

PROBLEMS AND USE OF STRUCTURE IN THE CLASSIFICATION OF VEGETATION

THE DIAGNOSTIC EVALUATION OF STRUCTURE IN THE BRAUN-BLANQUET SYSTEM

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1. INTRODUCTION

It is a well-known fact that vegetation can be classified on the basis of quite different criteria; e.g. by physiognomy, structure, dynamic processes, floristical composition, and even – a scientifically less satisfying way – by habitat. It is not the aim of this study to give a critical review of these starting-points. The author's purpose is to consider the Braun-Blanquet system of vegetation classification, which is a system claiming to be based on floristical composition, and to analyse how far, in reality, structural criteria are involved in it. This article does not consider whether Braun-Blanquet syntaxonomy is the only valuable or even the best one. In fact it is, however, the most widely used and uniform system of vegetation classification, enabling us to compare plant communities over an area as large as (e.g.) Europe, and, therefore, also presenting a basis for such items as geographical comparison of habitats, vegetation mapping of large areas, or the analysis of geographical differences in the autecological behaviour of taxa.

It may thus be useful to see whether the higher units of this inductive system correspond to the units of the more or less deductive formation systems of the world, based on physiognomy and structure.

The International Botanical Congress of Brussels (1910) defined the concept of association as a unit of vegetation which is floristically, ecologically and physiognomically homogeneous. From this starting point BRAUN-BLANQUET (1913, 1928, 1932, 1951, 1964 etc.) has especially emphasised the diagnostic value of the floristic composition in its aspect of faithfulness, i.e. the rate, in which taxa appear to be bound to one or several communities (see also BECKING, 1957; POORE, 1955; CAIN and CASTRO, 1959; WESTHOFF *et al.*, 1951, 1965). At first sight such a system may appear an artificial one, since it deals with one feature of vegetation only. Against this viewpoint it may be argued, that the concept of faithfulness is a synthetic one, based on a number of analytical and synthetical characters of the vegetation such as abundance, dominance, sociability, vitality, fertility, stratification, periodicity and presence. As a matter of fact, this floristic classification is based on quite a complex of features

and not on a single one. Another objection, however, is more essential. The fundamental hypothesis of BRAUN-BLANQUET, formulated as early as 1913, states that the floristic composition represents all the other characters of the vegetation, since each taxon presents its own ecological amplitude, its specific genetic and historical background and its characteristic dynamic behaviour. Therefore, the floristic relations would be correlated with ecological, chorological and dynamical relations. For this reason the Braun-Blanquet system may be stated to be more a natural than an artificial one.

Since 1913, a number of investigations have proved this hypothesis to be valuable. Nevertheless the claimed correspondance has its exceptions, as is the case with most laws in biology. There are cases in which the floristic composition varies more or less independently of the other characters of vegetation. Such exceptions offer syn-taxonomical problems. We will restrict ourselves here to structural problems: (1) the problem arising when two or more plant communities or higher vegetation units appear to be floristically closely related, but quite different in structure; (2) a problem of relative homogeneity, viz. the case of vegetations with a complex mosaic pattern of structure, posing the question as to the level at which this complexity has to be taken into account in a classification system based on floristic composition.

Before entering into these topics the possibility of coordination between any formation system and the Braun-Blanquet system has to be considered (see also LAM, 1948; CAIN and CASTRO, 1959; DOING, 1962; VAN DONSELAAR, 1963; WESTHOFF *et al.*, 1965). The often abused term "formation" is used here in its original sense as given by GRISEBACH (1872) and applied a.o. by BEARD (1944) and CAIN and CASTRO (1959).

The Braun-Blanquet method is an inductive "micro-method", built into a hierarchical system. It operates with units which from low to high contain more lower units and are every time characterised by species with larger ecological amplitudes; at the same time, these larger units are related to more comprehensive ecosystems, greater structural variance and larger distribution areas. Until some years ago classes were the highest unit; recently BRAUN-BLANQUET (1964) has added class groups. A class group has few or no species in common, but it is characterised by taxa of higher rank consisting of vicarious species: e.g. the class group of deciduous forests on rich soils in the northern temperate zone. The class groups represent the ultimate classificatory possibility in a system having a floristic basis. It would be desirable now, to circumscribe the classes or class groups in such a way, that they fit in well with the units of a formation system. Even if purely floristically diagnostic criteria are used, this wish can be fulfilled, since a method based on floristic composition may lead to more than one possible system. An example is the mediterranean class of *Cisto-Lavanduletea* with the order *Lavanduletalia stoechidis* and *Helianthemetalia guttati*. The first order consists of low shrubs in an open habitat, the second of open grassland and herbaceous

communities. The latter however has a number of faithful species in common with the order *Festuco-Sedetalia*, dry grasslands of the extra-mediterranean region of Western and Central Europe, such as *Helianthemum guttatum*, *Jasione montana*, *Aira caryophyllea*, *Silene gallica*, *Trifolium striatum*, *T. subterraneum*, *Hypochoeris glabra*, *Vulpia bromoides*, *Filago gallica*, *F. minima*, *Poa bulbosa* and *Vicia lathyroides*. It would, therefore, be quite possible to split the *Helianthemetalia* from the *Lavanduletalia* and to join the former with the *Festuco-Sedetalia* in one class. BRAUN-BLANQUET too, has recognised the importance of this structural difference: in 1931 he joined the alliance of *Helianthemion guttati* to the *Lavanduletalia*, but in 1940 the former unit was given the rank of an order (BRAUN-BLANQUET, MOLINIER and WAGNER, 1940).

Joining the *Helianthemetalia* and *Festuco-Sedetalia* would result in a classification more homogeneous and logical from a structural viewpoint. The objection may be made, that a combination of a mediterranean and a non-mediterranean order to one class is undesirable, but such a chorological consideration has just as little to do with classifying on a floristic basis as a structural argument has. In this paper the author does not intend, however, to join the orders *Helianthemetalia* and *Festuco-Sedetalia*; more elaborate argumentation would be necessary. The case was only meant to present an example of how a certain group of communities can be classified in two structurally different ways, both on the basis of a floristic method.

Quite another approach in coordinating structural and floristical vegetation classification has been tried by VAN DER MAAREL and WESTHOFF (1964), who established a system of local dune plant communities primarily on structural, secondarily on floristical criteria.

2. CONCEPTS OF STRUCTURE IN SPACE AND TIME

One of the clearest expositions on the criteria used in classifying vegetation has been given by FOSBERG (1958), who distinguished between physiognomy, structure and function. Physiognomy, the aspect of vegetation, is a much less exact or objective feature than structure and function and leads to categories such as wood, shrub, swamp and desert. The systems of SCHIMPER (1898) and RÜBEL (1930) and also the "formation types" in the sense of DANSEREAU (1958) are physiognomical. On the contrary, according to FOSBERG (l.c.) structure is the order of vegetational components in space. The concept of structure has been defined in various ways. Many authors limit it to stratification and horizontal pattern; others, e.g. DANSEREAU (1958) include periodicity, life forms, growth forms, leaf characters and seed dispersal. FOSBERG (l.c.) proposes to limit the concept of structure to the spatial distribution of vegetation biomass and to exclude all adaptative phenomena which are functional – or presumed to be functional –; the latter should be brought together under the concept of function. The present author prefers a middle course and assigns to structure also: (1) structure in time (see below);

(2) spatial pattern based on the distinction of life forms which are easily distinguished morphologically, e.g. those defined by RAUNKIAER or by IVERSEN (1936). A similar concept of structure has – in an implicit way – also been used by CAIN and CASTRO (1959). The practical use of such a concept of structure has been proved by the symbol diagrams of DANSEREAU (1958), which have been applied by DANSEREAU and ARROS (1959) to their structural diagrams of 83 European associations.

It has to be stressed now that structure should not only be considered and studied in its static and spatial aspect. MARGALEF (1958, 1961) distinguished, within the concept of structure two aspects viz. the static or compositorian aspect, which I have discussed so far, and the dynamic or energetic. The latter deals with the energy flow in ecosystems. The present author will not agree with this viewpoint; in his opinion, this dynamic structural concept of MARGALEF has hardly anything to do with structure. Structure is a matter of form and not of energy. I shall elucidate the connection between the static and the dynamic aspect of structure from another viewpoint, that of systems theory.

As a result of succession analyses carried out for about twenty years on some hundreds of permanent quadrats in the various vegetation types of the Netherlands, VAN LEEUWEN (1960, 1962, 1964, 1965, 1966a, 1966b) has worked out the mutual relations between spatial structure and dynamic behaviour, i.e. between pattern and process, and has proposed an ecological systems theory, based upon the general systems theory of ROSS ASHBY (1958). This theory has proved to be useful in the first place in research on ecological gradients and borderline areas (see also TÜXEN and WESTHOFF, 1963; WESTHOFF, VAN LEEUWEN and ADRIANI, 1962; VAN DER MAAREL, WESTHOFF and VAN LEEUWEN, 1964; WESTHOFF, 1965; WESTHOFF and VAN LEEUWEN, 1965). In this theory, isolation and communication have been opposed to each other. Isolation appears to induce differentiation, whereas communication leads to equalisation. Differentiation in space is furthered by continuity in time; the reverse is also true: continuity in time effects a more differentiated spatial pattern. On the other hand, homogeneity in the spatial pattern and poverty in species are linked with disturbances, discontinuities in time. On the basis of these experiences two borderline ecosystem types have been discerned: the unstable or convergent limit and the stable or divergent limit.

A convergent limit is characterised by concentration effects, thus by easily recognisable, sharp contours, coarse-grained patterns and instability. A divergent limit is characterised by effects of spreading, thus only with difficulty recognisable, vague contours, fine-grained patterns and stability. Convergent limits are to be found in unstable transitional zones between ecologically extreme situations. More or less synonymous concepts are: ecotone, stress zone, tension belt, disturbance zone, noise environment, shuttle environment. The horizontal convergence is often combined with a vertical one (soil

hardening). Divergent limits are to be found in stable, transitional zones, with complex gradient structures. More or less synonymous is the concept of ecocline (see VAN DER MAAREL and WESTHOFF, 1964).

I shall return to these two types of border situations in discussing the increasing importance of structure in the Braun-Blanquet classification system.

3. RELATIVE INDEPENDENCE OF LAYERS AS A PROBLEM IN CLASSIFICATION

Different stands of vegetation may have one or more layers in common, whereas the remaining layers are different. HULT (1881) was the first botanist to make use of this phenomenon in classifying communities. He described sixteen "twin formations", e.g. the *Pineta polymorpha*: these formations had *Pinus sylvestris* dominant in the tree layer (combining stand), and whereas in one formation *Vaccinium myrtillus* and *Hylocomium splendens* formed the ground layer, in the other formation, their place was taken by *Calluna vulgaris* and *Cladina* spp. (alternating stands). The older school of Russian plant sociologists further developed the method (KELLER, 1927; SUKACHEV, 1928; KATZ, 1929; ALECHIN, 1932). KATZ produced the concept of homologous series of twin communities, in which both structure and ecology are taken into account. In one of the first analyses of vegetation on the Dutch dunes this method was similarly applied (BIJHOUWER, 1926). In a somewhat different way the idea has been developed by LIPPMAN *et al.* (1934) and by DU RIETZ (1921, 1932, 1936) and his students; the latter named the stratal units, considered by them as independent ones, Sozietäten, later on Konsozionen, whereas the former named them "unions", a term approved by the International Botanical Congress of Amsterdam (1936). These concepts present special cases of the synusia concept of GAMS (1918). It has been shown (e.g. by CAIN and CASTRO, 1959) that such a classifying method is functional for northern Eurasia, viz. in boreal areas with a relatively simple vegetation structure, where many species are able to dominate alternatively; in warmer areas with more complicated structure and decreasing dominants it is not practical however. According to CAIN and CASTRO (l.c.) a classification system on a synusial basis can be useful only in regions whose floras are poor in species and where environmental conditions are critically limiting; they refer to ROACH (1952), who studied a mountainous area of volcanic origin. Certainly the difference between extreme and non-extreme habitats is of great importance; it will be shown below that such twin formations are not bound to boreal and alpine circumstances, but are to be found even in the tropics. My viewpoint, however, is not so much whether it is possible to classify vegetation on the basis of synusiae, but what the consequences of relative layer independence are for the Braun-Blanquet system.

A simple example showing that in some cases structure has always been the main diagnostic criterion in this otherwise floristical system,

is presented by deciduous swamp woods compared with the stands of tall herbs derived from them after cutting ("Hochstaudenfluren"). The floristical resemblance between certain swamp woods and certain herb swamps is so great, that they could very well be joined into one alliance, a consequence, however, which no author as yet has drawn: these communities are assigned to different classes. It is true that the floristical difference between a well developed canopy of *Alnetum glutinosae* and a *Valeriano-Filipenduletum* or *Filipendulo-Geraniumetum* is still considerable. The difference decreases when we deal with an open *Alnetum*-coppice; but all syntaxonomists of the Braun-Blanquet system agree that only optimally developed stands may be used for classifying purposes. However, there are also, and especially on mineralised peat soils, alder marshwoods belonging to the alliance *Alno-Padion* - e.g. the *Macrophorbio-Alnetum* -, which only show small floristical differences with a comparable *Valeriano-Filipenduletum* in the same area, and it is only on structural grounds that it can be justified in assigning these associations to different classes, viz. *Quercu-Fagetea* and *Molinio-Juncetea*.

Just the opposite solution however has been given in the case of the *Rhodoro-Vaccinion*, as it has been dealt with by BRAUN-BLANQUET, SISSINGH and VLEIGER (1939). The climatic climax of the upper subalpine zone in large parts of the Alps is the *Rhodoro-Vaccinietum*. This association has been divided into four subassociations: *mugetosum*, with *Pinus mugo*; *cembretosum*, with *Pinus cembra*; *calamagrostidetosum* and *extrasilvaticum*, i.e. without a tree layer. In this case, therefore, communities of different formations have been joined into one association indeed. It is true that the *Rhodoro-Vaccinietum pinetosum* and *cembretosum*, open mosaic communities near the timber line, can hardly be considered to be woodland; especially as the succession tendency of the subassociation *cembretosum* is so easily disturbed by man, that a *Pinus cembra* canopy is hardly to be found anywhere. If such a well-developed canopy were described, it might be considered an association of its own, but still as a part of the alliance *Rhodoro-Vaccinion*.

Similar situations are found in subarctic and circumboreal Fennoscandia, Russia and Siberia. In wind-exposed habitats near the timber line occur the communities of the *Loiseleurio-Vaccinion*, consisting mainly of "Spaliersträucher" such as *Loiseleuria procumbens* and *Diapensia lapponica* and of lichens. In the next lower zone birch woods and birch-pine woods occur, e.g. *Cladonio-Betuletum tortuosi* and *Hylocomio-Betuletum tortuosi*, the "twin formations" described by HULT and KATZ. The latter have been joined to the alliance *Phylodoco-Vaccinion*, which together with the *Loiseleurio-Vaccinion* have been assigned to the *Vaccinio-Piceetalia*, although the structures of these alliances differ considerably. However, any botanist who knows these vegetations personally will agree that any other syntaxonomical approach to these little floristical differences between woodland and nanophanerophyte carpets would be difficult.

A comparable situation in Ireland has been described by BRAUN-

BLANQUET and TÜXEN (1952). The eu-atlantic Irish association of the deciduous woodland alliance *Quercion roboris-petraeae* has been named by them *Blechno-Quercetum*. On very wet and nubulous slopes of maritime mountains (McGillycuddy reeks, Co. Kerry) a community of *Luzula maxima* occurs, which should be considered a degradation stage of woodland. BRAUN-BLANQUET and TÜXEN described this community as *Blechno-Quercetum extrasilvaticum*, although in these surroundings no single tree can be found. This solution seems an odd one, but after having visited the classical spot the present author agrees that within the Braun-Blanquet system no other description would be logical or practical.

A similar problem is offered by the wooded raised bogs in the baltic area. Their nanophanerophyte communities with more or less scattered trees in them have been described as a class *Vaccinetea uliginosi* with the order *Vaccinietalia uliginosi* and the alliances *Betulion pubescentis*, *Piceo-Pinion uncinatae* and *Pino-Ledion palustris*. LOHMEYER *et al.* (1962) have rejected these higher units and joined them to woodland alliances, but this solution is clearly at variance with the syntaxonomic trend of today. Situations of the above kind are not only found in the cool North or the wet atlantic West, but equally in the mediterranean region. A good example is the garigue of southern France, the *Rosmarino-Ericion*, and especially its association *Rosmarino-Lithospermetum*. The structure of this association has been studied in detail by BARKMAN (1958b). It presents a number of subassociations, of which four may be mentioned, constituting a degradation cline from woodland to dwarf shrub formation: *R.-L. pinetosum halepensis*, a "savanna" of Aleppo pine; *R.-L. ericetosum multiflorae*, a homogeneous closed dwarf shrub community; *R.-L. helianthemetosum*, a mosaic complex of dwarf shrub stands and open herb vegetations; and finally *R.-L. schoenetosum*, where dwarf shrubs are minor components. In this case also communities with considerably different structures have been joined into one association. DANSEREAU and ARROS (1959), who consider structure as a major diagnostic feature, are strongly opposed to this example of classification, their attack being directed against GUINOCHET (1955).

Even in the tropics situations are found where the vertical bond between the vegetation layers is only loose and the stands consist of more or less independent synusiae. MEYER DREES (1951) described such a case from the savannas of the Indonesian island of Timor. In these savannas scattered tree groups of various densities occur, on a certain substrate *Eucalyptus alba*, on another *Acacia leucophloea*, etc. In the Eucalyptus savanna in particular the herb layer under the trees appeared nearly the same as in the open stands. In spite of the great difference in structure it was necessary, therefore, to join the grassland community and savanna into one association. MEYER DREES (l.c.) however did not like this solution and would prefer to distinguish locally dominante communities on the basis of constancy (Scandinavian method). Similar patterns were recorded from Timor mangrove.

VAN DONSELAAR (1963) investigated the savanna vegetation of Surinam on soils with alternating water levels. He found that the Braun-Blanquet method was appropriate to these vegetation types and he was the first botanist in the northern part of South America to develop a system of associations, alliances, order and classes. He too met the problem that, in some cases, the undergrowth of savanna tree stands differed so little from the open herb vegetation without a tree layer, that both had to be reckoned as the same association. Contrary to MEYER DREES (l.c.) and DANSEREAU and ARROS (l.c.) however, VAN DONSELAAR is quite convinced that the floristical principle must preponderate and that, in this case, it would be unlogical to try to place tree stand and grassland in different classes. He prefers an association system quite separate from a formation system of the same vegetations and independent of each other.

The examples mentioned show that the problem of twin formations with rather independent layer synusiae, in other words the phenomenon of stands differing little in floristical but strongly in structural respects, is bound to extreme habitat conditions. Certain abiotic or even biotic environmental factors preponderate here (master factors) and outdo the ecological influence of a tree layer on its undergrowth. In subarctic, boreal and subalpine areas cold winters, snow cover and wind are all-important; in oceanic climate the high air humidity; on wooded raised bogs the deficiency of nutrients and oxygen in the soil; in the savannas of Timor and Surinam the extremely alternating water levels, in the mediterranean garigue the frequent burning by man. In these cases structure has a minor ecological importance indeed, so that it should not be overestimated as a diagnostic criterion. So I agree with VAN DONSELAAR (l.c.) as to his syntaxonomic solution for the present problem, which does not mean that I agree with his principal objections against the coordinating of floristical and structural systems.

4. THE INCREASING WEIGHT OF STRUCTURE IN THE BRAUN-BLANQUET METHOD

Hitherto I nearly took for granted, that all layers of a stratified community should be studied in their totality as a single phytocenosis; the unistratal concept of LIPPMAA and DU RIETZ has only been mentioned (see also CAIN and CASTRO, 1959). Without entering deeply into this matter, it should be remarked that this assumption does not hold in all cases. Epiphyte communities (see BARKMAN, 1958b) are generally held to be an exception, because their habitat is rather independent of the soil. However, it is not always easy or even possible to separate the epiphyte community from the phanerogam stand; moreover, the limit between epiphytic communities and cryptogamic communities on the soil surface is often difficult to draw. This problem of microcenoses has been thoroughly dealt with by BARKMAN (1965). Apart from such problems, Zürich-Montpellier workers generally agree that synusiae rooting together in the

same substrate have to be considered one total plant community. There are, however, exceptions also to this rule. TÜXEN (1950) described the "Schleiergesellschaften" (liane blanket communities) of river banks and similar convergent ecotones as an alliance *Calystegion sepium*. We have here to do with an outpost of a type of vegetation structure which is much better developed in the tropics. In fact, the associations of the *Calystegion sepium* are synusial units, although they are not claimed to be so. This solution should not be recommended, because of analytical difficulties. It is hardly possible in making sample plot analyses (relevés) to separate the blanket lianes from the other species which are also rooting in the same substrate. The result would be a subjective choice as to which species should be included in the list and which not.

Yet a special case is presented by the water vegetations. Previously the different strata of water communities, viz. the bottom or isoetid layer, the suspended or elodeid layer, the swimming-and-rooting or nymphaeid layer and the only just swimming or lemniid layer, have generally been joined into one association, although the analogy with terrestrial vegetations is not very obvious. In fact, the hydrophyte strata appear to be much less interdependent than the terrestrial ones; for the greater part they do not live in the same micro-habitat. This fact has been taken into account firstly in subdividing the lemniid strata into separate units: the alliance *Lemnion*, the order *Lemnetalia* and the class *Lemnetea* (MIYAWAKI and TÜXEN, 1960). DEN HARTOG and SEGAL (1964) and SEGAL (1965) have followed up the consequences of this development. They composed a system based not so much on strata as on life form synusiae, thus splitting up the former class *Potametea* into the classes *Potametea* s.s., *Ceratophylletea*, *Utricularietea*, *Stratiotetea* and *Lemnetea*. An important argument in its favour is the pioneer character of most hydrophyte communities, which brings about rapidly changing structures with often monospecific vegetation masses; a problem which will be dealt with below.

Not only in the case of the *Potametea*, but also in that of helophyte communities of the orders *Phragmitetalia* and *Montio-Cardaminetalia* there are many examples of coarse mosaic patterns, in which large monospecific clusters of individuals (often clones) are alternating. Often such a pattern is bound to primary abiotic habitat differences: for instance in *Scirpo-Phragmitetum*, *Typha angustifolia* dominates on soft mud, *Scirpus lacustris* in the deepest zone most exposed to wind and waves, etc. A general analytic procedure in the Braun-Blanquet method is that such a pattern, brought about by primarily abiotic factors, leads to the distinction of several associations within this pattern. However, the large association *Scirpo-Phragmitetum*, first described by W. Koch in 1926, as yet has not been split up, but undoubtedly such a splitting will prove to be desirable in near future; a unit like the *Scirpo-Phragmitetum* is becoming an anachronism.

There are, indeed, many examples showing that the Braun-Blanquet method in recent years, mostly in Western and Central Europe, is more and more insisting on structure as a diagnostic

criterion. This development is obvious in pioneer communities as well as in terminal (climax) ones. In 1936, the stands of *Salicornia europaea* and *Spartina stricta* on northwestern-atlantic marine mud flats were still considered to compose one association (BRAUN-BLANQUET and DE LEEUW, 1936); more recently they have even been made into two classes, *Thero-Salicornietea* and *Spartinetea* (TÜXEN and OBERDORFER, 1958; LOHMEYER *et al.*, 1962; BEEFTINK, 1962, 1965). One reason for this change is the great difference in life forms: the stands mentioned present two synusia, the former a therophyte, the latter a geophyte one. However, a more important factor is that here we have to do with pure stands very poor in species. A careful analysis always points out that a well-developed *Salicornia* stand and an equally well developed *Spartina* stand have no single species in common, so that they do not have any floristical relation (as far as phanerogams are concerned). This situation, common in pioneer vegetation, will urge us more and more to what PIGNATTI (1964) called "the inflation of the higher vegetation units". It is essential to realise that in such cases we have to do with patterns of unstable habitat, i.e. communities of convergent ecotones or convergent areas which in the course of time are exposed to irregular major ecosystem fluctuations and changes. Other examples are the *Ruppietea* of the poikilohalinic (brackish) water, the *Cakiletea* of the tidal marks on the sea shore, and the *Plantaginetea maioris* of the border areas between the extremes of wet and dry, salt and fresh, trodden and untrodden, and soil rich and poor in nutrients. In all such cases the analysis of vegetation is relatively simple, but the development of a hierarchic system is difficult; as an overstatement it might be said that every two associations from this type of environment represent two classes. (See also VAN DER MAAREL, WESTHOFF and VAN LEEUWEN, 1964).

In contrast to this category are the stable, divergent gradient communities, rich in species, with fine-coarsed pattern and vague contours, living in a stable environment where fluctuations (if any) are rhythmic and regular. In such cases vegetation analysis is more difficult: the problem is where the limits between the relevés have to be drawn and which level of homogeneity should be taken as a basis for classification. As a result of this problem, the syntaxonomy of the woodland margin communities in particular, the "mantles" (shrub) and "skirts" (borderlines of tall herbs), was somewhat neglected up to about 1950. In later years however this situation changed, at least in Western and Central Europe, on account of a gradual refining of analytical methods and of special attention to the close and intricate contact of two or more adjacent communities gradually merging into each other within a complicated divergent border pattern.

TÜXEN (1952) made an important development on the Braun-Blanquet system in a classification which is to a larger extent based on structure. He joined the mantle communities of woodland margins with comparable communities of shrubs and hedges into one newly

described order, named *Prunetalia spinosae*. This order was assigned to the class *Quercu-Fagetea*, described as early as 1937 by BRAUN-BLANQUET and VLIEGER. The admission of the order *Prunetalia* is contrary to the generally accepted subdivision of the *Quercu-Fagetea*. This consequence could have been avoided if all newly described shrub and mantle associations had been left near their edaphically and chorologically corresponding woodland associations, so that each shrub association would be placed in the same alliance at least as its comparable woodland companion. This solution, which has already been tried by JAKUCS (1961) is possible, because by far the most shrub associations have a part of their faithful and differential species in common with the corresponding (often adjacent) forest associations. TÜXEN, however, (l.c.) choose another way, with the result that, in this case, the structural criteria have superseded the floristical ones. It must be added that this renovation has been agreed with all over Europe and that it has induced much new valuable research. The next consequence was to raise the *Prunetalia* to the rank of a class. This has been effected independently by three authors: the Spanish botanists RIVAS GODAY and BORJA CARBONELL (1961) described the class *Rhamno-Prunetea* (referred to in TÜXEN, 1962); TÜXEN (1962) himself proposed the name *Crataego-Prunetea*; DOING (1962) the name *Sambucetea*. For the sake of priority *Rhamno-Prunetea* is the valid name. The *Prunetalia* are structurally similar and phytogeographically vicarious to that thorn shrub formation of the mediterranean mountains and southern continental areas, which was first described by ADAMOVIČ (1909) under the name "šibljak". DOING KRAFT (1955) was the first to take the latter formation into account in the frame of the Braun-Blanquet system by giving them provisionally the order name "*Cotinetalia coggygriae*". *Prunetalia* and *Cotinetalia* are deciduous shrub communities, Aestifruticeta in the sense of RÜBEL (1930). A parallel sere is formed by the two mediterranean evergreen shrub types, Durifruticeta in the sense of RÜBEL (l.c.), which were distinguished by ADAMOVIČ (l.c.) as "macchia" – in the plains – and "pseudomacchia" at somewhat higher altitudes, between macchia and šibljak. DOING KRAFT (1955) completed this system by designating the *Prunetalia* as "pseudo-šibljak".

In refining the analysis of divergent vegetation pattern MÜLLER (1962) has advanced further by resolving the old so-called "Steppenheide-problem" syntaxonomically. He described and developed a quite new class of "Hochstaudenhalden" or "Saumgesellschaften", i.e. the tall herb communities on the margins of woodland mantle, which he named *Trifolio-Geranietea sanguinei*. Along with the further refining of analysis goes a stronger accentuation of structure as a diagnostic feature. In fact, the alliances and associations all newly described by MÜLLER (l.c.) within this class *Trifolio-Geranietea* have been so faintly characterized – they hardly present any faithful or even good differential species with a comforting selectivity – that nobody would have brought them into a separate class if no structural arguments were available. This weak floristic characterization,

however, has nothing to do with poverty in species: these very communities are extremely rich in species. The problem of characterization in this case is directly dependent on the vague contours within the mosaic pattern: the presence optimum, i.e. the relative accumulation of any species in a given community compared with the adjacent communities, is always small. In this case, too, the Braun-Blanquet system attains to a limit of possibility, but for just the opposite reasons from those of the case in pioneer communities. The most extreme case of a phytocenosis rich in species on a divergent habitat, where a maximal rate of energy flow within internal rhythmic dynamic processes coincides with a great stability of the ecosystem as a whole, is the tropical rain forest, where hundreds of tree species occur on a quadrat mile, and every species is represented by very few individuals. As yet, the Braun-Blanquet system is not suitable for this community type. This is, however, exceptional. As we have shown above, the increasing use of structure provides the Braun-Blanquet system with a greater flexibility and more possibilities of being applied in different ecosystem types. The most important point is the gradual shifting from dogmatism to pragmatism. We may conclude with BRAUN-BLANQUET: "There are no right and wrong systems, only good and bad ones".

5. AN ATTEMPT AT CLASSIFYING THE VEGETATION CLASSES OCCURRING IN THE NETHERLANDS INTO STRUCTURAL UNITS

5.1. *Introduction*

In the last twenty years, the Braun-Blanquet system of classification of European vegetation has considerably changed, as may have appeared in the preceding chapters. As far as I know, a completely up-to-date survey has not been published. The most recent syntaxonomic survey of the vegetation of Northwestern and central Europe (except for the alpine areas) has been published by LOHMEYER *et al.* (1962); this survey has been taken over by ELLENBERG (1963) and OBERDORFER (1964).

It seemed worth while to try to classify the units of this system into a structural classification. An attempt is presented below. For the sake of surveyability only the classes are given, as they are the highest units which have been described in this region. The author prefers to restrict himself here to Dutch vegetation. This restriction is not a big disadvantage, since the bulk of the classes of non-alpine W. and Central Europe occur in the Netherlands. As authors' names should only be added when such are desirable to avoid confusion, such names have been omitted if they are also found in the surveys of LOHMEYER *et al.* (l.c.), ELLENBERG (l.c.) and OBERDORFER (l.c.). More recent or deviating class names have been provided with their authors' names; references relating to these classes may be found in BEEFTINK (1962, 1963), DOING (1962), DOING KRAFT and WESTHOFF (1959), DEN HARTOG and SEGAL (1964), SEGAL (1965), TÜXEN and WESTHOFF (1963).

An attempt has been made to define the structural units given below in terms of spatial arrangement and life form spectra only. (Edaphical factors which are not essential for this classification are only given in brackets as an aid to better understanding). The only exception is group 2, vegetations of rocks and walls; as yet, it is not possible to define this unit otherwise than in an ecological way.

A term for the structural units presented here has been avoided. It seemed not quite appropriate to design them as "formations". The scheme is meant to be provisional only. It might appear to be practical to lump some units (e.g. 12, 13 and 14), and to split up some others (e.g. 2, 5 and 6), to get a better-balanced system.

5.2. Scheme of structural units with the 37 classes assigned to them

1) Vegetations consisting of hydrophytes and amphiphytes (growing in an aquatic habitat and not or hardly emerging from it).

Classes: *Lemnetea* – *Charetea* (KRAUSCH, 1964) – *Potametea* – *Ruppieteae* (J. TX., 1961) (DEN HARTOG et SEGAL, 1964) – *Zostereteae* – *Littorelleteae*.

2) Vegetations of rocks and walls.

Class: *Asplenietea rupestris*.

3) Ephemeral vegetations with a pioneer character, consisting mainly of summer therophytes, built up from a single to many species (on open, haloid soils rich in ammonium and (or) nitrates, nearly always in convergent habitats).

Classes: *Thero-Salicornieteae* – *Cakiletea* – *Bidenteteae* – *Isoeto-Nanojunceteae* – *Chenopodieteae* – *Secalineteae*.

4) Pioneer vegetations consisting mainly of rhizome geophytes and poor in species (on marine mudflats and the coastal ridge of sea dunes).

Classes: *Spartineteae* – *Ammophiletea*.

5) More or less open, secondary, instable vegetations, consisting of several species, mainly made up of perennial plants: chiefly hemicryptophyta rosulata, scandentia et scaposa (on more or less disturbed soils rich in nitrogen, always in convergent habitats).

Classes: *Epilobieteae* – *Plantagineae maioris* – *Artemisieteae vulgaris*.

6) Communities consisting mainly of helophytes (in swamps and springs).

Classes: *Phragmiteteae* – *Scheuchzerio-Cariceteae nigrae* (syn.: *Parvo-cariceteae*) – *Montio-Cardamineteae*.

7) Closed and open grassland communities consisting mainly of hemicryptophytes – the bulk of them being hemicryptophyta caespitosa –, a considerable number of therophytes – for the larger part winter annuals –, and next, if any, geophytes and chamaephytes (on dry soils and on the ecotone between dry and salt habitat).

Classes: *Sedo-Sclerantheteae* – *Festuco-Brometeae* – *Violeteae calaminariae* – *Sagineteae maritimae* (TÜXEN et WESTHOFF, 1963).

8) Closed (rarely open) grassland communities consisting mainly of hemicryptophytes – the bulk of them mostly hemicryptophyta caespitosa –, exceptionally mainly chamaephytes, but differing from the previous group by the smaller content or absence of therophytes (on damp to wet, fresh or salt soils).

Classes: *Molinio-Juncetea* (BRAUN-BLANQUET, 1947) – *Arrhenatheretea* – *Asteretea tripolium* (BEEFTINK et WESTHOFF, 1960).

9) Closed, sometimes more open communities of tall perennial herbs, mostly hemicryptophyta scaposa, chamaephytes and lianes; often bordering shrubs and forming an intricate mosaic pattern with shrub communities (in divergent ecocline habitat, mostly on dry calcareous soils).

Class: *Trifolio-Geranietea sanguinei*.

10) Communities of nanophanerophytes with a mostly conspicuous – sometimes predominating – layer of bryophytes: tussocks of raised bogs; heaths and moorlands.

Classes: *Ombro-Sphagnetetea* – *Nardo-Callunetea*.

11) Shrubs or Fruticeta (on dry to wet soils, mostly in divergent habitats).

Classes: *Rhamno-Prunetea* (RIVAS GODAY et BORJA-CARBONELL, 1961); *Franguletea* (DOING, 1962) – *Salicetea purpureae*.

12) Poorly stratified deciduous forests (but with lianes); undergrowth poor in species, especially poor in therophytes and nanophanerophytes, but always with a certain amount of telmatophytes in the sense of IVERSEN (1936); moss layer either not very conspicuous (though often rather rich in species) or consisting of sphagnoid chamaephytes (azonal swamp woodlands and “carr” on wet peat soils).

Class: *Alnetea glutinosae*.

13) Poorly stratified deciduous forests (but with lianes); in boreal, baltic and montane Europe also acicular forests. Undergrowth poor in species, without any telmatophytes, but often with abundant or even dominant nanophanerophytes; moss layer often conspicuous (azonal woodlands on poor, very acid, dry to damp mineral soils).

Class: *Quercu-Piceetea* (DOING et WESTHOFF, 1959) (syn.: *Quercetea roboris-petraeae* and *Vaccinio-Piceetea* lumped together).

14) Richly stratified forests; undergrowth rich in species and consisting of many life forms, but rarely with a conspicuous amount of nanophanerophytes (zonal woodlands on rich, dry to damp, mineral soils or mineralised peat soils with a crumb structure).

Class: *Quercu-Fagetea*.

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