20 THE BRAUN-BLANQUET APPROACH

VICTOR WESTHOFF AND EDDY VAN DER MAAREL

Contents

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20 THE BRAUN-BLANQUET APPROACH

20.1 Introduction

We shall, in this last chapter, treat the floristic-sociological or Braun-Blanquet approach to classification and interpretation of communities. Before elaborating the details of the approach, we may state its essence in three ideas:

(i) Plant communities are conceived as types of vegetation, recognized by their *floristic composition*. The full species compositions of communities better express their relationships to one another and environment than any other characteristic.

(ii) Amongst the species that make up the floristic composition of a community, some are more sensitive expressions of a given relationship than others. For practical classification (and indication of environment) the approach seeks to use those species whose ecological relationships make them most effective indicators; these are *diagnostic species* (character-species, differential-species, and constant companions).

(iii) Diagnostic species are used to organize communities into a *hierarchical classification* of which the association is the basic unit. The vast information with which phytosociologists deal must, of necessity, be thus organized; and the hierarchy is not merely necessary but invaluable for the understanding and communication of community relationships that it makes possible.

The reader will see how far the elaboration of this three-part theme has led the members of the 'school of Braun-Blanquet.' The results are (like community relationships) complex. We fear lest the reader should lose sight of the heart of the approach — the floristic perspective — for the abundance of technical details that follow. The latter are only the skeleton of the approach. Furthermore, if we do not press the physical comparison too far, its body is the still-growing corpus of basic and applied research and the resulting knowledge of and insight into communities. This review must deal mainly with the skeleton of the approach; we cannot in the space we have discuss adequately the kinds of understanding of communities that have come from it. We ask the reader to recognize wherein this account must stop short, and to seek if he is interested a further feeling for what the approach offers by observing or reading studies applying it. On the other hand, we shall pay some attention (especially in sections 20.8 and 20.9) to recent developments in phytosociology that are not part of the BRAUN-BLANQUET approach as such but may be of value since they introduce concepts and methods that relate the floristic-sociological approach to other approaches.

Textbooks and reviews on the floristic-sociological approach have been published in most European countries, Argentine, India, Japan and the U.S.A. (see the bibliography by MAAREL, TÜXEN & WESTHOFF, 1970, Exc.[1]). Recent accounts include GOUNOT (1969), WESTHOFF & HELD (1969), and KNAPP (1971). Useful accounts in English are BECKING (1957), WHITTAKER (1962), KÜCHLER (1967) and SHIMWELL (1972).

20.2 **History**

The origin and history of the approach have been reviewed elsewhere and can be stated only briefly here (see GAMS 1918, BRAUN-BLANQUET 1921, and DU RIETZ 1921, as well as BECKING 1957, WHITTAKER 1962, and SHIMWELL 1972). The systematic description of plant communities and the idea of community types can be traced from great students of plant geography, HUMBOLDT (1805), SCHOUW (1823), HEER (1835) and GRISEBACH (1838). From their work two main approaches developed, the physiognomic and the floristic. The physiognomic approach developed as its principal unit the formation, a unit characterized by physiognomy or vegetation structure (POST 1862, GRISEBACH 1872, WARMING 1895; see article 13). Through the work of students dealing with smaller-scale units (esp. LECOQ 1844, 1855, THURMANN 1849, LORENZ 1858, KERNER 1863 and DRUDE 1890, in southern and central Europe, POST 1862, HULT 1881 and CAJANDER 1903 in northern Europe) there developed the essential idea of the floristic-sociological approach: plant communities as units of classification based primarily on species composition. From LORENZ (1863), MÖBIUS (1877) and DAHL (1908) a parallel approach to biotic communities can be traced. (See BALOGH 1958 and WHITTAKER 1962 for review and references.)

Much of the further development leading to the BRAUN-BLANQUET approach was centered in Zürich (STEBLER & SCHRÖTER 1893, SCHRÖTER 1894, SCHRÖTER & KIRCHNER 1902, BROCKMANN-

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[1] This and many other bibliographies to be mentioned in this contribution have been published in *Excerpta Botanica Sect. B Sociologica* (R. TÜXEN Ed). They will not be listed in the references, but indicated with 'Exc'.

JEROSCH 1907) and Montpellier (FLAHAULT 1893, 1898, 1901, PAVILLARD 1901, 1912). A main outcome of this period was a full hierarchy for vegetation classification—vegetation-type, formation-group, formation, subformation, stand-type down to local variants (Nebentypen) and geographic variants (Fazies). The stand-type was called the 'association' and considered the basic unit. FLAHAULT & SCHRÖTER (1910) agreed on the following definition, presented to the Third International Botanical Congress in Brussels, 'An association is a plant community of definite floristic composition, presenting a uniform physiognomy, and growing in uniform habitat conditions. The association is the fundamental unit of synecology.' (translation following PAVILLARD 1935b).

From this background BRAUN-(BLANQUET) carried out a monographic study of alpine vegetation (1913). In this, and the essay by BRAUN-BLANQUET & FURRER (1913), attention was focused on 'Charakterpflanzen' or character species — species that possess 'fidelity' (relative restriction) to a given association. GRADMANN (1909) had advocated the approach through floristic composition and the use of character species ('Leitpflanzen'). The key ideas in BRAUN-BLANQUET's treatment were: (i) The study of communities should be based on a fundamental unit, comparable to the species. (ii) This unit should be the association, and associations should be defined by their possession of character-species. (iii) Each association consists (like a species) of 'individuals,' and the association (like the species) can be described from samples of its individuals. (iv) Each sample ('Aufnahme,' relevé) should be chosen so as to represent adequately such an individual, and it should include analysis of the complete species assemblage. (v) Associations should be grouped into higher units not by physiognomy, but by floristic composition.

Additions to the approach came in further publications. BRAUN-BLANQUET (1915) added the 'Assoziationsgruppe' (later called the Verband, alliance) as a unit above the association, also defined by character-species. BRAUN-BLANQUET (1918) added the subassociation, as a deviation from the typical association expressed in a constant floristic difference, and the facies as a subordinate unit possessing merely quantitative differences. BRAUN-BLANQUET (1921) outlined essentially the full system, including the analytical scales (20.4.5) and the 'sociological progression' (20.3.4) for arranging communities by their levels of organization. BRAUN-BLANQUET (1925) pressed the claims of fidelity or 'Gesellschaftstreue' as the key to vegetation systematics, against the disagreement of northern schools. In the same essay he introduced the 'characteristic species combination' (charakteristische Artenkombination after SCHMID, 1923) as the ultimate community diagnosis, comprising both character-species and constant companion species. KOCH (1925) and BRAUN-BLANQUET & JENNY (1926) added the concept of differential-species for the characterization of subordinate units, and the order as a unit above the alliance. BRAUN-BLANQUET & PAVILLARD (1922, 1925, 1928) in their *Vocabulaire* codified the analytic and synthetic procedures of the approach. Finally the science of plant sociology and its application were spelled out more fully in the first edition of the textbook of BRAUN-BLANQUET (1928, 1932).[1])

From these beginnings the influence of the approach spread through western and central Europe. We cannot review that spread, but will mention such leaders as PAVILLARD, ALLORGE and MOLINIER in France, TÜXEN and OBERDORFER in Germany, SZAFER and PAWŁOWSKI in Poland, FURRER in Switzerland, SOÓ in Hungary, KLIKA in Czechoslovakia, HORVAT, HORVATIĆ and WRABER in Yugoslavia, BORZA in Rumania, GIACOMINI and TOMASSELLI in Italy, BOLOS in Spain, LEBRUN in Belgium, and DE LEEUW in the Netherlands. References for these authors are found in BRAUN-BLANQUET (1964, 1968). BRAUN-BLANQUET's own work began at Zürich and continued from 1927 onwards at Montpellier, where he still leads the S.I.G.M.A., Station Internationale de Géobotanique Méditerranéenne et Alpine. A second centre was established 1932 at Stolzenau, West Germany under Reinhold TÜXEN, a pre-eminent leader of the approach and former director of the Zentralstelle (later, Bundesanstalt) für Vegetationskartierung, who has done much to give the approach its value in application. From TÜXEN's centre the approach spread to various non-European countries as well, and notably to Japan.

During its spread the approach has been known by several names: French-Swiss (or Swiss-French) school, Zürich-Montpellier school, Middle European-Mediterranean school, and Sigmatism (TANSLEY 1922, DU RIETZ 1936, BRAUN-BLANQUET 1959, 1968, EGLER 1954, BECKING 1957, WHITTAKER 1962, TÜXEN 1969a). Most of these terms lack specificity or are unclear. Moreover we feel that the time has passed for the word 'school' with its implications of a fixed system. We prefer in this article the most direct name, viz. BRAUN-BLANQUET approach, whilst we may characterize the essential ideas in the term, the 'floristic-sociological approach.'

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[1]) One notes through this development of the full range of concepts the continuing contribution of BRAUN-BLANQUET himself, that has given the approach its present character (GAMS 1972 to the contrary).

20.3 **General Concepts**

20.3.1 CONCRETE VS. ABSTRACT UNITS

Much dispute has centered on the nature of the plant community. This will be briefly reviewed as far as the BRAUN-BLANQUET approach is concerned. (See further PAVILLARD 1935, WESTHOFF 1951, 1970, WHITTAKER 1962, BRAUN-BLANQUET 1964.)

Concepts of the plant community include: (i) the organismal concept (CLEMENTS 1936, TANSLEY 1920): the community as a 'superorganism.' (ii) the concept of social structure (PACZOSKI 1930) and many early Russian authors such as SUKATSCHEW (1929). (iii) the individualistic concept (GLEASON 1926): the community as a changeable mixture of 'individualistically' distributed plant species. (iv) the concept of population structure (WHITTAKER 1953, 1962, 1970): the community as a system of interacting species and vegetation as a complex population pattern.

The BRAUN-BLANQUET approach takes a practical, intermediate position that recognizes the heterogeneity of species distributions but emphasizes nonetheless the interactions between plants in the community, which has a certain individuality because of relative discontinuities between communities in the field. Definitions of plant community or phytocoenose range from the more superficial, 'any collection of plants growing together which has as a whole a certain unity' (TANSLEY 1935), to the more profound, 'a plant community (+animal community = biotic community) is a working community; the species composition of which is in a sociologic-dynamical equilibrium in competition for space, minerals, water and energy, in which each component affects all others and which is characterized by harmony between environment and production and phenomena expressing life in form, colour and temporal course' (TÜXEN 1957).

As shown by TÜXEN's definition, the community concept may be broadened from the plant community to the biotic community of plants and animals: producers, consumers and decomposers. In a further broadening of perspective the biotic community (= biocoenose) plus its environment or biotope is treated as a functional unit, the ecosystem. The concept of ecosystem has become most familiar from its expression in English-language ecology by TANSLEY (1935), but the concept is largely identical with FRIEDERICH's (1927, 1958) 'holocoene' and the 'biogeocoenose' of SUKACHEV (e.g. 1954, 1960) and other Russian authors. Though by far the greatest development of the BRAUN-BLANQUET approach has been in application to plant communities, biotic communities are clearly amenable to parallel study (section 20.7.2). Tüxen (1957, 1965b) has emphasized this possibility and stressed the influence of Friederichs and Thieneman (e.g. 1956) on his own views.

The term plant community and its German equivalent 'Pflanzengesellschaft' have been used in both concrete and abstract senses, which has caused dispute and confusion (see Tansley 1920, 1935, Du Rietz 1921, Alechin 1926, Pavillard 1935, Westhoff 1951, 1965, Whittaker 1956, 1962). The floristic-sociological approach has always stressed the distinction between the concrete and the abstract community. The classification units were, naturally, abstract units. Concrete plant communities were often, especially in forestry, referred to as stand (Bestand), whilst concrete representatives of associations were even called association-individuals (Pavillard 1912, Braun-Blanquet & Pavillard 1922). This term has been much disputed and criticized (most thoroughly by Whittaker 1962) and we consider it now as of only historic interest.

Westhoff (1951, 1965) has acknowledged the distinction between concrete and abstract communities in separate definitions, which were linked to a general definition of vegetation. For the concrete plant community the term phytocoenose (Gams 1918) was proposed, for the abstract community the term phytocoenon (Maarel 1965, specifying the general term 'coenon' proposed by Barkman et al. 1958, Westhoff et al. 1959).

The term (phyto)coenon may be proposed as a suitable international term which may replace the terms community-type (Whittaker 1956, 1962) and nodum. The latter term has been suggested by Poore (1956, 1962), but has been used in a more specific meaning by Williams & Lambert (1961) in their 'nodal analysis' (cf Ivimey-Cook & Proctor 1966).

For biotic communities parallel terms: biocoenose and biocoenon may be used (Maarel 1965). For partial communities Mörzer Bruyns' (1950) term merocoenose can be used with merocoenon as the abstract equivalent. Layer communities could be called, stratocoenose-stratocoenon. For specific subcommunities consisting of plants of the same stratum, life-form and seasonal relations the couple, society-synusia may be reserved. (See further article 16.)

In conclusion we present Westhoff's (1951, 1970) definitions in a slightly adapted form. Vegetation is defined as a system of largely spontaneously growing plant populations, growing in coherence with their sites and forming an ecosystem with these sites and all other forms of life occurring in these sites. (Thus are excluded all assemblages of mobile plants and collections of plants growing in arrangements set up by man such as flowerbeds and arboreta.)

A phytocoenose is defined as a part of a vegetation consisting of interacting populations growing in a uniform environment and showing a floristic composition and structure that is relatively uniform and distinct from the surrounding vegetation.

A phytocoenon is defined as a type of phytocoenose derived from the characterization of a group of phytocoenoses corresponding with each other in all characters that are considered typologically relevant.

20.3.2 FLORISTIC-SOCIOLOGICAL CLASSIFICATION UNITS

Phytocoena include such various kinds of vegetation units as formations defined by physiognomy, dominance-types defined by major species, forest site-types defined by undergrowth composition, and noda derived by quantitative comparisons or numerical procedures. The approach of BRAUN-BLANQUET has its own, formal hierarchy of units, of which none of those just mentioned is a part. The fundamental unit of the hierarchy is the *association*, a unit that corresponds in function to the species as the fundamental unit of idiotaxonomy, or the classification of individual organisms. The word 'association' has had a long, complex, and argument-afflicted history as different schools sought to determine its meaning to their preference (WHITTAKER 1962, SHIMWELL 1972, see also articles 14, 17 and 18). In an earlier definition by BRAUN-BLANQUET (1921) 'the association is a plant community characterized by definite floristic and sociological (organizational) features which shows, by the presence of character-species (exclusive, selective, and preferential) a certain independence.' MEIJER DREES (1951) defined the association as ' a plant community identified by its characteristic taxon combination, including one or more (local) character-taxa or differentiating taxa.' A similar conception was agreed on during a Symposium on Plant Sociological Systematics at Stolzenau in 1964 (in TÜXEN 1968b, especially OBERDORFER 1968) and a later colloquium at Rinteln (see DIERSCHKE 1971). We shall return to characterization of the association (20.6.2) but emphasize that, in keeping with the floristic-sociological perspective, the association is defined by its *characteristic species combination* including character- and differential-species as well as companions (Begleiter) with high presence values (over 60%). The Sixth Botanical Congress at Amsterdam, 1935, accepted definition of the association by characteristic or differential species in the sense of BRAUN-BLANQUET as one of three resolutions given in article 18.3.6.

As basic units associations, like species, are to be grouped into a hierarchy of higher units. Associations are classed into alliances, alliances into orders, orders into classes, and classes into divisions (20.6.4-5); associations are divided into lower units of the hierarchy (20.6.7). All these units are coena as defined above; but the coena of the formal system of BRAUN-BLANQUET may be termed *syntaxa* (BARKMAN et al. 1958, WESTHOFF et al. 1959). Thus the parallelism in the classification of organisms and phytocoenoses is realized: to the species as a fundamental unit corresponds the association, to the taxon for units on any level corresponds the syntaxon, to (idio)taxonomy for the practice of classification corresponds syntaxonomy, to (idio)systematics as the broader study of relationships among organisms corresponds synsystematics.

20.3.3 DIAGNOSTIC SPECIES

Syntaxa are defined by diagnostic species (character-species, differential species, and constant companions). *Character-species* are species that are relatively restricted to the stands (or samples) of a given phytocoenon, and therefore characterize it and indicate its environment (Fig. 1). In ideal, a group of character-species is used for the characterization of a syntaxon of the BRAUN-BLANQUET classification on any level from the association to the class. To serve as character-species for an association, a species should have a relatively narrow distribution even if it is not simply restricted to the association. (Degrees of restriction to a given syntaxon, which are termed degrees of *fidelity* or Treue, are discussed in 20.5.6.) Note that the concept does not say that the species need be important in phytocoenoses; very minor species may have diagnostic value.

The German term is 'Charakterart'; this has been variously translated into English as characteristic species (BRAUN-BLANQUET 1932), which seems unsatisfactory, faithful species (POORE 1955a, BARKMAN 1958a, BEEFTINK 1962, MOORE 1962, WESTHOFF 1959), and character-species (BECKING 1957, WHITTAKER 1962). The latter, most direct translation, is our preference. HEIMANS (1939) introduced 'kensoort' in Dutch to avoid the germanism 'karaktersoort'; and the Dutch kensoort returned to German as *Kennart* (TÜXEN 1950: 99). Most phytosociologists writing in German now use that term, which is accepted in the third edition of BRAUN-BLANQUET's (1964) text. Syntaxa are most often defined by the fundamental units of idiotaxonomy — species —, but this is not always the case. Sometimes plant subspecies, varieties, or ecotypes may contribute to the definition of lower-level syntaxa or geographically vicariant

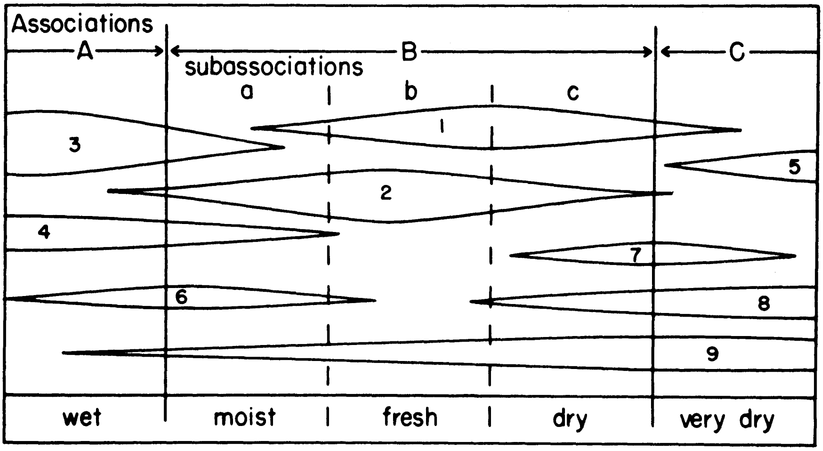

Fig. 1. Diagnostic species along a moisture gradient. Species 1 and 2 are character-species for association *B*, and have their populations centered in (or largely confined to) that association. Species 3 and 4 are character-species for association *A*, and species 5 is a character-species for association *C*. Species 4 and 6 are differential-species for subassociation *a* of association *B*, and species 7 and 8 are differential-species for subassociation *c* of association *B*. In each case presence of the differential-species distinguishes the moist, or dry, subassociation from the "typical" (fresh) subassociation *b*. Species 9 is a more widely distributed species that might help characterize association *B* as a constant companion for that association. Species 9 might also be a character-species for a higher syntaxon, such as an alliance uniting associations *B* and *C* with other associations.

associations. Sometimes a genus or subgenus may be used to define a higher syntaxon, as the alliance Spartinion is defined by the fidelity of any species of the genus *Spartina* (BEEFTINK 1965, 1968, see also PIGNATTI 1968a: 72, WESTHOFF apud PIGNATTI 1968a: 74). It is therefore appropriate to broaden character-species to character-taxon (BARKMAN et al. 1958) as we shall do here following Dutch use of 'kentaxon' (WESTHOFF & HELD 1969). The German equivalent is of course 'Kenntaxon'.

Character-species characterize syntaxa by their normal occurrence in phytocoenoses of that syntaxon, contrasted with their absence less frequent occurrence or smaller total estimate in phytocoenoses of all other syntaxa. It is possible also to distinguish closely related syntaxa by the presence and absence of certain species without concern for the broader distributions of those species. Two subassociations of an association may be characterized by the fact that samples of one normally include species 4 and 6, whereas samples of the other normally lack these species (Fig. 1). These species function as *differential-species* that distinguish the two subassociations. Differential-species, as the second class of diagnostic species, define syntaxa on the basis of the distributional boundaries of species (without regard to fidelity for the syntaxa in question), and are used primarily to define lower syntaxa.

Since being introduced by KOCH (1925) and BRAUN-BLANQUET (1925) as 'Differentialart', the concept has entered English as differential species (BRAUN-BLANQUET 1932, WHITTAKER 1962) or differentiating species (BECKING 1957), whilst in German the term *Trennart* has come into general use (TÜXEN 1950, 1952, BRAUN-BLANQUET 1959, 1964a) in parallel with Kennart. The use of differential-species has been further developed by SCHWICKERATH (1931, 1942, 1954a) and TÜXEN (1937, 1950, 1952). Differential-species and Trennart are synonyms, and these are largely synonymous also with differentiating species; but we shall here use 'differentiating species' for the more informal use of diagnostic species of unassigned syntaxonomic position in the synthetic phase of research (20.5), and speak of differential-species and differential-species groups for the formal characterization of syntaxa (20.6). A further recent development is the concept of 'character-combination' (after the Dutch kencombinatie) introduced by WESTHOFF & HELD (1969) following BEEFTINK (1965, 'differentiating species combination'). The essential concept is the exclusiveness to a syntaxon of the combination of species (or taxa), whilst none of them need be a character-taxon.

A third group of species with diagnostic value are the constant companions (20.5.3) which occur in most relevés of a syntaxon but are not designated as character- or differential-species. Constant companions are added to the character-taxa to form the 'characteristic species (taxon) combination' for associations and higher taxa. Although BRAUN-BLANQUET (1925) introduced this concept rather early and repeatedly (e.g. 1959, see MOORE 1962) stressed its relevance there has been doubt amongst critics (e.g. POORE 1955-1956). Of course, as BRAUN-BLANQUET (e.g. 1932: 68) remarked for associations, these syntaxa are established best which possess a high proportion of both characteristic and constant species.

20.3.4 SOCIOLOGICAL PROGRESSION

BRAUN-BLANQUET (1921) sketched an 'arrangement of the plant communities according to their sociological progression.' The idea of this arrangement was again a parallel with idiobiology, specifically with the arrangement of taxonomic groups by evolutionary level. Levels of structural and organizational development were chosen as criteria for arranging phytocoenoses from moving aero- and hydroplankton communities on the lowest level to the tropical rain forest at the highest level. Other communities are arranged between these according to increasing stratification, complexity, presence of dependent communities, species richness, diversity of growth-forms, and assumed intensity of species interactions. Thus BRAUN-BLANQUET (1921) summed up many of the structural-successional trends much later commented on by ODUM (1969)! The scheme was later modified in detail, and increasing stability was added as a criterion. BRAUN-BLANQUET (1964) arranges higher syntaxa (classes and orders) in the progression.

WAGNER (1968) called the sociological progression a 'purely artificial division principle' (cf. ELLENBERG 1963). Of course, no phylogenetic meaning should be imputed to its sequence. Yet the sociological progression is useful, as a principle at right angle to the levels of the hierarchy, in arranging syntaxa in surveys. Its use is illustrated in vegetation monographs by TÜXEN (1937), OBERDORFER (1957), ELLENBERG (1963), OBERDORFER et al. (1967), WESTHOFF & HELD (1969), and others. It may be of interest that it has appeared also as an axis of broad-scale ordination of syntaxa (MAAREL 1972a, see 20.9.2).

20.3.5 NATURAL CLASSIFICATION

The problem of 'natural' classification has been discussed in another article (12.1.2). It has been accepted by BRAUN-BLANQUET and others that associations are abstract units. A degree of continuity or gradualness in transitions between phytocoena is recognized, but considered not to preclude classification. 'We are convinced that the plant cover of the earth in all its dimensions can be divided into phytosociological groupings of higher and lower rank; their delineation may be either sharp or less sharp and gliding.' (BRAUN-BLANQUET and TÜXEN in comment on GOODALL 1963, translated.)

American research in gradient analysis has led to interpretations that may seem in conflict with those of BRAUN-BLANQUET. The American work of WHITTAKER (1951, 1954, 1956, 1962, 1967, articles 2 and 3) and CURTIS (CURTIS & MCINTOSH 1951, CURTIS 1959, MCINTOSH 1967, article 7) developed in parallel to Russian work of RAMENSKY (1930, article 17) toward the concept expressed by WHITTAKER (1970) as 'the population structure of vegetation.' In this concept the population structure of the individual phytocoenose may be analysed through dominance-diversity and species-importance relations, and niche differentiation among plant species expressed in stratification and functional differences among them. The phytocoenose is then conceived as a 'system of interacting, niche-differentiated and partially competitive species.' The vegetation of an area, on the other hand, is to be approached through gradient analysis, studying the manner in which species populations are distributed along environmental gradients and combined into phytocoenoses. Species are differently distributed from one another, so that undisturbed phytocoenoses intergrade continuously in most areas. 'In relation to patterns of environmental gradients, communities form complex and largely continuous population patterns.' (WHITTAKER 1970, article 3.9.)

It is further recognized that, 'Because of environmental interruptions and some relative discontinuities inherent in vegetation itself, the pattern may also be considered a complex mixture of continuity and relative discontinuity' (WHITTAKER 1956: 32). Vegetational continuity by no means precludes useful classification (WHITTAKER 1956, 1962, 1970). Gradient analysis implies a vision of vegetation, regarded as a coherent pattern of intergrading phytocoenoses, different from that of phytosociologists who tend to see it in terms of a typology of phytocoena (see, however, 20.7.4 on complexes). Yet we think that the difference between the concept of the gradient approach and BRAUN-BLANQUET's is clearly one of degree — of emphasis of continuity vs. discontinuity where both are present, of species individuality vs. species groupings where both are realistic, and of gradient analysis vs. classification where both are possible. We judge the difference between less extreme students of gradient analysis, and of the BRAUN-BLANQUET approach, to be one of emphasis and perspective, not one of fact or understanding.

Given the individuality of species distributions and some degree of continuity between phytocoenoses, classification is not strictly natural in the sense defined in article 12.1.2. BRAUN-BLANQUET (1951a: 561, 1959: 147) has considered argument on the naturalness of classification pointless. TÜXEN (1955), in response to a criticism of ELLENBERG (1954b), interpreted phytosociological classification through the concept of *types* as ideal concepts, recognized in an empirical way from 'correlation concentrates,' i.e. groups of correlated characters. That which is evident and characteristic of a type is always its nucleus, not its periphery; types are not pigeonholes but foci in a field of variation. GLAHN (1968, see also RAUSCHERT 1969) elaborated the concept of vegetation type, distinguishing as its three aspects: (i) The vegetation type as identity: repetitions of certain observations are approached via intuitive integration, resulting in vegetation-type concepts based on recurring combinations of species. (ii) The vegetation type as maximal correlative concentration: The joint floristic-sociological and ecological approach leads to types as correspondences of recurring species combinations with recurring combinations of environmental factors. (iii) The vegetation type as systematic category: A hierarchic system is feasible as a result of an integrative, inductive process grouping the initial types into higher and higher ranks on the basis of common species combinations. The similarity of this statement to the theory of classification developed at greater length by WHITTAKER (1962) may be noted. Relative naturalness of classification in this perspective is to be judged by success in embodying the maximum number of significant relationships among phytocoena and species in the structure of the hierarchy. We assert that compared with other classifications the BRAUN-BLANQUET approach, with its floristic emphasis and maximum use of species distributional relationships for classification, does not fall short.

20.4 **Analytical Research Phase**

20.4.1 RECONNAISSANCE AND CHOICE OF PLOTS

An analysis of the vegetation is as a rule preceded by a preliminary survey of the area, when this is little known to the investigator. This reconnaissance (see CAIN & CASTRO 1959) includes a study of the general vegetation pattern, and the establishment of the apparent relations of the various vegetation types with geology, topography and soil conditions. The next step, 'primary survey,' including a superficial description of the major communities, is mostly passed over in the BRAUN-BLANQUET approach.

A vegetation analysis starts with the choice of stands (phytocoenoses) on the basis of the reconnaissance. Within the stand one sample plot is laid down, often covering a large part of the stand. The analysis of this plot is called the *relevé*. The BRAUN-BLANQUET approach has often been criticized for the subjectivity of its sampling procedure. However, subjectivity of stand choice must be accepted in the procedures of many empirical sciences. A selection of relevés is desired that will effectively represent the variation in the vegetation under study, the samples being so chosen that they will not represent different phytocoena disproportionately and will not include mixed, incomplete, or unstable stands. For this purpose of equitable representation of different kinds of communities with most useful relevés, a subjective, 'stratified' sample selection is far superior to sample choice by random points on a map.

Relevés may be undertaken without classification as a purpose. They may then serve for the study of vegetation dynamics on a given area (periodicity, fluctuation, or succession) or another ecological purpose, e.g. the study of the ecology of a certain taxon or ecotype by describing its pattern in relation to the pattern of the vegetation. In most cases, however, relevés are intended to be used for some form of classification or ordination. In that situation, the only preconception in this choice is the demand for uniformity of the stand.

'Uniformity' may better express what is sought than 'homogeneity.' This chapter is not the place for a treatment of the mathematical aspects of homogeneity in vegetation; we may refer to POORE (1955, 1956), ELLENBERG (1956), DAHL (1957, 1960), BECKING (1957), LAMBERT & DALE (1964), BRAUN-BLANQUET (1964), MAAREL (1966b) and GOUNOT (1969) for general considerations, to GOODALL (1952, see also his bibliography, 1962 Exc.), DAHL & HADAČ (1949), DAHL (1957), GREIG-SMITH (1964) for aspects of homogeneity in the distribution of plant individuals, to GOODALL (1961) and GREIG-SMITH (1964), for pattern analysis, to RAUNKIAER (e.g. 1934), GUINOCHET (1955), DAHL (1957), CAIN & CASTRO (1959) for the relation between homogeneity and frequency distribution and to CURTIS (1959), GODRON (1966) and GOUNOT (1969) for infrastand similarities and information measures as approaches to homogeneity.

The first condition is that no obvious structural boundaries or variation in stratification are visible within the stand. The second criterion is uniform floristic composition. It is usual to look for joint patterns of dominant and/or abundant species and then to delimit a stand where qualitative changes in patterns occur, i.e. where one or more species drop out and others come in. In many cases an experienced field worker is able to judge this rapidly. In many cases however the changes in pattern are quantitative rather than qualitative. The species composition differs little from one site to an adjacent one, but the relative proportions of abundance and cover do vary. It is usual to make separate relevés in any case where the abiotic habitat factors show a clear discontinuity or at least a marked transition.

Many species cause pattern heterogeneity only by their growth form or their aggregation or shoot clustering. In such a case one may try at first to study this biotically heterogeneous pattern as one single stand, i.e. with one relevé. However, the situation becomes different as soon as the crowding of one major species leads to the establishment of one or more other species which appear to be locally bound to it. A simple example is the establishment of a dwarf shrub patch in a herbaceous vegetation, e.g. a clone of *Salix repens* in open dune grassland. When one or more species are found particularly bound to that dwarf shrub patch we prefer to consider the latter as a separate phytocoenose which has thus to be analysed with a separate relevé. However, there are exceptions to this rule. E.g. OBERDORFER (1970, Canaries) and WERGER (1973, South Africa) report stable savanna mosaics consisting of a dwarf-shrub and grassland and a low tree and shrub phytocoenose. Such mosaics are considered one vegetation type, since one does not find locally more extensive patches of either phytocoenose without adjacent patches of the other one.

In intermediate or doubtful cases, such as a swamp community with tall tussocks of sedges (*Carex hudsonii*) alternating with wetter hollows, it will be advisable, at least when the type of vegetation pattern is unknown, to follow both procedures, viz. analysing the pattern as a whole as well as relevés of tussocks and hollows separately. It will then turn out later which relevé is more useful for the classification purpose.

20.4.2 BOUNDARIES

As was said before, the recognition of distinct stands may presuppose the occurrence of discontinuities in the field. Although according to the opinion of BRAUN-BLANQUET workers such discontinuities are mostly to be observed, it is obvious that boundaries between stands are less sharp in some cases than in others. In such cases the boundary may be detected by means of a belt transect analysis or a 'line taxation.' Such transects consist of a series of small quadrats laid down at right angles to the extension of the boundary zone. By comparison of quantitative data on species occurrences in the quadrats the boundary zone can be discerned from the uniform phytocoenoses. MAAREL (e.g., MAAREL & LEERTOUWER 1967) and FRESCO (1972) refined boundary analysis by constructing 'differential profiles,' in which can be shown degrees of change between adjacent quadrats along a gradient. For similar techniques see article 5.4.4.

In general we may distinguish between two types of boundary zones which are, according to the relation theory of LEEUWEN (1965–1970, WESTHOFF 1971a, b, WESTHOFF & LEEUWEN 1966, SHIMWELL 1972), the limes convergens and the limes divergens. The *limes convergens* zone, or convergent limit, is characterized by sharp

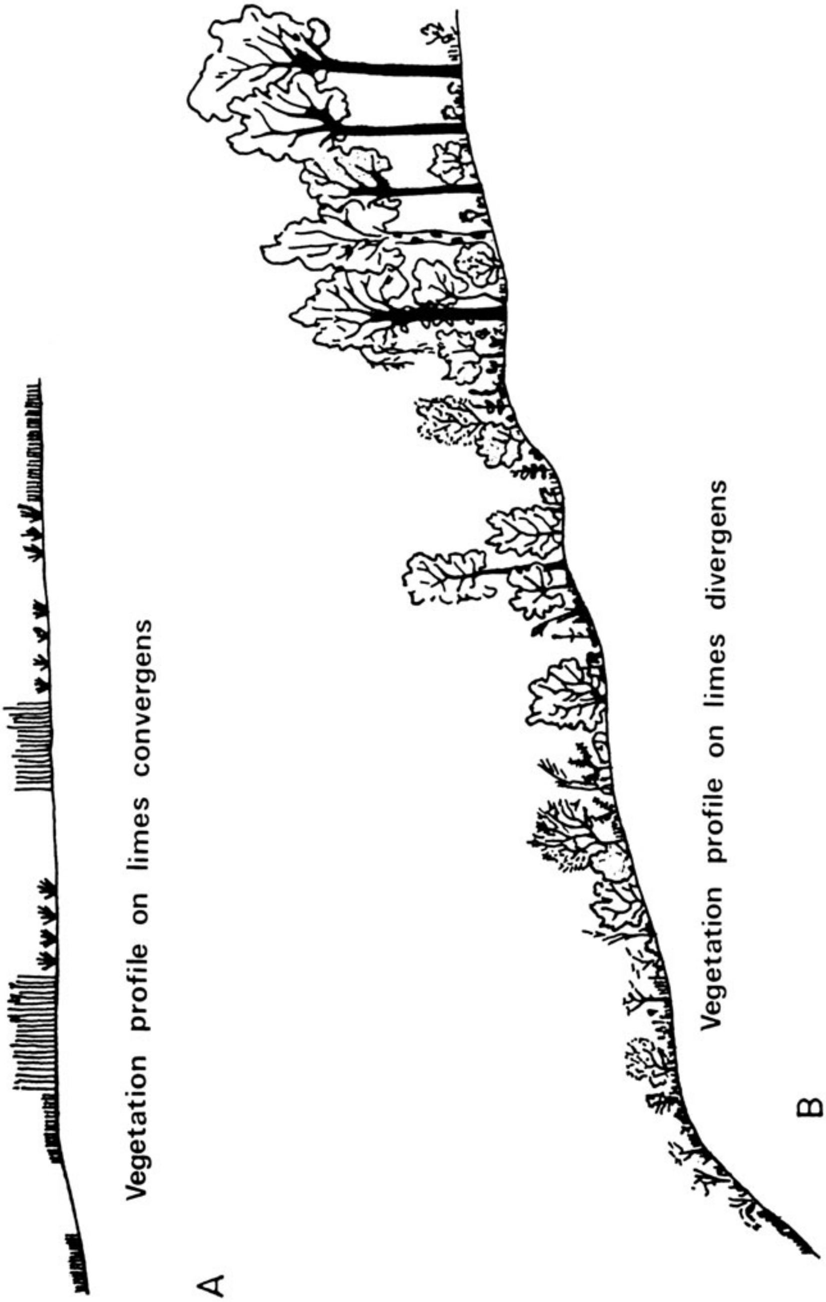

Fig. 2. Vegetation profiles corresponding to the limes convergens and limes divergens zones (LEEUWEN 1965).

vegetational boundaries on either side of which uniform phytocoenoses occur, with few species represented, some by many individuals, in coarse-grained patterns. The corresponding environment is unstable, i.e. with sharp fluctuations in vertical direction (e.g. water-table or phreatic level) or in horizontal direction (e.g. deposition of flood marks). A typical synsystematical unit of this type is the Agropyro-Rumicion crispi.

The *limes divergens* zone, or divergent limit, is characterized by numerous small-scale boundaries in phytocoenoses merging continuously into each other, with many species generally represented by few individuals in fine-grained patterns. The corresponding environment is stable and determined by a gradient. A typical series of divergent synsystematical units is Mesobromion-Trifolion medii-Carpinion betuli. Fig. 2 shows a vegetation profile belonging to these types of boundary. According to MAAREL (e.g. 1966a), LEEUWEN (1966) and WESTHOFF (1971a) the ecotone concept of LIVINGSTONE and CLEMENTS (e.g. WEAVER & CLEMENTS 1938, CURTIS 1959) could be applied to the limes convergens zone, whilst the ecocline concept as derived from HUXLEY's cline concept (WESTHOFF 1947, MEIJER DREES 1951) may be considered an equivalent of the limes divergens zone.

The delimitation of stands within ecotones generally gives no difficulties, except for pattern problems already discussed. Gradients of vegetation-and-biotopes (ecoclines) can be approached by belt transects following the direction of variation, which transects have to be divided into sample plots (not necessarily quadrats) small enough to be uniform. Recently JAKUCS (1972) gave examples of this approach in 'grassland-shrub-woodland' transitions within the range of the Quercetea pubescenti-petraeae in Hungary.

20.4.3 MINIMAL AREA AND PLOT SIZE

The size of the sample plot is largely dependent on the structure of the vegetation under study, but may be affected also by the size of the stand. In many cases the stand is sufficiently small to be analysed largely in one relevé. In many other cases, however, this is not possible, and then the plot should be large enough that all species of regular occurrence in the stand should be present in the sample plot. In extremely uniform phytocoenoses which are very poor in species, e.g. salt marshes, where differences in abundance and cover are of major concern, these differences should be considered in establishing the size of the sample plot.

These conditions refer to the minimal area concept (see also articles 5.2.1, and 18.3.3). Without treating this concept in detail we may give some comments relevant to the phytocoenose description. First the minimal area as an analytical concept (for the phytocoenose) has to be distinguished from the synthetic minimal area (for the phytocoenon). The analytic minimal area should be defined for a stand under study as a representative area, e.g. as an adequate sample of species of regular occurrence in the stand; the size decision may, but will not necessarily, be based on the total number of species in the stand or the usual minimal area curve (BRAUN-BLANQUET 1964, CAIN & CASTRO 1959, DU RIETZ 1921, 1930, GOODALL 1952, 1961, GREIG-SMITH 1964, HOPKINS 1957, MAAREL 1966b, TÜXEN 1970c and 1970 Exc., VESTAL 1949). A synthetic minimal area, in contrast, is subject to many current definitions (e.g. BRAUN-BLANQUET 1964, CAIN & CASTRO 1959, and WESTHOFF 1951 — who explicitly defined it as 'the minimal surface which has as a rule to be occupied by a sample of a plant community if the normal specific assemblage will be able to develop'). The size decision in this case involves not merely the stand itself but the 'normal' composition of stands representing a phytocoenon. It is clear that before judging this in the field one should know from synthesis the characteristic species combination. Nevertheless many authors, including BRAUN-BLANQUET (1964), describe the normal species-area determination, applied analytically to the stand, as the way to find the minimal area.

TÜXEN (1970c) presented numerous examples of species-area curves ending in a horizontal part, implying that at the sample size where the horizontal part begins, full species representation or saturation has been reached. Tüxen consequently spoke of 'saturated communities,' which he found among homogeneous communities of various organization levels. He cited various authors who found curves of the same type, including DU RIETZ (1921).

Most authors, e.g. BRAUN-BLANQUET (1964), CAIN & CASTRO (1959), HOPKINS (1955), and MAAREL (1966b) have found curves that never reach an asymptote. It is true that many of their curves refer to either relatively small or relatively large areas. It remains unclear in which situation which type of species relation can be expected — the ARRHENIUS-type of a log-log relation (cf. PRESTON 1962), the ROMELL-type of a log-linear relation (cf. HOPKINS 1955, DAHL 1957, WILLIAMS 1964, MAAREL 1966b), or the KYLIN-type of saturation relation. BALOGH (1958), and MAAREL (1966b), quoting FREY (1928), who presented the three types, interpreted them as referring to very uniform and species-poor environments (limes convergens type!), highly variegated and

TABLE I

Minimal area values in square meters for various communities

Epiphytic communities	0.1–0.4
Terrestrial moss communities	1–4
Hygrophylous pioneer communities (Isoeto-Nanojuncetea)	1–4
Dune grasslands (Koelerio-Corynephoretea)	1–10
Salt marshes (Asteretea tripolii)	2–10
Pastures (Lolio-Cynosuretum)	5–10
Mobile coastal dune communities (Ammophiletea)	10–20
Hay meadows (Arrhenatheretalia)	10–25
Heathlands (Nardo-Callunetea)	10–50
Alpine meadow and dwarfshrubs (Elyno-Seslerietea)	10–50
Calcareous grasslands (Festuco-Brometea)	10–50
Chaparral, temperate sclerophyll shrubland	10–100
Weed communities (Secalietea)	25–100
Scrub communities (Rhamno-Prunetea)	25–100
Steppe communities	50–100
Temperate deciduous forest (Querco-Fagetea)	100–500
Mixed deciduous forest (North America)	200–800
Tropical secondary rainforest	200–1000
Tropical swamp forest	2000–4000

species-rich situations (limes divergens type), and intermediate types or (BALOGH) 'normal homogeneous stands', respectively.

Table I presents some minimal area values for community types, taken from various sources. (See TÜXEN, 1970 Exc. for a bibliography). They range from a few dm^2 for certain epiphytic communities to one hectare or more for climax tropical rain forests. In general the plot size is taken somewhat larger than the minimal area. It will be clear that plot size should not vary too much within one vegetation type. The shape of the plot is not standardized and may depend on the situation. If possible, a quadrat of rectangular shape is to be preferred.

20.4.4 DESCRIPTION OF STRUCTURE AND STRATA

Vegetation layering is an important structural character. Mostly only four principal layers are distinguished as the tree, shrub, herb, and moss layers. The latter is also named field layer or thallophyte layer (which is less adequate, because many of the larger fungi do not belong to it). These principal layers may be further subdivided. In the relevé as many layers are distinguished as is considered appropriate or necessary. For each layer height and coverage degree in per cent, mostly with 5–10% intervals, are estimated. For tree and shrub layers the age is estimated and additional data on stem diameter, number of dead or fallen trees, and occurrence of epiphytic communities are gathered.

Stratification can be more accurately described with the help of diagrams in which the total or combined cover of each layer is indicated (HULT 1881, BRAUN-BLANQUET 1928, cf. CAIN & CASTRO 1959, KNAPP 1971). These diagrams are related to vertical profiles, as have frequently been presented for tropical rain forest (see article 13.4.2) and by ZONNEVELD (1960) for the freshwater tidal delta of the Rhine. Both however have their own special uses. The profile can show exactly the structure of a given phytocoenose; in the coverage-stratification diagram a pattern typical for a phytocoenon can be generalized (CAIN & CASTRO 1959). A more formal method is that of DANSEREAU (1957, DANSEREAU & ARROS 1959) for the description and recording of vegetation on a structural basis (see article 13.3.3).

It is possible to classify different strata into separate synusial units. This approach is treated in detail by BARKMAN (article 16). The BRAUN-BLANQUET approach however considers the main strata of a given stand as a single phytocoenose which has to be analysed as a whole, at least as far as terrestrial communities are concerned. The main arguments are: (i) The different strata are rooting in a common substratum; (ii) The layers are ecologically closely interrelated; (iii) The plants of all other layers have originally been part of the field layer and they must pass through one or more layers as they develop from seedlings to their mature life-form stature. The layered community is, then, a dynamic totality (see WEBB et al. 1967b on the vertical integration of the rain forest).

The situation in aquatic communities of higher plants is less clear however. Here the coherence of layers is much looser, or absent. DU RIETZ (1930a) has proposed a stratification scheme, which was modified by HARTOG & SEGAL (1964) (see also article 16.4.3). Layers are distinguished according to rooting or non-rooting of plants and the positions of leaves in relation to the water surface. The layers are named by growth-forms after representative genera, e.g. the isoetid layer.

An additional analysis can be made of subterranean layers. For a treatment of root stratification see BRAUN-BLANQUET (1964: 59–62). Bibliographies of root studies were given by WILMANNS (1959 Exc., 1966 Exc.) and TÜXEN & WILMANNS (1973 Exc).

20.4.5 FLORISTIC ANALYSIS

20.4.5.1 *Cover and Abundance*

The description of structure is followed by an inventory of taxa, at least of phanerogams, pteridophytes, bryophytes and lichens.

TABLE II

The combined estimation (cover-abundance) scale of Braun-Blanquet, compared with the cover-abundance scale of Domin (See Evans & Dahl 1955). The subdivisions 2m, 2a, and 2b are proposed by Barkman et al. (1964). The ordinal transformation is discussed in 20.5.4.

Braun-Blanquet, cover-abundance		ordinal transform	Domin	
			+	one individual, reduced vigor
r	one or few individuals	1	1	rare
+	occasional and less than 5 % of total plot area	2	2	sparse
1	abundant and with very low cover, or less abundant but with higher cover; in any case less than 5 % cover of total plot area	3	3	< 4 %, frequent
2	very abundant and less than 5 % cover, or 5–25 % cover of total plot area			
2m	very abundant	4		
2a	5–12.5 % cover, irrespective of number of individuals	5	4	5–10 %
2b	12.5–25 % cover, irrespective of number of individuals	6	5	11–25 %
3	25–50 % cover of total plot area, irrespective of number of individuals	7	6 7	26–33 % 34–50 %
4	50–75 % cover of total plot area, irrespective of number of individuals	8	8	51–75 %
5	75–100 % cover of total plot area, irrespective of number of individuals	9	9 10	76–90 % 91–100 %

The taxa are listed according to the layer in which they grow. Plants which appear to be structurally transgressive, i.e. occurring in more than one layer, have to be recorded in each of these layers separately.

Taxa occurring only outside the sample plot (but within the stand) are noted in parentheses. Next, the quantitative occurrence of each taxon is estimated. In the Braun-Blanquet approach two criteria are considered most useful: abundance and coverage degree. Abundance relates to the density of the individuals of a given species in a plot. Cover degree is measured as the vertical projection of all aerial parts of plants of a given species as a percentage of the total plot area. The term 'dominance,' often used as a synonym for coverage, is less appropriate.

Abundance and cover degree are usually estimated together in a single 'combined estimation' or 'cover-abundance' scale. The five-point scale in Table II, from BRAUN-BLANQUET (1928, see also article 18.4.1) is in general use. Several authors (e.g. TUOMIKOSKI 1942, DOING 1954, EVANS & DAHL 1955, BARKMAN et al. 1964) used more detailed scales of combined estimation; the BRAUN-BLANQUET symbol 2 especially was refined. The more elaborate scales are useful for special purposes, e.g. for an accurate record of change of abundance and cover by succession on permanent sample plots in the course of years (DOING 1954). However, they often suggest more accuracy than can really be justified. Only values obtained by one investigator should then be compared (cf. CAIN & CASTRO 1959: 142–143, MAAREL 1966b). We have recently introduced as a refinement of scale interval 2 (taken from BARKMAN et al. 1964) the scale subdivisions 2m, 2a, and 2b given in Table II. This elaboration, which brings the total number of scale values to 9, has proved to be useful and reliable.

20.4.5.2 *Sociability*

Sociability or gregariousness is an expression of horizontal pattern of species. It is a measure of the degree of clustering (contagion) of the plant units of a species. A plant unit (WILLIAMS 1964) may be an individual or a shoot or a sprout-forming part of an individual. Measurement of sociability goes back (again) to HEER (1835).

In the floristic-sociological approach sociability is estimated with the following scale (BRAUN-BLANQUET 1928, 1932, 1951, 1964).

1. growing solitary, singly.
2. growing in small groups of a few individuals, or in small tussocks (caespitose), e.g. *Corynephorus canescens* in shifting sands.
3. growing in small patches, cushions or large tussocks, e.g. *Carex hudsonii* as a hummock builder in eutrophic swamps; *Silene acaulis* and *Saxifraga oppositifolia* in alpine swards.
4. growing in extensive patches, in carpets or broken mats, e.g. stands of *Hedera helix*, *Lamium galeobdolon*, *Asperula odorata* etc. in deciduous temperate forest.
5. growing in great crowds or extensive mats completely covering the whole plot area; mostly pure populations, e.g. *Erica tetralix* in *Erica*-heath; *Sphagnum rubellum* or *S. pulchrum* in raised bogs.

A variant of scale value 5 (5̤, loose or open 5) was proposed for populations with a cover degree of over 75% consisting, however, of plants which are sufficiently separated as to leave space for other species. Similar variants can be used for loose cover of 51–75% $\underset{\dots}{(4)}$ and 26–50% $\underset{\dots}{(3)}$ (MELTZER & WESTHOFF 1942, BRAUN-BLANQUET 1964).

In the relevé sociability values are written immediately behind the combined estimation values, e.g. *Scirpus maritimus* 1.1.

During the last decade several investigators (see FUKAREK 1964) expressed the opinion that the diagnostic value of sociability has been overestimated and that a certain sociability degree is a specific character of most taxa. Other authors (BRAUN-BLANQUET 1964, SCAMONI & PASSARGE 1963, WESTHOFF 1965) do not agree with this view. Only a few species have a fixed degree of aggregation based upon their innate manner of growth. The degree of gregariousness of most species is much influenced by habitat conditions and competition, and therefore is of major phytosociological importance. Sociability may also change considerably during the course of a succession; many examples are given by the authors quoted above. On the other hand, the variation in sociability will be correlated with variation in cover degree to some extent.

Sociability is commonly considered as an expression of vitality. However in various situations this is not so. JAKUCS (1970, 1972) remarked that character-taxa of the Trifolio-Geranietea (thermoxerophilous woodland fringe communities or 'Saumgesellschaften') tend to grow with sociability 1 in their optimal habitat, whilst they form polycorms with reduced vitality in suboptimal habitats. Facies of species are often connected with extreme or disturbed habitats (see 20.6.7).

20.4.5.3 *Vitality and Fertility*

Further variables in the performance of a species are its vitality and its fertility, representing vegetative and generative development respectively. BRAUN-BLANQUET (e.g. 1932, 1964) developed a scale of relative 'thriving' (Gedeihen) with four categories indicated by symbols (BRAUN-BLANQUET 1932).

●, 1 Well developed, regularly completing the life cycle (an extraordinary vitality is indicated with 'lux', luxurious).

⊙, 2 With vegetative propagation but not completing the life cycle.

○, 3 Feeble with low vegetative propagation, not completing the life cycle.

○○, 4 Occasionally germinating but not vegetatively propagating.

BRAUN-BLANQUET (1964) slightly altered the symbols and gave them numbers from 1 to 4, as above.

BARKMAN et al. (1964), following VARESCHI (1931) and ZOLLER (1954), stated that for many species vitality and fertility are independent or even negatively correlated parameters. They proposed separate scales for these.

20.4.5.4 *Periodicity*

In addition to vitality the seasonal phase in the life cycle of each plant, its 'phenological state' is recorded. Various scales are in use, the first one being that of GAMS (1918). BRAUN-BLANQUET (1964: 67 and 510) presented two scales (which are very similar). As was stated by GAMS (1918), ELLENBERG (1939, 1954a) and others (see also the bibliography by BALÁTOVÁ-TULAČKOVÁ, 1970 Exc.) one incidental record during the relevé is really not sufficient, a complete phenological diagram should be desired for each community. For a relevé at a given time, however, appropriate abbreviations may be used — v. (vegetative), fl. (flowering), fr. (fruiting), etc.

20.4.6 RELEVÉ PROTOCOLS

The various structural and floristic data discussed so far are written in standardized form either in field note books or on special protocol forms. These notes are preceded by some notes on the following items:

1. Date; running number; topographic locality (as detailed as possible); altitude; exposure and inclination; geology of substrate. If possible the location should be indicated on a detailed map.
2. Size and shape both of the plot and of the entire uniform stand; character of adjacent vegetation; soil profile; phreatic level; depth and differentiation of root system.
3. Character and intensity of human and animal influence, e.g. pasturing, burning, mowing, treading, manuring, irrigation.

Table III presents an example of a relevé, taken from MELTZER & WESTHOFF (1942). For each species are recorded the scale numbers for cover-abundance (before the period) and sociability (after the period), the phenological abbreviation, and the vitality symbol.

TABLE III

Protocol of a relevé (translated from MELTZER & WESTHOFF 1942)

Nr. 39462. 1st August 1939. Terschelling, Bessenplak S of beacon near beach mark 6. Gridnr. G5.61.43 in IVON-system (Institute for Vegetation Research in the Netherlands). Stand very uniform, Empetrum heath on slope of 6 m tall parabolic dune, exposition NNE, inclination 30°.

Habitat:	shadowed, moist soil, by day not strongly heated and rarely desiccating. Slight shifting of sand. Little human and animal influence.	
Profile:	A_0:	2 cm semi-decayed material.
	A_1:	5 cm dark humus containing sand.
	C:	bright, white dune sand.
Sample plot	100 sq m.	

Herb layer cover 100 %, 20–40 cm			
Polypodium vulgare	2.3	v.	●
Empetrum nigrum	4.4	fr.	●
Hieracium umbellatum	1.1–2	fl.	●
Festuca rubra subvar. arenaria	+.1	fr.	●
Hypochoeris radicata	+.1	fr.	●
Calamagrostis epigeios	+.1	fl.	●
Jasione montana	+.1	fl.	●
Carex arenaria	1.1	v.	⊙
Ammophila arenaria	2.2	v.	○
Salix repens	+.2	fr.	●
Viola canina var. dunensis	r	v.	⊙
Moss layer cover 100 %, 2–5 cm			
Hypnum cupressiforme var. ericetorum	3.3	v.	⊙
Pleurozium schreberi	3.3	v.	⊙
Dicranum scoparium	2.3	v.	⊙
Mnium hornum	2.3	v.	●
Lophocolea bidentata	2.2	fr.	●
Eurhynchium stokesii	+.3	v.	⊙
Plagiothecium denticulatum	+.2	fr.	●
Polytrichum juniperinum	+.3	v.	○
Peltigera canina	+.2	v.	●
Parmelia physodes	+.1	v.	⊙
Cladonia alcicornis	+.2	v.	⊙

20.5 **Synthetical Research Phase**

20.5.1 STEPS IN SYNTHESIS

The analysis of stands is only the first step in the description of vegetation units. After relevés have been collected, they must be compared. This is the start of the synthetical phase which leads to the distinction of coena and, if wished for, the final classification of syntaxa. To this purpose, a number of relevés are tabulated in a matrix, which is usually named a relevé table or community table.

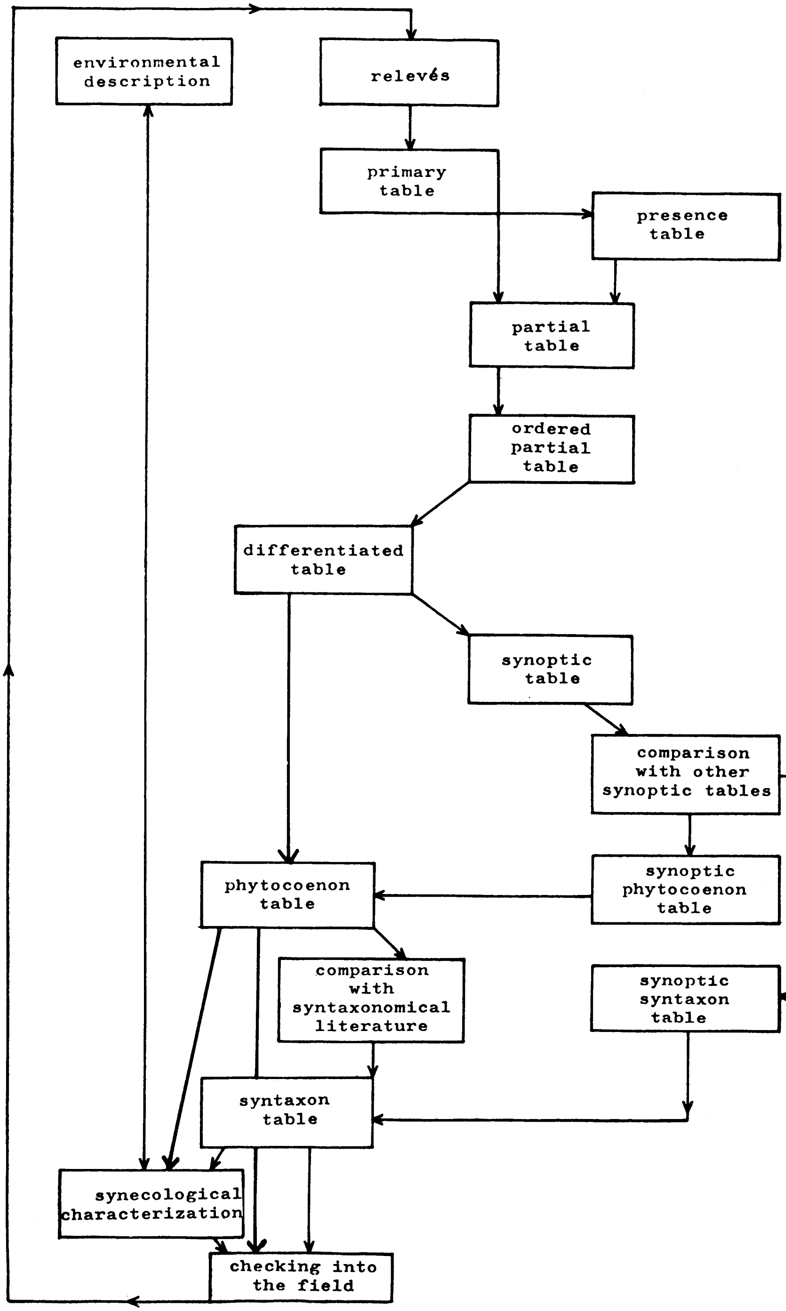

Fig. 3. Scheme of steps in the synthetic procedure.

Such a table is also called a primary or raw table (Rohtabelle). Each primary table is then rearranged into a structured table in which one or more uniform phytocoena are distinguished and characterized. After consultation of the relevant syntaxonomical literature (and possible further revision), this phytocoenon table or community table may then be presented as a syntaxon table, often for an association.

When environmental data such as soil analyses are available the vegetation types arrived at can be characterized synecologically. Finally the coena, or syntaxa, are checked in the field, e.g. whilst mapping the vegetation of the area under investigation or during the reconnaissance of a neighbouring area. This may lead to the collection of new relevés. Thus vegetation classification in the BRAUN-BLANQUET approach is essentially an iterative process, or one of successive approximation in the sense of POORE (1956). Fig. 3 shows the various steps in synthesis. SHIMWELL (1972) also outlines in English (cf. KNAPP 1958 and ELLENBERG 1956) the steps of the procedure.

The checking of units is an essential part of the method; this point seems not to be recognized by all critics of the BRAUN-BLANQUET approach (e.g. POORE 1955–56). MOORE (1962) explained that the misapprehension that the fidelity concept rests on a circular argument (e.g. POORE 1955a) is based on the failure to recognize the checking step: 'In present practice, associations are not distinguished in the field at all, but only when editing the tables of relevés. The first step involves describing uniform tracts of vegetation, *not* representative stands of a presumed association. Only when sufficient relevés have been accumulated and analysed one can discern the associations. Of course, in observing continental phytosociologists at work in their own homeland whose vegetation they know, one may be misled as to their methodology. They will now have reached the second stage of checking the reality of units already distinguished. They will not necessarily make this clear to a visiting inquirer.'

20.5.2 PRIMARY TABLE

In the primary table all taxa are listed at the left hand side of a sheet of squared paper; to each relevé a single vertical column is assigned. Each item in any column should contain either a dot or dash (in the case that a taxon is absent in the corresponding relevé) or else a combined estimation value (or an actual coverage per cent) and preferably a sociability value too. It may be convenient at this preliminary stage to group the species under separate headings according to strata and to separate phanerogams and cryptogams. The addition of new species from the later relevés produces a characteristic tailing off to the right of the table. Each row of the table represents a species (in a given stratum). Comparison of the rows of the table enables us to judge the distribution of any taxon over the relevés; comparison of the columns may lead to preliminary conclusions on relative similarities of the relevés.

The primary table should be rearranged several times, in order to establish groupings of relevés by rearrangement of columns as well as to group taxa with similar distributions in the table by rearrangement of rows. Before we discuss this rearrangement procedure (20.5.5) some concepts and techniques should be discussed.

20.5.3 PRESENCE, CONSTANCY, HOMOTONEITY

Presence is the occurrence of a taxon in a vegetation table. It is usually measured as a degree by the number of relevés in which the taxon occurs (regardless of abundance and cover) expressed as a percentage of the total number of relevés compared. *Presence degree* (Stetigkeit) can thus be calculated from any number of relevés, regardless of the difference in size of the plots.

When plots of equal size are compared the corresponding per cent occurrence for a taxon is named 'constancy' (Konstanz). (Frequency, in contrast with these, is an analytical concept dealing with the distribution of a taxon within subsamples from a given stand.) Presence degree and constancy are determined from stands of different and often widely distributed localities. Constancy determinations on plots of equal size were especially favored by the Uppsala school (article 18), starting with DU RIETZ et al. (1920), although the first such measurements, by BROCKMANN-JEROSCH (1907) had used plots of various sizes. In the BRAUN-BLANQUET approach presence degree has been termed 'Stetigkeit' and distinguished from 'Konstanz'; but confusion has resulted from the translation of both concepts as 'constancy' in some statements in English (e.g. BRAUN-BLANQUET 1932, MORAVEC 1971).

Constancy and presence degree can be given in exact percentages, or in percentage classes. It is usual to distinguish five classes, noted in Roman figures:

Class:	Percentage of plots in which taxon occurs:
I	1-20
II	21-40
III	41-60
IV	61-80
V	81-100

The numbers of taxa falling into these classes are often presented in a 'constancy diagram.' Such diagrams are important characteristics of vegetation units and provide useful tools to check the uniformity or homogeneity of a table. This synthetic homogeneity concept, however, should be distinguished from analytical homogeneity. Barkman (1958a: 316–317) designated these concepts as 'intensive homogeneity' and 'extensive homogeneity.' However, as Dahl (1970, apud Tüxen, 1970c: 101) pointed out, the latter term has been designated as *homotoneity* (Nordhagen 1943, Dahl 1957, 1960). This term was long overlooked in the Braun-Blanquet approach, but now receives common use (e.g. Tüxen 1970c, Moravec 1971). Homogeneity is an analytic concept, based on comparing different plots of the same size taken from an individual stand, whereas homotoneity is a synthetic concept, based on comparing similar plots from different stands of the same community-type or phytocoenon.

Homotoneity (see also 20.8.4) has been judged with the help of constancy diagrams; especially in North-European approaches (see further article 18). The classical interpretation, based on Raunkiaer's (e.g. 1934) 'law of frequency,' of a constancy diagram is that the following relation between the constancy classes exists: $S_{I} > S_{II} > S_{III} \gtreqless S_{IV} < S_{V}$ (the reversed J-shape). In very homotoneous tables class V may equal class I (U-shape). When classes III and IV include more species than class V, the table is considered heterotoneous (cf. Guinochet 1955, Cain & Castro 1959, Moravec 1971). According to Maarel (1972, in Maarel & Tüxen 1972: 209), the reasoning of Williams (1964) and observations of Barkman (1958a) showed that constancy class I is more or less dependent on the total number of relevés. Between the other classes the following relation exists in homotoneous tables: $S_{IV}+S_{V}/S_{II}+S_{III}$ is slightly over 1, whilst $S_{III}+S_{IV}+S_{V}/S_{II}$ is mostly about 2.

A second feature with which the homotoneity of a table can be easily checked is the variation in the number of taxa within the relevés of the table. In most cases well-developed stands of a phytocoenon do not differ much in number of species. A high variance of that number is reason to suppose that the table is heterotoneous, which may mean that more than one phytocoenon is represented in it (Hofmann & Passarge 1964). After the relevés have been classed into groups according to their number of taxa, we may obtain the frequency distributions of these classes, which will indicate this variation. A table comprising relevés belonging to two different coena may produce a curve with two or more peaks (Knapp 1971).

Apart from superficial inspection of homotoneity some simple measures have been proposed on the basis of constancy figures and species numbers (see Moravec 1971 for a survey). The following symbols, all corresponding to one vegetation table, are used: M is the number of relevés: S_m is the total number of species and $\bar{S}$ the mean number of species per relevé; S_v, etc. is the number of species falling into constancy class V, etc. C_i refers to the constancy per cents for species of the constancy class(es) indicated by the subscript to the summation sign, or for the prevalent species P — those belonging to the group of species with the highest constancy values, the number of which (S_p) approaches the average number of species ($\bar{S}$).

Amongst the measures based on constancy figures are:

1. The ratio S_V/S_{IV} (Dahl 1957).
2. Basic homotoneity coefficient $\frac{1}{S_m}\sum_{IV+V} C_i$ (Moravec 1971).
3. 'Homogeneity value' $\frac{1}{S_p}\sum_{p} C_i$ (Raabe e.g. 1952).
4. Index of homogeneity (Curtis 1959) $\frac{\sum_{p} C_i}{\sum_{S_m} C_i S_m}$
5. Mean constancy for all species $\sum_{S_c} C_i/S_m$

6. Corrected homotoneity coefficient (Moravec 1971). This is coefficient 2 with an 'oscillation factor,' determined by the difference in species number between the richest and the poorest relevé.

Tüxen (1970c) presented curves for various communities ending in a horizontal line (section 20.4.3); one may derive a 'minimal relevé number' from such curves. In fact Tüxen based his saturation quotient on tables containing about this minimal number of relevés. Other observations suggest that the number of species grows continuously with the number of relevés (e.g. Etter 1949, Barkman 1958a, Dahl 1957, 1960, Williams 1964). Dahl (1961) based an 'index of uniformity' on this relation (see 20.8.4)

and BARKMAN adapted KLEMENT's heterogeneity index by omitting species with a constancy of less than 10 %.
7. 'Saturation quotient' $100\bar{S}/S_m$ (TÜXEN 1970c).
As Tüxen mentioned this measure is the reciprocal of the homogeneity (i.e. heterogeneity) value of DAHL & HADAČ (1941). WHITTAKER (1972) suggested use of $BD = (S_m/\bar{S}) - 1$ as a measure of beta diversity (article 3.6). PFEIFFER's (1957) homogeneity value was reduced to TÜXEN's measure by MORAVEC. KLEMENT (1941) used the same measure under the same name as DAHL & HADAČ did, as was mentioned by BARKMAN (1958a), who concluded that this index is largely dependent on the total number of relevés in the table.

In conclusion we think it would be more realistic to base a saturation quotient explicitly on species with a minimum constancy value, e.g. species from constancy classes II–V, and to measure the rate of increase in total species number separately. For measurement of homotoneity we suggest the mean similarity coefficient for the relevés (see 20.8.5).

20.5.4 SPECIES WEIGHTS

Species may be weighted in synthetical procedures such as fidelity determination, assignment of syntaxa to higher units and calculation of spectra. Weighting is usually with the combined estimation value or some transformation of this. SCHWICKERATH (1931) used 'Artmächtigkeit' — and when species groups were concerned 'Gruppenmächtigkeit' (species and group importance value, MAAREL 1972b) — based on BRAUN-BLANQUET figures and arbitrary numerical values for symbols + and r. TÜXEN & ELLENBERG (1937) and BRAUN-BLANQUET (1946) used the Deckungswert (cover value) and Gruppenwert (group value) by taking average coverage percentages for BRAUN-BLANQUET values 2–5 and arbitrary values for 1, + and r. The latter procedure has received more application than that of SCHWICKERATH, although TÜXEN & ELLENBERG stressed its limited applicability, which was also criticized by WESTHOFF (1947), MEIJER DREES (1949), SISSINGH (1950).

DAGNELIE (1960) suggested the use of an arc-sine transformation as is usual with percentage scores. His rounded figures appear to be identical with the original BRAUN-BLANQUET values. Various other transformations have been applied, including those of ETTER (1949), BARKMAN (1958a), BARKMAN et al. (1964), MAAREL (1966b), SCHMID & KÜHN (1970), MOORE (MOORE & O'SULLIVAN 1970) and LONDO (1971). (See MAAREL, 1972b for a review.)

Without discussing this problem here (see MAAREL 1972b) we are in favour of a simple 'ordinal transformation' of the extended nine-point BRAUN-BLANQUET scale (Table II). This produces also partial accordance with the DOMIN scale in its modification by EVANS & DAHL (1955), which is much used in Scandinavia and Britain.

20.5.5 TABLE REARRANGEMENTS

The development of phytosociological tables has been stressed by the leaders of the floristic-sociological approach as a crucial procedure. E.g. BRAUN-BLANQUET (1951a, b) wrote (transl.): 'Appropriately elaborated association tables are comparable with thorough species diagnoses. By means of the tables the considerable detailed work from the minute floristic analyses of the lower vegetation units becomes accessible and evaluable. From the table it also appears whether one has worked seriously and reliably; the tables are the proper touch-stone of the concerned plant sociologist.'

At the same time the table method is said to be difficult to learn, at least by written instructions. TÜXEN & PREISING (1951) spoke of 'special aptitudes, a view of the interrelations in the tabular picture, and broad experience in the sociology, synecology and syngenetics of plant communities,' that are all needed for mastering the ordering of tables. Although personal instruction in the technique is important, as numerous pupils of BRAUN-BLANQUET and TÜXEN can confirm, it may be admitted that early BRAUN-BLANQUET sociology paid insufficient attention to explicit statements of the table techniques.

KNAPP (1948, 1958) and ELLENBERG (1956) presented detailed accounts of the table technique as it had been developed by TÜXEN in the 1930's at the Zentralstelle für Vegetationskartierung. ELLENBERG's scheme (1956: 46, slightly altered) is as follows (see Fig. 3):

(1) rearrangement of the first matrix to a 'presence table';
(2) tracing of table-differentiating species, mostly with the aid of 'partial tables';
(3) rearrangement of taxa and relevés according to the empirically established occurrence of groups of differentiating species; the result is a 'differentiated table';
(4) compilation of every relevant differentiated vegetation table into a 'synoptic table' ('Übersichtstabelle');
(5) determination of fidelity by comparing an adequate number of

synoptic tables ('zusammenfassende Übersichtstabellen' in the sense of ELLENBERG l.c.);

(6) rearrangement of the differentiated table into a final syntaxon table ('charakterisierte Tabelle' in the sense of ELLENBERG l.c.).

Similar schemes were presented by MOORE (1962), SCAMONI & PASSARGE (1963), FUKAREK (1964), KÜCHLER (1967), GOUNOT (1969), KNAPP (1971) and SHIMWELL (1972). The steps 1, 2 and 3 are the basic ones; they are essential for any local classification of relevés into phytocoena. Step 4 is preliminary to 5. Steps 5 and 6 have to do with the next level of investigation: the establishment of a (perhaps provisional) syntaxonomical classification.

TÜXEN (1970b) recommended to start with a preliminary procedure aiming at the exclusion of relevés with deviant numbers of species that suggest fragmentary or heterogeneous stands. Such relevés are thus excluded from successive rearrangements and fidelity calculations and are not considered in an association diagnosis.

The first rearrangement of a primary table aims at listing the species after their degree of presence. In the presence table it may become apparent, whether the relevés vary irregularly, or whether certain combinations of species are found recurrently. In the latter case such groups may be more or less mutually exclusive and serve as groups of differentiating species. Those are not likely to be found in the presence classes V and I; they will mostly belong to the intermediate classes II, III and IV. The supposed differentiating species are underlined or boxed in the presence table. These differentiating species, which are provisional sets of diagnostic species (see 20.3.4), are used to rearrange the table.

The next step is to set up a partial or extracted table in which only the species thought to have diagnostic value are given and used to rearrange both columns and rows. During the rearrangement of a provisional partial table, the differentiating species are written on the left hand side of the paper and the rows arranged in their corresponding groups, and the relevés (columns) are rearranged to show a diagonal order of species groups from the left to the right of the table. To simplify the rearrangement of the relevés dictation or transfer strips are used.

When the partial table has been worked out, the complete table (thus containing again the temporarily omitted species) is rearranged accordingly so that the differentiating groups appear clearly. Now we have the 'differentiated table.' The species with a high presence values indicate the degree of coherence or homotoneity of the table. The species with intermediate and lower presence values used in differentiating groups represent the heterotoneity of the table. After comparing the sizes of the two groups, one may decide how many phytocoena the table includes and whether the table should be divided, or combined with others for further treatment.

Step 4 from Ellenberg's scheme comprises the replacement of each uniform table or partial table by a column in which for each participating species the presence degree is indicated (either as a percentage or a class value). Such a table (which may consist of only one column) is called Übersichtstabelle by Ellenberg but is also known as Sammeltabelle, synthetische Tabelle and Stetigkeitstabelle. Following a recent denomination by Doing (1969a) and Tüxen (1970b) we propose the neutral name 'synoptic table.'

After comparison of the synoptic table with those from other types of vegetation from the same region an idea can be formed about the local diagnostic species groups in the table under study (step 6). The differentiating groups used may represent recognized diagnostic groups, or may represent approximate groupings that should be revised on the basis of broader knowledge of diagnostic groups, or may represent diagnostic groups for newly recognized phytocoena. With those species, as well as the constant taxa, a phytocoenon may then be identified or described. Here we could speak of a synoptic phytocoenon table, from which the corresponding relevé-table or 'phytocoenon table' (Gesellschaftstabelle) can be rewritten. When moreover the synoptic table is compared with the literature and with tables from similar vegetation types from other regions, character-taxa may be found and a syntaxonomic interpretation may follow. The synoptic table now serves as a synoptic-syntaxon-table and the corresponding (rewritten) relevé-table is now a syntaxon-table. The latter will often be an association table. The fidelity research implied in steps 5 and 6 will be discussed in 20.5.7-8.

The rearrangement method might be criticized with the objection that the table pattern may be 'an artefact imposed by the clever shuffling of data and not mirroring any reality in nature,' as it has been expressed by Moore (1962) in his refutation of this objection. In reality, the characterized table is, first, an effective organization of information, an ordering of species and relevés in relation to one another (and biotope properties). Second, it is considered a working hypothesis to be tested by further observation. It should receive confirmation: (i) from further floristic data, critically and impartially collected; (ii) from mapping the units distinguished; and (iii) from the evidence of relationships between the vegetational units and environment. The groups of differentiating taxa may be presumed to indicate ecological differences in one or more specific major biotope factors or correlated sets of factors, such as phreatic level, humus, carbonate content, amount of soil hardening; salt content, or frequency and duration of periodical inundation by sea water; exposure; shade; rate of pasturing or mowing; etc. The resulting hypotheses have to be checked by continued ecological research. If the work has been well done, the differentiating groups should have indicator value in relation to environmental factors (see 20.7.6), and the phytocoena as kinds of communities should bear consistent, reliable relations to kinds of biotopes.

20.5.6 MECHANICAL MEANS FOR REARRANGEMENT

The 'classical' rearrangement technique by manual ordering of taxa and relevés, as it has been rendered above, is a time-consuming procedure and a potential source of errors. Attempts to simplify and mechanize the procedure have been made by several investigators. The most simple means is the use of cardboard strips, usually for the relevés and thus for the columns of the table.

Various systems of blocks (wooden, plastic, or aluminium) have been developed (WILMANNS 1959, MARGL 1967, MÜLLER et al. 1972). TRENTEPOHL (1968) showed a magnetic device which seemed to be less vulnerable to manual disordering of the blocks.

For tables with a large number of relevés or a large number of species the use of punched cards is obvious. Three types of cards are in use — the edge-punched card, the visual punched card, and the machine punched card. COTTAM & CURTIS (1948) initiated use of cards with the third and most advanced type. Examples of the use of edge-punched cards are found with EMBERGER et al. (1957), GOUNOT (1957) and ZONNEVELD (early sixties, internal undated reports Netherlands Soil Survey Institute).

ELLENBERG & CRISTOFOLINI (1964) intensively used visual punch cards, mainly for sorting relevés. The corresponding cards are laid on a light-table and then compared with a standard card — e.g. one containing the characteristic species combination of a certain syntaxon. ELLENBERG (1968) published a version of this technique where combined estimation values of species are taken into consideration, however at the expense of space on the card. According to ELLENBERG, this apparatus is only efficient if the number of relevés is large, at least 200 to every table. As MÜLLER et al. (1972) stated, this technique may be useful where the vegetation has already largely been classified and the vegetation units described, and where additional relevés need only to be arranged and included in existing tables. Further use of machine punched cards in phytosociology has been described by DAGNELIE (1960), BECKING (1961), GROENEWOUD (1965) and many others; whilst recently a number of computer-based table rearrangement programmes have been developed; this will be discussed in 20.8.1 and 20.8.6.

20.5.7 DETERMINATION OF FIDELITY

The next step in the synthetic procedure is the determination of fidelity. By comparing a number of tables — if possible all available tables covering the vegetation of a given area — it is possible to discern character-species in the sense discussed in 20.3.3. As indicated there, the criteria are the distribution of the species in different coena; fidelity is the degree to which a species is concentrated in one coenon, vs. dispersed with more even occurrence in several coena. Species distributions in the tables are observed on the basis of measures already discussed — presence degree, combined estimation value, vitality, and sociability. It should be emphasized that these measures are relevant to a species' fidelity only as they differ between different coena. Character-species can as well be minor species as major ones; there is no necessary relation between fidelity and dominance. In the classification of European forests, more significance is attached to the fidelity of shrubs, herbs, and mosses, both because tree species are often widely distributed in different coena, and because disturbance has brought extensive replacement of natural tree species.

Five degrees of fidelity have been distinguished (BRAUN-BLANQUET 1921, 1928, 1932, 1951, 1964) in the relation of a species to the given coenon.

A. Character-taxa.

Fidelity degree 5: *Exclusive taxa* (treue): taxa completely or almost completely confined to one phytocoenon (vegetation unit);

Fidelity degree 4: *Selective taxa* (feste): taxa occurring with clear preference for one phytocoenon but also, though with a considerably lower presence degree, in other coena;

Fidelity degree 3: *Preferential taxa* (holde): taxa present in several coena, perhaps with about equal presence degree, but with a higher combined estimation value and (or) with a higher vitality degree in one particular coenon;

B. Companions.
Fidelity degree 2: *Indifferent taxa* (vage): taxa without pronounced preference for any coenon.

C. Accidentals.
Fidelity degree 1: *Strange taxa* (fremde): taxa having a definite presence degree optimum and mostly also a cover-abundance optimum outside the considered coenon. These are often accidental intruders from neighbouring coena or relics from a coenon that preceded in succession.

Table IV

Determination of fidelity according to Szafer and Pawłowski (Braun-Blanquet 1932)

F = fidelity degree;
A = cover-abundance combined estimation;
C = presence or constancy class;
V = vitality.

F	in phytocoenon under consideration		in comparable phytocoena	
	C	A	C	A
5	IV–V	3–5	I–II	+–2(1)
	IV–V	+–2	I	+–2
	I–III	+–5	absent or very rare	
4	IV–V	3–5	II–III (IV) (relic or pioneer)	+–2(1)
	IV–V	+–2	II–III	+–1(2)
	III–IV	+–2	I–II (III)	+–1(2)
	I–III	+–2	I (rare)	+
3	I–V	3–5	I–V	+–2
	C, A various	V normal	C, A lower	V reduced
2	C, A, V various		similar	
1	I	+–1	higher	
	V reduced			
	– outskirts and disturbed parts of the stand(s) –			

As early as 1927, Szafer & Pawłowski gave a quantitative outline for the determination of the fidelity class. It has been taken over, with slight modifications, by Braun-Blanquet (1928, 1932, 1951, 1964) and it is presented here with slight alterations (Table IV). In this table the comparison is between a phytocoenon that is being studied and comparable phytocoena. It seems logically incorrect to specify in such a table 'the given association' versus 'other associations.' as Braun-Blanquet (l.c.) has done in all editions of his manual.

Becking (1957) has modified the scheme of Szafer & Pawłowski (1927) considerably, especially in omitting the possibility of obtaining fidelity degree 5 with a low presence degree. However, it has been crucial in the Braun-Blanquet approach that faithful species need not be constants, and apart from diagnostic implications (see 20.6.1) one cannot simply change this principle.

20.5.8 Geographical Effects on Fidelity

Since the beginning of the Braun-Blanquet approach (Braun-Blanquet 1921) it has been recognized that the diagnostic value of character-taxa is geographically limited. Naturally enough this recognition has become more and more general with the growing geographical extension of phytosociological knowledge. The vegetation of a region with a uniform climate and a uniform geological history usually shows great uniformity in the ecological amplitudes and therefore in the sociological positions of its species. Most species however occur in larger, climatically and geologically heterogeneous areas and present different ecological amplitudes or habitat relations in different parts of their areas. In many cases these differences in local habitat response within the species are correlated with genetic differences: we are dealing then with ecotypic variation. In other cases genetic differences, if present, are not evident. Geographic variation in habitat response may involve such shifts in topographic or other local distribution, as tend to compensate for difference in climate (law of relative habitat constancy, cf. Walter & Straka 1970, article 3.2).

A number of species which behave as xerophytes in Central Europe, e.g. *Bromus erectus*, *Koeleria gracilis*, *Carex humilis*, *Peucedanum cervaria*, are bound to humid soils of cool northern exposures in the Mediterranean. Species which are real woodland plants in a continental climate may present much wider amplitudes in oceanic climates: e.g. *Osmunda regalis*, *Listera ovata*, *Dryopteris filix-mas*. On the contrary a number of thermoxerophilous species are indifferent to soil conditions in Central Europe, whereas in the cooler and more humid climate of NW-Europe they are strictly confined to calcareous soils. *Iris pseudacorus*, a species of wet eutrophic swamps in Central and Western Europe, grows in moderately damp grassland in the perhumid Western Irish climate. *Schoenus nigricans*, in Central Europe faithful to calcareous marshes or fens, occurs in Ireland both in fens and in ombrotrophic blanket bogs. Even within a much more limited geographical range the differences in ecological amplitude may be considerable. Within The Netherlands,

	Artemisietum maritimae typicum								
	Initial phase with Artemisia maritima					Typical form			
	4)			5)					
Number of relevê	53136	53134	53133	52390	52371	52338	54081	53022	55
Locality[1]	Ka	Kà	Ka	Ka	Ka	He	Ko	Ba	
Habitat[2]	cr	cr	cr	dike	dike	cr	cr	ab	
Salinity flood-water[3]	p	p	p	p	p	p	e	p	
Date	2-9-53	2-9-53	2-9-53	21-8-53	20-8-52	5-8-52	13-8-54	5-8-53	5-8-
Surface in m^2	2x12	2x12	3x10	2½x20	4x12	2x25	3x20	3x15	3
Coverage in %	98	95	95	95	100	100	100	100	1
Character-taxon of the association									
Artemisia maritima	5.4	4-5.4	5.4	4.5.5	4.3-4	2.1	2-3.1-2	2.1-2	2.
Differential-taxa of the subassociations									
Armeria maritima	-	-	-	-	-	-	-	-	
Agrostis stolonifera var. compacta subvar. salina	-	-	-	-	-	-	-	-	
Atriplex hastata	-	-	-	2-3.2	3.3	-	-	-	
Character-taxa Armerion maritimae									
Festuca rubra f. litoralis	+.2	+.2	1.2-3	-	+.2	5.5	5.5	5.5	5
Glaux maritima	-	-	-	-	-	+.1	-	+.1-2	
Juncus gerardii	-	-	-	-	-	-	-	-	
Parapholis strigosa	-	-	-	-	-	-	-	-	
Character-taxa Puccinellion maritimae									
Puccinellia maritima	+.2	+.2	-	-	+.1-2	-	-	-	+
Halimione portulacoides	2.2-3	2-3.3	2.2-3	+.1-2	1.1-2	+.1-2	1.1-2	+.2	1-
Bostrychia scorpioides	-	-	+.2	-	-	-	-	-	
Character-taxa Glauco-Puccinellietalia									
Spergularia marginata	-	+.1	-	-	-	-	1.1	1.2	+.1
Limonium vulgare ssp. vulgare	-	-	+.2	-	+.1-2	+.1-2	1.1-2	+.2	1.1
Character-taxa Asteretea tripolii									
Aster tripolium	+.1	+.1-2	+.1	-	+.1	+.1	1.1-2	2.1-2	1-
Triglochin maritima	-	-	-	-	-	-	+.2	-	+
Plantago maritima	+.2	+.2	+.2	-	+.1	+.1-2	-	+.2	+
Character-taxa Thero-Salicornion, Thera-Suaedion and Spartinion									
Salicornia europaea	-	-	-	-	-	-	-	-	
Suaeda maritima	-	+.1	-	+.1	+.1-2	-	+.1	-	+
Spartina townsendii	-	+.2	-	-	-	-	-	-	
Other taxa									
Elytrigia pungens	-	-	-	+.1-2	1.1-2	1-2.1	-	-	+
Atriples littoralis	-	-	-	+.1	-	-	-	-	
Lolium perenne	-	-	-	-	-	-	-	-	

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[1] Localities :
Ka + Kaloot near Borssele (South Beveland);
He = "Slikken van de Heene" (St. Philipsland);
Ko = Marshes near Kortgene (North Beveland);
Ba = Marshes near Baarland (South Beveland);
Sp = Spieringschor near Kamperland (North Beveland);
Kats = Marsh near Kats (North Beveland);
Wa = Marshes east of Waarde (South Beveland);
Bath = Marshes west of Bath (South Beveland);
Os = Marshes west of Ossendrecht and
Li = "Galgeschoor" north of Lilloo (Belgium).

	Artemisietum maritimae armerietosum				Artemisietum maritimae agrostidetosum							
					Typical form				Fragment			
98	52343	54092	54089	52051	53043	53054	52207	53071	54130	54133	54139	54152
Ka	He	Sp	Sp	Kats	Wa	Wa	Bath	Bath	Os	Os	Os	Li
cr	ac	cr	cr	cr	ab	ab	cr	cr	cr	ac	cr	ac
p	p	e	e	e	m	m	m	m	m	m	m	m
55	5-8-52	14-8-54	14-8-54	4-9-52	6-8-53	6-8-53	3-7-52	6-8-53	2-9-54	2-9-54	2-9-54	2-9-54
12	100	3x25	4x20	2½x12	5x10	6x8	1½x15	2x10	5x50	10x20	2x15	4x20
00	95	100	100	90	100	100	100	100	100	100	100	100
-2	1-2.1	2.1-2	2.1-2	2.1	3.1-3	3.1-2	2.1-2	3.1-2	-	-	-	-
-	1-2.2	1.2	1.2	+.2	-	-	-	-	-	-	-	-
-	-	-	-	-	4.5	5.5	2.2	2.2-3	3.2-3	3.5	1.2	3.5
-	-	-	-	-	1.1	1.1	1.1	+.1	1.1	2.1-2	1.1-2	-
5	5.5	5.5	5.5	5.5	3.5	2.5	5.5	5.5	4.5	4.5	5.5	4.5
-	1.1	+.1	-	1.1	2.1-2	1.1-2	-	-	-	-	-	+.1
-	-	-	-	+.2	-	-	-	-	-	-	-	+-1.1
-	1.1-2	-	-	-	-	+.1-2	-	-	-	-	-	-
2	-	+.2	-	-	-	-	-	-	-	-	-	1.2
2	+.1-2	1.1-2	+.1-2	1.2.1	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-	-	-	-
2	-	1.1	1.1	+.1	+.1-2	+.1-2	-	+.1	-	-	-	-
2	1.1-2	2-3.2	2.2	+.1-2	+.2	-	2.1-2	+.2	-	-	-	-
2	-	2.1-2	+.1-2	+.1-2	+.1-2	+.1	1.1-2	+.1	+-1.1	+.1	2.1-2	-
2	-	+.2	+.2	1.2	-	-	+.1-2	-	-	+.2	-	+.2
2	2.2	+.2	+.2	1.2	2.2	1-2.2	+.2	+.1-2	-	-	+.2	+.1-2
	-	$+.1^{o}$	-	$+.1^{o}$	-	-	-	-	-	-	-	-
1	-	1.1	-	-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	+.1	-	-	-	-	-
1	-	+.1-2	+.1	+.2	-	+.1-2	+.1-2	+.2	+.2	+.2	2.1-2	-
-	-	-	-	-	-	-	-	-	-	-	-	-
-	-	-	-	-	+.2	-	-	-	-	-	-	-

---

[2] Habitats :
cr = on elevated creek banks;
dike = at the foot of the dike, where tidal drift is washed ashore;
ab = on elevated parts with an abrasion edge;
ac = on highly accreted parts in the marsh.

[3] Salinity flood water :
e = euhaline;
p = polyhaline and
m = mesohaline.

[4] Variant with Halimione portulacoides

[5] Variant with Atriplex hastata

Orchis morio is faithful to the Mesobromion of dry chalk in Southern Limburg, whereas it is bound to moorland (Calluno-Genistetum molinietosum) in the Pleistocene part of the country, to mesohalinic peat soil (community of *Orchis morio* and *Ophioglossum vulgatum*) in the brackish Holocene parts of Holland (sensu stricto) and to a narrow ecotone at the margin of wet heather dune slacks on the West Frisian islands (cf. WESTHOFF & HELD 1969). *Hymenophyllum peltatum* is in the major part of Ireland bound to damp oakwood, but on the extremely oceanic cliff of Slievemore on Achill Island (Co. Mayo) it thrives freely in the open air in between *Calluna vulgaris* and *Empetrum nigrum* (PRAEGER 1934).

Consequently, one and the same species can be a character-taxon for association *A* in one area and for association *B* in another one. BRAUN-BLANQUET (1964: 100) concluded that the validity and diagnostic value of character-taxa for a given association are mostly restricted to a climatically uniform area. It follows that a typology of character-taxa with respect to their geographical extension of their validity may be useful.

BRAUN-BLANQUET (1928, 1932) gave a first distinction between general and regional character-taxa. Later (1951a) he mentioned absolute, territorial and local character-taxa (cf. ELLENBERG 1956). The distinction between territorial and local was unclear, however; apparently it refers to the size of the range of the association in which the taxon shows fidelity. As BARKMAN (1958a) pointed out the replacement of general by absolute suggests a change of criterion, i.e. from range of fidelity to degree of fidelity, which was in fact realized in BRAUN-BLANQUET's definition of 'Absolute Treue.' With BARKMAN we think that these two criteria should be used independently. A third criterion is the relation between the range of the character-taxon and the range of the corresponding syntaxon.

MEIJER DREES (1951) elaborated this criterion and came to four possibilities: 1) ranges of taxon and syntaxon coincide, 2) taxon range forms part of syntaxon range, 3) syntaxon range forms part of taxon range and 4) ranges differ but overlap. MEIJER DREES maintained BRAUN-BLANQUET & MOOR's term 'regional' which he applied to all cases in which the taxon is a character-taxon throughout the common range of taxon and syntaxon, contrasted with the term 'local' for cases in which the taxon is a character-taxon only in part of the common area.

The corresponding scheme was taken over by BECKING (1957, 1961) who incorporated it moreover in a complex scheme in which also the degrees of fidelity were considered. BARKMAN (1958), who wished to maintain the more obvious meaning of the terms local and regional, adopted the eight types of MEIJER DREES (1951), but largely renamed them. Finally KNAPP (1971), who only mentioned MEIJER DREES and BECKING, refined the division into four types of geographical character-taxa in the taxon-bound sense of MELTZER & WESTHOFF (1942): viz. 'local', 'territorial or regional,' 'region-' and 'absolute.' The following scheme may be given as a summary:

i) Local character-species, with fidelity restricted to an area that forms only part of the total area of the syntaxon.

ii) Regional character-species, with fidelity for the total area of the syntaxon, but with the species area exceeding that of the syntaxon. Subcategories could be distinguished in relation to BRAUN-BLANQUET's phytogeographical typology including provinces and sectors.

iii) General character-species, with fidelity for the total area of the syntaxon, and the species area coinciding with the syntaxon area.

20.5.9 PHYTOCOENON CHARACTERIZATION

After a primary table has been rearranged into a phytocoenon table, presence values have been calculated, and the fidelity and differentiating value of the taxa towards neighbouring communities have been established, the corresponding phytocoenon can be characterized. First the general structure can be described. Mostly the presence class of each species is indicated at the right hand side of the table, in some cases the presence per cent. To the right of the presence figure the range of the combined cover-abundance estimation values may be given.

Then, according to procedures described above the faithful, differentiating and constant taxa may be indicated. The diagnostic value may be only provisional, when the relevés come from a limited area or when insufficient other material could be compared. We are dealing here with the first of three phases of systematic phytosociology, viz. the local phase. The taxa that are of lowest presence degree and lack diagnostic value (mostly of presence class I) are often presented in an addendum to the table. In many cases the description of phytocoena does not immediately lead to a formal classification. Without this, the phytocoenon tables may summarize much of what phytosociology seeks to understand of relations amongst species, kinds of communities, and environments. When data are thus organized into phytocoenon tables, however, the stage is set for the syntaxonomic treatment next to be discussed.

20.6 **Syntaxonomical Research Phase**

20.6.1 SYNTAXON TABLE CHARACTERIZATION

The syntaxonomical research phase starts when a phytocoenon is to be fitted into the hierarchic system of syntaxa. The phytocoenon table is then interpreted by consulting the relevant syntaxonomic literature, especially synoptic syntaxon tables. Questions in this are: (i) Which already described association can be recognized in the characteristic taxon combination of the phytocoenon; (ii) which lower units could be recognized on the basis of the established differentiating taxa; (iii) which taxa can be recognized as character- or differential-taxa from higher units already distinguished?

Careful treatment of these questions may lead to the conclusion that the phytocoenon under study is one already recognized, or that it must be described as a new syntaxon, or that part of the existing hierarchy must be redefined. Here, as ELLENBERG (1956: 57) said 'begins the range of the 'tact' of which BRAUN-BLANQUET, 1951: 18 spoke.' The expression 'sociological view' ('soziologischer Blick') is relevant. Though some of the decisions on phytocoenon similarity are objective, the essential role of judgement and experience in a typological discipline should be recognized.

The results of these considerations are expressed in the structuring and labeling of the phytocoenon table, which now becomes a syntaxon table. Usually the highest unit treated in a given syntaxon table is the association. In such an association table the subordinate units distinguished are presented as well. Table V presents an example of an association table of an already recognized association, viz. the Artemisietum maritimae, as it occurs in a region not systematically described before, the southwestern Netherlands.

When a number of related associations have been described, their regional descriptions might be presented together in a synoptic syntaxon table. An example of such a table is presented in Table VI. Both tables, composed by W. G. BEEFTINK (cf. BEEFTINK 1962, 1965, 1968), whose cooperation is gratefully acknowledged, will be discussed in the subsequent paragraphs.

20.6.2 CHARACTERIZATION OF THE ASSOCIATION

As was discussed in 20.3.2 the association concept of the BRAUN-BLANQUET approach was always based on the presence of a characteristic taxon combination, including character-species. However, as the number of described associations grew, the role of character-taxa gradually diminished whilst the diagnostic importance of differential-taxa increased. In some association descriptions character-taxa are not mentioned separately but are given together with the differential-taxa ('Kenn- und Trennarten'). This led to the character-combination concept which in fact recognized the possibility that none of the participating taxa is a character-taxon in a strict sense, but rather the correlated occurrence of taxa is the essential 'character' of the phytocoenon.

BRAUN-BLANQUET (1964: 122) seemed to confirm this development when he stated that 'the essential association features' should be found in a stand in order to assign it to that association and then defined this as follows: 'primarily the normal characteristic species combination should be present, that is a minimum number of character- and differential-species and some of the more important companions.' However, during recent colloquia and symposia of the International Society for Plant Geography and Ecology the presence of at least one character-taxon was demanded by others, especially by OBERDORFER (1968); see also the following discussions, during the 1964 symposium at Stolzenau (TÜXEN 1968: 132–141) and DIERSCHKE (1971). DIERSCHKE (1971) even stated that 'the basic unit for the Prodromus is the association, the rank of which is determined by the constant occurrence of at least one character-species and which is defined by its characteristic species combination.' This definition may be considered the standard from which, however, vegetational circumstance may force some departures.

20.6.3 GEOGRAPHIC PROBLEMS WITH ASSOCIATIONS

Many of the problems with character-taxa result from complexities in the geographic behaviour of species in relation to coena, as discussed above (20.5.8). The difficulties led ELLENBERG (1954b) to speak of 'the crisis of the character species doctrine' and to propose a much more local delimitation of associations without general character-species. As ELLENBERG (1956) added, the use of geographically restricted 'local character-species' for associations is then appropriate. The local establishment of associations emphasized by ELLENBERG (1954b) had, in fact, been common practice by then for some 20 years, as TÜXEN (1955) stated in a reply to ELLENBERG, whilst referring to BRAUN-BLANQUET & MOOR (1938) and TÜXEN (1937). In fact OBERDORFER (1957, but also

Table VI

Classification of salt-marsh communities in the SW Netherlands according to the Braun-Blanquet method by W.G. Beeftink

Classes	Thero-Salicornietea	Spartinetea			
Orders	Thero-Salicornietalia	Spartinetalia			
Alliances	Thero-Salicornion	Spartinion		Puccinellion maritimae	
Associations	Salicornietum strictae	Spartinetum maritimae	Spartinetum townsendii	Puccinellietum maritimae	Halimionetum portulacoidis
Column	1	2	3	4	5
Number of relevés	14	24	30	124	40
Character-taxa of the associations					
Salicornia europaea coll.[1]	100(1-3)	33(+-2)	14(+-2)	78(+-2)	40(+-1)
Spartina maritima	14(+)	100(2-4)	-	6(+)	-
Fucus vesiculosus var.lutarius	-	79(+-5)	7(2-3)	4(+-2)	-
Spartina townsendii agg.	86(+-1)	79(+-2)	100(3-5)	50(+-2)	35(+-2)
Puccinellia maritima [2]	25(+-1)	33(+-1)	30(+-1)	100(3-5)	92(+-2)
Halimione portulacoides	8(+)	-	33(r-1)	83(+-2)	100(3-5)
Artemisia maritima	-	-	-	5(+-1)	-
Armeria maritima	-	-	-	6(+-1)	-
Carex extensa	-	-	-	-	-
Puccinellia distans	-	-	-	-	-
Puccinellia fasciculata	-	-	-	-	-
Puccinellia retroflexa	-	-	-	-	-
Scirpus maritimus var. compactus[3]	-	-	27(+-2)	-	-
Faithful taxa Puccinellion maritimae					
Bostrychia scorpioides	-	17(+-4)	14(+-2)	21(+-4)	37(+-4)
Character-taxa Armerion maritimae					
Juncus gerardii	-	-	-	2(+)	-
Festuca rubra f litoralis	-	-	-	14(+-2)	62(+-1)
Glaux maritima	-	-	10(r-1)	50(+-2)	15(+-1)
Parapholis strigosa	-	-	-	-	-
Agrostis stolonifera var. compacta subvar. salina	-	-	-	-	-
Character-taxon Puccinellio-Spergularion salinae					
Spergularia salina	-	-	-	-	-
Character-taxa Glauco-Puccinellietalia					
Spergularia marginata	-	-	7(r-+)	73(+-2)	42(+-2)
Limonium vulgare ssp vulgare	8(+)	8(+)	30(r-+)	73(+-2)	60(+-2)
Character-taxa Asteretea tripolii					
Aster tripolium	50(+-2)	33(+-2)	77(r-2)	98(+-2)	97(+-2)
Triglochin maritima	8(+)	-	27(r-2)	86(+-4)	62(+-2)
Plantago maritima	-	-	20(r-1)	65(+-4)	65(+-2)
Other taxa					
Suaeda maritima	50(+-1)	12(+-2)	37(+-1)	64(+-2)	60(+-2)
Atriplex hastata	-	-	77(+-2)	25(+-2)	5(+)
Elytrigia pungens	-	-	7(r-+)	1(+)	22(+)
Lolium perenne	-	-	-	-	-
Plantago coronopus	-	-	-	-	-
Phragmites communis	-	-	-	-	-

Addenda: Column 1: Zostera noltii 29(+-2); Column 7: Centaurium pulchellum 17(+-2), Carex
Centaurium pulchellum 57(r-2), Carex distans 29(r-2), Juncus maritimus 29(r-1),
rum 14(r), Sonchus arvensis 14(r), Trifolium repens 14(r), Centaurium littorale
22(+-1), Potentilla anserina 8(+-1), Plantago major (24+-2), Leontodon autumnali
caria inodora 11(+)°, Bromus mollis 8(+), Ranunculus sceleratus 16(+-1)°, Poa an
Cirsium arvense 5(+-1), Poa trivialis 3(3), Hordeum secalinum 3(1), Taraxacum sp.
3(+), Senecio vulgaris 3(+), Anagallis arvensis 3(+), Leontodon nudicaulis 3(+);
tricaria inodora 10(r)°, Bromus mollis 10(+), Sagina maritima 40(+-2), Juncus bu
Column 11: Bromus mollis 8(r); Column 12: Ranunculus sceleratus 5(+), Cochlearia

1. In the alliances Thero-Salicornion and Spartinion represented by S. stricta Dum.
2. Preferential character-taxon of the association; also selective character taxon of the
   the order Glauco-Puccinellietalia.
3. Also character-taxon of the alliance Halo-Scirpion.

Asteretea tripolii

Glauco-Puccinellietalia

	on maritimae	Armerion maritimae			Puccinellio-Spergularion salinae			Halo-Scirpion
etum	Halimionetum portulacoidis	Artemisietum maritimae	Juncetum gerardii	Junco-Caricetum extensae	Puccinellietum distantis	Puccinellietum fasciculatae	Puccinellietum retroflexae	Halo-Scirpetum maritimi
	5	6	7	8	9	10	11	12
	40	61	64	7	37	10	12	19
	40(+-1)	30(+-1)$^{\circ}$	42(+-1)$^{\circ}$	14(+)$^{\circ}$	35(+-2)$^{\circ}$	70(r-2)$^{\circ}$	100(1-2)$^{\circ}$	-
	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-
	35(+-2)	13(+)	20(+-2)	-	8(+)$^{\circ}$	-	17(r)	37(+-2)
	92(+-2)	43(+-2)	31(+-2)	14(+)	62(+-1)	90(r-3)	25(r-1)	26(1-3)
	100(3-5)	98(+-3)	62(+-1)	-	5(+)	-	-	-
	-	93(+-3)	59(+-1)	-	8(+-1)	-	-	-
	-	2(+)	90(+-3)	14(r)	-	-	-	-
	-	-	-	100(1-4)	-	-	-	-
	-	-	-	-	100(1-5)	20(r-2)$^{\circ}$	17(r-+)	-
	-	-	-	-	-	100(2-4)	17(r)	-
	-	-	-	-	-	-	100(1-4)	-
	-	-	-	-	32(+-2)$^{\circ}$	10(+)$^{\circ}$	8(r)$^{\circ}$	100(3-5)
	37(+-4)	5(+-2)	-	-	-	-	-	-
	-	-	86(+-5)	100(2-4)	14(+-2)	30(+)	-	5(+)
	62(+-1)	100(3-5)	97(+-5)	86(+-3)	35(+-3)	10(r)	-	-
	15(+-1)	33(+-1)	98(+-3)	100(2-3)	35(+-3)	30(r-2)	-	11(+)
	-	5(+-1)	64(+-3)	43(+-2)	19(+-2)	10(+)	8(+)	-
	-	-	11(+-1)	100(+-3)	65(+-2)	30(+-2)	-	42(+-4)
	-	-	-	-	97(+-3)	80(+-2)	100(r-2)	-
	42(+-2)	72(+-2)	47(+-1)	14(+)	19(+-1)	20(1-2)	8(+)	-
	60(+-2)	66(+-2)	91(+-3)	57(r-2)	3(+)$^{\circ}$	-	-	-
	97(+-2)	100(+-2)	72(+-2)	71(r-1)	65(+-3)	100(r-3)	100(+-4)	74(+-2)
	62(+-2)	29(+-1)	77(+-2)	29(+)	5(+-1)	50(r-2)	8(r)	16(+-1)
	65(+-2)	72(+-3)	98(+-3)	100(+-2)	11(+)	-	8(+)	-
	60(+-2)	31(+-1)	20(+-1)$^{\circ}$	-	38(+-1)$^{\circ}$	30(r-1)$^{\circ}$	8(1)$^{\circ}$	-
	5(+)	11(+)	5(+)$^{\circ}$	-	62(+-2)$^{\circ}$	40(r)$^{\circ}$	-	63(1-3)
	22(+)	31(+-2)	28(+-2)	-	30(+-2)	-	-	32(+-2)
	-	-	2(+)	-	30(+-3)	10(r)	-	-
	-	-	2(+)	29(+)	11(+-1)	10(1)	25(+)$^{\circ}$	-
	-	-	2(+)	43(r-+)$^{\circ}$	30(+-3)	10(r)$^{\circ}$	67(r-2)$^{\circ}$	11(+-2)

llum 17(+-2), Carex distans 5(+), Sagina maritima 2(+), Solanum dulcamara 2(+); Column 8:
maritimus 29(r-1), Lotus tenuis 29(2), Hippophae rhamnoides 29(r-+), Trifolium fragife-
ntaurium littorale 14(+)$^{\circ}$; Column 9: Polygonum aviculare 41(+-2), Elytrigia repens
Leontodon autumnalis 5(+), Trifolium repens 11(+)$^{\circ}$, Coronopus squamatus 8(+-2), Matri-
us 16(+-1)$^{\circ}$, Poa annua 11(+-2), Cochlearia officinalis 11(+), Festuca arundinacea 8(+),
3(1), Taraxacum sp. 5(+), Sonchus arvensis 3(+), Poa pratensis 3(+), Solanum nigrum
on nudicaulis 3(+); Column 10: Centaurium pulchellum 10(+), Plantago major 20(r)$^{\circ}$, Ma-
40(+-2), Juncus bufonius 40(r-2), Hordeum marinum 10(r), Samolus valerandi 10(r);
us 5(+), Cochlearia officinalis 5(+), Atriplex littoralis 5(+).

stricta Dum.
racter taxon of the alliance Puccinellion maritimae and exclusive character-taxon of

1968 and OBERDORFER et al. 1967) also worked with local character species, though always in close connexion with alliance character-species.

This local association approach as such has been criticized from another point-of-view by SCHWICKERATH (1942, 1954a, 1963). This author emphasized that geographically differentiating taxa should be used in the delimitation of syntaxa, but whenever a series of geographically different syntaxa should have one or more character-taxa in common they should be grouped together into one association. SCHWICKERATH especially criticized the splitting up of the Xerobrometum by BRAUN-BLANQUET & MOOR (1938).

To solve the problem use of different terms for more localized, vs. more widely distributed, phytocoena has been suggested. KNAPP (1942, 1948, 1958) introduced the concept of chief-association (Hauptassoziation) for the type of association SCHWICKERATH was referring to. MEIJER DREES (1951) defined it as follows: the smallest unit possessing absolute or regional character-species. Absolute = general or regional is meant here in the sense of BRAUN-BLANQUET & MOOR (1938) and MEIJER DREES, i.e. not occurring outside the association's range. KNAPP (1971) later mentioned the concept rather incidentally as referring to character-species that are valid 'at least within an entire flora-region.' The more local units comprised in a Hauptassoziation were called Gebietsassoziationen, or 'regional associations'. PASSARGE (1968) and PASSARGE & HOFMANN (1968) elaborated the suggestion by KNAPP towards a separate system of historic-geographical units besides the usual edaphic-ecological units. 'Regional' (territorial or provincial) associations could then be distinguished as parallel but subordinated units to the 'elementary association,' with which the chief-association is identical. PASSARGE & HOFMANN (1968) subjected the regional association to a trinary nomenclature as is applied in zoological systematics for geographical races.

This brings us back to OBERDORFER (1957, 1968) who sharply distinguished between 'association,' 'regional-association' and 'geographical race.' (See also MÜLLER 1968). A regional association ('Gebietsassoziation') has a limited distribution-area; it is characterized by a combination of regional (or local) character-taxa, corresponding with SCHWICKERATH's geographically differentiating taxa, and general alliance character-taxa. A geographical race is a regional expression of a larger, regional or general association, without such a typical combination of territorial and alliance character-taxa. As OBERDORFER (1968) remarked, it will often be very difficult to distinguish between the two levels. Geographical races have not yet found a place in the formal hierarchy but have nonetheless frequently been described, particularly in Germany (e.g. OBERDORFER 1957), Czechoslovakia (e.g. NEUHÄUSL & NEUHÄUSLOVÁ-NOVOTNÁ 1972) and Poland (e.g. MATUSZKIEWICZ 1962).

We have thus a surfeit of terms and concepts. To resolve this matter we refer to the remarks on character-taxa (20.5.8) and adopt the distinctions made by OBERDORFER and others under three terms for units of expanding geographic extent: the local association, regional association, and (general) association. Clearly these intergrade, but in principle they should possess local, regional and general character-taxa, respectively. Groups of related regional associations, which are in fact vicariant associations (cf. PASSARGE 1968) could be called 'vicariant association groups'; this term seems more appropriate than either chief or elementary association. Another acceptable name for the vicariant association-group is collective association (cf. MEIJER DREES 1951).

We shall now briefly discuss the Artemisietum maritimae association as presented in Table V. It is characterized by one character-taxon, *Artemisia maritima* which has, according to Table VI, a high fidelity degree (at least in the investigated area) and which is, according to the synchorological data presented by BEEFTINK (1965) as well as chorological data on the species, a territorial character-taxon. It follows from Table VI that most of the salt marsh associations in the southwestern Netherlands are typified by few but generally 'good' character-taxa (fidelity degrees 4 or 5). The normal characteristic taxon combination of the Artemisietum maritimae in the southwestern Netherlands consists of *Artemisia maritima*, *Festuca rubra* f. *litoralis*, *Limonium vulgare* ssp. *vulgare*, *Aster tripolium* and *Plantago maritima*. BEEFTINK has listed most of the taxa under a specific head so that the companions are few and simply called 'other taxa'. Note the four relevés at the right end of the table, that lack the character-taxon and are considered a fragmentary syntaxon.

20.6.4 HIGHER UNITS (ALLIANCE, ORDER, CLASS)

When a new association is recognized, it must be placed in the system of higher units. The assignment of an association to an alliance (and other higher units) is primarily based on comparison of floristic relationships. As in plant taxonomy (cf. DAVIS & HEYWOOD 1963) the terms relation(ship) and affinity refer only to the possession of common characters. They do not refer to syngenetical (successional) links; we may compare with SOKAL & SNEATH'S

(1963) emphasis of phenetic relationships. Group importance values of the character- (and differential-) taxa of the relevant alliances are calculated, either on a presence-absence or on a quantitative basis, and compared (cf. WESTHOFF 1947, RAABE 1957). It may occur that the affinity towards two alliances (or orders or classes) is almost equal. An example of close relationship towards two alliances is presented by the Artemisietum maritimae. Generally the Armerion maritimae alliance is the obvious higher unit, as follows from tables V and VI, but the subassociation Artemisietum maritimae typicum is also clearly related to the Puccinellion maritimae. In fact the association was once assigned to the Puccinellio-Salicornion alliance (BRAUN-BLANQUET & LEEUW 1936) from which the Puccinellion maritimae was split off, but later (e.g. TÜXEN 1937, BEEFTINK 1965, WESTHOFF & HELD 1969) it was considered part of the Armerion maritimae. In cases of doubt equal use is made of structural, physiognomical and synecological considerations (cf. OBERDORFER 1957, WESTHOFF & HELD 1969).

It may also be the case that in a little-known area a number of new associations are described; and some of these may bear so little relation to known alliances (etc.) that they should be classified into new higher units. As was introduced in 20.3.2, various higher units above the association level, viz. the alliance, the order, and the class are characterized in the same way as the association. Species equally occurring in a group of related associations but faithful to that group, become character-taxa for higher units to which they are faithful. Contrary to most associations the higher units generally do possess a number of regional or general character-taxa of high fidelity. When an alliance character-taxon shows a preference for one association within an alliance, it may be used both as alliance character-taxon and as differential-taxon for an association within the alliance. The species is then termed a 'transgressive character-taxon.' Species may of course bear similar character- and differential- relations to orders vs. alliances, and classes vs. orders. Interpolated units like the suballiance and suborder are characterized by character-taxa and/or differential-taxa. Their use is to be avoided; but the suballiance has had some use.

Formal definitions for higher syntaxa and instructions for their ranking have not been agreed upon (cf. PIGNATTI 1968b, DIERSCHKE 1971). In practice the number of related associations tends to determine the number of the higher units classifying these. Growth in number of associations expresses its influence upward, in growth in the number of alliances, etc. For example, TÜXEN (1937) described 94 associations and 41 alliances for northwest Germany;

in TÜXEN (1955) the numbers were 189 and 76. In the Netherlands the number of described alliances grew from 39 (WESTHOFF et al. 1946) to 85 (WESTHOFF & HELD 1969). PIGNATTI (1968b) called the attention to the 'inflationary' character of this phenomenon. His suggestive title stimulated much discussion (TÜXEN 1968b: 89—97), which produced few solutions apart from plans for cooperation and standardization now being realized in the European Prodromus of plant communities.

20.6.5 UNITS ABOVE THE CLASS

The growing number of classes, as well as the extension of the BRAUN-BLANQUET approach to various, and floristically different parts of the world, lead to the introduction of units above the class. The grouping above the class originally proposed by BRAUN-BLANQUET, the 'vegetation circle' was a phytogeographical rather than a sociological unit. BRAUN-BLANQUET (1959) and TUXEN (1970a) on a suggestion of SCHMITHÜSEN sought to establish a new unit, the *class group* (cf. TÜXEN 1963: 213—218).

The class group (TÜXEN 1970a) is a set of territorially defined, largely vicariant classes analogous with the 'vicariant association group' (20.6.3). The characterizing taxa are in this case *genera* with vicariant species in different floristic provinces or regions; for example the classes Querco-Fagetea silvaticae (Europe), Querco-Fagetea grandifoliae (North America), and Querco-Fagetea crenatae (East Asia) form a class group: Querco-Fagea, with the suffix -ea probably taken from JAKUCS (e.g 1972). Curiously, BRAUN-BLANQUET (1964) presented the class group under a different name 'community kingdom' (Gesellschaftsreich) and apparently as a somewhat different phytogeographical concept. Although he first (p. 140) stated that this unit 'takes together classes floristically related by vicariant species and identical higher categories', he concluded that community kingdoms should coincide with SCHMITHÜSEN'S (1961) vegetation kingdoms established by means of vicariant classes.

TÜXEN'S class group should not be confused with the geographically determined class-group of SCAMONI et al. (1965). However, according to the elaboration given by PASSARGE (1968) and PASSARGE & HOFMANN (1968), these class groups correspond actually to the usual European classes. It is questionable whether PASSARGE & HOFMANN'S (1968) complicated system of two hierarchies can be integrated in the BRAUN-BLANQUET system. TÜXEN (1971) strongly rejected such an integration.

Three other treatments of higher units deserve mention. (i)

CHAPMAN (1952, 1959) used terms like Coeno-Salicornietalia for groups of higher units dominated by species of one widely distributed genus. For such a unit the name Coeno-Salicornietum should be preferred. (ii) The concept of 'vegetation type' was developed by HADAČ (e.g. 1962, 1967) for groups of more or less similar classes. The vegetation type is based on the occurrence of common species (indicating or 'bezeichnende' species). However, the floristic basis of these units seems to be rather loose, and as HADAČ admits the vegetation types are 'practically formations'. (iii) JAKUCS (1961) also used the class group concept, which he later (e.g. 1972) named 'division' and for which he introduced the suffix -ea. HADAČ (1967) concluded that the division is largely identical with his vegetation type, which term should then have priority. The identity seems to be real, but for it the term 'vegetation type' is least descriptive and most confusing; *division* should be preferred. BOLOS (1968) presented a system of divisions for classes occurring in Spain. As term and concept the division is consonant with the hierarchy.

In conclusion, a division may be defined as a syntaxon above the class level that unites related classes within a floristic region (or province) on the basis of common division character-taxa. The character-taxa may be species, or genera, or both. Let us call this a 'vertical' unit in the sense that it unites lower units sympatric in a given region. The class-group concept, in contrast, is comparable with the vicariant association group in that it joins units on the same level from different floristic territories. It is in this sense a 'horizontal' unit. Its character-taxa will more usually be genera than species. Therefore the name 'vicariant class group' may be proposed, defined as a group of classes allopatric in geographic occurrence, but linked by the occurrence of vicariant species in one or more genera. Since two units would be distinguished in this way, it may be questioned whether the suffix -ea should be used for both. It seems logical to reserve this suffix for the division, for which it was proposed.

The definition of the division is not physiognomic. We suggest that, the difference in definition notwithstanding, divisions may converge in practice with the formations of Anglo-American ecology (article 13), as broad physiognomic units limited to a given region or continent. Vicariant class groups, in contrast, would link floristically related phytocoena of different continents. Thus the Querco-Fagetea-group would comprise forest phytocoena with genera in common in Europe, eastern North America, and western Asia, whilst a Spartinetea-group would comprise a set of more narrowly defined phytocoena (*Spartina* associations) in the salt marshes of the world.

20.6.6 HORIZONTAL AND VERTICAL CLASSIFICATION

Thus we follow the suggestion of KNAPP (1948), to classify independently by two principles, the one on an edaphic-ecological ('vertical') and the other on a historic-geographical ('horizontal') basis. This suggestion has been amply discussed (WESTHOFF 1950, MEIJER DREES 1951, BARKMAN 1958a, BEEFTINK 1965, SCAMONI et al. 1965, PASSARGE & HOFMANN 1968, PASSARGE 1968). All authors agree with the incorporation of both viewpoints in syntaxonomy. MEIJER DREES emphasized the vertical approach, because syntaxonomy should build upward from locally classified associations. BEEFTINK suggested that the choice of the criterion would depend on the peculiarities of the vegetation concerned: for some phytocoena with disjunct distributions the stronger floristic relations and preferred grouping would be horizontal whereas for other phytocoena the more natural grouping would be vertical. PASSARGE & HOFMANN use both principles on each level, with the geographical units subordinated to the corresponding edaphic units, which makes the system very complicated (cf. TÜXEN 1971, in his critical review of PASSARGE & HOFMANN 1968).

We would modify BEEFTINK's suggestion in recommending that the main-axis of the classification should be 'vertical' on all levels of the hierarchy. Given the main direction of the classification as vertical, secondary to this, 'horizontal' vicariant groupings may be recognized on any syntaxonomic level. We have mentioned such groupings for associations (20.6.3) and higher syntaxa (20.6.5); we may now trace the problem and the principle into the lower syntaxa.

20.6.7 LOWER UNITS (SUBASSOCIATION, VARIANT, FACIES)

Associations are on the one hand joined into higher units, and on the other divided into subordinate units. As in idiotaxonomy the former procedure is compulsory, the latter facultative. The lower syntaxa are mostly characterized by differential-taxa. Usually, also, the syntaxa below the association level are described as deviations from average or typical situations. Thus to complete the syntaxonomy on a certain level a 'typical' subassociation (variant, etc.) and one or more 'deviant' syntaxa are described and characterized in parallel.

Variations within an association have been approached in three directions; to the edaphic-ecological ('vertical') and historic-geographical ('horizontal') may be added a syndynamical (successional) point-of-view. It has been proposed repeatedly that different syntaxa should correspond to these approaches each of which could form a hierarchy of subordinate units. Thus the subassociation might be based on local edaphic or micrometeorological differences within the association, the variant on geographical or climatological differences (with the terms vicariant and geographical race as synonyms), and the phase on differences in successional status. This distinction is in accordance with the original approach of BRAUN-BLANQUET (1928, 1932, BRAUN-BLANQUET & PAVILLARD 1928). SCHWICKERATH (1942) and DUVIGNEAUD (1946, 1949) distinguished five types of differential-taxa on the basis of differences in nutrient status, moisture conditions, successional status, geographical area, and human influences.

The system was further extended by the incorporation of the sociation, a unit defined by the dominant species of its strata (see article 18). This suggestion of NORDHAGEN (e.g. 1937) was acknowledged by the 1935 Botanical Congress (see DU RIETZ, 1936). In the Netherlands it has become common practice to describe species-poor communities without character-species but with one or more dominants as sociations or consociations (WESTHOFF 1947, 1949, BEEFTINK 1965, WESTHOFF & HELD 1969). Contrary to DU RIETZ (1930b, 1936, 1965) the sociation and consociation are considered of association-rank (BRAUN-BLANQUET 1955, MAAREL et al. 1964). They may be assigned to an alliance and higher syntaxa (WESTHOFF & HELD 1969).

From the beginning many communities have been described without receiving a definite syntaxonomic position. They are often called 'community of ......' ('Gesellschaft von ......') (cf. ELLENBERG 1956, NEUHÄUSL 1963, FUKAREK et al. 1964). These units can be either provisional local coena, which might later be ranked in the system when more evidence is available, or coena without character-species or dominants. BARKMAN et al. (1958) and WESTHOFF et al. (1959), proposed the term 'consortium' for the latter units.

An additional term for subordinate units, 'form,' is used in different ways for syntaxa of lower rank. It may mean a unit of no specified rank (as seems to be the case with SCHUBERT 1960, for example). It is also used in relation to altitude (OBERDORFER 1957, 1968, BRAUN-BLANQUET 1964) or moisture conditions (DUVIGNEAUD 1946). The 'Ausbildungsform' is considered the lowest unit in the hierarchy apart from the facies by TÜXEN (1970a, cf. SCHUBERT 1960, PASSARGE 1968).

The distinction of local-edaphic and geographic units has been maintained by BRAUN-BLANQUET (1951, 1964), MEIJER DREES (1951), OBERDORFER (1957, 1968), BARKMAN (1958b) and others.

Under the influence of Tüxen (1937) the variant became a subunit under the subassociation (Braun-Blanquet 1951a, 1964) rather than a differently defined (geographic) unit. In line with this practice we suggest as the downward extension of the primary hierarchy, for units based on local variations: association, subassociation, variant, subvariant, and facies. The last two may be often unneeded, but facies may be ecologically significant and useful as indicators in some cases (Krause 1954). Geographic races of lower syntaxa would be separately indicated by the territories in which they occur (Oberdorfer 1957, Müller 1968).

The *subassociation* is indicated with the suffix -etosum. Of the various ecological possibilities and corresponding symbols of Duvigneaud (1946, 1949) *d* and δ may be used for subassociations differentiated by nutrient and moisture status, respectively. Schwickerath (e.g. 1942), Duvigneaud (1946) and Meijer Drees (1951) showed how subassociations of an association may in fact indicate the transitions of that association towards related associations. The subassociation 'typicum' may then be considered as the 'nucleus' of the association (cf. Fig. 1); in fact this term is commonly used for the subassociation that lacks differential-species. Westhoff (1965, Westhoff & Held 1969) observed that many subassociations of the latter type were relatively poor in species, and particularly poor in character-species of the association. Such units were indicated as 'inops' (= having shortage of); the 'typical' Querco-Betuletum is an example of such an 'inops'-subassociation.

The next lower rank is called the *variant*. According to Braun-Blanquet (1964: 124) a variant would not be characterized by differential-species, but 'either by a strong prominence of certain species, which cannot be considered as differential-taxa, or by a slightly deviating species assemblage.' This criterion is, however, diagnostically too vague. Most phytosociologists share the opinion that a variant also must be characterized by differential-species. The same holds for the next lower rank, the subvariant. The variant-differentiating taxon (taxa) may be differentiating only because of its 'strong prominence,' i.e. its higher combined estimation values in one variant compared with others and not because it is clearly present resp. absent. In most cases the variant is distinguished within the subassociation; but it is also possible to divide an association directly into variants, if the mutual differences are considered too small to justify the rank of subassociation. Below the variant the subvariant may be used if needed.

The lowest unit is the *facies*. It is not even characterized by differential-taxa; it thus does not employ diagnostic-species and is not part of the formal hierarchy. A facies is usually characterized by the dominance, in a high cover degree (scale 4 or 5), of one of the species belonging to the normal floristic assemblage of an association. It is not usual to consider a stand as a facies if this dominance is a normal feature of that association. Since, for instance, dominance of *Fagus sylvatica* is normal for any association assigned to the alliance Fagion sylvaticae, it is not appropriate to construct such a coenon as 'a *Fagus* facies of the Fagetum.' A facies, therefore, is a deviation phenomenon. It may be brought about by special, and sometimes by extreme conditions of abiotic factors, but in many cases it is the result of human disturbance (e.g. MELTZER & WESTHOFF 1942, KNAPP 1971). Examples are a facies of *Rubus* sect. *Sylvatici* or *Rubus* sect. *Heteracanthi* in a stand of Querco-Carpinetum, or a facies of *Acorus calamus* in a stand of Scirpo-Phragmitetum. It is often possible to deduce an effect of human disturbance from the appearance of a certain facies.

20.6.8 NOMENCLATURE

Formal nomenclature of syntaxa started with the naming of associations by BRAUN-BLANQUET (1913), following precedents of CAJANDER (1903), BROCKMANN-JEROSCH (1907) and RÜBEL (1912). The first general proposals were discussed at the Brussels Botanical Congress (FLAHAULT & SCHRÖTER 1910); the nomenclature of associations and other syntaxa developed gradually thereafter. With the growth of the number of described syntaxa the need for standardization and rules increased. A start toward systematic nomenclature was made in 1933 (BRAUN-BLANQUET 1933b), and DAHL & HADAČ (1941) proposed a coherent set of rules based on the code of botanical nomenclature. During the Stockholm Botanical Congress BARKMAN (1953a) proposed a general set of rules and MEIJER DREES (1951) a complete system of nomenclature. These were discussed in a number of papers in *Vegetatio* vol. 4. Contributions by BACH et al. (1962) and RAUSCHERT (1963) appeared later, and BRAUN-BLANQUET (1964) reported on the discussion and presented 7 rules. The next phase started during the Symposium on Plant Sociological Systematics at Stolzenau, 1964, where MORAVEC (1968) introduced a set of 26 articles and urged a general acceptance of these amongst active plant sociologists. A special Working Group is now preparing a code for the new Prodromus project (see TÜXEN 1968b: 152, MORAVEC 1968, 1969, 1971, NEUHÄUSL 1968).

Some instructions for the construction of names and some proposed general rules for nomenclature of syntaxa follow.

According to MORAVEC (1971) five necessary principles are:
1. Each syntaxon (with definite rank, position and delimitation) has only one correct name.
2. Each name can be correctly used for one syntaxon only.
3. The correct name is established according to rules based on the priority principle.
4. The association is the fundamental nomenclatural unit (syntaxon).
5. The validity of nomenclatural rules is retroactive.

20.6.8.1 *Construction of Names*

For the standardization of syntaxon names, the following procedure is in general use.

To the generic part of the names of one or two (not more) characteristic (not necessarily faithful) taxa of a syntaxon a suffix is added. These suffixes are specific for the different syntaxonomic ranks, see Table VII. The suffix '-etum' for the association goes back to classical Latin and has been in use since HUMBOLDT (1805). The suffix '-ion' for the alliance was proposed by Moss (1910) and taken over by BRAUN-BLANQUET (1921: 347). The suffix '-etalia' for the order was presented in BRAUN-BLANQUET (1928). For the class, up to 1932 (BRAUN-BLANQUET, FULLER & CONARD) no specific suffix was used, since the classes were designated by circumscriptions such as 'communities of maritime dunes' (later the class Ammophiletea). In 1934 MEIER & BRAUN-BLANQUET proposed the suffix '-etales' for the class, but (BRAUN-BLANQUET et al. 1939) this suffix was later changed into '-etea'. The suffix '-etosum' was introduced by BEGER (1922).

If we are dealing with an association or alliance that is sufficiently characterized by one taxon (e.g. by a faithful dominant character-taxon), the genus name of the taxon is used with the appropriate suffix (-etum, -ion), followed by the species name in the genitive. For example the association Ericetum tetralicis is named after *Erica tetralix*, and the alliance Alnion glutinosae after *Alnus glutinosa*.

In some cases the specific epithet has been replaced by a geographical adjective indicating the area characteristic of the syntaxon, e.g. Agropyretum boreoatlanticum for the association of *Agropyron junceum* (syn. *Elytrigia juncea*) of the North Atlantic Coast. In this case this has been done to distinguish it from a different association of *Agropyron junceum* occurring in the Mediterranean. In recent decades, however, there is a tendency to avoid such geographical names as far as possible and to replace them by bigeneric names. In the case of orders and classes and, though less frequently, alliances the specific epithet is omitted when the context leaves no doubt – for example, 'Fagion' instead of 'Fagion sylvaticae' in a European context.

When a syntaxon was to be named after two characteristic (not necessarily faithful) taxa, the name of the second taxon was provided with the appropriate suffix; whilst the name of the first taxon was joined with the second one by the suffix -eto. Examples are the association Querceto-Betuletum, the alliance Alneto-Ulmion, the order Glauceto-Puccinellietalia, and the class Querceto-Fagetea. However in many cases this suffix was abbreviated to a connecting vowel after the stem of the first name, e.g. Alneto-Padion became Alno-Padion. Bach et al. (1962) proposed to do this systematically, mainly on the argument that, for example, 'Querceto-Betuletum' could mean a mixture of, or transition between, a *Quercus* stand and a *Betula* stand, which is of course something quite different. This proposal has been widely accepted. However, the correct choice of the connecting vowel, especially in the case of the third Latin declension and with names derived from Greek words, gives difficulties. Bach et al. (1962) and Rauschert (1963) gave directions for a large number of cases.

There are two reasons for choosing a bigeneric name. The first and more obvious is that a combination of two names should characterize the syntaxon better. The first name may be a dominant, generally the second name represents the character-taxon considered diagnostically most important. The other reason was already mentioned, viz. monogeneric names with a geographical adjective are replaced by bigeneric names, in which the first name comes from a species characteristic for the geographical region originally indicated. The example given above, the Agropyretum boreo-atlanticum, has been renamed in fact the Minuartio-Agropyretum (Tüxen 1955).

In some cases the nomenclature is at variance with the standard procedure. The following deviations should be mentioned:

(1) Contractions. It has become general use to follow the proposal by Koch (1925) to replace clumsy terms like 'Potamogetonion' (and, later on, also 'Potamogetonetalia' and 'Potamogetonetea') by 'Potamion', 'Potametalia' et 'Potametea'. However, Oberdorfer et al. (1967) proposed to return to the complete and cumbersome names.

(2) In special cases descriptive adjectives or substantives are in-

cluded in the name. 'Magnocaricion' indicates an alliance characterized by tall sedges; 'Macrophorbio-Alnetum' is meant to characterize a moist woodland (carr) association in which 'macrophorbiae' (tall forbs, Hochstauden) form a group of differentiating species.

(3) Finally, sometimes specific epithets have been used instead of generic ones. This was common practice in the early days of alpine phytosociology; BROCKMANN-JEROSCH (1907) and RÜBEL (1912), for example, used the names 'Curvuletum' and 'Firmetum' instead of 'Caricetum curvulae' and 'Caricetum firmae.' Later this practice has been applied only very rarely; a rather recent example is 'Alno-Padion' (KNAPP 1942, MATUSZKIEWICZ & BOROWIK 1957), to designate an alliance characterized by *Alnus glutinosa* and *Prunus padus.*

20.6.8.2 *Validity, Changes and Authors' Names*

Various rules have been proposed for the settlement of the validity of syntaxon names. A name should have been published after 1900 in printed form, available at least in generally accessible libraries. Publication of a name should be combined with an adequate diagnosis.

For associations and lower-rank units this would include the presentation of a table with the complete floristic composition of at least three relevés and the assignment of a type-relevé. For higher units the listing of character- and differential-taxa and the assignment of a type-unit of the next lower level would be required. Such types are called nomenclatural types.

When two or more correctly published names appear to refer to one and the same syntaxon, the oldest name has priority. When a syntaxon is divided into two or more units of the same rank, the original name goes to that new unit that contains the nomenclatural type.

When the valid name of a taxon used in a syntaxon name changes, corresponding change in the syntaxon name should be considered. In any case a syntaxon name should be changed when one of the name-giving taxa appears to be a younger homonym of a different legitimate name. For example, the Isoëtetum setacei should become the Isoëtetum delilei, since *Isoetes setacea* (Box ex) DELILE appeared to be a homonym of *Isoetes setacea* LAM. = *I. echinospora* DUM. and was then renamed *I. delilei* ROTHMALER.

No agreement has been yet reached on the – still very frequent – simple nomenclatural changes. E.g. *Carex nigra* (L.) REICH-

ARD appears to be the correct name for *C. fusca* ALL. Should the order Caricetalia fuscae now be renamed the Caricetalia nigrae? MORAVEC (1968) would say not; WESTHOFF would say yes and in fact (WESTHOFF & HELD 1969) changed this name.

Rules for the citation of authors' names have also been proposed, more or less parallel to those of idiobotanical nomenclature. The name of the author(s) who published a valid name is added to that name together with the year of publication. When this name refers to a previously published but invalid name, the earlier author's name is added in the form, Thero-Airion TÜXEN ex OBERDORFER 1957. When a name is changed, e.g. when the syntaxonomic level is changed, the author of the changed name is added between brackets. When a syntaxon is given a new contents or delimitation, both old and new authors are mentioned connected with the abbreviation em. (= emendavit).

These proposals were advanced by MORAVEC (1968). PIGNATTI (1968b: 87) recommended dropping authors' names to avoid the description of new syntaxa by authors who primarily want to have their names immortalized. In the discussion following, p. 89—97, there was agreement on omitting author's names when no confusion could occur, especially with higher units and when a prodromus can be referred to.

20.6.9 SCHEME OF SYNTAXA

All in all phytosociological nomenclature may be considered a necessary evil. Contrary to the opinion of DOING (1962, 1966, 1970) that a rigid system of nomenclature should be abandoned for practical reasons, we would emphasize that the value of the system for ordering information and communicating among phytosociologists outweighs its difficulties. We would further state that descriptions of formal phytosociological syntaxa should either be published in strict accordance with nomenclatural rules, or they should not be published as such.

Table VII presents the current syntaxa and their nomenclature, as discussed so far. Examples together with their denominating taxa are added. The variant (and the facies) are given here without suffixes. The geographically determined syntaxa (20.6.3, 20.6.5), which have not yet been agreed upon, are not included.

TABLE VII

Scheme of Syntaxa

Levels and units of the formal hierarchy from highest (Division) to lowest subvariant, with suffixes and examples of the construction of names after denominating taxa.

Syntaxon	Suffix	Examples	Denominating taxa
Division	-ea	Querco-Fagea	genus Fagus
Class	-etea	Phragmitetea	Phragmites australis
		Querco-Fagetea silvaticae	Quercus robur Fagus sylvatica
Order	-etalia	Littorelletalia	Littorella uniflora
		Festuco-Sedetalia	Festuca and Sedum L. div. spp.
Alliance	-ion	Agropyro-Rumicion crispi	Agropyron repens, (syn.: Elytrigia repens) and Rumex crispus
		Alnion glutinosae	Alnus glutinosa
Suballiance	-ion (-esion)	Ulmion carpinifoliae (Ulmesion)	Ulmus carpinifolia
Association	-etum	Ericetum tetralicis	Erica tetralix
		Elymo-Ammophiletum	Elymus arenarius, Ammophila arenaria
Subassociation	-etosum	Arrhenatheretum elatioris brizetosum	Briza media
Variant		ibid., Salvia variant	Salvia pratensis
Subvariant		ibid., Bromus subvariant	Bromus erectus

20.7 **Extension of the Approach**

20.7.1 OTHER GEOGRAPHIC AREAS

From its center of origin in the Alps and the western Mediterranean the BRAUN-BLANQUET approach spread into many European countries and Japan. Larger parts of the Mediterranean and Euro-Siberian, and smaller parts of the Sino-Japanese, floral regions have been synsystematically described. Still, a considerable part of the original working area is insufficiently known, particularly the eastern Mediterranean, Russia and Scandinavia (see the map presented by DIERSCHKE 1971). Expansion of the approach's influence continues, and we shall give a short survey of more recent literature applying the approach outside its European homeland. The survey cannot be exhaustive; only regions will be mentioned in which substantial work has been done. For further references the reader is referred to *Excerpta Botanica Sectio Sociologia* (bibliographic contributions to which are indicated below as 'Exc.'). This series can also serve as a survey of phytosociological work in the three regions mentioned above, with bibliographies for almost all European countries.

Japan may deserve special attention. The phytosociological study of Japan was initiated by SUZUKI/TOKIO and developed especially by MIYAWAKI and his pupils (see MIYAWAKI 1960 and 1966a, 1971a Exc.). Of special interest is the manner in which the Japanese communities are compared with Mediterranean and Indo-Malaysian communities. Other comparative studies in Japan include OHBA (1972), in which various vicariant salt marsh associations were described, partly belonging to the 'European' class Asteretea tripolii; TÜXEN, MIYAWAKI & FUJIWARA (1972) on the class Oxycocco-Sphagnetea in which Europe and North America (work of R. KNAPP and A. DAMMAN) are included; and TÜXEN (1966a) on holarctic Honckenyo-Elymetea communities. These studies were all based on extensive relevé tables and close cooperation between European and Japanese phytosociologists. From these studies the concept of vicariant class group developed (see TÜXEN 1970a and 20.6.5). Vegetation mapping on a phytosociological basis has reached a high level in Japan (see MIYAWAKI 1966b, 1971b, Exc. for a survey of maps).

The *arctic-subarctic* region has only occasionally been described. Iceland is becoming relatively well-known; a general survey is in preparation by R. TÜXEN based on phytosociological excursions by HADAČ, BÖTTCHER, the International Society for Plant Geography and Ecology, and others. Newfoundland was partly described by DAMMAN (1964). The research on Oxycocco-Sphagnetea by DAMMAN in Canada was already mentioned under Japan as was the study of TÜXEN (1966a). See also STEINDÓRSSON (1966, Exc.) for Iceland, BÖCHER (1961, Exc.) for Greenland, and HANSON (1959, Exc.) for Alaska.

The *west and central Asiatic* (Irano-Turanian) region has been described in a fragmentary way. An extensive survey of xerophytic and summer-dry hygro- and mesophilous communities of Afghanistan was presented by GILLI (1969, 1971), who could reasonably establish associations, though not as sharply delimited as in Europe because of the large number of species in most communities. HARTMANN (1968, 1972) published accounts on mountain grassland and scrub communities.

For the *Macaronesian* region the Canaries are relatively well-known through work of RIVAS-GODAY & ESTEVE CHUECA (1965), OBERDORFER (1965), LEMS (1968), and SUNDING (1969), as well as

LOHMEYER & TRAUTMANN (1970) who reviewed this literature (see also references in SUNDING 1969-70, Exc.). Studies on the Azores and the Cape Verdes were listed by PINTO DA SILVA & TELES (1962, Exc.). OBERDORFER (1970) reported on some plant communities on the Canaries and described complex, stable, mosaics of succulent scrubs and open sclerophyllous woods, which are amongst the most complicated communities of the world and should be studied as complexes (cf 20.7.4 and the South-African Kingdom below).

Rather numerous, though still scattered phytosociological studies have been carried out in the *North-American* and *Canadian* regions, starting with the description of Long Island by CONARD (1935) including 71 associations. CONARD (1952) also published on the vegetation of Iowa and DANSEREAU (1957) on the middle St. Lawrence Valley. TOMASELLI (1958, quoted in KÜCHLER 1967) described plant communities in eastern Kansas. Monographs are concentrated on forest communities (except for the studies of LOOMAN e.g. 1969 on grasslands). They include those of MEDWECKA-KORNAŚ (1961) in the Montreal area, GRANDTNER (1966) in Quebec, KORNAŚ (1965) in North Carolina, CRISTOFOLINI (1967) in Tennessee, JANSSEN (1967) in Minnesota and KRAJINA (1969) in British Columbia. KNAPP (1957, see also 1965) presented a preliminary survey of higher phytosociological units, viz. 72 classes, some of which were divided into orders and later (KNAPP 1964) extended it to the whole holarctic Kingdom.

The *Indo-Malaysian* and the *Polynesian* subkingdoms are practically phytosociological terra incognita. Some studies have been made in India (BHARUCHA & MEHER-HOMJI 1963, Exc., GUPTA 1966, 1967, Exc., MEHER-HOMJI 1969, Exc., MEHER-HOMJI & GUPTA 1972a,b, Exc.).

The *African* territory has been studied rather intensively, here and there. French studies on the North African desert region culminate in the monograph of QUÉZEL (1965), which presents a coherent survey of over 100 desert communities largely fitted into a syntaxonomic system (see also ROUSSINE & SAUVAGE 1961, Exc.). Relatively intensive studies have been performed in the West African rain forest region by LEBRUN (e.g. 1960), LEBRUN & GILBERT (1954) and SCHNELL (1952). The associations and higher units described are all based on relevés and range from xerophytic and hydrophytic pioneer communities to climax forests. LEBRUN concludes that the BRAUN-BLANQUET approach is very well applicable. Savanna studies in this area include those of DUVIGNEAUD (1949), ADJANOHOUN (1962), and DEVRED (1956). In Moçambique a first phytosociological inventory was carried out by GOMES PEDRO & GRANDVAUX BARBOSA (1955), see also PINTO DA

Silva & Teles (1962, Exc.). Knapp (1965, 1966a) presented preliminary surveys of higher units for West, Central and East Africa and reviewed the literature for some countries (Knapp 1969—70, 1971a,b, Exc.).

Phytosociological research in *South Africa* started recently and is now expanding rapidly (Edwards 1967, Taylor 1969, Zinderen Bakker 1971, Werger 1973, see Werger for references). Werger et al. (1972) presented the first account of plant communities in the Cape Kingdom, including vegetation types of the famous 'Fijnbos' formation. Their experiences with the Braun-Blanquet approach in this extremely varied mosaic of species-rich communities are comparable with that in European xerotherm woodland-scrub-borderline communities (cf. Jakucs 1961, 1972).

The *Caribbean* region has also been treated in general phytosociological studies, e.g. Knapp (1965). Detailed descriptions of savanna vegetation in Surinam have been published by Donselaar (1965, 1969), who found the Braun-Blanquet approach applicable. The North Surinam open savannas could be grouped into one class. A special problem was formed by the floristic similarities between community types of deviating structure. Donselaar considered the floristic relations as decisive, as did Werger et al. (1972) for similar situations in Fijnbos communities of the Cape. Earlier Surinam work is mentioned in Boerboom (1970, Exc.). *Brazilian* rain forest descriptions are very limited (Veloso 1962 in Braun-Blanquet 1964, Donselaar 1965). The *Andean* region has received more attention; Oberdorfer (1960), Schmithüsen (1960), Eskuche (1968, 1969) described various scrub and forest communities, and Kohler (1968, 1970) desert and coastal communities. See also Eskuche (1967, Exc.) for this, and adjacent regions in South America. Knapp(1966b) presented a survey of higher vegetation units in *Patagonia.*

The Braun-Blanquet approach has thus been applied in nearly all floristic regions, and to almost all types of vegetation. The approach should in principle be universally applicable; and in fact no difficulties have been met in its expansion out of Europe more fundamental than those encountered in Europe. The principal directions of difficulty are: (i) In species-poor vegetation in the North and the Antarctic, character-taxa may be difficult to find and use, and species dominance (and the sociation as a unit) may be more emphasized (see article 18). (ii) Rich tropical vegetation confronts the approach with such a wealth of species as to make application more difficult; physiognomy has been more emphasized in the tropics as a means of recognizing phytocoena. (iii) Delimitation of uniform stands becomes difficult in mosaic structures of open xerothermic scrubs and woodlands, such as found in the Canaries and South Africa (cf. 20.4.1).

20.7.2 BIOTIC COMMUNITIES

Approaches to the classification of animal communities are diverse (WHITTAKER 1962); applications of the Braun-Blanquet approach have mostly been concentrated on the analysis of one or more animal groups in plant communities already described. General bibliographies were presented by RABELER (1957b, 1964, Exc.). More or less complete descriptions of biotic communities are restricted to marine benthic environments, in which animals and plants were used together to construct a hierarchy according to Braun-Blanquet principles (ROGER MOLINIER 1960).

The following conclusions may be drawn from work on biotic communities (cf. BRAUN-BLANQUET 1951, 1953, 1964, RABELER 1937, 1960, 1962, 1965, WESTHOFF & WESTHOFF-JONCHEERE 1942, MÖRZER BRUYNS 1950, WHITTAKER 1962, MAAREL 1965, TÜXEN 1965a and BARKMAN article 16 in this volume):

1. Species from most animal groups form characteristic combinations, often indicated as 'communities.' Mostly they are merely taxocoenoses (cf. MAAREL 1965).
2. The local distribution pattern of such groupings may coincide with that of the plant communities in which the groupings have been established, but mostly it is of a larger, sometimes of a smaller scale.
3. Most animal groupings are primarily bound to specific abiotic factors like soil surface moisture or to vegetation structural features (or, rather, to the micrometeorological features determined by them).
4. The plant community can be characterized by animal species groups, although the number of faithful animal species is low. As long as the synusial structure of animal communities is not sufficiently known, the phytocoenoses are the most realistic framework for biocoenotic studies. This implies that attempts like that of QUÉZEL & VERDIER (1953) to create a separate hierarchy of 'communities' of members of one – or a few – animal groups is unrealistic when these communities are in fact taxocoenoses.

20.7.3 MICROCOMMUNITIES AND SYNUSIAE

Since these community-types are treated by BARKMAN (article

16), we refer only to some current literature. The Braun-Blanquet approach has been applied to various kinds of microcommunities and synusiae. Bibliographies have been composed for: epiphytic communities (Barkman 1962, Exc., 1966, Exc.), marine algal communities (Hartog 1967 Exc.), epigeic moss and lichen communities (Hübschman & Tüxen 1964, Exc., Tüxen 1964, Exc., 1968/1969, Exc.) and soil inhabiting communities (Apinis 1969, Exc.) Classification systems have been developed by Hartog (1959) and Boudouresque (1971) for marine algal communities; Hartog distinguished associations which were grouped into formations, Boudouresque presented a complete hierarchic system. Broad classification systems of moss and lichen communities have been presented by Klement (1955), Koppe (1955), Barkman (1958), Wilmanns (1962). From these studies one may conclude that the Braun-Blanquet system is generally applicable to microcommunities and synusiae, and that it is advantageous to approach the latter through a classification separate from that for phytocoenoses (see also article 16.5 for references).

20.7.4 Community Complexes

A 'complex' is a set of contiguous or continuous communities forming a mosaic or pattern. Complexes can thus be studied on various levels from the microtopography of bogs to whole landscapes. Small-scale topographic complexes may often be studied without direct concern for successional relationships, even though the communities may have developmental relations to one another (as in bogs) or to the potential natural vegetation (Seibert 1968). In situations where man has drastically changed the vegetation pattern as well as the substrate or in geologically young systems such as coastal dunes it may be more realistic to approach complexes directly in their local mosaic or zonation structure. A difficult type of complex is the 'superposition complex' (Überlagerungskomplex) within which rapidly changing community patterns occur, e.g. with aquatic or with ephemeral communities (cf. Müller 1970).

For communities related by successional process the concept of community ring (Gesellschaftsring) was mentioned by Krause (1952) and developed by Schwickerath (1954b) and Schmithüsen (1961). The ring comprises the series of communities that are syndynamically related to a terminal community. Seibert (1968) translated the concept as 'circle of communities', a term that unfortunately invites confusion with Braun-Blanquet's (1932, 1964) 'circle of vegetation' or 'Vegetationskreis'. The English-language terms 'climax-complex' and 'successional complex' (see article 14.4.2) may well be preferred.

Study of broader topographic and edaphic complexes in relation to climax theory was initiated by TÜXEN. (For an English account of TÜXEN's views, see KÜCHLER 1967). TÜXEN & DIEMONT (1937, see also TÜXEN, 1933) developed the parallel concepts of 'climax swarm' and 'climax group' for spatially contiguous stable communities (Dauergesellschaften) that occur in the same climate, but differ in consequence of direction of exposure in mountains (swarm), or soil parent material in lowland areas (group). TÜXEN (1933) proposed also the term 'paraclimax' for a widespread stable community the characteristics of which are determined by soil development, and not climate alone. TÜXEN furthermore recognized a series of climax-regions for Europe, each characterized by a number of character-associations bound to it in their distributions, together with companion-associations (Begleitassoziationen) of wider distribution in more than one climax-region. The latter idea is a development beyond the climax-complex of BRAUN-BLANQUET (1928, 1964) and others; it characterizes regions not by a single, somewhat hypothetical climatic climax (Schlussgesellschaft), but by associations used as diagnostic-communities.

TÜXEN (1937) also recognized the coherence between the various substitute communities (Ersatzgesellschaften), both the completely cultural and the semi-natural ones, which may occur in the space that could be (and may actually partly be) occupied by a terminal community. Such locally coherent communities were consequently called 'contact communities.' The recognition of the coherence of substitute communities in their potential development towards one terminal community led TÜXEN (1956) to the concept of *potential natural vegetation*. This concept is defined in relation to a given habitat, as the vegetation that would finally develop (terminal community) if all human influences on the site and its immediate surroundings would stop at once, and if the terminal stage would be reached at once. With the latter restriction abiotical (e.g. macroclimatological) changes during this development are meant to be excluded. Although in many cases the potential natural vegetation may be identical with the original vegetation and interpretable as such, the distinction of this concept is useful for the following reasons: (i) There may have been no 'original' vegetation at all, since man has influenced the ecosystem under consideration at least as long as the present climate (and thus the present climax complex) lasts; (ii) Man may have induced irreversible changes in the ecosystem, so that the presumed 'original' vegetation can never establish again; (iii) reconstruction of the original vegetation may theoretically be possible in some cases, but precarious in practice.

Further discussion of climax interpretation is beyond our purposes here; we refer to WHITTAKER (1953), DANSEREAU (1957), SCHMITHÜSEN (1961) and BRAUN-BLANQUET (1964). We mention as significant, however, the phytosociological study of community complexes over wide geographic areas by KRAUSE (1952). KRAUSE observes the consistency of community composition over extensive areas together with the occurrence of vicariant communities, particularly between eastern and western Europe. The community-complex of a given area is shaped both by its macroclimate, and by local factors producing mosaic-like community relationships. Regions are characterized by different complexes, and different prevailing or dominant communities. Complexes give way to other complexes through geographic distance in three ways: (i) compression of communities into smaller areas and exclaves, (ii) increasing floristic impoverishment until a given community can be traced only in infrequent fragments, and (iii) the replacement of dominant communities by vicariants suited to other climates. For further discussion of vegetation areas and regions see SCHMITHÜSEN (1961), BRAUN-BLANQUET (1964), and SEIBERT (1968).

20.7.5 APPLIED PHYTOSOCIOLOGY

The floristic-sociological approach has been applied in many neighbouring disciplines. Early indications of this application were presented by BRAUN-BLANQUET (1930) and by TÜXEN (in BRAUN-BLANQUET & TÜXEN 1932) who observed several non-botanical sciences with which phytosociology might have mutual relationships: geology, hydrology, geomorphology, climatology, soil science, animal sociology (see 20.7.2), geography, archaeology, palaeobotany (particularly palynology), nature conservation and land use planning. Applications of phytosociology were often based on vegetation maps. Above all, under TÜXEN the Zentralstelle (later Bundesanstalt) für Vegetationskartierung (Federal Institute for Vegetation Mapping) at Stolzenau/Weser, West-Germany, developed vegetation mapping and its application in land interpretation and management and thereby contributed considerably to the acceptance of phytosociology as a significant applied, as well as basic science. Many studies at the Institute, models of such research, can be found in the series *Angewandte Pflanzensoziologie* (Stolzenau/Weser) and *Mitteilungen der Floristisch-Soziologische Arbeits-*

gemeinschaft (Neue Folge, Stolzenau). See also TÜXEN (1956) for a survey of maps, BRAUN-BLANQUET (1969) for a survey of TÜXEN's work, and KÜCHLER (1967) for an English account of floristic-sociological vegetation mapping.

Since applied phytosociology will be the subject of other volumes of the *Handbook*, we present here only a survey of main applied floristic-sociological literature and bibliographies. General publications on agriculture and forestry include textbooks by KNAPP (1949) and ELLENBERG (1950, 1952, 1954a) as well as the series *Angewandte Pflanzensoziologie* (Stolzenau) and the symposia on Vegetation Mapping, Anthropogenic Vegetation, Plant Sociology and Palynology, Landscape Ecology and Experimental Phytosociology of the International Society for Plant Geography and Ecology (TÜXEN 1963, 1966b, 1967c, 1968a, 1969b). Further general references are found in *Excerpta Botanica, Sectio Sociologica.*

An important general conclusion may be drawn from applied research: detailed floristic-sociological description of vegetation combined with adequate analysis of its environment provides a basis for applied phytosociology in many fields of research which can be of great social importance, at least in the cultural landscapes of Europe.

20.7.6 STRUCTURAL CONSIDERATIONS

BRAUN-BLANQUET established the association on a floristic-sociological basis, but since the floristic-sociological characters of an association are supposed to reflect all other characters a floristicsociologically uniform association might be expected to be structurally uniform as well. The original association concept thus implied the physiognomic uniformity of the association. As WESTHOFF (1967) showed, it is not always true that floristically consistent units are also structurally uniform. Many examples are known of considerable structural differences – even on the formation level – within associations or higher syntaxa (e.g. BARKMAN, 1958b). In a number of cases the discrepancy between floristic and structural uniformity has been solved by a refined syntaxonomic treatment.

An example is the Salicornieto-Spartinetum BRAUN-BLANQUET & DE LEEUW (1936) of NW-Atlantic mud flats. This association was considered a mosaic of patches of two different life forms, hence of two different structural types. New relevés taken separately from the two kinds of patches revealed them to be floristically different, which led to separated associations (cf. BEEFTINK 1962, 1965). These associations were in fact assigned to separate classes, viz. Spartinetea and Thero-Salicornetea (e.g. BEEFTINK, 1962). A second example from a very different situation is the classification of scrub and mantle communities separately from the woodland classes to which they used to be assigned. TÜXEN (1952) created for these the order Prunetalia spinosae which he later (1962) placed in a separate class Rhamno-Prunetea (after RIVAS GODAY & BORJA CARBONELL).

Besides attempts to use structural criteria in floristic-sociological classification various suggestions for an integration of the latter system with physiognomic systems have been put forward. A connexion between the syntaxonomical class and the physiognomic formation has been sought by DOING (1962) and PASSARGE (1966, 1968, SCAMONI et al. 1965). PASSARGE (1966) adopted a formation definition that was based on the original concept of Grisebach (See BEARD, article 13), as well as a growth-form definition from SCHMITHÜSEN (1961): a phytosociological formation is a sociological vegetation unit dominated by related growth-forms and hence showing a uniform physiognomy. Informal arrangements of classes within formations have been presented by ELLENBERG (1963) and WESTHOFF (1967), WESTHOFF & HELD (1969). One could also think of connexions between formations and either of the floristic-sociological units above the class, viz. the division and the vicariant class group.

20.7.7 INDICATOR GROUPS

One of the essential bases of applied phytosociology is the use of indicator groups of species. It is consistent with – indeed it expresses – the perspective of the BRAUN-BLANQUET approach that species are used, on the basis of their distributions, as indicators of biotope characteristics and other factors, and that when possible groups of species are thus used. Groups of species may often give much more effective indication of environmental factors than dominant species, or other single species alone, or abundance relations that may be much affected by disturbance. Discussions of indicator use of species have been given by, among others, DUVIGNEAUD (1946), ELLENBERG (1950), WHITTAKER (1954a) and TÜXEN (1970b). We may consider indicator species in four contexts – in connexion with synsystematic, biotope or ecological, successional, and geographic indication. In each of these, but particularly in the biotope-ecological function, it is possible to use indicator species in a perspective of either classification or gradient analysis.

20.7.7.1 *Indicators for Classification*

One direction of development – the synsystematic use of groups of species as indicators for syntaxa – is implicit in the BRAUN-BLANQUET approach. The concept was developed further, however, with the distinction of differentiating taxon groups (SCHWICKERATH 1942, 1954a, DUVIGNEAUD 1946), and the idea of sociological groups (SCAMONI & PASSARGE 1959, 1963, DOING 1962, 1969b). The latter are established as groups of species that are distributionally related, and that consequently occur in and characterize, particular syntaxa; the idea is related to that of 'commodal' species (WHITTAKER 1956). SCAMONI et al. (1965) constructed a sort of 'sociological profile' by arranging relevés for phytocoena and determining the distribution of sociological groups over the units compared. Treatment in terms of syntaxonomical groups has been developed by SEGAL & WESTHOFF (1959) and MAAREL (1969 et seq.).

Clearly, groups of species should indicate characteristics of biotopes or habitats, as well as the particular phytocoena that occur in those biotopes. The concept of ecological groups — sets of species that, because of their similar distributional response to environmental factors, tend to occur together and to indicate properties of biotopes — may be traced from DUVIGNEAUD (1946, 1949). Ecological groups have had most extensive application by ELLENBERG (1950, 1952, 1956), who relates them both to environmental factors and to the syntaxa of the BRAUN-BLANQUET approach. By describing species responses to various important factors — such as pH, lime, moisture, nitrogen — one may arrive at integrated ecological characterizations of species (ELLENBERG 1956, compare article 5.4.1.) Ecological groups have been used also by investigators of the Centre d'Études Phytosociologiques et Écologiques at Montpellier (GOUNOT 1969, GUILLERM 1971, DAGET et al. 1972).

A third application is recognition of geographic indicator groups that express geographic-historic influences and may characterize vicariant phytocoena. SCHWICKERATH (1942) and OBERDORFER (1957) have used geographic groups in dealing with vicariant associations. Given classification of species into geographically defined groups, or areal types, it is possible to characterize communities by geographic spectra, based on representation of these groups. The geographic perspective has been developed by MEUSEL et al. and by MØLHOLM HANSEN and BÖCHER in the Danish school (see article 18.5.3-4), and in the United States WHITTAKER (e.g. 1954b, 1960) has compared areal-type spectra of communities.

20.7.7.2 *Indicators for Gradient Relations*

Community spectra may intergrade, perhaps continuously, along major axes of biotope characteristics, geography and climate, and succession. Spectra (per cent representation of different species groups) may consequently be used to indicate position along these axes. There seems to have been little application of indicator groups to the study of succession, though the recognition of 'decreaser, increaser, and invader' groups in response to grazing disturbance (article 4.2.1) should be noted. Study of gradients of geographic spectra also has been limited, though ELLENBERG (1950) deals with climatic indicator groups, and article 3 (Fig. 8) illustrates a gradient in geographic spectra. A third possibility, use of representation of ecological groups to indicate position along environmental gradients, has had such extensive development as to be beyond review here. Use of ecological groups in direct ordination is discussed in articles 2—5 and 8; use in indirect ordination in article 9. The most extensive application in phytosociology is that of ELLENBERG (1950, 1952, 1956). ELLENBERG classified European species (weeds in agricultural fields, and plants of meadows and pastures) into ecological groups on the basis of their responses to various environmental factors. Weighted averages (see 2.2.3.1) for samples expressed their positions in relation to these factors. At the same time the relation of the species to syntaxa was known, and it was consequently possible to interpret the relations of the syntaxa to one another and environment. The technique thus created a multidimensional direct ordination, and belongs also to section 20.9.1.

20.8 **Numerical Techniques**

There remain to be discussed two (closely related) recent developments in phytosociology – numerical techniques and ordination. For review of similarity measurements and approaches to numerical classification we refer the reader to GOODALL's articles (6 and 19) in this volume. We discuss briefly, however, work in this direction employing the BRAUN-BLANQUET approach.

20.8.1 STORAGE OF RELEVÉS

Although the numbers of relevés treated in syntaxonomical studies may be very high – often several thousands – the number of storage systems is low. Most individual phytosociologists and their institutes work with an archive of relevé note books and tables. Such is the case at syntaxonomic centres like the Station Internationale de Géobotanique Méditerranéene et Alpine (S.I.G.M.A.) at Montpellier and the former Bundesanstalt für Vegetationskartierung at Stolzenau (data from the latter are now at Tüxen's Arbeitsstelle für theoretische und angewandte Pflanzensoziologie at Todenmann über Rinteln, West Germany). Some archives have been set up with visual punched cards. The only such archive of some size seems to be that of the Geobotanical Institute Rübel at Zürich including about 5500 forest relevés from Switzerland (Ellenberg 1968).

Besides incidental use of machine punched cards in the application of computer techniques, two archive systems based on computer hardware are known to us: the system of the C.E.P.E., Centre d'Études Phytosociologiques et Écologiques at Montpellier and the system of the Working Group for Data-Processing of the International Society for Plant Geography and Ecology. The C.E.P.E. system (see Emberger 1968) has the following characteristics: (i) The basic unit is the relevé, which is defined as the whole of ecological and phytosociological observations at a particular site. (ii) General vegetation structure, situation of the site, general climate and soil are described by means of measurements or estimations of numerous factors. (iii) For each factor a code is devised with, in most cases, 10 classes. (iv) All coded determinations of general features are punched in three 'parent' relevé cards, 'Cartes-Maîtresse-Relevé' (CMR) of which columns 1—71 (except for CMR 3) are used. (v) Each taxon from the relevé is treated separately for each vegetation layer in which it has been observed. Coded determinations include vegetation layer, abundance, and dominance (in separate 0—9 codes), pattern within the site, phenological state, vitality and life-form. The corresponding punched cards are called 'detailed cards', Cartes Détail (CD) and used only from column 72 onwards. (vi) Species are enumerated from 0001—4779 according to the Quatre flores de France by Fournier (1961). Cryptogams are provisionally enumerated from 5000 onwards. (vii) Data per species per layer are combined with CMR data, which results in three combined cards.

In this way a relatively large archive arises, which has the advantage of being rapidly accessible to all kinds of spectrum and correlation calculations.

The 'Working Group' was established in 1969 during the International Symposium at Rinteln after a proposal by S. Pignatti, G. Cristofolini and D. Lausi (Trieste). One major aim (see Maarel 1971) was the treatment of relevés in such a way that the data could be readily stored and retrieved. An outline of the system has been presented by CRISTOFOLINI et al. (1969); its main characteristics are: (i) The basic unit is a full relevé table, either published or in manuscript form. (ii) Rows of relevé tables are punched – from column 21 onwards. Cover-abundance values per species are coded either as direct BRAUN-BLANQUET symbols or in a 0—9 transformation code (Table II). (iii) In the first 20 columns coded data on publication, table number in publication, and taxon number are punched. (iv) Taxa are coded with 7 digits, 4 for the genus, 3 for the species – as yet no space is left for infraspecific taxa. The genus enumeration is according to the world survey *Genera Siphonogamarum* by DALLA TORRE & HARMS (1900—1907, reprint 1963). Species enumeration is as yet restricted to European species (Russia not included), according to *Flora Europaea* as far as possible, otherwise according to a provisional enumeration based on six large standard floras of Europe. Additional provisional codes for cryptogams are being developed. (v) A separate punched card is used for bibliographical data on the paper (or set of unpublished tables). (vi) A separate set of punched cards is used for general data on the site and its situation, for each relevé in each table. This part of the system is still in development. The Montpellier system, which is already elaborated in this respect, could be taken as a starting-point.

The Working Group decided to concentrate activities on salt marsh communities. Some 3400 relevés (including 576 Spartinetum relevés) have been stored in punched card decks and on magnetic tape.

20.8.2 SPECIES CORRELATION

The study of species correlation was introduced by VRIES (e.g. VRIES et al. 1954, DAMMAN & VRIES 1954). The plexus of grassland species he presented (article 7, Fig. 3, p. 169) was taken over in the textbooks of ELLENBERG (1956) and BRAUN-BLANQUET (1964), who underlined VRIES' conclusion 'that the resulting species groups broadly coincide with the associations of the Zürich-Montpellier school.'

Measurement of species distributional similarities may be based on either binary or quantitative data. Distributional similarity based on binary (presence and absence) data may be termed 'species association,' that based on quantitative representation in relevés, may be termed 'species correlation' (see article 6). In the BRAUN-BLANQUET approach the quantitative weightings may be either the abundance-cover scale (20.4.5.1) in individual relevés (or a transformation of that scale), or presence degrees (20.5.3) in different phytocoena. Species association seems to be more appropriate for the detection of species groups in relevés representing an extensive range of community difference, whilst correlation studies are more appropriate for intensive study within the range of broadly overlapping species (cf. GREIG-SMITH 1964). The use of species correlation in the establishment of sociological groups is obvious, but phytosociologists using such groups have hardly applied this technique. The studies of HEGG (1965; see article 7, Fig. 7, p. 174) and STOCKINGER & HOLZNER (1972) may, however, be mentioned as examples (see also article 7).

The detection of ecological groups has been particularly developed by phytosociologists using factor analysis and principal component analysis. DAGNELIE (1960, see also article 9) described the use of factor analysis for the establishment of sociological groups, and the use of joint species-environmental factor analysis for the establishment of ecological groups. GODRON (1966) used species correlations for the checking of 'imbricating' ecological groups; GUILLERM (1971) and DAGET et al. (1972) constructed ecological profiles of species against environmental factors. LACOSTE & ROUX (1971) and ROMANE (1972) used 'factor analysis of correspondences' in which floristic and environmental variables were analysed in combination to arrive at ecological-sociological groups.

Another such method was developed by FRESCO (1971) as part of his 'compound analysis.' He constructed overlapping species groups based on similarities between species with respect to their loadings on eigenvalues extracted in subsequent factor analyses. This method could be applied to very large data sets, e.g. the first selection of salt marsh data (1296 relevés, 245 species). From this salt marsh treatment (with an arbitrary similarity level) 65 such groups were derived which could be interpreted roughly as alliance character-species groups.

20.8.3 FIDELITY TESTS

Although it seems obvious to use tests on the significance of the exclusiveness or differentiating value of species (or species groups) for a given vegetation type, phytosociologists have hardly done so. MEIJER DREES (1949) suggested the use of the *t*-test for the significance of the difference between the group amounts of species groups in different relevés of a set. In his example the relevés were assigned to a particular association and the two species-groups examined were syntaxonomic groups for two orders; the problem was the assignment of the association to one or the other order. For such situations Goodall (1953b) used Fisher's discriminant function, which is more powerful but also more laborious.

Goodall (1953b) also proposed an index of fidelity for a species based on the ratio of constancy values for that species in two communities, which could be tested with the χ^2 test or by exact calculation of P. In addition he suggested the use of this index as an 'indicator value' for the comparison of the constancy of a species in one community with that in various other communities — Goodall spoke of 'all other communities in the area.' In usual phytosociological terms Goodall's indicator value is the real fidelity index and the application of this measure to the two-community comparison would be an 'index of differentiation.' Such tests may have limited value, particularly because of the non-random selection of relevés from which they are derived (Goodall 1953b). Still, their use may be experimented with for syntaxon diagnoses from tabular summaries.

20.8.4 Relevé Similarity

Measurements of similarity between relevés have long been accepted as one basis of grouping these into phytocoena (Braun-Blanquet, 1928, 1932). Various coefficients of similarity and dissimilarity are in use in phytosociology, including the formulas of Jaccard and Sørensen (article 6, formulas 39 and 40). Recently an anonymous 'similarity ratio,' which was introduced by Wishart (1969) in Clustan, a set of classification programmes, was used by Kortekaas & Maarel (1972). This formula reads

$$\textstyle\sum_i x_i y_i / \sum_i x_i^2 + \sum_i y_i^2 - \sum_i x_i y_i ,$$

and is thus a generalisation of Jaccard's formula. Comparatively little use has been made of direct dissimilarity measures (Groenewoud 1965, Maarel 1966b). Similar formulas, most of them derived from Sørensen's formula, are in use for the comparison of sets of relevés or the calculation of average similarity within a set (cf. Sørensen 1948, Raabe 1952, Češka 1966, 1968, Frydman & Whittaker, 1968, Maarel, 1969). Weighting of species may use presence values or a combination of presence with an importance value. Ellenberg (1956) as well as Pignatti & Mengarda, see Pignatti 1964, suggested the use of a similarity coefficient in the assignment of a relevé to a type by comparing it with a 'standard' or average relevé, e.g. one consisting only of the normal characteristic species combination. Hofmann & Passarge (1964) and Scamoni et al. (1965) determined similarity between relevés and sets of relevés with reference to the sociological groups ('group affinity').

20.8.5 MEASUREMENT OF HOMOTONEITY

Homotoneity we have defined as the homogeneity of a community table, the relative consistency of the relevés the table comprises (20.5.3). In addition to the simple measures mentioned in 20.5.3, the mean similarity coefficient for the relevés, as calculated in a direct way by Češka (1966), is a convenient measure, particularly in classifications based on relevé similarity. Either the average of all interrelevé similarity values within a table, or the average relevé similarity with the average for the table (i.e. the centroid of the relevé cluster) may be used. See also article 6 and 20.8.4 and 20.8.8 on similarity measures.

Alternative techniques based on species relationships include the use of positive interspecific correlation by Goodall (1953a), association analysis (Williams & Lambert 1959), and information analysis (Williams et al. 1966) (see article 19.5.1.5 and 19.5.2.5). Maarel (1966b) derived an information measure that is related to that of Williams et al. and appeared to be a useful heterogeneity coefficient in a study of a local grassland community complex. Godron (1966) developed an information measure, based on Brillouin's information formula, for determination of the heterogeneity within a series of contiguous quadrats in the field. The frequencies of the species occurring in the set determine the value of this measure. It could also be used for heterotoneity in sets of relevés and in that case is rather similar to the formula of Williams et al. (1966).

Dahl (1957, 1960) derived an index of uniformity from the Fisher model (logarithmic series) for species-individual and species-area relations ($S = \alpha \log_e(1+N/\alpha)$, S is number of species, N number of individuals, and α a diversity index, see Williams 1964). Dahl considered the species-relevé relation to be similar and defined the diversity parameter for a table as $(S_m - \bar{S})/\alpha \log M$ (see symbols and formulas in 20.5.3). The index of uniformity is accordingly defined as $\bar{S}/\alpha$. A clear relationship with Curtis' (1959) index was shown by Dahl (1957).

20.8.6 NUMERICAL CLASSIFICATION

Of the various numerical classification techniques which are described in article 19, only a few are in use in quantitative phytosociology. Direct use of similarity matrices was developed by Polish phytosociologists (MATUSZKIEWICZ 1948, FALIŃSKI 1960) and by GUINOCHET (1955, GUINOCHET & CASAL 1957), who spoke of the 'differential analysis of CZEKANOWSKI' (after the Polish originator of the approach). See further article 7.3.1.

Agglomerative clustering techniques (19.5.2) based on similarity coefficients like the JACCARD and SØRENSEN indices were used by SØRENSEN (1948), LOOMAN & CAMPBELL (1960), MAAREL (1966b), MOORE & O'SULLIVAN (1970), MOORE et al. (1970) and KORTEKAAS & MAAREL (1972). Agglomerative techniques can be profitably combined with re-allocation techniques (cf. WISHART, 1969). The relevé-groups arrived at in these classifications could generally be typified with characteristic species combinations and connected with syntaxonomical units.

IVIMEY-COOK & PROCTOR (1966) applied nodal analysis (association analysis followed by an inverse species clustering) to salt marsh, fen and woodland data. They obtained tables with clear blocks of relevés and species and concluded that the results confirmed the arrangement of the data arrived at by traditional phytosociological methods. The technique was considered particularly useful for the detection of differentiating species. Moreover they found minor lines of division which had not been obvious in previous studies.

20.8.7 TABLE REARRANGEMENT

A successful nodal analysis should produce an ordered table. A number of special techniques for table rearrangement have been developed, from the early work of BENNINGHOFF & SOUTHWORTH (1964) to the more recent of MOORE (1972, MOORE et al. 1970, MOORE & O'SULLIVAN 1970). The following computer programmes are known to us:

i) BENNINGHOFF & SOUTHWORTH (1964), G. W. MOORE et al. (1967), LIETH & MOORE (1971). This programme finds species clusters by application of LIN's algorithm for the 'travelling salesman problem.' It is applied to species with intermediate presence in the table. Additionally, relevés are sorted. Final table ordering is by hand.

ii) J. J. MOORE (1971, last version). This programme 'PHYTO' rearranges both species and relevés. It finds pairs of species with intermediate presence values and high co-occurrence values. Opposing pairs are used as differentiators. Further arrangements are dictated by the user, either through suspected mutually exclusive species or through preferred order of species and relevés.

iii) SPATZ (1969, 1972 last version). This programme forms groups of relevés on a similarity basis. Differentiating species are defined as species with presence of $> 50\%$ in one group and $< 10\%$ in all others. Output includes a synoptic table with synthetic figures.

iv) SCHMID & KÜHN (1970). This programme calculates D^2 values and forms groups on lowest D^2 basis. Differentiated tables can be dictated.

v) ČEŠKA & ROEMER (1971). This programme finds species-relevé groups through iteration. Diagnostic species are defined as in programme 3 (values vary from 50 vs. 10 to 66 vs. 33). A relevé is considered a member of a group if it contains at least 50 % (or 66 %) of the diagnostic species of that group. Groups are arranged in order of size and within-group similarity. Final arrangement is usually by hand.

vi) JANSSEN & MAAREL (1972, JANSSEN 1972). This programme is based on programmes HIERAR and RELOC of the CLUSTAN set (WISHART 1969) with a choice of 10 similarity coefficients. It starts with an allocation of relevés to groups, either at random or as determined by previous classifications and phytosociological experience. Group arrangement is based on group properties, particularly the relation between relevé number and species number, or alternatively on position along the first component of a principal components analysis of groups. Species are arranged so as to form a diagonal structure in the table. Significance of positive differentiating value of species in one or more groups is determined by a χ^2 test. Final arrangement is usually through MOORE's PHYTO-programme.

vii) STOCKINGER & HOLZNER (1972). This programme finds species groupings through similarity analysis. Relevés are sorted according to occurrence of species groups.

It follows from this description that all programmes require the personal finishing touch of the user; this is felt to be not an inconsistency but rather a matter of efficiency. Most designers claim a considerable gain in accuracy, since re-writing tables by hand is no longer necessary. The speed of the programmes will depend on type of computer and size of the table. Programmes i, ii, v, and vii are most adapted to tables with comparatively many relevés and few species, programmes iii and iv to tables of the reverse form. Programme vi has a larger capacity, but requires preliminary experience to be fully efficient.

20.8.8 NUMERICAL SYNTAXONOMY

Numerical syntaxonomy has been mainly restricted to the characterizing of various syntaxon levels by average similarity. Various coefficients of similarity and dissimilarity are in use in phytosociology. 'Coefficients of community' comparing samples by the per cents of their species shared have been used most, with about equal interest in the formulas of JACCARD and SØRENSEN (article 6, formulas 39 and 40). Formulas using importance values for species (cover-abundance in relevés, especially) include the 'percentage similarities,' notably the CZEKANOWSKI index (article 6, formula 50). Similar formulas are in use for comparing sets of relevés (representing different phytocoena), or calculating average similarity within sets (see SØRENSEN 1948, RAABE 1952, ČEŠKA 1966, 1968, FRYDMAN & WHITTAKER 1968, MAAREL 1969, 1972a). Comparison of sets of relevés may use presence per cents, or mean cover-abundance values, for the species in these sets. Numerical classification is further discussed in article 19.

SØRENSEN (1948) concluded that grassland groupings with similarity levels of 0.40 roughly corresponded with syntaxa on the alliance level. ELLENBERG (1956) stated that the average similarity of relevés within one association is between 0.25 and 0.50, whereas subunits may be distinguished by levels above 0.50 (JACCARD values, which are 10% lower than SØRENSEN values on the average). LOOMAN & CAMPBELL (1960) calculated SØRENSEN values of > 0.70 within subunits belonging to one grassland association, whereas values between subunits were all < 0.50. HOFMANN & PASSARGE (1964) presented group affinity values between various woodland associations and subassociations. Within associations values were mostly > 0.60, between typical subassociations of related associations values were mostly between 0.30 and 0.50. RAABE (1952) obtained affinity values (KULCZIŃSKI coefficient) between associations and alliances of weed, salt marsh and alpine communities. Within-alliance values were between 0.40 and 0.50, between-alliance values were 0.20 to 0.40. Within salt marsh associations values varied more widely, from 0.30 to 0.80, and here the influence of geographical distance between local representatives of associations was evident.

NEUHÄUSL & NEUHÄUSLOVÁ-NOVOTNÁ (1972) studied within- and between- group similarities (SØRENSEN values) of many woodland associations of the alliance Carpinion. Within-group similarities of locally established associations and lower units were generally over 0.55. When larger areas were involved, these values were lower but still over 0.45. Similarities between associations and between lower units were always lower, mostly 0.10 to 0.20. These calculations made possible some improvement in the delimitation of Carpinion associations (which, as the authors stated, must be checked by renewed phytosociological table studies). KORTEKAAS & MAAREL (1972) carried out a numerical analysis of European *Spartina* communities involving an agglomerative classification with relocation of 576 relevés. They arrived at four separate dendrograms each comprising relevés dominated by one of the *Spartina* species. On various levels of the hierarchy groups were inspected for character-species and compared with the existing syntaxonomy (BEEFTINK & GÉHU, in prep). For these communities values of the similarity indices between 0.40 and 0.60 could be connected with the association level, 0.61—0.70 with the subassociation level and 0.71—0.80 with the variant level. Figure 4 presents the dendrogram for the *Spartina maritima* relevés. Each 'subassociation' had exactly one 'good' differential-taxon. The examples suggest that in related communities a reasonable parallel between syntaxonomical level and similarity level can be established. Furthermore, the

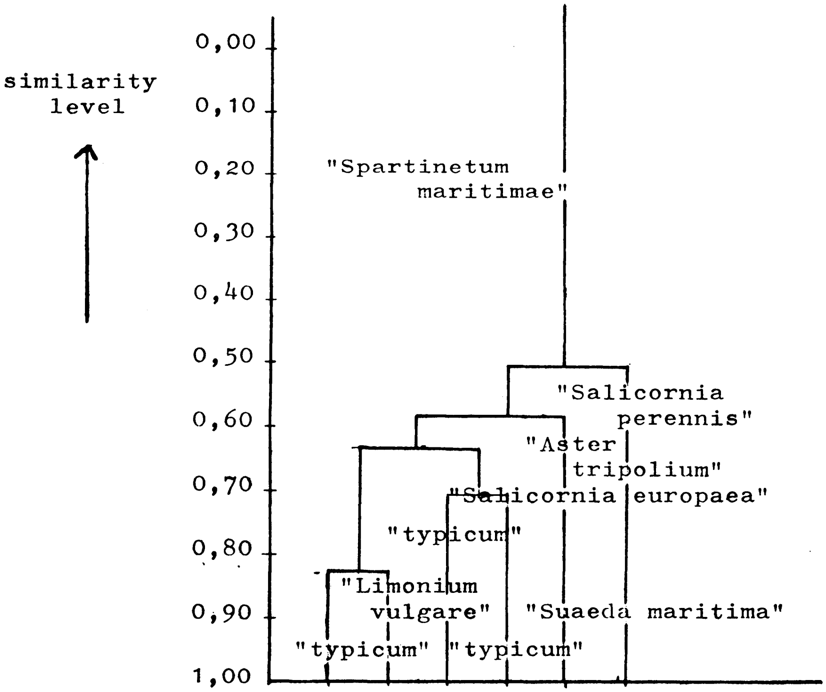

Fig. 4. Dendrogram of Spartinetum maritimae relevés. (KORTEKAAS & MAAREL, 1972).

similarity values for a given syntaxonomic level in different vegetation types are similar, suggesting that various authors have made comparable intuitive judgments of relative similarity for various kinds of communities. Similarity measurements should thus be thought a useful aid to synsystematics.

20.9 **Ordination**

'Ordination' refers to the arrangement of entities (generally samples, or species) in a uni- or a multidimensional order (RAMENSKY 1930, GOODALL 1954, articles 1 and 2.) Ordination is often considered to stem from the concept of vegetation as a continuum, whereas the floristic-sociological classification may seem to assume discontinuity. It may consequently be argued whether ordination is appropriate in phytosociology. Even if we assume for the moment that associations are generally discontinuous with one another, there is no reason ordination cannot be used as an aid to understanding the relations of relevés and lower syntaxa to one another and environment, within the association. On a different level, ordination and the perspective of gradient analysis can well be applied to the relations of associations and higher syntaxa as wholes, to one another and environment. We feel consequently that ordination is a fully acceptable supplementary approach in phytosociology.

There has been some dispute, mainly between BRAUN-BLANQUET (1939, 1951b, 1955) and GAMS (1918, 1941, 1954) on the question 'linear or multidimensional system in plant sociology.' GAMS emphasized the multidimensional relationships of plant communities, without indicating the way of constructing an appropriate system, as BRAUN-BLANQUET remarked. WAGNER (1954, 1968) observed that many syntaxa show multidimensional relationships to various syntaxa of the next higher level. The 'flexibility' ELLENBERG (1954b) demanded at lower syntaxonomic levels could be thought of in this perspective. Surely it is true both that linear arrangements into hierarchies are possible and valuable, and that study of multidirectional relationships may be rewarding.

20.9.1 INFORMAL ORDINATION

A number of approaches that represent ordination but do not employ similarity measurements have been applied in phytosociology. In many ordered phytocoenon tables a suspected underlying environmental gradient is chosen as a basis for ordering that may be completed by inspection of ecological groups (Moore et al. 1970). Often a moisture gradient is chosen and a 'dry' a 'typical' and a 'moist' subassociation are arranged within an association table. The unidimensional approach known as compositional ordination (article 2) has a phytosociological precursor in the approach of Schwickerath (1931 et seq.), in which relevés of one association were arranged on the basis of representation of diagnostic species groups. The development of weighted-average ordinations by Ellenberg (1950, 1952) has been referred to (20.7.7.2).

More abstract two- or many-dimensional schemes including Russian examples (discussed in article 5) were recommended by Gams (1941, 1961). The approach of Duvigneaud (1946) was an early floristic-sociological ordination without numerical basis. A number of phytosociologists have presented patterns ('mosaic charts', 2.3.3) of phytocoena in relation to environmental gradients (see Duvigneaud 1946, Wagner 1954, 1968, Ellenberg 1952, Fig. 5, 1963, Zonneveld 1960, Hegg 1965, and article 18, Fig. 1, p. 555).

20.9.2 FORMAL ORDINATION

The first ordination of relevés on the basis of their similarities is found in the Polish approach of Matuszkiewicz & Traczyk (1958), and Faliński (1960). They constructed 'dendrites' as arrangements that can be ecologically interpreted (cf. Gams 1961, 1967, and article 7).

Ordination in the sense of axis construction was first applied in phytosociology by Dagnelie (1960) on beechwoods (see article 9). A comparable factor analysis on heathlands was presented by Fresco (1969). Groenewoud (1965), Moore et al. (1970) and Maarel (1972a) applied principal component analysis to similarity matrices. The Wisconsin polar ordination of Bray & Curtis (1957), or slightly modified forms, was applied in Dutch work (unpublished MSc theses, Universities of Utrecht and Nijmegen, Maarel 1966b, 1969, Maarel & Leertouwer 1967, Londo 1971) and further by Rogers (1970). Lacoste & Roux (1971) applied factor analysis of correspondences (see 20.8.2) to relevés assigned to various subalpine associations and subassociations.

Ordination can be applied also to phytocoena (or syntaxa), with each phytocoenon treated as a composite sample with its species composition summarized as presence per cents or mean importance values. One may then conceive of environmental gradients

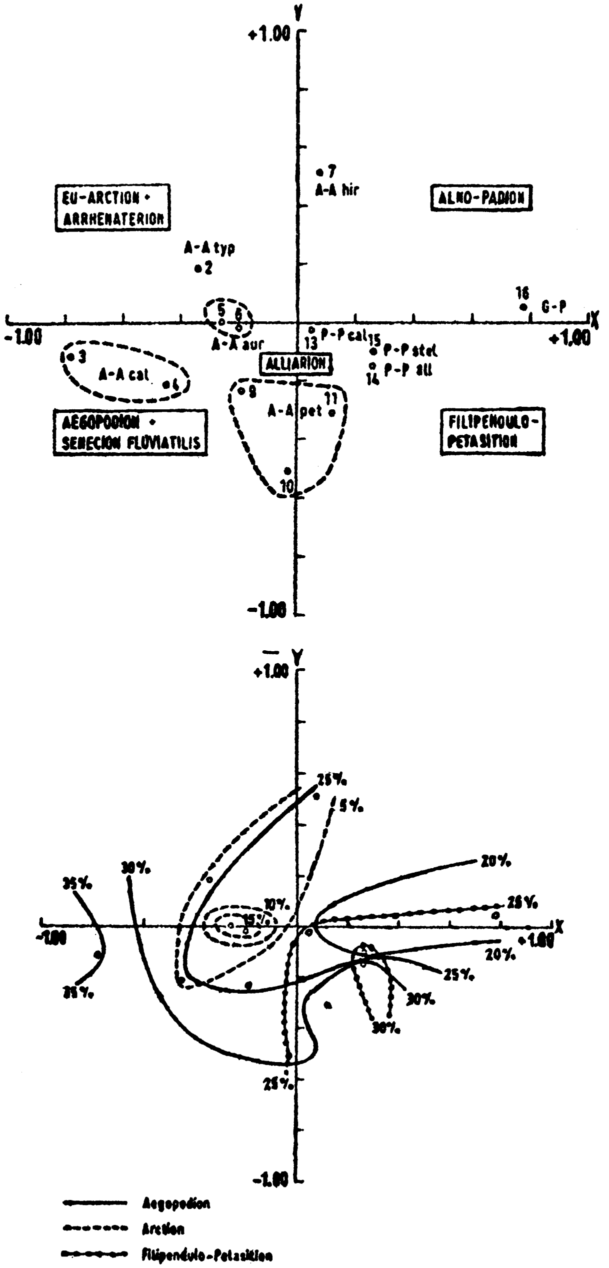

Fig. 5. Ordination of nitrophilous edge communities described by Tüxen (1967a), from Maarel (1969).

relating these phytocoena as a multidimensional habitat space (GOODALL 1963, WHITTAKER 1967) in which the centroids of the phytocoena (as clusters of relevés) are ordinated. ORLOCI (1966) carried out such an ordination by principal component analysis; GITTINS (1965), CRAWFORD & WISHART (1966, 1967), FRYDMAN & WHITTAKER (1968), MAAREL (1969), and WHITTAKER (1972) applied polar ordination to community-types. Mostly the similarities between types were measured by presence or constancy values. All the resulting ordinations were effective and easily interpretable. An effective approach to interpretation is the plotting of contour lines for biotope measurements (e.g. FRYDMAN & WHITTAKER 1968), to determine the relationship between axes and environmental factors, and the plotting of community-types and representation of diagnostic groups (FRYDMAN & WHITTAKER 1968, MAAREL 1969, WHITTAKER 1972) to show the relation of these to environment and one another. Fig. 5 illustrates the latter technique (see further articles 2, 8, and 9).

When no appropriate environmental data are available it is possible to interpret the ordination by plotting the distribution of syntaxonomical groups. Figure 5 presents an example. Nitrophilous edge communities, bordering woodlands and scrubs, as described by TÜXEN (1967a) are ordinated and the ordination space is characterized by various alliances. The associations are reasonably separated in the ordination space, except for the Agropyro repentis-Aegopodietum. The subassociation with *Chaerophyllum hirsutum*, in particular, is distinct and has a considerable representation of Alno-Padion species. Patterns of three alliances are presented. Lines with equal percentage amounts of one alliance are called 'isocenes' and outlined. The greatest difference in the set of types is between the relatively dry, open nitrophilous Agropyro repentis-Aegopodietum calystegietosum sepium from anthropogenic edges at low altitudes, and the relatively moist and shaded Geranio phaei-Petasitetum along streamlets in the montane region. WHITTAKER (1972) and FRYDMAN & WHITTAKER (1968) presented a similar approach with similar results. Besides species populations, species groups, and environmental measures, various spectra can be plotted in an ordination field. RAUNKIAER life-forms, for example, showed clear distribution patterns when thus plotted by FRYDMAN & WHITTAKER (1968).

Other uses of ordination include applications to succession (MAAREL 1969, LONDO 1971) and ordinations based not on species composition but on structural characters, life-forms or sociological (syntaxonomic) groups (KNIGHT 1965, GOFF & COTTAM 1967, MAAREL 1969, WHITTAKER 1972). MAAREL (1972a) used

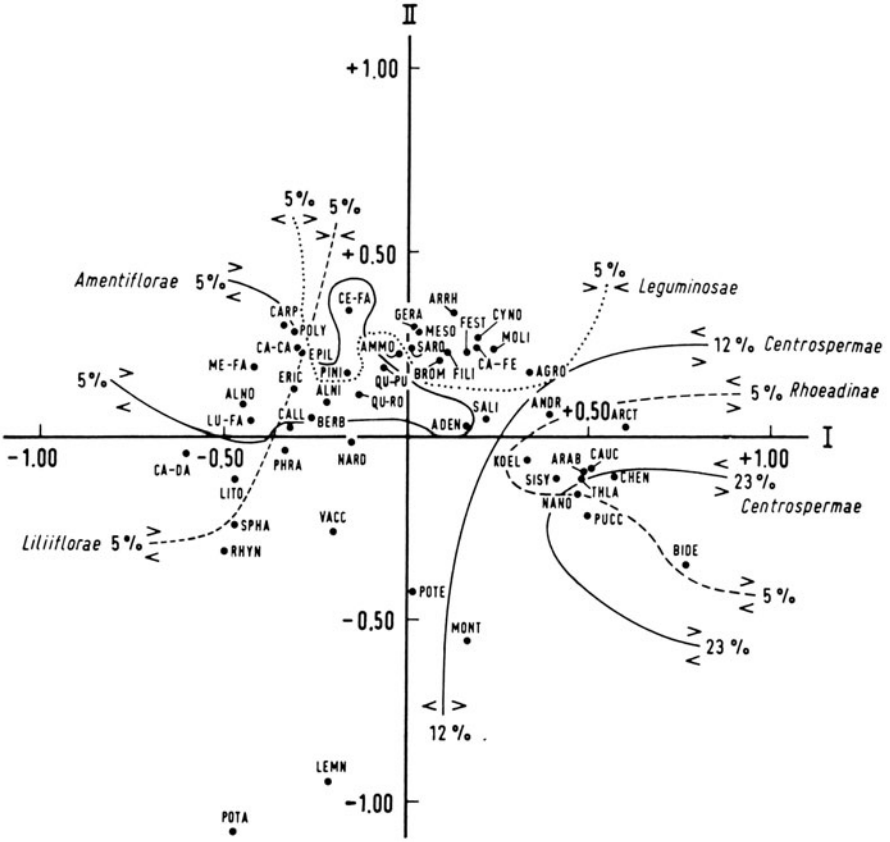

Fig. 6a. Ordination of 51 European associations and lower syntaxa on the basis of their plant order spectra, dimensions 1 and 2. (MAAREL, 1972a).

higher idiotaxonomical units as attributes to compare and ordinate vegetation types. Figure 6 presents some results of an ordination of 51 associations and subassociations belonging to 49 alliances, and thus covering almost the entire variation in central and western Europe. The corresponding similarity matrix was based on representations of plant orders in synoptic tables, mainly from OBERDORFER (1957). The first line of variation shows the sociological progression from pioneer comminities, with alliances such as the Bidention (BIDE) and Nanocyperion (NANO) on the right, to mature communities like the Fagion (—FA) and Carpinion (CARP) on the left. Most grasslands, marshes, and heathlands are intermediate. This variation is illustrated by isolines of various idiotaxonomic orders, e.g. Centrospermae vs. Liliiflorae. The second axis involves a moisture gradient from wet (Eu-Potamion,

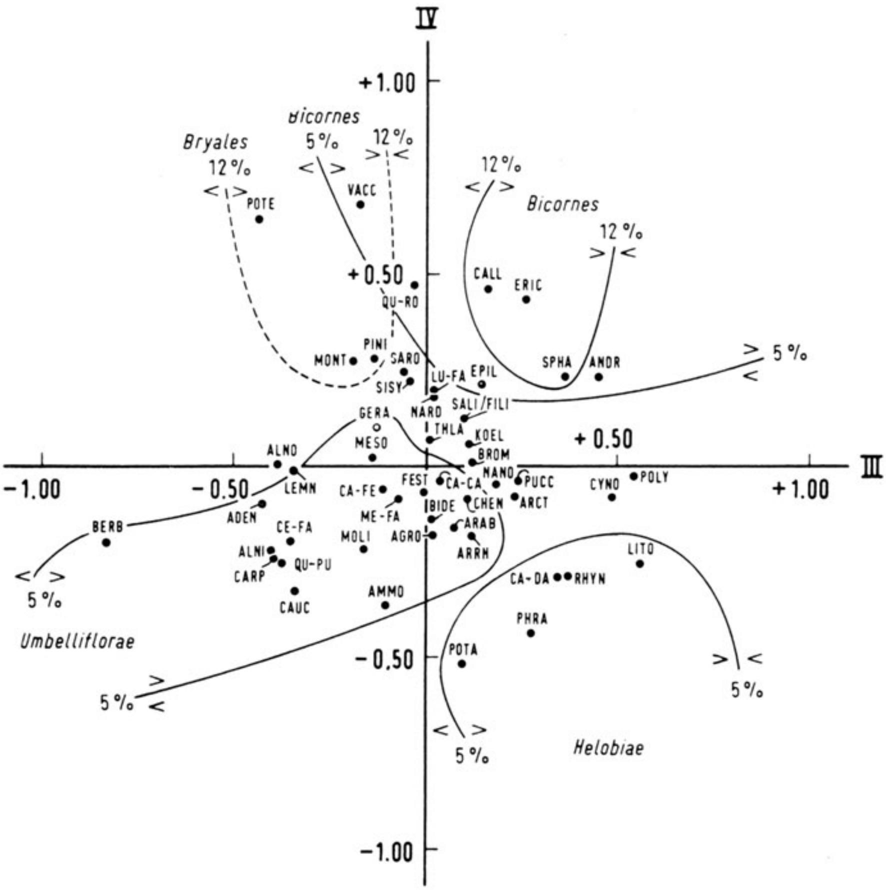

Fig. 6b. Ordination of 51 European associations and lower syntaxa on the basis of their plant order spectra, dimensions 3 and 4. (Maarel, 1972a)

POTA, below) to dry, (Mesobromion, MESO, upper middle). Between axes III and IV (Fig. 6b) two more or less oblique lines of variation can be discerned. The third axis may be tentatively interpreted as a shading gradient from Polygonion avicularis (POLY) and Phragmition (PHRA) below, to Cardamino-Montion (MONT) and Vaccio-Piceion (VACC) above, from prevalence of Helobiae to that of Bryales. The fourth axis runs from raw humus soils with a relatively high C/N ratio to soils with a low C/N ratio and high microbiological activity (Ericion tetralicis, ERIC, with Bicornes, upper right, to Caucalion, CAUC, with Umbelliflorae, lower left). We regard Fig. 6 as representing only a first venture in broad-scale ordination of phytocoena; its significance may be in its demonstration of possibility.

20.10 **Conclusion**

In perspective, these numerical techniques and ordinations should be seen as ancillaries to the BRAUN-BLANQUET approach. We re-emphasize the essential ideas with which we began: the floristic approach to understanding, the functional value of diagnostic species for classification and environmental indication, and the utility of the hierarchical classification for ordering knowledge and expressing understanding. Given this as the approach, then the numerical techniques serve to reduce labour, and ordinations to enhance interpretation. Ordination without prior classification has accomplished significant research in American ecology, but ordinations in different areas are not easily coordinated with one another. It is the European experience that the BRAUN-BLANQUET approach provides such coordination of the work of different investigators through its classification, whilst the classification provides a context that increases effectiveness of ordination. On the one hand prior classification makes possible the ordination of phytocoena, rather than an often unmanageable number of relevés; on the other hand the known relationships of species groups and phytocoena to one another and environment give basis for interpreting an ordination. The ordination should, in turn, express and further clarify those relationships.

We return to another theme – the complexity of the BRAUN-BLANQUET approach as a technical system. The complexity has causes; these include the numerousness of species and phytocoena, the multifarious distributional relations of species to one another and phytocoena, and the many directions of environmental, geographic, and developmental relationships amongst species and phytocoena. The complexity of the BRAUN-BLANQUET system is thus a response of science to the complexity of vegetation. It is no real statement of preference that the approaches through physiognomy and species dominance are 'simpler'; it is not necessarily true that they are, and to the extent that they are, they are only because they do not treat and coordinate so wide a range of information. We thus express our judgement (or our bias) that in the study of vegetation one approach has most fully faced the demands for a method that is both detailed and generalizing, both locally intensive and integrative of the results from different local areas – and that that one approach is BRAUN-BLANQUET'S.

This judgement we must balance with another. The BRAUN-BLANQUET approach is very demanding of research effort by many investigators, if the vegetation of extensive areas is to be known through it. The effort has been possible in Europe and some other areas but is not yet possible everywhere — there are not phytosociologists enough. The approach may be particularly difficult to initiate in an area lacking prior studies to offer suggestions toward classification and diagnostic species groupings, unless the initiator is experienced in the approach. This difficulty is one reason for the importance of approaches through physiognomy and dominance in many areas; by these approaches knowledge of vegetation may be gained that might not otherwise be obtained at all. It is true also that the physiognomic and other approaches may reveal vegetational relationships that are important, but are outside the main concerns of the BRAUN-BLANQUET approach. The statement that BRAUN-BLANQUET's is the most fully developed approach to vegetation is thus no rejection of the contributions of others amongst the many ways for the ordination and classification of communities.

20.11 SUMMARY

(20.1) Amongst the central ideas of the approach are that: (i) classification and interpretation of communities should be based on their full floristic composition, (ii) with emphasis on diagnostic species, whose relative restriction to samples characterizes communities and indicates their environments and (iii) which may be used to organize the communities into a formal, hierarchical classification. (20.2) This floristic-sociological approach to vegetation had its origin in southern European phytosociology centered in the cities of Zürich and Montpellier, but especially in the ideas of BRAUN-BLANQUET.

(20.3) It is important to distinguish particular, concrete plant communities or phytocoenoses, and abstract classes of plant communities; the term phytocoenon is recommended for the latter. The phytocoena of the formal BRAUN-BLANQUET hierarchy are termed syntaxa, in analogy with the taxa into which individual organisms are classified. Syntaxa are characterized by diagnostic species of three types: character-species are centered in or relatively restricted to a particular syntaxon compared with all others, and therefore characterize it and indicate its environment; differential-species distinguish two closely related syntaxa by presence in most samples of the one and absence in most samples of the other; constant companions are not restricted to a given syntaxon but help to characterize it and indicate its relationships to higher units. In addition to the hierarchy, syntaxa may be arranged along a sociological progression from simple and poorly organized to complex and highly differentiated communities. The BRAUN-BLANQUET classification is considered natural in the sense that its syntaxa (though their limits may be arbitrary) are consistent with a large number of relationships between environment, species populations, and biocoenoses.

(20.4) The research procedures include three phases — analytical, synthetical, and syntaxonomical. In the analytical phase samples or relevés representing kinds of phytocoena to be studied are taken in the field. The relevés should be chosen to represent the phytocoena to be studied, and each should sample a uniform area of sufficient size to represent that phytocoenose adequately. A relevé includes information on environment and location and a list of all plant species in the sample area, with species recorded by strata and rating scales (for combined cover and abundance, and if possible sociability, vitality, and periodicity).

(20.5) In the synthetical phase the relevés are compared with one another to derive a preliminary classification. A set of relevés are first listed in their full species composition in a primary table. Species of intermediate presence values are emphasized in seeking groups of differentiating species that characterize some of the relevés but not others. Partial tables are prepared using these species to rearrange the relevés into groups characterized by the groups of differentiating species. When the rearrangement is satisfactory, the data from all species are recopied into a phytocoenon table in which boundaries may be drawn to mark off differential-species groups and phytocoena. A synoptic table may now be prepared in which each column summarizes data for species occurrence in the relevés of a phytocoenon. By use of synoptic tables the phytocoena under study may be compared with others from the same area in a search for character-species. Problems in the recognition of character-species, including geographic differences in fidelity of species to phytocoena, are discussed.

(20.6) In the syntaxonomical phase the studied phytocoena may enter the formal hierarchy. The phytocoenon table is revised into a formal syntaxonomic table indicating the character-species and differential-species groups represented. If the phytocoenon represents a new association, this is named and placed in the hierarchy in which associations are grouped into alliances, alliances into orders, orders into classes. Syntaxa on all these levels may be defined by character-species; in some cases character-genera are used for higher units. Apart from the hierarchy, associations (and other syntaxa) from different geographic areas may be grouped by floristic affinities, especially as marked by vicariant species. Associations are divided into subordinate units: subassociations and variants characterized by differential-species, and facies as the lowest-level units, characterized by quantitative differences in species representation. Associations are named on the basis of one or two characteristic species and the suffix -etum. Further rules of nomenclature for associations and other syntaxa are discussed, and an outline of the syntaxa is given.

(20.7) Various extensions of the approach are described. Applications to vegetation outside the European homeland are summarized. The approach is applied also to biotic and animal communities, and to stratal and life-form subcommunities to produce a separate classification of these into synusiae. Complexes (mosaics or patterns of contiguous or continuous communities) can be studied on various levels from the microrelief of bogs to whole landscapes. Mapping of phytocoena is valuable in applied phytosociology and land management. For applied work, diagnostic species groups can be used to indicate environment. Species can also be classed into ecological groups by their distributional responses to environmental gradients, and representation of ecological groups can be used to indicate position of a phytocoenose along an environmental gradient.

(20.8) Numerical techniques are being developed to store relevés, to measure homogeneity of phytocoenon tables, and to aid in sample rearrangement in tables and the earlier stages of classification. (20.9) Ordinations are possible on either a less formal basis, using relevés or phytocoena along known environmental gradients, or on a more formal basis using quantitative comparisons amongst samples to arrange them along abstract axes. Ordinations can be applied to phytocoena (each summarizing data from several relevés) as well as to individual relevés. Results to date indicate that this is a promising means of clarifying relationships amongst species and syntaxa.

(20.10) Numerical techniques and ordination are aids to the essential floristic-sociological procedures of the BRAUN-BLANQUET approach. Despite the complexity of the procedures, the approach is felt to be flexible to different kinds of vegetation and research purposes, productive of understanding of the relations of species and samples to one another and environment, useful for applied purposes, and valuable for its coordination of the results from different areas into a single classification. It is judged the most fully developed and most widely useful approach to the classification and interpretation of vegetation.

20.12 Additions to the Second Edition

No essential changes affect the BRAUN-BLANQUET approach as treated in the first edition. Our additions are mainly references to a (selected) number of publications that came to our notice after the manuscript for the first edition was completed. They will be given by sections.

(20.2-3) **History and General Concepts**

The history of the BRAUN-BLANQUET approach was studied in further detail by MAAREL (1975) on the occasion of BRAUN-BLANQUET's 90th birthday. VAN DER MAAREL emphasizes the crucial position of BRAUN's work in the development of phytosociology, with the conclusion that it is a synthesis of ideas and approaches from the entire 19th century in a framework that has incorporated many developments of the 20th century.

(20.4) **Analytical Research Phase**

The book by MUELLER-DOMBOIS & ELLENBERG (1974) presents full information on the relevé method and compares various methods of measuring species quantities, without giving any preference for one particular method. An important new French contribution was published by GUINOCHET (1973), who paid special attention to the choice and delimitation of sample plots.

(20.4.3) MINIMAL AREA AND PLOT SIZE

WERGER (1972) discussed minimal area and emphasized that no analytical minimal area can be found through a species-area curve. He suggested (cf. MAAREL, 1966b*) an optimal relevé-size representing a given fraction of the total information in the stand. MORAVEC (1973a) tried to establish a minimal area through analysis of similarity between multiple plots of increasing size (as was done earlier by MAAREL, 1966b* following GOUNOT & CALLÉJA, 1962).

(20.5) **Synthetical research phase**

Again the book by MUELLER-DOMBOIS & ELLENBERG (1974) may be mentioned as a general reference. For homotoneity MORAVEC (1973b) proposed an empirical correction for small sets of relevés as well as a simplified calculation for large sets.

(20.6) **Syntaxonomical Research Phase**

Further evidence is presented by MUELLER-DOMBOIS & ELLEN-

BERG (1974) on the geographical variation in habitat preference of many species and the consequently limited significance of character-species. The authors regret the increasing splitting of associations and emphasise alliances as general units, recurring in similar forms in many areas, which largely fulfil the requirements once set up for the association.

An important approach to plant communities with an insufficient number of character-species was developed by KOPECKÝ & HEJNÝ (1974, see also 1973 and KOPECKÝ 1974). They distinguish 'basal' and 'derivate' communities in addition to the cenologically saturated communities that can be fully characterised as syntaxa. Basal communities are composed of species with relatively broad habitat amplitudes. They may arise either after disturbance of saturated communities, or during a succession on newly formed anthropogenic sites. They lack character and differential species on the association level, but may show them on the alliance, the order or even only the class level. KOPECKÝ & HEJNÝ propose a special nomenclature for those communities. E.g. a basal community (BC) characterised by dominance of *Urtica dioica* and *Aegopodium podagraria* in which only class character-species occur is indicated BC Urtica-Aegopodium (Galio-Urticetea).

A derivate community is characterised by a dominating species showing, at least regionally, a narrow amplitude and a rapid spread from diaspores. It may develop as a special form of a basal community during primary succession, or, again, by disturbance of a saturated community, or during the disintegration of a basal community due to disturbance. Derivate communities (DC) are indicated as are basal communities; for example, within the range of the BC Urtica-Aegopodium (Galio-Urticetea) may occur a DC Chaerophyllum aromaticum (Galio-Urticetea). This approach may be applied to all kinds of anthropogenic plant communities (cf. BRAAKHEKKE & BRAAKHEKKE-ILSINK 1976) as well as to communities in naturally disturbed or otherwise extreme environments.

Nomenclature of syntaxa has reached a milestone through the publication of the Code of Phytosociological Nomenclature in *Vegetatio* (BARKMAN et al. 1976).

(20.7) **Extension of the approach**

The number of applications of the Braun-Blanquet approach in non-European areas has further increased. The reader is referred to numerous contributions in *Vegetatio*, the new periodical *Phytocoenologia*, and Symposium volumes (notably GÉHU 1975 on coastal dunes).

Many references are found in new issues of *Excerpta Botanica Sociologica* and also in *Fortschritte der Botanik* (Progress in Botany) volumes 36 and 37.

With respect to community complexes a new development can be mentioned: the distinction of ‘sigmassociations’ or association complexes, coherent series of associations characterizing certain landscapes (Tüxen 1973, Géhu 1974). Also syntaxa on higher levels can be described in such a framework, with the general term sigmasyntaxon. The approach is similar to the description of vegetation complexes in recent Dutch landscape ecological descriptions (cf. Maarel & Stumpel 1975).

As to indicator groups, a recent synthesis of ecological knowledge on European plant species by Ellenberg (1974) can be mentioned.

(20.8) **Numerical techniques**

The Working Group for Data-Processing in Phytosociology ended its research. The results are now to be published in *Vegetatio*, starting with a general survey of activities and perspectives (Maarel et al. 1976, see also Maarel 1974).

The use of ‘‘analyse factorielle des correspondences’ (reciprocal averaging or correspondence analysis, article 11, Hill 1973, 1974) has shown further successes in the delimitation of plant communities and the establishment of characterising species groups, particularly through the work of Lacoste (1975, 1976). The Montpellier group proceeded in establishing ecological groups by applying correspondence analysis to floristic and environmental data (Bottliková et al. 1975) (see also Guinochet 1973).

With respect to numerical classification Coetzee & Werger (1975) considered the Braun-Blanquet approach in its essence superior to association analysis, whilst Stanek (1973) found it as effective as a sum-of-squares agglomeration technique. This is a divisive polythetic classification and an approach in that direction through the method of indicator species analysis as suggested by Hill et al. (1975) seems very promising.

Table rearrangement procedures have been treated at length by Mueller-Dombois & Ellenberg (1974) mainly on Ellenberg’s (1956*) original test data, with applications of numerical methods divised by Spatz (1972*, Spatz & Siegmund 1973). Stöckinger & Holzner (1973) proceeded with their approach through the erection of correlated species groups. Dale & Quadraccia (1973) used display on monitors in an interactive table sorting. Dale & Webb

(1975) applied a two-parameter analysis, i.e. an analysis which is symmetric in its use of species and relèves, in such a way that relevé groups are established during the divisive procedure at a point where discontinuities between relevé groups change to continuities within them.

The table rearrangement program TABORD (JANSSEN 1972*) has been further extended and implemented in various centres; JANSSEN (1975) devised a simple clustering procedure for the division of very large data-sets (up to 6000 relevés) into smaller groups manageable with TABORD.

The attempts towards a numerical syntaxonomy of *Spartinetum* communities by KORTEKAAS & MAAREL (1973) proceeded. A comparison with the classical syntaxonomy became possible through the publication of the *Spartinetea* issue of the *Prodrome* of European plant communities (BEEFTINK & GÉHU 1973), the first issue of this series, a new milestone in traditional European phytosociology. The comparison showed substantial agreement whilst some new lower rank syntaxa were suggested by the numerical output.

(9.9) **Ordination**

For the rapidly growing literature on phytosociological ordination we may refer to ORLÓCI (1975), various contributions in *Vegetatio* and, of course, the companion volume of this book. Like LACOSTE (1974, 1976) with correspondence analysis, many phytosociologists have used principal component analysis to obtain effective boundaries between community types (e.g. BOUXIN 1975, FEOLI 1973, GILS et al. 1975, and PIGNATTI & PIGNATTI 1975). DALE & CLIFFORD (1976) further explored the possibilities of using higher taxonomic ranks in the classification of vegetation (cf. MAAREL 1972*).

(9.10) **Conclusion**

The general effectiveness and efficiency of the BRAUN-BLANQUET approach was emphasised once more, by WERGER (1974). PIGNATTI (1975), contemplating the future of phytosociology, concluded that neither a one-sided if sophisticated mathematical phytosociology, nor a sterile perfecting of the hierarchic system of syntaxa should be desired. The approach should instead seek first summarization and fundamental understanding of relations of plant communities to one another and environment, and second increasing application of this knowledge to the conservation and management of our natural heritage.

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*References to publications already listed in the first edition are marked with *; new publications are in a separate list at the end of the References.

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