can talk with confidence of named units which mean nothing to us, and, on the other hand, the opinion is often expressed abroad that British vegetation has not been described. This may seem to us an unjust aspersion when we look at Tansley's *British Islands and their Vegetation*, a work perhaps unequalled in any other country in Europe; and, certainly, it is rooted in an ignorance of the British viewpoint as great as is our ignorance of the continental. But it contains a grain of truth.

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The two principal continental schools, with which this discussion is concerned, are those which have become known as the Zürich-Montpellier, of which the principal exponent is Dr Braun-Blanquet, and the Uppsala (or 'Nordic-Alpine' according to Gams, 1939 and 1941). The most extensive and organized attempt at a classification of vegetation has been carried out by the former, and Nordhagen (1936) has brought Norwegian descriptive material into line with the arrangement of this school.

This series of articles embodies the results of a study of the methods of some of the continental plant sociologists. In Part I an exposition is given of the techniques and aims of the Zürich-Montpellier school, the data for which are derived partly from personal experience of the system in action at Montpellier, where I spent two months through the kindness of Dr Braun-Blanquet, and partly from the extensive literature of that school. In this part, I have tried to argue the case for the system from the point of view of one who believes in it, while indicating those points which British ecologists find difficult to accept. In Part II certain practical modifications and refinements are discussed in the light of British criticism, of the literature of the Scandinavian and other schools, and of my own practical field experience. Part III will contain contributions towards a vegetation survey of the Breadalbane area in Perthshire (with particular reference to the mountain communities), carried out by these modified methods; and Part IV a critical discussion of certain aspects of the Braun-Blanquet system (in relation to the description and classification of vegetation), and of the possible advantages which a system of the kind that I have used might possess in the study of British vegetation.

It is hoped to show that, although the historical and logical development of Braun-Blanquet's system is quite comprehensible and its accomplishments considerable, it is based on unacceptable premises; but that empirical techniques based on those of the continental plant sociologists may be a useful tool in the solution of ecological problems.

II. PHYTOSOCIOLOGY OR ECOLOGY?

According to many authors plant sociology (or phytosociology) is defined as the discipline which concerns itself with the study of vegetation as such, with its floristic composition, structure, development and distribution, whereas the term ecology is restricted to the study of the habitat (cf. Tansley, 1920). This divorce of the study of vegetation from the study of the habitat has not appealed to British, as it has to many continental, botanists, a fact which may be due to the different climates of opinion in which vegetation study has arisen and developed in Britain and in Europe. For the continental phytosociological systems have grown out of a preponderant initial interest in classical taxonomy and phytogeography, the British in physiology.

This divergence in aim and difference in origin has led to a lack of sympathy between the two. The phytosociologists have naturally become concerned with producing a complete description and classification of vegetation, while the British ecologists, once the early enthusiasm for primary survey had diminished (Tansley, 1947), devoted themselves to the investigation of the physiological relationship between plant and habitat (and hence autecology), with the study of succession and development, and with the perfection of methods for the objective description of the plant community as a basis for more exact synecological studies. Points of contact between these two schools of thought have become fewer because their aims are nearly mutually exclusive; intensive work on ecological problems and in the field of experimental taxonomy have raised doubts on the

validity of the premises on which the plant sociologists have built their classification. On the other hand, the view expressed by Tüxen (1942) that the plant can measure habitat factors better than any instrument is symptomatic of the scepticism with which the sociologist regards intensive ecological investigation, in spite of the fact that the only exact knowledge which he possesses of the tolerance of species has been obtained by extrapolation (often unjustified) from original instrumental measurements.

Mention of the phytosociological systems in British literature is scanty, and is mostly devoted to criticism of small parts of their technique without considering their relation to the whole (e.g. minimal area by Pearsall, 1924; and constancy diagrams by Ashby, 1935). The present state of affairs with reference to the Braun-Blanquet system is expressed by Tansley (1939): 'I am unable to form an opinion as to the validity or usefulness of the terminology of plant communities invented by Dr J. Braun-Blanquet, and have therefore had to forego any attempt to consider its possible application to British vegetation.' (The only serious attempt to apply the method was made by Tansley & Adamson in their study of the vegetation of the British Chalk (Tansley & Adamson, 1920).

It is, of course, illegitimate to generalize about 'continental phytosociologists'; for the schemes of classification which have been put forward are many and various (Brockmann & Rübel, 1912; Warming & Gräbner, 1933; Du Rietz, 1930; Gams, 1918, 1941, as well as many others), and the volume of literature produced on the subject is prodigious; neither do I intend to review all this literature. But the methods proposed by Braun-Blanquet have been accepted and used by very many botanists, particularly in middle and north-west Europe, the Mediterranean region and even in the tropics, and a detailed discussion of his methodology and techniques will raise numerous questions which can be discussed with reference to those other prevailing schools of phytosociology.

In this discussion I want to make clear the following points:

(1) What the Braun-Blanquet school is attempting to do (and the differences from the British outlook which this reveals);

(2) How far the methods used do accomplish the purposes for which they were designed; and

(3) Whether these methods can be profitably adopted by British ecologists for their original purpose or modified for some different though related purpose.

III. The Braun-Blanquet system

The most notable achievement of the Braun-Blanquet system is the *Prodromus der Pflanzengesellschaften*, which contains in a number of volumes the diagnoses and classification of the described communities of the north-west European and Mediterranean regions, treated separately. These volumes are considered as the prelude to a world-wide classification of plant communities according to the principles enunciated by Braun-Blanquet. Further extensive treatments of particular regions have also been made by these methods: for example, Nordhagen (1936), 'Versuch einer Einteilung der subalpinen-alpinen Vegetation Norwegens'; Tüxen (1937), 'Die Pflanzengesellschaften Nordwestdeutschlands'; Westhoff, Dijk, Passchier & Sissingh (1946), *Oversicht der Plantengemeenschappen in Nederland*; and Lebrun, Noirfalaise, Heinemann & Vanben Berghen (1949), 'Les associations végétales de Belgique'. All these accounts use similar nomenclature and are comparable. They can thus be used directly as a basis for discussion and argument. It is

noticeable that British vegetation is rarely referred to. Duvigneaud (1949), 'Classification phytosociologique des tourbières de l'Europe', is a notable exception, but even in that work many units which occur in Britain are not mentioned, because they cannot be recognized in our literature.

In essence these classifications are based on the following principles:

(1) The fundamental unit of vegetation is the Association,* which is an abstraction, obtained by the comparison of a number of lists made in selected sites in the field. It is defined entirely by floristic composition, *not* by habitat; but is thought to be also an ecological reality (i.e. to occupy a definite habitat) (Braun-Blanquet & Jenny (1926) and elsewhere).

(2) The description and the foundation of the Association is the Association Table (for an example see Table 1), which portrays in tabular form the species lists of communities which are thought to belong to the Association, together with some index of the quantity with which each species occurs.

(3) The tables are not necessarily reproduced in full in the Prodromus or other classifications, but each Association is 'characterized', which means that to each is appended a key diagnosis, which distinguishes it from other related Associations. Braun-Blanquet has selected one character of the Association as the most valuable for diagnosis—'fidelity', by which he means the complete or partial restriction of certain species of narrow ecological amplitude to one particular Association. Thus each Association is characterized by a number of species of high fidelity to that particular Association.

(4) The associations are arranged in a hierarchy of Alliances, Orders and Classes and are finally included in a Circle of Vegetation, which is defined by Braun-Blanquet as 'including the totality of the communities and species connected with it that are confined or largely confined to a natural vegetation region'.

(5) Just as the Ranales head the usual taxonomic arrangement of the dicotyledons, so the Classes of vegetation are arranged according to the 'principle of sociological progression'; that is, the simplest communities, those with the least internal integration, occur first and those with the highest integration (the woodlands) come last.

Why is it that British ecologists have taken no part in this movement? The reasons are, no doubt, many and complex; but some factors can be certainly identified. As interest in primary survey has decreased since the early years of the century, and has been largely replaced by more strictly ecological studies, there has been correspondingly less incentive to examine much of the Continental descriptive literature. Further, any system which treats plant communities as apparently static is suspect in a climate of opinion dominated by a dynamic approach like that of Clements, Cowles and Tansley. There are those, too, who think that no attempt should be made to describe and classify vegetation units until we are sure what is the essential nature of the plant community. All these amount to a lack of interest in what the Continental plant sociologists are trying to accomplish. Others criticize more actively. They criticize the continental methods for subjectivity and inexactitude; fidelity, they say, is not an adequate criterion for distinguishing or classifying vegetation units; the units are not separated from each other by clear lines, and are grouped in such a way as to obscure successional series; too little account is taken of

* When the word 'Association' is used henceforth it will refer to the Association in the sense of Braun-Blanquet. For a definition of this usage see p. 233. If it is used in other senses, e.g. that of Clements or of Tansley, this will be explicitly stated in the text. For a survey of the nomenclature of the vegetation units see Appendix.

ecotypic differentiation and change of tolerance of species throughout their range; and, finally, vegetation is of such a nature that it cannot be classified in a hierarchy. All these objections are raised and others. Answers to some of them, at least, will be given later. For the present, it is as well to realize that Braun-Blanquet would be the first to admit that his system is not a natural classification and that it is not perfect. What he does maintain, however, is that it is the only suggested system which has been extensively applied.

In the sections which follow I shall attempt to show with examples the procedure which is used at each stage in the process of description and classification. It is important in criticizing the methods to try to understand why they have been selected and how well they are suited to the end which they are designed to attain.

IV. Braun-Blanquet methodology

By 1921, after extensive plant sociological studies in the Alps and the Cevennes, Braun-Blanquet had formed definite ideas about the fundamental concepts of his system, which he published under the title 'Principien einer Systematik der Pflanzengesellschaften auf floristischer Grundlage'. These have been little modified since. This section is an attempt to present a connected account of Braun-Blanquet's methodology, drawing the data from all available sources,* A discussion of this topic is necessary in order to understand the significance of the practical techniques. In many points I do not agree with the views expressed, but my own will become clear at a later stage. The few comments which I have made are inserted in double brackets.

The Braun-Blanquet school may be taken to hold the following views:

A. *Ecological and floristic systems*

The theoretical and philosophical basis of community systematics has not kept pace with the rapid description of new communities. Descriptions are thus not made according to generally accepted principles, to the detriment of both ecological and chorological studies, which must be devoted to clearly defined communities. The goal is a system in which all plant communities may be arranged, which is 'as far as possible natural but at the same time practical'. This is likely to be modified in future; but, if the basic principles can be correctly defined, the modification may well be slight.

'The most immediate task of plant sociology is the recognition, distinction and classification of community units', using those characteristics of communities which seem most important and recognizing that not 'every collection of plants can be referred to a definite community'; for mixtures, undeveloped and degenerate stages, and purely accidental aggregates frequently occur. The recognition of communities is a matter of practice and depends greatly on the talent of the worker. Recognition must be followed by characterization 'so that the community can always again be recognised by another person'. Characterization involves the description of the organization, development, economy and distribution of a community. Present external factors are not alone responsible for the determination of a plant community. Historical plant geography may have a considerable influence. This, taken together with the difficulty of measurement and

* These sources are threefold: practical experience both in the field and in the laboratory under the tutelage of Dr Braun-Blanquet; the literature specifically cited in the text; and wide reading among the literature of various pupils and followers of Braun-Blanquet. The last mentioned are very numerous and have not been individually noted; most of them are to be found in the Communications of S.I.G.M.A. and the periodical *Vegetatio*.

our ignorance of the exact effects of habitat factors is a strong argument against basing the characterization of communities on habitat alone.

There remain the physiognomic-ecological and floristic approaches as possible bases for a system. Of these the former depends on 'as natural as possible a system of life forms', and that is so far from attainment that it cannot be used as the basis for classification. Thus there remains only a system founded on floristics. (In his address at the Stockholm Botanical Congress in 1950 Braun-Blanquet reiterated these points, and dealt also with two other possible classifications, the chorological, according to the distribution patterns of species, and the syngenetic, according to successional series. The former he dismissed because the units distinguished by it were too vast; the latter because the climax is largely hypothetical and because the number of anthropogenic communities, which could not be grouped into true series, was rapidly increasing.)

The basic unit of the floristic system, the Association, is not identical with the smallest unit; the latter, in agreement with the views of Raunkiaer, is a community which is a unit both qualitatively and quantitatively (that is, in specific composition, and arrangement, degree of cover, etc., of the component species), while the association is a unit built up of units which are qualitatively (but not quantitatively), similar. In species-poor areas (e.g. Scandinavia) the smaller units may be extensive, and there is a tendency to call *them* associations. This is to distinguish too far, for the predominance of one or another species in a particular spot may be purely accidental.

The Association is an abstraction conceived from examination of a number of stands found in the field, each of which should have the minimum of characters which personify the association under all circumstances. Stands which for some reason do not reach this minimum standard are known as fragments and must be omitted from the tabular representation of the association. 'These tabular collections will be the more valuable, the more thorough the attention which is paid to the characters of the community. The complete table gives not only a survey of the floristic complement and of the sociological and diagnostic worth of the species but it permits also an assessment of the width of variation of the association and gives points of reference for identifying the optimum of the community. The table taken as an whole, if it is based on a considerable number of stands, gives an ideal synthetic association which is hardly met with in nature.' This is especially valuable for comparative geographical studies. People should, however, be careful to look on the association table as an artificial product based on summation rather than as the embodiment of the natural Association.

The classification is founded on floristic and organizational characteristics of the community, but the value of any one characteristic in organization or succession on the one hand, and in diagnosis on the other, may be very different; thus, species of high fidelity are of great importance in diagnosis, whereas the dominants are often of little.

B. *Characteristics of the community*

(1) *Fidelity*

Fidelity is defined as 'das mehr oder minder Gebundsein der Arten an bestimmte Pflanzengesellschafter'. It has developed naturally from the concept of 'fidelity to habitat' (*Standortstreue*), and is of the greatest value for the diagnosis and characterization of the association. The term 'faithful species' (*Charakterart, espèce caractéristique*) is applied to those species which show a certain degree of fidelity towards any particular association.

The term *Charakterart* has been applied in varying senses in the past, particularly to those species which are important or appear regularly in any community, but its use is properly restricted to those of high fidelity.*

Competition restricts the range of tolerance of faithful species in natural associations; thus, plants can in its absence be grown under a wider range of conditions (e.g. in gardens). The grade of fidelity must be determined empirically by examining the behaviour of species under natural conditions. Restriction of tolerance may be due to historical factors, as in relict species (e.g. *Hieracium stelligerum* in the *Saxifraga cebennensis-Potentilla caulescens* association), or in new apomicts (*Hieracium* or *Alchemilla* spp.).

Faithful species may be divided into three categories, due to:

'*a*. Einseitige, ganz spezielle Anpassung an bestimmte physikalischchemischeFaktoren. Hieher zählen u.a. viele Charakterarten von Fels-, Felsschutt-, Sand- und Wassergesellschafter.

'*b*. Direkte Abhängigkeit von andern Organismen, Pflanzen oder Tieren, oder von bestimmten Organismengruppen. Viele Charakterarten der Wald-, Gebüsch-, Heide-, Moor-, und Wiesengesellschaften sind hieher zu rechnen. Manche davon leben zaprophytisch, hemiparasitisch oder auch parasitisch ....

'*c*. Konkurrenzverhältnisse. Durch den scharfen Wettbewerb besser angepasster Arten warden andere, deren Gedeihen sonst nichts in Wege stünde, auf ganz bestimmte Gesellschaften zurückgedrängt, wo sie der Konkurrenz Stand zu halten vermögen. Als beispiel seien bloss die Charakterpflanzen der *Agrostomma* Assoziation unserer Kornfelder erwähnt, die ausserhalb dieser anthropogenem Gesellschaft dem Wettgewerb der bodenständigen Arten nicht gewachsen sind.'

Species of groups (*a*) and (*b*) above are of different value in plant-sociological studies; for the former are independent of other organisms and their autecology is thus an expression of the ecology of the whole community in which they grow, but this is not the case with the latter, which are dependent and which only appear in full strength when the community is mature. Thus the appearance of a number of faithful species of this kind in a community is a sign that it is a well-developed example of the association.

Determination of degrees of fidelity should be undertaken in an area which is phytogeographically uniform, and not too small. The ideal is to examine the fidelity of species over their whole range; but, although this is easy with those of restricted distribution, it has not often been done with widely ranging species. Evidence so far accumulated suggests that it may be necessary to distinguish three grades of fidelity, namely, 'local', 'regional' and 'general'. For example, *Goodyera repens* is 'exclusive' (see p. 239) to the *Pinus sylvestris* association in most of France, in the West Alps it is 'selective' and in Switzerland it is only 'preferential'; the reason for this is the presence in the two last of nearly allied communities. There is much evidence to show that species which are of high fidelity regionally become less faithful in other regions and other different climatic conditions. A xerophilous plant is likely to have much higher fidelity to the communities in which it occurs in a moist climate than it will in a region with a dry climate. The con-

* Contrary to these suggestions and to the *Vocabulaire de sociologie végétale* (Braun-Blanquet & Pavillard, 1925), I do not use 'characteristic species' as the English equivalent of the German *Charakterart*, because in current British and American ecological usage it is applied to the constants and dominants (in a descriptive and not very precise way), and this is in keeping with the actual meaning of the word. 'Faithful' has been adopted as the obvious adjective to apply to species of high fidelity.

clusion is reached: 'Der indikative Wert der Charakterarten kann daher nur unter Berücksichtigung des geographischen Momentes zu voller Geltung gelangen.'

It should be possible to distinguish every association on purely floristic grounds without recourse to speculation about habitat or to vague physiognomic concepts; and, of the floristic characters, fidelity is the most important. Indeed, it is doubtful whether a community without faithful species should be considered as an Association at all. For they represent the stable element in the Association around which the other species may show great fluctuations, which may be purely accidental. A change in fidelity will take place only gradually in the course of thousands of years. No faithful species are thus likely to be found in recent types of habitat conditions, which will account for the lack of well-defined communities with faithful species in, for example, north England, and middle and north Sweden, as compared with the species-rich areas of southern Europe, which often have an unbroken continuity of vegetational history from the Tertiary. ((This in direct contradiction to the point of view expressed in Braun-Blanquet and Tüxen, 1952.)) Insistence of the presence of faithful species in the Association will prevent the undue splitting of vegetation into small units. Although the impossibility of giving a satisfactory precise definition of an Association is recognized, the field sociologist '*muss* dem Begriff einen bestimmten Denkinhalt verleihen, am fruchtbringend Arbeiten zu können'. The following definition is thus proposed:

'Die Assoziation ist eine durch bestimmte floristische und soziologische (organisatorische) Merkmale gekennzeichnete Pflanzengesellschaft, die durch Vorhandensein von Charakterarten (treuen, festen oder holden) eine gewisse Selbständigkeit verrät.'

(2) *Presence, Constancy and Dominance*

Among the synthetic characters of the Association other than Fidelity are Presence. Constancy and Dominance. As all these three have been used as the bases of classification in one system or another, it will be necessary to consider what Braun-Blanquet thinks about them.

By Presence is meant the occurrence of a species in any stand of an association, with the two conditions that the stand should be at least as large as the minimal area of the association and that it should contain the characteristic combination of species. When a certain number of lists have been entered on the association table, the species can be grouped according to their degrees of presence. Thus those which occur in 80–100 % of the stands are known as 'Presence 5', those in 60–80 % as 'Presence 4', etc. The species of Presence 5 may be known as the 'Constants' of the association. Constancy is determined by 'those investigations of Presence which are made with plots of sharply limited area', and only such studies can be treated by mathematical statistical methods. ((Owing to the original subjective choice even this is only partially true.)) The same conditions about 'minimal area' and the 'characteristic combination of species' are made as for the determination of the degree of presence. It is noted that the constancy curve and diagram correspond for the abstract Association to the frequency curve and frequency diagram for the stand. ((Species of constancy class 5 seem also to be known as constants.))

The Constants are, however, rejected as a characteristic for distinguishing and classifying associations for the following reason: the unit to be distinguished must be more or less uniform in ecology (response to factors of the habitat), and the faithful species because of their narrow tolerance give the best measure of the ecology of the vegetation; in com-

parison the constants are unreliable. Of them Braun-Blanquet writes: 'It appears from the available studies that species of the higher constancy classes can readily replace one another in different stands of the same Association. The writer cannot share the opinion that a composite framework of definite "constants", always present and unchangeable, must be considered as an essential prerequisite of the association. This is because the constants of an association can be replaced by non-constants without lessening the unity of the Association, unless, indeed, those constants are the species which determine the whole character of the community.' ((This whole argument depends of course on Braun-Blanquet's definition of the Association.))

It is believed also that dominants are replaceable and should not be used to characterize the association; and that they, being frequently species of wide tolerance, may often dominate communities which are ecologically different. ((Examples of this state of affairs are numerous; *Fagus sylvatica* in the different beechwoods on the Chilterns (Watt 1934), *Molinia coerulea* in the Molinietum mediterraneum on the south French littoral, in Fen *Molinieta* in England (e.g. Wicken) and in the West of Scotland.))

V. Field technique

The next step is to describe the field practice of adherents of the Braun-Blanquet school; for descriptions in the literature of the methods used are singularly reticent about some of the points which British ecologists find most difficult to understand or to accept. It should constantly be remembered that the techniques used in the field, and later in the composition of tables, have developed simultaneously with the methodology which I have outlined above; and, although influence has been reciprocal, the former are now completely adapted to obtain the kind of result required by the latter. If this is realized it becomes easier to understand the subjective elements of the system, its insistence on careful choice of material, and on experience and discrimination in the working plant-sociologist. For this reason I shall recapitulate the main points of Braun-Blanquet's argument developed in the preceding section.

(1) Associations do exist, and can with skill be recognized. They may be variable and may grade gradually into others which are nearly related ecologically or stand close in a successional series; but, in spite of this, they have a degree of reality.

(2) Smaller units with uniform dominance or constancy may be distinguished within the Association, often to be separated from one another by differential species; but the association is the smallest plant sociological unit which contains faithful species.

(3) It is desirable, though perhaps not essential, to recognize the Associations before making synecological studies, in order that these studies may be concerned with real units and that the results from them can be generalized to apply (with reservations) to similar vegetation elsewhere. From this point of view some British synecological studies are criticized as being merely studies in the autecology of the dominant.

Braun-Blanquet thus believes (and brings forward arguments or evidence in support of his beliefs) that associations can be recognized and characterized; that each has an optimum composition and ecology, and that it is the plant sociologist's task to approximate to a full description and understanding of both.

The following description of field technique is drawn partially from published accounts (e.g. Braun-Blanquet, 1932), and, in places where these are inadequate from my own interpretation of the actions in the field of various plant sociologists with whom I have worked.

A. *Choice of site*

The whole procedure of the distinction and classification of units is based on the description of carefully chosen sample plots (*relevés*, *Aufnahme*). It is regarded as most important that each of these sampling sites should be uniform. This is the essential prerequisite of all phytosociological systems, and it is unfortunate that one cannot define with precision what is meant by 'uniformity'. It includes the concept of homogeneity, although, in fact, statistically significant tests for homogeneity are never made. This is for three main reasons: that the use of statistical techniques on every stand would excessively slow down the accumulation of results; that statistical techniques can hardly be applied in many of the situations where surveys should be made; and that the stands of vegetation are often far too small.

Actually, the uniformity is subjectively assessed by using all the properties of the vegetation which can be directly observed. Among these are uniform form or distribution of the dominant (or, if there is no single dominant, the most abundant species), life form, or habitat in as far as this can be assessed (i.e. by such criteria as evenness of slope and aspect, similarity of drainage conditions and uniformity of soil profile). If, for example, an otherwise uniform area is found to contain a small depression with a different flora, or a large stone with epilithic lichens, these would be omitted for the purpose of the survey. (By the term 'different flora' is meant different in kind not in quality. For instance, if the hollow contained the same species as the surrounding area but in different relative abundances, this would not constitute a 'different flora' in the sense used; but if it contained species otherwise absent in the uniform area, i.e. 'differential species', it would be considered 'different' and omitted from the survey plot.) This distinction may be difficult to uphold in some communities, but if sites are chosen at first in places where large 'uniform' stands of vegetation can be found the finer mosaics and transitions can usually be interpreted later. But if no 'uniformity' can be found, the method breaks down. In examining a list made with these techniques the reader naturally assumes that the area fulfils these conditions of uniformity, and any departure from them in practice would be actively misleading.

Ideally all the uniform areas (or stands) in a particular region should be examined, and comparisons made between them. In practice one finds, however, that as the investigation progresses some associations are already known, and it is possible to ignore (for the purpose of studying this one association), those stands which do not exhibit to the full the characteristics of the association.

B. *Description of the stand*

Having chosen a uniform stand and decided upon its limits the plant sociologist next makes a description of it (*relevé*, *Aufnahme*). Braun-Blanquet uses a standard technique for this, which, he believes, gives him all the information he requires with the least expenditure of time and energy.

He first notes the major environmental features, the geographical location, the altitude, aspect and slope, the geological substratum and any other points about the habitat which may have a bearing on the ecology of the stand. This may be supplemented by a small sketch map of the site marking the bounds of neighbouring communities. The unit of

study is the stand, and, if it is at all possible, the whole stand is then described by the following technique:

(1) Note the average height and the percentage cover of each layer of the vegetation separately. The percentage cover is taken as an estimate of the space covered by a vertical projection of all the above-ground parts of the plant. If it is impossible to give an estimate that is reliable (e.g. moss-cover in closed grassland), it is better to note the difficulty experienced rather than give an erroneous estimate.

(2) List all the species present in the stand, being careful not to go outside the previously defined uniform area. The list should be as comprehensive as possible and should certainly include all vascular plants, mosses, liverworts and lichens. If any specimen cannot be readily identified in the field, it should be labelled and carried home. Systematic determination should be as exact as possible.

(3) Give every species listed an index of cover-abundance and of sociability. The cover-abundance index used by Braun-Blanquet and all the followers of the orthodox Zürich-Montpellier school is as follows:

5, covering more than $\frac{3}{4}$ of the area;
4, any number of individuals covering $\frac{1}{2}$–$\frac{3}{4}$ of the area;
3, any number of individuals covering $\frac{1}{4}$–$\frac{1}{2}$ of the area;
2, very numerous or covering at least 5% of the area;
1, plentiful but of small cover value;
×, sparsely or very sparsely present, cover very small.

In this scale the larger figures have to do with cover, the smaller with abundance. In this way two difficulties are avoided; that of assessing the cover of very numerous small individuals, and that of deciding what is an individual in many of the vegetatively reproducing plants of high cover. On the other hand, it does stress the value of cover for indicating the relative importance of the various species within the community.

To complete this picture in symbols of the plant community Braun-Blanquet includes an index of sociability for each species:

Soc. 1, growing one in a place singly;
Soc. 2, grouped or tufted;
Soc. 3, in troops, small patches or cushions;
Soc. 4, in small colonies, in extensive patches or forming carpets;
Soc. 5, in great crowds, pure populations.

To clarify the description of sociability even further, Braun-Blanquet writes: 'The density of the stand of individuals or shoots is indicated by a dotted or solid line under the figure. Thus *Typha minima* (Soc. 5) means an open but large patch of *Typha minima*, and *Calluna* (Soc. 5) indicates a large, dense closed stand of heather.'

(4) Note the total area of the stand described.

(5) Add any additional relevant information on vitality of the species, the structure of the community, the presence or absence of seedlings, etc.

(6) Dig a soil pit and describe the profile and root layering; and take samples to the laboratory for analysis.

This constitutes a unit description, and it is from examination and comparison of numbers of these that the association tables are drawn up.

I have described above a case where it was possible to describe the whole stand. This is not always so; for the stand may be too large for the investigator to be able to estimate cover accurately, or even in some cases to examine all parts of the stand in the same detail. If it should prove impossible to examine the whole stand, the following procedure is recommended to replace that given in paragraphs (2)–(4) above.

(2) Mark out a small area in the middle of the stand, the initial size of which should be chosen on considerations of convenience. 1 sq.m. will usually be suitable for grassland communities; $\frac{1}{4}$ sq.m. may be easier to examine in bryophyte communities or in a stand with numerous small therophytes; 4 or 16 sq.m. may be more suitable in woodland.

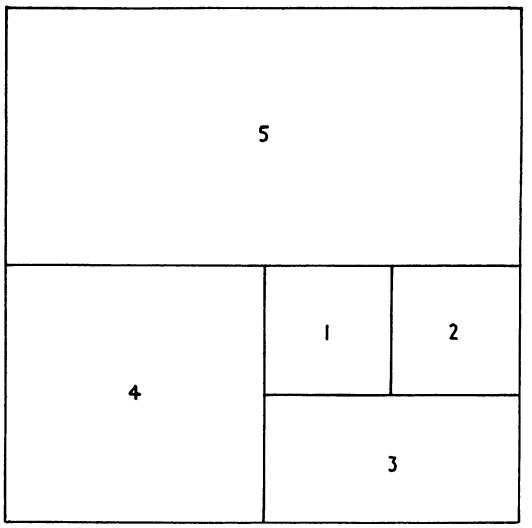

Fig. 1. Arrangement of quadrats of increasing size

Let us say that the initial size is 1 sq.m. Note this size, and then list all the species which occur in this marked area of 1 sq.m. The area should then be doubled by laying out another square metre alongside and touching the first, thus converting the square into a rectangle (2×1 m.), and any species occurring in the second square metre but not in the first should be added to the list. Continue by doubling again to a square (2×2 m.) and add any new species; then to a rectangle (2×4 m.) and so on until the number of new species added per increase of area becomes small. (See Fig. 1, and, for the lay-out of field notes, p. 257 in Part II.) If the number of species continues to increase quickly with each successive increase of area, the initial choice of uniform area is at fault; if it rises suddenly in a second step it indicates that the area has passed the limits of one community into another.

(3) Give each species indices of cover-abundance and sociability within the total area listed in detail.

(4) Note any additional species which occur outside the sample area and within the stand. They should be denoted with ($\times$). Give the final size of the sample area, followed in brackets by the area of the whole stand, or, in a very large stand, the area which it has been possible to examine. Thus 16 (400) sq.m. means that the cover-sociability figures refer to a plot of 16 sq.m. in a stand of total area 400 sq.m., or in an area of 400 sq.m. examined in a much larger stand.

A sample plot of this kind is considered an adequate substitute for a description of the whole stand, because it is said to be as large as the 'minimal area' of the association. (For a discussion of the concept of minimal area see Part II, p. 265.)

VI. Association tables

The grouping of the lists from sample plots into association tables is one of the most important, if not the most important, part of the technique of Braun-Blanquet's plant sociology. Of it he writes: 'The preparation and study of these tables is the work of years; but since they are fundamental to the determination of fidelity and the delimitation of the association, they cannot be omitted.' The aim is to tabulate together lists which are similar in order to produce a description of the association. These tables are never final; for, as additional lists are made or as more detailed ecological information is accumulated, it may be found necessary to divide the table of what was originally one association into two, or to combine two which were originally thought separate.

It is impossible to lay down general rules for the building up of tables, but in the light of experience of the Montpellier school the general lines of their procedure may be indicated. The tables are made on squared paper, with the list of species down the left margin and the index numbers of the sample plots along the top. It is convenient to arrange the species in groups, trees, shrubs, grasses etc., leaving a space between each group for the filling in of additional species which may appear in subsequent sample plots. The most conspicuous details of the habitat may also be tabulated at the top of the sheet. All those lists which are thought similar should now be entered on the table. The bases for recognizing similarity may be many and various, and may include, for instance, dominance by the same species, constancy of certain species, similarity of physiognomy and habitat and the regular occurrence of species which are already suspected to have a narrow amplitude.

It cannot be sufficiently emphasized that, although the criterion used is floristic, it is claimed that the units distinguished are ecologically real. The situation is analogous to that in systematics where morphological characters are used as a primary basis of classification, and as the only basis of a descriptive classification, but no genetic evidence should be ignored and the morphological classification is thought to be a reflexion of the genetic—an assumption which more often than not is vindicated. It should, however, be borne in mind that, as in the analogical case, certain floristic characters of the community may not reflect the ecology.

From inspection of the table it should be apparent what lists differ noticeably from the rest. These differences may be of various grades; if they concern common species the lists may belong to different 'variants' or 'facies' of the Association, or they may be of sufficient importance to necessitate dividing the table into two or more different Associations. This will depend on the meaning assigned to the term Association.

According to Braun-Blanquet these decisions can only be made by having recourse to a consideration of the fidelity of the various species; and this stage (that of distinguishing Associations by faithful species) is one about which the literature is singularly reticent. Apart from the proviso that it requires much time and experience we are told nothing; and observation of the system in use has done nothing to unravel this problem for me. I cannot, therefore, provide any connected and logical account of the distinction of Associations by the Montpellier school, because I believe that the process itself is muddled

and haphazard. The nearest approach to a logical procedure is in the ideal instance when all the vegetation of a region has been described, which is the only situation in which degrees of fidelity *can* properly be assessed.

If this is the case indices of fidelity to the vegetation units *as initially distinguished* can be given immediately. The various grades of fidelity recognized are as follows (Braun-Blanquet, 1932):

A. *Characteristic (faithful) species*

Fid. 5, exclusive species (treue); species completely or almost completely confined to one community. E.g. *Viola cenisia*, *Papaver alpinum* in the Thlaspeetum in the Alps, *Delia segetalis* in the Centunculo-Anthoceretum of Central Europe.

Fid. 4, selective species (feste); species found most frequently in a certain community but also, though rarely, in other communities, e.g. *Phyteuma pedemontanum* in the Caricetum curvulae, *Crepis biennis* in the Arrhenatheretum of Central Europe.

Fid. 3, preferential species (holde); species present in several communities more or less abundantly but predominantly or with better vitality in one certain community, e.g. *Luzula luzulina* and *Pirola uniflora* in the Piceetum of the Alps and the Tatra.

B. *Companions*

Fid. 2, indifferent species (vage), species without pronounced affinity for any community.

C. *Accidentals*

Fid. 1, strange species (fremde); species that are rare and accidental intruders from another plant community or relicts of a preceding community, e.g. *Peucedanum palustre* or *Carex elata*, relicts of the Caricetum elatae in the Molinietum; *Ammophila arenaria* as a relic in the shrub communities of the coastal dunes.

Braun-Blanquet also gives a chart for the determination of the various indices of fidelity.

Once the degrees of fidelity of the various species are determined the associations are distinguished by the species faithful to them (fidelity grades 5, 4 and 3) instead of by the other criteria used initially (e.g. dominance, lifeform, habitat).

This must mean either that the associations are in fact distinguished on grounds of dominance and the faithful species are used merely as an additional and sensitive diagnostic character; or that the associations are determined in the field because species of known narrow amplitude are present, and the later determination of degrees of fidelity is a circular argument. If the first alternative is true, faithful species are unnecessary for delimitation of the association (and, because of the difficulties involved in the use of them, undesirable); if the second, the validity of the units determined by them is questionable.

The difficulty one finds in discovering the exact procedure used is, I think, due to the curious and illogical mixture of the two which the Zürich-Montpellier school apply. This is the more so in regions where not all the communities have been described. When the community being studied has a high degree of integration (which is usually associated with dominance or some over-riding habitat factor), the associations determined by the school are convincing; but in many instances this is not so.

The good association table thus takes the form of a series of lists (the more the better, but it has been suggested that a minimum is desirable), which are more or less similar in

Scheme for the determination of fidelity of the species of a given Association

P = degree of presence: A = degree of abundance (total estimate, see p. 236).

Relationship of species with approx. same vitality and sociability		
In given Ass.	In other Ass.	Examples
Fidelity 5:		
—	P 1; A to 1	*Juncus trifidus* in the Trifidi-Distichetum of the Tatra
P 4–5; A 3–5	P 1–2; A to 1	*Schoenus nigricans* in the Schoenetum nigricantis of Central Europe
P 4–5; A ×–2	P 1; A ×–2	*Ribes petraea* in the Mughetum of the Tatra
P 1–3; A any degree	Lacking or very rare	*Chamorchis* in the Firmetum of the Tatra, *Listera cordata* in the Piceetum of the Alps
Fidelity 4:		
P 4–5; A 3–5	P 2–3; A ×–2	*Pinus mughus* in the Mughetum of the Tatra
—	P 3–4; A ×–1 (as association relicts or pioneers)	*Ammophila arenaria* in the Ammophiletum
P 4–5; A ×–2	P 2–3; A ×–1 (2)	*Saussurea alpina* in the Elynetum of the Alps
P 3–4; A ×–2	P 1–2 (3); A ×–1 (2)	*Koeleria gracilis* in the Xerobrometum of Germany
P 1–3; A ×–2	P trifling; A v. trifling	—
Fidelity 3:		
P anything; A 3–5	P ×–3; A ×–2	*Trisetum flavescens* in the Trisetetum flavescentis in the Alps
P anything; A anything	P and A trifling or rather trifling; or A trifling vitality reduced	*Empetrum nigrum* in the Empetreto-Vaccinietum in the Alps
Fidelity 2:		
P, A and vitality in two or more Ass. approx. equal	P, A and vitality in two or more Ass. approx. equal	—
Fidelity 1:		
P 1; A ×–1 vitality reduced	P 1; A ×–1, vitality reduced	*Prunus avium* seedlings in the Piceetum or the Fagetum
Species occurring only on the outskirts or on disturbed parts of the stand	P 1; A ×–1, vitality reduced	*Rumex alpinus* in the Triseetetum flavescentis; *Sibbaldia procumbens* in the Arabidetum coeruleae

floristic complement and which have a number of faithful species, as defined above. These may vary from species with a high degree of presence and abundance to others which are very scarce. Within a particular region the association is defined by these species. The table of the Quercetum ilicis galloprovincialis in Braun-Blanquet (1936), La Chênaie d'Yeuse mediterranéene' (Quercion ilicis) (*S.I.G.M.A. Comm.* no. 45) is a superb example of an association table (Table 1). In this instance the dominant also happens to be a species faithful to the association.

A table such as this gives an admirable idea of the general floristic composition of the association and the range of conditions under which it will occur. From closer inspection it may also be possible to detect possible correlations between the presence and abundance of certain species and features of the habitat, correlations which can then be examined in greater detail. It represents, in fact, a concise summary of a great deal of ecological investigation. The lay-out followed in this table is that usually adopted by the followers of the Zürich-Montpellier school. The species list is headed by those faithful to the association, arranged in order of presence and abundance; the remaining species follow according to their decreasing degrees of fidelity.

Substratum géologique	...	Calc. miocène				C. éocène		
Numéros des relevés	...	1	2	3	4	5	6	7
Altitude s. m. (m.)	...	60	70	70	120	180	70	150
Exposition	...	N.E.	plat	plat	plat	S.W.	S.W.	S.E.
Inclinaison		5°	—	—	—	2°	1–2°	5°
Age approx. des troncs (ans)	...	30–40	30	15	30–40	20–25	25–30	25–30
Hauteur des arbres (m.)	...	6–8	8	5–6	6–7	6–7	5–8	6
Degré de couverture des arbres (%)	...	95	100	100	90	100	95	100
Degré de couverture des strates inf. (%)	...	80	—	40	70–20	30–5	20–5	—
Surface (mq.)	...	100	100	100	100	<100	100 (500)	<200
Caractéristiques:								
MP.	Quercus ilex	5.4	5.5	5.5	5.5	5.5	5.5	4.3
NP.	Ruscus aculeatus	3.2	3.3	1.2	2.2	1.2	2.2	(+)
MP.	Phillyrea media	1.2	.	+	.	+	+	(+)
P.sc.	Lonicera implexa	1.1	+	+	1.1	2.1	1.1	.
H.caesp.	Carex distachya	2.2	+	+	.	.	+	.
P.sc.	Rosa sempervirens	+0.2	1.1	+	2.2	.	(+)	1.1
MP.	Viburnum tinus	+0.2	1.2	.	1.2	2.3	(+)	(+)
MP.	Arbutus undedo	.	.	.	+	.	.	.
H.ros.	Viola scotophylla*	1.1	+	+	2.1	.	.	1·1
H.ros.	Stachys officinalis*	+	.	+	+	.	1.1	+
H.ros.	Asplenium ad. nigrum ssp. o opt.*	+0.2	.	.	.	.	.	.
H.scap.	Calamintha ascendens	.	.	.	.	+	(+)	.
H.caesp.	Luzula Forsteri*	.	.	.	.	.	.	.
T.rept.	Moehringia pentandra	.	.	.	.	.	.	.
H.caesp.	Carex olbiensis	.	.	.	.	.	.	.
G.rh.	Epipactis latifolia*	.	.	+	.	.	.	.
G.rh.	Epipactis microphylla*	.	.	.	.	.	.	.
Caractéristiques de l'Alliance:								
P.sc.	Asparagus acutifolius	1.1	1.1	1.1	1.2	1.1	+	1.1
P.sc.	Smilax aspera	2.2	2.1	2.1	+	2.2	2.2	3–4.3
P.sc.	Clematis flammula typica	+	+	+	1.2	1.1	1.1	+
Ch.suff.	Teucrium chamaedrys*	+	+	+	+	+	1.1	+
MP.	Pistacia terebinthus	+	.	+	+	+	.	+
P.sc.	Lonicera etrusca	+	+	+	.	+	.	+
Ch.suff.	Euphorbia characias	+	.	.	+	+	.	+0.1
NP.	Rhamnus infectoria	.	.	.	+	.	.	.
H.caesp.	Oryzopsis paradoxa	.	.	.	+	.	.	.
H.sc.	Lathyrus latifolius ensifolius	.	.	.	.	.	.	.
H.scap.	Rumex intermedius	.	+	.	.	.	.	.
NP.	Bupleurum fruticosum	.	.	.	.	+	.	.
Caractéristiques de l'Ordre:								
P.sc.	Rubia peregrina	1.1	1.1	2.2	1.2	1.1	1.1	1.1
MP.	Rhamnus alaternus	+	+	.	1.2	+	(+)	+
~~MP.~~	~~Pistacia lentiscus~~	~~.~~	~~.~~	~~.~~	~~.~~	~~+~~	~~+0.2~~	~~.~~
MP.	Quercus coccifera	+0.2	.	+	.	+0.2	+0.2	.
MP.	Phillyrea angustifolia	(+)	.	.	+0.2	.	+0.2	.
NP.	Jasminum fruticans	.	.	.	+0.2	+	.	.
NP.	Daphne gnidium	.	.	.	.	.	.	+
Compagnes:								
P.sc.	Hedera helix	1.2	2.1	4.3	1.2	1.3	.	+
H.ros.	Carex Halleriana	1.2	+	+	.	+0.2	+	+
P.sc.	Rubus ulmifolius	+	1.2	+	+0.2	+	.	1.2
H.caesp.	Hieracium Wiesbaurianum	1.1	+	(+)	+	.	+	.
Ch.sc.	Brachypodium ramosum	+	1.1	.	+	.	+	(+)
P.sc.	Osyris alba	1.2	1.1	.	+0.2	1.2	.	1.2
MP.	Quercus pubescens	(+)	+	.	.	+	+	1.1
MP.	Juniperus oxycedrus	.	.	.	.	+	+	2.1
MP.	Crataegus monogyna	.	+	+	+	.	(+)	+
MP.	Buxus sempervirens	3.3	.	.	.	+0.2	.	.
H.ros.	Ranunculus bulbosus v.	+	.	+	.	+	(+)	.
T.e.	Geranium purpureum	.	+	.	.	+	.	.
MP.	Prunus mahaleb	.	.	.	+	.	.	.
H.scap.	Bupleurum rigidum	(+)	+	+	.	.	.	+
H.scap.	Silene italica	+	+	.	+	.	+°	.
H.caesp.	Brachypodium silvaticum	(+)	.	.	.	.	.	.
NP.	Erica scoparia	.	.	.	.	.	(+°)	1.2
Ch.suff.	Helleborus foetidus	.	.	.	.	.	.	+
NP.	Prunus spinosa	.	+	.	.	.	.	.
MP.	Erica arborea	.	.	.	.	.	.	.
MP.	Acer monspessulanus	.	.	.	.	.	.	.
NP.	Coronilla emerus	+	.	.	.	.	.	+
MP.	Sorbus domestica	.	.	.	.	.	.	.
H.scap.	Clinopodium vulgare	+	.	.	.	.	.	.
H.scap.	Inula conyza	.	.	.	.	.	.	.
G.b.	Arum italicum	.	.	.	+	+	.	.
MP.	Spartium junceum	.	.	.	.	.	+°°	.
G.b.	Aristolochia rotunda	.	.	.	.	.	.	.
MP.	Ligustrum vulgare	.	.	.	.	+	.	.
Ch. suff.	Thymus vulgaris	+°	.	.	.	.	.	.
T.sc.	Lathyrus aphaca	.	+	.	.	.	.	.
H.ros.	Asplenium trichomanes	.	.	.	.	.	.	.
P.sc.	Clematis vitalba	.	.	.	.	.	.	.
Ch.suff.	Cephalaria leucantha	.	.	.	.	.	.	.
	Mousses:							
	Drepanium cupressiforme	1.2	+	.	+	.	1.3	+
	Eurhynchium circinnatum	1.2	.	1.2	(+)	+	+	.
	Scleropodium purum	2.3	1.2	.	.	.	.	+0.2
	Brachythecium rutabulum	1.2	.	+	.	.	.	+
	Fissidens decipiens	.	.	+	.	.	.	.
	Fissidens taxifolius	.	.	.	.	.	+	+
	Fissidens incurvus	.	.	.	.	.	+	.
	Rhynchostegium megapolitanum	+	.	.	.	.	.	.

Table 1. *Quercetum ilicis galloprovincialis*

Calc. crétacé			Calcaire jurassique compact											Bas	
8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	2
190	40	400	480	220	135	280	180	200	230	250	220	150	300	25	2
S.E.	N.	N.	S.	W.	S.E.	N.	E.	W.	W.	N.	plat	plat	N.	N.	N
5°	5°	—	30°	2°	5°	5–10°	10°	10°	2°	2°	—	—	10°	5–10°	5–
25	60–100	10–15	30–40	15	20	100	30–40	20	15–20	10	30	15–20	30–50	30–50	40
5–7	8–12	3–5	4–5	4–5	4–5	10	6–8	4–5	4–5	3–4	5–8	5	8	6–8	5
90	100	90	100	100	95	85	100	90	100	90	90	100	100	100	1
10–5	—	—	—	—	10–3	75	—	—	—	—	—	—	40	70	8
100	<200	<200	—	100	<100	100	100	100	100	100	<500	100	100	100	1
						(300)	(200)			200				(200)	(2
5.5	5.5	3.2	5.4	5.5	5.5	3.3	5.4	5.4	4.3	5.4	5.5	5.5	5.5	5.5	5
+	2.2	1.2	+	2.2	2.2	1–2.2	2.2	+	+0.2	1.2	1.2	2.2	+	3.4	3
+0.2	1.1	+	1.2	+	1.1	1.1	1.2	(+)	+0.2	1.2	+	+0.2	+	1.2	
1.1	+	1.1	+	2.1	+	.	+	+	+	2.1	1.1	2.1	(+)	2.1	1
.	.	.	.	.	1.2	+	+	+	+	1.2	+	1.2	+	+0.2	1
1.1	+	+	+	+	+	.	1.1	+	+	1.1	+	+	+	2.1	
1.2	.	2.2	.	2.2	+0.2	+	1.1	2.1	2.2	.	.	.	.	+	
+	+	2.2	.	2.2	.	.	+0.2	1.2	2.2	+0.2	1.2	+0.2	+	.	((
+	+	+	+	+	.	+	+	+	+	1·1	+	+	+	.	
.	+	.	.	.	.	+	.	.	+	+	+	(+)	+	.	
.	+	.	.	.	.	+0.2	.	.	.	.	.	(+)	.	+	(
.	+	+	.	.	.	.	.	+	.	+	+	+	+	.	
.	.	.	.	.	.	+	.	.	.	.	.	.	+	.	
.	+	.	.	.	(+)	.	.	.	.	.	.	.	.	.	
.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	
.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	
.	.	.	.	+	.	.	.	.	.	.	(+)	.	.	.	
+	+	+	1.2	2.1	+	1.1	1.1	+	+	2.2	1.1	2.1	+	+0.2	
2.3	2.1	1.1	1.2	3.2	2.1	1.2	2.1	1.2	1.1	2.2	1.2	2.1	2.3	3.4	2
1.1	+	+	.	+	+	+	+	+	+	1.1	1.1	1.1	+	1.1	
+°	.	+	1.1	.	.	+	(+)	.	+	+	+	.	(+)	+	
(+)	+	.	+	1·1	.	.	+0.2	+	+	1.2	1.1	+	.	(+)	
.	.	+	+	.	.	+	.	.	.	.	+	.	(+)	(+)	
.	+	+°	+	.	+°	.	+	+	.	.	+	.	.	.	
.	.	.	+	.	.	.	+	.	.	.	+	+	.	.	
.	.	.	.	.	+	.	+	.	.	+	.	.	.	+	
.	.	+	.	.	.	.	.	.	.	.	.	+	.	.	
.	.	.	.	.	.	.	.	.	.	.	.	(+)	.	.	
.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	
1.1	+	+	1.1	.	1.1	1.1	.	1.1	+	+	+	+	1.1	2.1	2
+	.	+	.	+	+	.	.	.	+	+	+	+	.	(+)	
+0.2	.	.	.	1·2	+0.2	.	+0.2	+0.2	.	+	1.2	+	.	+0.2	+
+	.	.	.	.	+0.2	.	.	+	.	.	.	.	.	+0.2	
.	.	.	.	.	.	.	.	.	.	.	+	+	.	+0.2	
.	.	.	+	.	+0.2	.	+	.	.	+	.	+	.	.	
.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	
(+)	1.1	+	+	.	1.1	1.1	.	+	+	+	+	(+)	3.2	3.2	
+	+	.	+	1.2	.	+	+	+0.2	+	+	+	+	+	1.2	
+	+	+	+	+	+	.	+	+	+	+	+	+	+	+	
+°	+	.	.	.	.	+	.	.	+	+	+	+	(+)	+	(
+°	1°1°	.	1.1	1.1	+	.	.	+	+	.	+	+	.	+	
(+)	+	+	1.2	.	.	.	.	+	1.1	1.2	+	+	2.2	2.2	1
+	.	1.2	.	.	.	+	.	.	1.2	.	.	.	+	.	
(+)	+°	1°1°	.	+	.	(+)	.	+	+	.	.	.	+	.	
.	1°	.	+	.	.	.	.	.	.	.	.	.	.	.	
.	3.2	2.2	2.2	1.2	.	3.4	2.2	+0.2	+0.2	1.2	+	1.2	+	.	
.	+	.	+	+	+	.	.	+	+	+	.	+	+	.	
.	+	.	.	.	+	+	+	.	.	1.1	+	1.1	.	+0·1	+
.	.	+	.	.	+	.	+	.	+	+	+	+	.	.	
+°	.	.	.	+	.	.	.	.	+	.	+	+	.	.	
.	.	.	.	.	.	+	.	.	.	.	.	+	.	.	
.	.	+	.	+	.	.	.	+	.	+	.	+	.	.	
.	.	.	.	.	.	.	.	.	.	.	.	.	+°	.	
(+)	.	.	.	.	.	(+)	.	.	+	+	+	+	+	.	
.	.	.	.	.	.	.	.	.	+	+	+	+	.	.	
.	.	.	.	.	.	.	.	.	.	.	.	(+)	.	+°	
.	.	+	.	.	.	.	.	.	.	1.1	+	.	.	.	
.	.	+	.	.	.	.	.	.	+	+	.	.	(+)	.	
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+°°	.	.	.	.	.	.	+	.	.	.	+	+	.	+°°	
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.	.	.	+	+	.	.	+	.	.	.	.	.	.	.	
.	+	+	+0.2	.	.	+	1.2	.	.	.	+	1.2	+	1.2	+
1.2	+	+	.	.	+0.2	+	2.3	.	.	.	+	+	.	2.3	
(+)	1.2	.	.	.	.	.	+0.3	.	.	.	.	.	.	+0.2	
+	+	.	.	.	.	+	.	.	.	.	1.2	+	.	.	
.	.	.	.	(+)	.	+	.	.	.	.	1.2	+	.	1.2	
.	+0.2	.	.	.	.	.	.	.	.	.	.	.	+	+	
+	.	.	.	.	.	+	.	.	.	.	.	.	+	.	
.	+	.	.	.	.	+	.	.	.	.	.	.	.	.	

	Basalte		Schistes	Alluvions quatern. siliceuses						Substr. siliceux			
2	23	24	25	26	27	28	29	30	31	32	33	34	
5	25	90	200	40	75	50	40	20	60	35	550	5	
.	N.	S.W.	N.W.	plat	plat	plat	N.W.	plat	N.	N.	W.N.W.	plat	
10°	5–10°	5–10°	20°	—	—	—	2°	—	5°	20°	5–10°	—	
-50	40–50	60–80	40–50	30	100–200	150–200	100	40	80–100	20–80	80–100	50–70	
-8	5–7	6–8	8–12	6–7	8–12	15–20	10	8	10	5–10	10–12	8–10	
00	100	90	100	100	90	100	90	90	95	80	95	90	
0	80	90–30	40–5	—	80–30	90	80–30	80–20	80–30	90	—	—	
00	100	100	100	100	100	500	100	100	100	100	100	100	Pré-
00)	(200)	(500)	(200)	(200)	(200)		(200)	300	(500)	(600)	(200)	(500)	sence
.5	5.5	4.4	5.5	5.5	5.5	5.5	5.4	3.2	5.5	2.2	5.5	4.4	34
.4	3.2	2.2	2.2	+0.2	3.4	3.3	3.3	2–3.3.	4.4	(+)	2.2	(+)	34
.2	+	.	1.1	+	2.2	+	+	1.2	+0.2	1.1	1.1	1.2	31
.1	1.1	.	1.1	+	1.2	+	+	.	(+)	1.1	1.1	1.1	30
0.2	1.2	1.2	+0.2	2.2	2.2	+0.2	1.2	2.2	2.2	1.2	+	+	26
.1	+	.	+	.	.	.	.	.	.	.	.	+	24
+	.	4.4	.	(+)	1.2	4.4	3.2	2.2	2.2	3.2	.	(+)	24
.	((+))	(+)	1.2	.	+	.	(+)	1.2	1.2	3.2	+	+	22
.	.	(+)	.	.	.	.	.	.	.	(+)	+	.	21
.	.	.	.	(+)	1.1	+	+	1.1	1.1	+	.	1.1	20
+	(+)	+0.2	+.02	.	.	+0.2	+	(+)	+0.2	+	1.1	+	15
.	.	.	.	.	.	.	.	.	.	.	.	.	10
.	.	.	.	.	.	.	+	.	+0.2	(+)	+	.	6
.	+	.	.	.	.	.	.	.	.	.	.	.	3
.	.	.	.	.	.	.	.	.	.	.	.	.	2
.	.	.	+	.	.	.	.	(+)	(+)	.	.	.	4
.	.	.	.	+	.	.	.	.	.	.	.	.	3
0.2	+	1.1	+	+	1.2	+	+	1.1	+	(+)	1.1	+	34
.4	2.2	+0.2	3.2	.	+0.2	1.2	.	.	(+)	2.1	2.2	+	32
.1	+	+	(+)	(+)	.	1.1	1.1	+	(+)	.	.	(+)	30
+	.	+	.	(+)	1.1	.	+	(+)	+	(+)	+	.	25
+)	.	.	.	.	(+)	+	.	.	.	.	(+)	.	19
+)	.	+	.	(+)	.	+	.	+	+	.	.	.	16
.	.	.	.	.	.	.	.	.	.	.	.	.	11
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.	.	.	.	.	.	.	.	.	.	.	.	.	3
.1	2.1	1.1	2.2	2.1	1.1	1.1	1.1	2.2	1.1	1.1	1.1	1.1	32
+)	.	.	.	.	1.2	2.1	(+)	+	(+)	(+)	+	+	24
0.2	+0.2	.	.	.	1.2	.	.	.	.	(+)	.	+	15
0.2	.	.	+.02	(+)	1.2	+0.2	+	.	+0.2	(+)	.	.	15
0.2	+	+	+	.	+0.2	+0.2	.	(+)	+	.	.	.	13
.	.	.	.	.	.	.	.	.	.	.	+	.	8
.	.	.	(+)	.	.	.	.	(+)	.	(+)	.	.	5
.2	+	(+)	1.2	1.2	1.2	2.2	2.2	2.2	+		3.4	(+)	30
.2	1	1.2	.	1.2	+0.2	1.2	1.2	1.2	+0.2	(+)	+	.	29
+	+	.	+	1.1	1.2	.	.	(+)	+	(+)	1.1	(+)	29
+	(+)	(+)	.	(+)	+	+	(+)	(+)	(+)	.	.	.	22
+	.	+°	+°	.	+0·1°	.	+	.	+°	+	+	.	20
.2	1.2	+0.2	.	(+)	.	1·2	.	2.2	.	.	.	.	21
.	.	+	.	1°	(+)	+	+	1.2	+	.	.	.	17
.	.	+	.	+	.	.	(+)	(+)	(+)	.	+	.	17
.	.	.	(+)	+	(+)	+	+	(+)	+	.	+	.	15
.	.		+0.2	.	.	.	.	.	.	.	.	.	15
.	.	.	.	.	.	.	.	.	.	(+)	.	.	15
0·1	+0.1	.	.	.	.	.	.	+	.	(+)	+	.	13
.	.	.	(+)	.	.	.	.	.	.	.	(+)	.	10
.	.	.	.	.	+	.	.	.	.	.	.	.	10
.	.	.	(+)	+	.	.	+	.	+	.	.	.	10
.	.	.	.	.	.	+	.	1.1	.	(+)	+	+	11
.	.	.	+0.2	.	+°	.	+°	+°	+°	+	.	(+)	10
.	.	.	.	.	.	.	.	.	.	.	.	.	8
.	.	.	.	+	.	.	.	.	.	.	.	.	6
+°	+°	.	.	.	.	.	.	(+)	.	2.2	.	+	6
.	.	.	(+)	.	(+)	.	.	.	.	.	(+)	.	6
.	.	.	.	.	.	.	.	.	.	.	.	.	6
.	.	.	.	.	.	+	.	+	+	.	.	.	5
.	.	.	.	+	.	.	.	+	.	.	.	(+)	5
.	.	.	.	.	+	.	+	.	.	.	+	.	5
.	.	.	.	.	.	.	+°	.	.	.	.	.	5
+°°	.	.	.	+°°	.	.	.	.	.	.	.	.	4
.	.	.	.	.	.	.	.	.	.	.	+	.	4
.	(+)	+	.	.	.	.	.	(+)	.	.	.	.	4
.	.	.	.	.	.	+	+	.	.	.	.	.	4
.	+	.	.	.	.	.	.	.	.	.	.	.	4
.	.	.	.	(+)	.	.	.	.	.	.	.	.	4
.	.	+	+	.	.	.	+	.	.	.	.	.	4
.	.	.	.	.	.	.	.	.	.	.	.	.	3
.2	+0.2	.	(+)	(+)	+0.2	.	+0.2	.	+0.3	1.2	+	.	20
.3	.	1.2	.	+0.2	.	+0.2	.	.	1.2	.	.	.	18
0.2	.	.	.	1.2	+0.3	.	+0.3	.	1.3	2.2	.	.	12
.	.	.	.	+0.2	.	.	2.3	.	1.2	.	.	.	11
.2	.	.	(+)	.	.	.	.	.	.	.	.	.	7
+	.	.	.	.	.	.	.	.	.	.	.	.	5
.	.	.	.	.	.	.	.	.	.	.	.		4
.	.	.	.	.	.	+0.2	.	+	.	.	.		3

A. *Classification of higher units*

Associations which are nearly related ecologically are grouped into Alliances (termination -ion). Species of high fidelity are again used as the criterion for the same reasons as before. Fidelity is a relative concept, and so species of high fidelity to the Alliance have naturally a wider ecological amplitude than those faithful to the Association. Species which are faithful to one Association of an Alliance but which also occur in others of the same Alliance are included in those faithful to the Alliance under the designation of 'transgressive faithful species'. In the same way Alliances are grouped into Orders (-etalia), and Orders into Classes (-etea). The highest units seem to have been chosen initially on grounds of ecology and general life form, and faithful species for them have been supplied later (e.g. the Orders in Braun-Blanquet (1921) are distinguished by a key using habitat as the main criterion, and are given short ecological descriptions).

Below is reproduced an outline of the classification of the alpine and sub-alpine vegetation of Norway according to Nordhagen (1936). He does not name the Classes; but, in general, each of his orders belongs to a different Class. It will be seen that each Order coincides with a well-defined habitat type; and that most of them are easily recognizable in Scotland. The species after which the units are named are not always British species, and sometimes the naming is inappropriate.

1. Androsacetalia multiflorae. Communities of crevices on cliffs of acid rock.
   a. Saxifragion cotyledonis subarcticum.
2. Potentilletalia caulescentis. Communities of crevices on cliffs of basic rock.
   a. Asplenion viridis subarcticum.
3. Thlaspeetalia rotundifolii. Communities of basic scree.
   a. Arenarion norvegicae.
4. Myricarietalia germanicae. Communities of alluvium.
   a. Calamagrostidion neglectae.
5. Isoetetalia. Rooted aquatic communities.
   a. Isoetion lacustris.
6. Potametalia. Communities of aquatics.
   a. Potamion eurosibiricum.
7. Phragmitetalia. Reed beds, i.e. high-growing communities of swamps and lake-margins.
   a. Magnocaricion.
8. Scheuchzerietalia palustris. Oligotrophic communities of Monocotyledons (principally *Cyperaceae*) of wet ground.
   a. Scheuchzerion palustris.
9. Caricetalia goodenowii. Eutrophic-mesotrophic communities of Monocotyledons (particularly Cyperaceae) of wet ground.
   a. Caricion bicoloris-atrofuscae.
   b. Schoenion ferrugineae.
   c. Caricion canescentis-fuscae.
10. Montio-Cardaminetalia. Springs on base-poor and base-rich soils.
   a. Cratoneureto-Saxifragion aizoidis.
   b. Montio-Epilobion Hornemannii.

11. Arrhenatheretalia elatioris. Weakly manured pastures, mowing meadows and allied communities.
    a. Nardeto-Agrostidion capillaris.
12. Adenostyletalia or Aconitetalia. Tall-herb meadows.
    a. Aconition septentrionalis.
13. Chenopodietalia. Nitrophilous weed communities.
    a. Polygonion avicularis.
14. Elyneto-Seslerietalia. Grassland- and dwarf-shrub-communities of base-rich mountains.
    a. Elynion bellardii.
    b. Potentilleto-Polygonion vivipari.
15. Arabidetalia coeruleae. Communities on moist, base-rich detritus with affinities to snow-bed vegetation.
16. Salicetalia herbaceae. Snow-bed communities on acid detritus.
    a. Nardeto-Caricion rigidae.
    b. Cassiopeto-Salicion herbaceae.
    c. Ranunculeto-Oxyrion digynae.
    d. Allosoreto-Athyrion alpestris.
17. Caricetalia curvulae. Dry grasslands on acid mountains.
    a. Juncion trifidi.
18. Rhodoretalia ferrugineae. Dwarf-shrub communities of acid mountains.
    a. Loiseleurieto-Vaccinion uliginosi.
    b. Phyllodoco-Vaccinion myrtilli.
19. Ledetalia palustris. Dwarf-shrub communities of moor soils.
    a. Oxycocco-Empetrion hermaphroditi.

This system of Nordhagen has been reproduced as an example because the units which he has proposed can be discussed against the background of the communities which will be described from Breadalbane in Part III.

B. *Relation of succession to classification*

Braun-Blanquet criticizes the classification in one unit of the different stages of a sere, because the initial stages of two seres are often more closely related to one another than either is to the climax of its particular sere. The units of the Braun-Blanquet system, being based on level of organization, run across successional series. Associations occur at all levels (not only in the climax), and are conceived as stable steps in the process of development (cf. Braun-Blanquet & Jenny, 1926). ((This is comparable with the view expressed by Tansley 1920.)) Associations can be of two kinds, corresponding to the different kinds of fidelity (see p. 232); they may be either highly integrated, closed communities determined by the dominant species or the dominant life form (e.g. Quercetum ilicis), or collections of species which are loosely integrated, if at all, and which owe their presence to a certain type of habitat (e.g. scree) or to a regular pattern of interference (e.g. the Associations of the Rudereto-Secalinetea). They are in fact groups of communities which are repeated in more or less detail, at any level of organization, seral or climax. In the latter they are a much smaller unit than the Clementsian Association.

I am particularly indebted to Dr Godwin, for his guidance and encouragement in the preparation of this and the succeeding parts, and to Dr Braun-Blanquet for the hospitality

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APPENDIX

The nomenclature of vegetation units

Confusion in the nomenclature of vegetation units has been considerable. Gams (1918) and Du Rietz (1930) give tables of the correspondences between the usages of different authors.

At the International Botanical Congress of 1930 a committee was set up to make recommendations on standard usage. Du Rietz was elected recorder of this committee. Its recommendations were as follows:

(1) To use the term Sociation for vegetation units characterized mainly by dominance in the different layers, in the sense of the Scandinavian plant sociologists;

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

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

Dahl & Hadac (1941) believe that there is often in practice no such important distinction between Sociations and Associations.

Du Rietz (1936) proposes that a system of nomenclature for Synusiae should be adopted similar to the above for Biocoenoses. The successive categories in the two systems are as follows:

Synusiae	Biocoenoses
Society	Sociation
Union	Association
Federation	Alliance

(He also uses the term Consociation for groupings of sociations having a common dominant, either in the upper or the lower layer, though usually in the former.)

I have adopted these terms for units which correspond with their definitions, but without the implication that they can necessarily be grouped into higher units in this way. The additional term Nodum has been introduced to apply to an abstract unit (either Synusia or Biocoenose) of uncertain status. It corresponds to the term Taxon in systematics.

Gams (1932) uses the following further terms:

(1) Isoecia; abstract units built up of ecologically identical but floristically different Synusiae of different regions. (I question the use of the term 'identical').

(2) Isocoenoses; abstract units built up of floristically different but ecologically identical Consociations.

His Associations are not defined by faithful species but as composite vegetation units of Phytocoenoses which are formed by different but ecologically and geographically related dominant Societies.

The usage of Anglo-American authors is not considered here. Its correspondence with the above can be seen in the tables reproduced in the works cited above.

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