Acta Botanica Neerlandica **13** (1964) 367–393

A NEW CLASSIFICATION OF THE WATER-PLANT COMMUNITIES

C. DEN HARTOG
(*Rijksherbarium, Leyden*)
AND
S. SEGAL
(*Hugo de Vries Laboratorium, Amsterdam*)

(*received May 20th, 1964*)

Abstract

Up to the present the water-plant communities have been studied in the same way as the terrestrial plant communities. As water and land differ fundamentally as a habitat for plants it is not surprising that several ecological concepts, which have been developed for the terrestrial vegetation, can not be applied to the aquatic vegetation. In the water quite other factors are decisive for the development of communities than on the land.

The system of Braun–Blanquet, normally used for the classification of plant communities, is based on one complex character, the floristic composition of the vegetation. Although this character is highly estimated by us, we think, nevertheless, that a one-character system is of necessity artificial. To arrive at a more natural classification other criteria have also to be considered. The floristic composition of the vegetation on its own appears to be an insufficient character for the classification of the water-plant communities, as a consequence of the equalizing effect of the aquatic medium. In the system proposed the following characters have been applied: floristic composition, life-form spectrum, physiognomy, stratification and in some cases the ecology of the vegetation.

1. Introduction

In the last 20 years the knowledge of the vegetation of West and Central Europe has increased enormously. This has resulted in radical changes in the original classification schemes, particularly those of the weed communities, the wood communities and the halophyte communities. The classification of the water-plant communities changed little in that time. This, without doubt, must be ascribed to the small direct economic importance of the water plants and that the water is neglected as a habitat by many botanists.

The earlier classifications were completely based on the floristic composition of the communities, thus on one complex character only. The opinion that the base of the "pflanzensoziologische System auf floristischer Grundlage" of Braun-Blanquet is too narrow is gaining ground more and more among the phytocenologists. In addition to the floristic composition other criteria have to be accepted as well for the classification of communities, e.g. stratification, life-form spectrum, physiognomy and possibly the ecology of the vegetation. The more criteria used, the better will the classification reflect the reality.

With regard to the water-plant communities we have arrived independently of each other at the same conclusion, viz. that the existing classification is antiquated and has to be revised from a modern point of view. Independent of each other we have devised a new classification scheme. The two systems agreed on many points and had some interesting differences, due to the different methods of approach followed by us both. As it was considered undesirable to publish at the same time two systems which had more in common than they differed, we have tried to come to a synthesis of our ideas. At a meeting with Dr. V. Westhoff we reached agreement on almost all points and it was decided to make a joint publication on the new classification scheme of the water-plant communities.

2. Definition of the concept "water plant"

To begin with it has to be ascertained what we understand by water plants. It is not easy to give a useful definition of this group. The definitions given in the botanical literature vary considerably and often include plant types which are dependent on the water for only some stages of their life cycle. Raunkiaer (1934), who classified the plants according to their morphological adaptations to the unfavourable season, regarded hydrophytes as plants which have their vegetative parts submerged or floating at the water surface but not projecting into the air and which survive the unfavourable period in the form of submerged buds, these being either attached to a rhizome or lying completely free on the bottom of the water. This definition does not take into account the short-lived water plants, e.g. *Naias* species, *Trapa natans*, *Salvinia natans*, *Subularia aquatica* and *Azolla* species which are summer annuals in Europe and pass through the winter in the form of seeds or spores. Braun-Blanquet (1951) rightly classified these species in the life-form system of Raunkiaer as hydrotherophytes.

Not only the winter but also the summer is an unfavourable season for many water plants, as their habitat may become completely or partly dry. The adaptations for surviving the drought are quite different in the various water plants. Many of them develop more or less reduced, sterile land forms, e.g. *Potamogeton* species and *Nymphaea alba*. Other taxa, e.g. species of *Callitriche* and *Ranunculus* subgen. *Batrachium*, occur with land and water forms, both of which pass through their generative cycle. Further there are amphibious species, which flower by preference during the period of emergence although they are quite well able to achieve their generative cycle in the submerged condition, e.g. *Littorella uniflora*. Thus plants which survive the winter as hydrophytes when subjected to a drought can also belong to other groups in Raunkiaer's system. *Potamogeton natans*, for example, is in the winter a hydrophyte, but it survives a period of emergence as a hemicryptophyte. *Zannichellia palustris* ssp. *pedicellata* dies rapidly when emerged, but its seeds resist a protracted dry period, and so it behaves as a therophyte.

There are, however, also many terrestrial plants which tolerate a long-continued submersion quite well. Some even develop special water forms; these are unable to achieve their generative cycle when all vegetative parts are submerged or floating at the surface. These plants have to be regarded as hydrophytes, according to the definition of Raunkiaer, and indeed this author mentioned *Juncus bulbosus* and *Echinodorus ranunculoides* as hydrophytes, although they are unable to reproduce when they are submerged.

Iversen (1936), who classified the plants according to their morphological adaptations to the factor water, regarded water plants as plants which have their vegetative parts submerged or floating at the water surface but not projecting into the air, and which for the larger part are able to develop vegetatively and generatively reduced land forms. This definition comprises the hydrophytes as well as the hydrotherophytes of Raunkiaer's system. It is, however, not quite sufficient, as plants which are able to achieve their generative cycle in the submerged as well as in the emerged condition, were classified by Iversen as amphiphytes. These are defined as plants with emerged aerial leaves and hydromorphic leaves, or which are able to develop water forms. These water forms have enlarged vegetative parts but reduced floral parts in comparison with their land forms. He gives as examples some dwarf amphiphytes, among others *Eleocharis acicularis*, *E. parvula*, *Littorella uniflora* and *Pilularia globulifera*, which reproduce by preference when emerged but which are quite well able to pass through their reproductive cycle when submerged. Many species of *Callitriche* and *Ranunculus* subgen. *Batrachium* form in fact transitional cases between the amphiphytes and the limnophytes[1]). There are also several taxa of which the vegetative parts are completely adapted to the water and do not tolerate any desiccation, although they reproduce when they become emerged, e.g. the moss *Fontinalis* and the tropical Podostemonaceae. Arber (1920) wrote of the latter family that flowering and seed-setting take place with the utmost rapidity when the plants are exposed to the air, as it were their swan-song. In Iversen's system these taxa with "emergency-flowering" represent in fact a separate ecological group between the amphiphytes and the limnophytes. They have certainly to be regarded as water plants as they are unable to produce terrestrial forms.

Iversen further stated that it is quite well possible to consider the taxa with floating leaves to be amphiphytes as well, because their vegetative parts are as much adapted to aerial life as to life in the water.

---

[1]) The term "limnophyte" as used by Iversen (1936) is misleading. Generally words with the Greek prefix *limne* relate to fresh water and are used in contrast to marine terms. So the term limnophyte suggests that the plant concerned occurs in fresh water; the definition as given by Iversen, however, covers also the seagrasses and brackish-water plants. Secondly, the term had already been employed in the original version of Raunkiaer's life-form system for an other life form, but this was later replaced by the term helophyte.

From the foregoing lines it is clear that the separation of amphiphytes and limnophytes is very indefinite, as both groups are connected by a series of transitions. Although they show a wide range of diversity in their morphological adaptations to environmental circumstances the water plants by their limitation to the aquatic habitat form a closed group. Morphological characters seem, therefore, less suitable for a general definition of the concept water plant. However, a true water plant must be able to achieve its generative cycle when living in its normal habitat. This criterion has been used by us as base for the following definition:

Water plants are plants which are able to achieve their generative cycle when all vegetative parts are submerged or are supported by the water (floating leaves), or which occur normally submerged but are induced to reproduce sexually when their vegetative parts are dying due to emersion.

This definition excludes three groups of plants which figure often as water plants in the literature:

1. Plants which frequently occur completely submerged, maintaining themselves for years by vegetative reproduction, but which are not able to achieve their generative cycle under these circumstances. In very shallow water or when emerged their vegetative parts show a marked differentiation (development of erect aerial leaves) and sexual reproduction may take place, e.g. *Sagittaria sagittifolia f. vallisneriifolia* and *Sphagnum crassicladum* var. *obesum* (pseudohydrophytes).

2. Plants which root in the bottom and of which the basal parts are submerged almost continually, but whose leaves and inflorescences rise above the water surface, e.g. *Typha*, *Phragmites*, *Scirpus* subgen. *Schoenoplectus*, *Butomus*, etc. (helophytes).

3. Plants drifting freely on the surface with submerged root systems, but with all other vegetative parts and inflorescences rising above the water, due to their aerenchymatic structure, e.g. *Eichhornia crassipes*, *Calla palustris*, etc. (pleustohelophytes).

3. Morphological and ecological classification of water plants

The group of the water plants, as defined in § 2, can be subdivided according to several morphological and ecological criteria and various classifications of water plants have been published. It is not our intention to discuss them here in extenso. We will limit ourselves to the discussion of those systems which appeared to be of basic importance for the phytocenological classification proposed here, viz. the systems of Luther (1949) and of Du Rietz (1923, 1930).

Luther (1949) classified the water plants according to their mode of attachment to the substrate. He distinguished three groups.

1. Haptophytes: plants not penetrating into the substrate with their basal parts but attached to the surface of rocks, stones, wood and all kinds of other solid substrates.

This group comprises the majority of the benthic algae, all aquatic lichens, and most of the aquatic musci (*Fontinalis*, *Cinclidotus*) and liverworts (*Scapania undulata*, *Riella*). There are no haptophytes among the phanerogams in Europe. In the tropics the Podostemonaceae, occurring in cataracts and near water falls, belong to this group. Along the Pacific coasts of North America and Japan epilithic sea-grasses (*Phyllospadix*) occur.

2. Rhizophytes: plants with their basal parts penetrating into the bottom or covered by the substrate.

This group comprises the majority of the aquatic phanerogams and many algae (Charophyta; Vaucheriaceae; several Chlorophyta, e.g. *Caulerpa*).

3. Planophytes: plants floating freely in the water and whose assimilatory organs are submerged or float on the water surface. This group has been subdivided by Luther into the microscopical planktophytes (which will not be considered by us) and the macroscopical pleustophytes. The latter group contains thus all floating plants, which are not attached to a solid substrate. Luther distinguished three groups of pleustophytes:

a) The benthopleustophytes are plants which lie freely on the bottom. To this group belong some algae, e.g. *Cladophora aegagropila* and *Nostoc pruniforme*.

b) The mesopleustophytes are plants which float freely between the bottom and the surface of the water, e.g. *Lemna trisulca*, *Riccia fluitans*, *Utricularia vulgaris*, *Ceratophyllum demersum* and tangles of floating algae.

c) The acropleustophytes are plants which float on the surface of the water. The upper sides of their leaves are adapted to aerial life. This group contains *Lemna minor*, *Azolla filiculoides*, *Salvinia natans*, *Hydrocharis morsus-ranae*, etc.

Stratiotes aloides, of which the upper parts of the leaves usually arise above the water surface, is a transitional case between the acropleustophytes and the pleustohelophytes.

The separation between these three groups of pleustophytes is not very sharp, as many acropleustophytes sink to the bottom in autumn and rise to the surface again in spring. During the growth period the acro- and mesopleustophytes are clearly separated.

It has to be pointed out that some haptophytes, which have been loosened from their substrate, are able to propagate vegetatively in that condition and to behave as pleustophytes. Some species of *Enteromorpha* are well-known in this respect. When they have become detached from their substrate, they form thick masses which float just below the surface of the water.

Furcellaria fastigiata, *Rhodomela subfusca*, *Phyllophora brodiaei*, *Fucus vesiculosus*, *Sphacelaria* species, *Chaetomorpha linum* and *Cladophora* species form on the bottom of shallow still-water biotopes in the Baltic extensive vegetations of secondary benthopleustophytes, so-called "migration forms". The moss *Fontinalis antipyretica* forms an extensive loose-lying carpet on the bottom of some broads in the Netherlands.

Among the rhizophytes also species occur which can behave as pleustophytes, e.g. *Elodea canadensis* and *Myriophyllum spicatum*.

Secondary rhizophytes exist also. Detached *Fucus vesiculosus* can maintain itself under certain circumstances in the upper part of the intertidal belt between the subgrowth of low-lying salt-marsh communities. It propagates itself by proliferation and dichotomous splitting of the thallus, so forming dense carpets of "*Fucus lutarius*". Detached *Fucus vesiculosus* can become reattached by the byssus-threads of mussels; it is then transformed to "*Fucus mytili*" which also propagates by dichotomous splitting (DEN HARTOG, 1959a).

The classification of water plants according to their attachment to the substrate can be supplemented with another classification, based on the growth forms of these plants. The growth-form system of DU RIETZ (1923, 1930) seems to us the most useful for the study of water-plant communities, as its basic types are well-defined and easily recognizable. We have elaborated this system by extending the number of basic types. This was necessary, as the original definitions by Du Rietz were in some respects too wide, so that species with very different growth forms were classed into the same basic type. The definition of the elodeids, for example, comprised rhizophytes such as *Elodea canadensis* and *Potamogeton pusillus*, but also pleustophytes, such as *Ceratophyllum*.

The system of Du Rietz has been elaborated for the rhizophytes and the pleustophytes only. The growth forms of the haptophytes have not yet been classified into a general system. SCHIMPER and VON FABER (1935) distinguished a special *Podostemon* type for the haptic phanerogams. The growth forms of the epilithic algae have been summarized by DEN HARTOG (1955, 1959a). In this paper the haptophytes will not be considered.

In Europe 11 basic types can be distinguished.

1. Isoetids: rhizophytes with a short stem, a rosette of stiff radical leaves, and with or without stolons, e.g. *Isoetes lacustris*, *Littorella uniflora*, *Lobelia dortmanna*.

2. Vallisneriids: stoloniferous rhizophytes with a short stem and a rosette or bundle of long, flabby, linear radical leaves, e.g. *Vallisneria spiralis*.

3. Elodeids: caulescent rhizophytes with undivided, submerged leaves and without specialized floating leaves; generative parts rising above the water surface or not, e.g. many species of *Potamogeton*, *Elodea*, *Naias*, *Zannichellia*.
4. Myriophyllids: caulescent rhizophytes with finely dissected, submerged leaves and without specialized floating leaves; generative parts rising above the water surface, e.g. *Hottonia*, *Ranunculus circinatus* and *Myriophyllum*.
5. Batrachiids: caulescent rhizophytes with specialized floating leaves and spatulate or finely dissected submerged leaves; generative organs rising above the water surface or not. Tendency to develop terrestrial forms; e.g. several species of *Ranunculus* subgen. *Batrachium* and of *Callitriche*.
6. Nymphaeids: rhizophytes with a little or not branched stem and longly petiolated floating leaves, in some cases also with submerged leaves, e.g. *Nuphar*, *Nymphaea*, *Nymphoides* and *Potamogeton natans*.
7. Ceratophyllids: submerged pleustophytes with finely divided leaves and without floating leaves; in the summer near the surface of the water, but in the autumn sinking to the bottom, hibernating by turions, e.g. *Ceratophyllum*, *Utricularia*, *Aldrovanda*.
8. Hydrocharids: pleustophytes floating freely on the water surface with specialized floating leaves; hibernating by gemmulae or sporocarps, e.g. *Hydrocharis*, *Salvinia natans*.
9. Stratiotids: freely floating pleustophytes with stiff radical leaves of which the upper parts rise above the water surface; in autumn sinking to the bottom, hibernating by turions, e.g. *Stratiotes*.
10. Lemnids: small pleustophytes, floating freely on the water surface, with reduced fronds, of which the upper side is adjusted to air metabolism and the under side to life in the water, e.g. *Spirodela*, *Wolffia*, *Lemna minor*, *Ricciocarpus natans*, *Azolla*.
11. Ricciellids: small, submerged, lanceolate, furcate or reticulate pleustophytes, without adaptations to air metabolism, e.g. *Riccia* subgen. *Ricciella*, *Lemna trisulca*.

There are a few species which can be classified into more than one basic type. *Elodea canadensis*, for example, is normally an elodeid but detached shoots may behave as ceratophyllids. These are able, however, to fix themselves again by adventitious roots. *Polygonum amphibium* occurs as a nymphaeid water form and as a normal terrestrial plant. The water form of *Hippuris vulgaris* is an elodeid, the land form an helophyte. The land forms of the batrachiids achieve their generative cycles as well as the water forms.

The subdivision of the water plants according to their growth forms is of great importance for phytocenology, as the diverse vegetation units are composed of plants with very specialized growth forms, of which mostly one dominates.

In other systems the water plants have not been treated so extensively. RAUNKIAER (1934) who classified the plants according to their adaptations to unfavourable periods in their life cycle, distinguished only one group as water plants, the hydrophytes. IVERSEN (1936) developed a system of "hydrotypes" in which the plants were classified according to their morphological adaptations to the factor water. The water plants were dealt with under the term "limnophytes", and these were subdivided according to the system of Du Rietz, but in less detail. Their definitions of hydrophyte and limnophyte have been treated already in § 2.

More interesting is the system of POPLAWSKAJA (1948) who divided the waterplants, called "limnophytes" by her, into three groups:

1. The hydatophytes, which have no adaptation to aerial life and achieve their generative cycle completely submerged.

2. The "submerged" aerohydatophytes, the vegetative parts of which are completely submerged and whose inflorescences rise above the water surface, where pollination takes place.

3. The "floating" aerohydatophytes, the vegetative parts of which are partly submerged and partly floating at the surface and whose inflorescences rise above the water surface.

For the plants which are submerged only for a small part, but which are mainly exposed to the air, the term "hydrophytes" is applied.

HEJNÝ (1957, 1960) elaborated a system for the water and marsh plants of the Danube valley in Czechoslovakia based on their ecological adaptations to the factor water. Although his subdivision of the water plants, as defined in § 2, is not very detailed, his system in its totality is of great importance for the cenological study of waters with a fluctuating water level. Three of Hejný's 10 ecological groups together comprise the water plants:

1. The euhydatophytes, of which the vegetative parts are completely adapted to water life, and of which the inflorescences are submerged or rise above the water surface. This group thus contains the hydatophytes and "submerged" aerohydatophytes in the sense of Poplawskaja.

2. The hydatoaerophytes, which are bound to the water, but whose vegetative parts come into contact with the air, resulting in specially adapted floating leaves, and whose inflorescences rise above the surface of the water. This group coincides with Poplawskaja's "floating" aerohydatophytes.

3. The tenagophytes, an heterogeneous group of amphibious plants characteristic for banks along waters with a strongly fluctuating level. Some of the species involved are able to achieve their

generative cycle when submerged, e.g. *Littorella uniflora, Pilularia globulifera* and *Callitriche palustris* (isoetids, batrachiids), and have to be regarded as true water plants, according to the definition in § 2. The other tenagophytes are ephemeràl summer annuals of the alliance *Nanocyperion flavescentis* Koch 1926, and tolerate submersion quite well, but only pass through their generative cycle when above water.

It is regrettable that Hejný has not given clear definitions of his ecological groups. One can obtain a good impression of the composition of these groups from his extensive descriptions, but for the application of his system in other regions more rigid definitions would be of great help.

4. Some remarks on earlier classifications of water-plant communities

Although it is by no means our intention to give here a complete review of the development of the cenological classification of the water-plant communities before we present our new system some remarks have to be made about the earlier systems. The development in the classification of water-plant communities is demonstrated strikingly by comparing the system of Braun–Blanquet and Tüxen (1943) with the recently published work of Lohmeyer c.s. (1962).

In 1943 Braun–Blanquet and Tüxen gave a survey of the higher syntaxonomic units of Central Europe. At that time the system of the water-plant communities was still in a high measure undeveloped and consisted of merely two classes. This can be seen from the following extract.

Class 4: POTAMETEA
- order: POTAMETALIA
  - alliance: *Potamion euro-sibiricum*
- order: ZOSTERETALIA
  - alliances: *Ruppion maritimae*
    Zosterion

Class 5: LITTORELLETEA
- order: LITTORELLETALIA
  - alliances: *Littorellion*
    Helodo-Sparganion

In the recent survey of Lohmeyer c.s. (1962) the system of the water-plant communities is more elaborated, as can be seen from the following extract.

Class 1: LEMNETEA
- order: LEMNETALIA
  - alliance: *Lemnion minoris*

Class 2: ZOSTERETEA MARINAE
order: ZOSTERETALIA MARINAE
alliance: *Zosterion marinae*

Class 17: RUPPIETEA MARITIMAE
order: RUPPIETALIA MARITIMAE
alliance: *Ruppion maritimae*

Class 18: POTAMETEA
order: POTAMETALIA
alliances: *Eu-Potamion*
Nymphaeion
Ranunculion fluitantis

Class 19: LITTORELLETEA
order: LITTORELLETALIA
alliances: *Sphagno-Utricularion*
Hypericion elodis
Littorellion

The two alliances of the *Zosteretalia* in the old system have been raised to the rank of classes, *Zosteretea* (PIGNATTI, 1953) and *Ruppietea* (J. TÜXEN, 1960). Further the *Lemna* communities have been removed from the *Potametea* and placed in an independent class *Lemnetea* (KOCH and TÜXEN, 1954), as was suggested already by GAMS (1941). The separation of the pleustic *Lemnetea* from the *Potametea* did not mean that a consistent separation of the water-plant communities into floating and fixed ones was carried out. The fundamental importance of such a separation escaped the attention of the "floristic syntaxonomists", although the communities of the fixed water plants and those of the floating ones have not a single species or even a genus in common in Europe. RÜBEL (1933) gave, however, in his enumeration of the plant communities of Switzerland a subdivision of the aquatic communities, according to the attachment to the substrate. His formation class "Submersiherbosa", which contains all aquatic plant communities, was split into three orders. His system is given below.

Formation class: SUBMERSIHERBOSA
Order: POTAMETALIA: communities of rhizophytes.
alliances: *Potamion eurosibiricum*
Littorellion
Characion
Nanocyperion flavescentis

Order: HYDROCHARITETALIA: communities of pleustophytes.
alliance: *Hydrocharition*

Order: ENCYONEMATETALIA: communities of haptophytes.
alliance: *Encyonemation*

These orders are largely identical with the groups of classes in our classification. The alliances in Rübel's system agree partly with units in the system of BRAUN–BLANQUET and TÜXEN (1943). Both systems have a *Potamion eurosibiricum* and a *Littorellion.* The system of Rübel contains, moreover, a *Charion* ("*Characion*"), an alliance that surprisingly is not given in the system of BRAUN–BLANQUET and TÜXEN (1943) nor in the system of LOHMEYER c.s. (1962). The *Hydrocharition* of RÜBEL (1933) does not coincide with the *Lemnetea* in the system of Lohmeyer c.s.; it has a much wider conception.

When the systems of BRAUN–BLANQUET and TÜXEN (1943) and of LOHMEYER c.s. (1962) are compared with that of RÜBEL (1933) it is apparent that the arrangement of the higher units has been carried out according to different basic principles. Rübel considered the structure of the vegetation to be the basic criterion for the subdivision into orders. The second criterion was the dominant growth form and was used for characterizing the alliances.

The guiding principle for classification in the other two systems is said to be the floristic composition of the communities. However, the ecology of the habitat seems to play in these systems quite an important part as the higher syntaxonomic units are arranged in a series which exactly coincides with the ecological series from the richest to the poorest waters, as is shown in Table 1.

TABLE 1

Relation between the arrangement of the higher phytocenological units of the floristic systems and the salt-content of the water.

BRAUN–BLANQUET and TÜXEN (1943)	LOHMEYER c.s. (1962)	salt-content
	Lemnetea	
Zosterion	Zosteretea	marine
Ruppion	Ruppietea	brackish
Potamion	Potametea	eutrophic fresh water
Littorellion	Littorelletea	oligo- or dystrophic fresh water

Although the systems of BRAUN–BLANQUET and TÜXEN (1943) and RÜBEL (1933) are based on different principles, both are logical and supplement each other. On the contrary the recent, more differentiated system of Lohmeyer c.s. shows some aesthetic faults. In the first place, it seems somewhat unbalanced, as a structural character, viz. the bond of the aquatic communities to the substrate, has been introduced as a criterion for classification but has not been applied consistently. The *Lemnetea* were recognized as a separate class, but the other pleustophytic units were not removed from the *Potametea.*

Secondly, this system has a completely unnecessary break in the arrangement. Lohmeyer c.s. arranged the classes according to the concept of the "sociological progression", and the entirety of the aquatic plant communities, which together form a natural formation of specialized life-form types, is thus interrupted. The *Lemnetea* and the *Zosteretea* are classed respectively as class 1 and 2, while the *Ruppietea*, *Potametea* and *Littorelletea* respectively are given as class 17, 18 and 19. The *Lemnetea*, indeed, show a very low organization, but we do not see why the *Ruppietea* have been classed so much higher in the progressive series than the *Zosteretea*. These classes are very similar in their structural as well as in their physiognomic build up.

We prefer an arrangement in which the classes of the aquatic plant communities are united into a formation, as had been proposed by RÜBEL (1933).

The system of BRAUN–BLANQUET and TÜXEN (1943) as well as that of RÜBEL (1933) have been followed by several authors. It has to be mentioned, however, that SOÓ (1957) and KÁRPÁTI (1963), who followed Rübel by subdividing the *Potametea* into the *Hydrocharetalia* and the *Potametalia*, did not use the division of the water plants in rhizo- and pleustophytes as the separating character between the two orders.

Our classification scheme (§ 6) can be regarded as a synthesis of the classification of Rübel and that of Braun–Blanquet and Tüxen. Our scheme is, however, more elaborate, as we used the growth-form spectrum of the vegetation as a new criterion for classification, and so achieved a finer subdivision.

5. CRITERIA FOR THE CLASSIFICATION OF WATER-PLANT COMMUNITIES

It is of paramount importance for the phytocenologist to realize that the ecological circumstances in the water greatly differ from those on the land. Ecological concepts that have been worked out for the land vegetation can not be used for the aquatic vegetation without first having been critically considered. Terrestrial plants root in the bottom, from which they take up their water and mineral nutrition, while photosynthesis, respiration and transpiration take place in the air. The water plants, however, are almost completely dependent on the aquatic medium for their metabolism. They obtain their mineral salts, their oxygen and their carbon dioxide direct from the water. The bottom is a substrate for attachment and is only for a limited number of species a second source of mineral requirements. Many species, genera and even some families have become completely independent of a substrate and float freely in the water.

Many water plants are adapted to a certain extent to aerial life. Some species have developed floating leaves of which the upper sides are adapted to air metabolism, but of which the under sides are only suitable for life in the water. Many of the aquatic phanerogams are dependent on the air for their sexual reproduction. Most species have anemophilous flowers (*Potamogeton*, *Myriophyllum*), but species with entomophilous flowers are also known (*Stratiotes*, *Hydrocharis*, *Egeria densa*). Further, there are species which make use of the surface tension of the water for their pollination mechanism (*Vallisneria*, *Hydrilla*, *Ruppia spiralis*, *Elodea canadensis*). The number of phanerogam species with completely submerged pollination is rather small (*Naias marina*, *Zostera*, *Ceratophyllum*).

When, however, aquatic plants become completely exposed to the air, e.g. in temporarily dry ditches and ponds, or when the water level of a water body is lowered, most of them die. Some species, however, remain alive for a short period as their subterranean parts are protected from desiccation; other species develop stunted land forms which are not able to flower. Only a few species are able to maintain themselves and to achieve their reproductive cycle on the land as well as in the water (*Callitriche*, *Ranunculus* subgen. *Batrachium*, *Polygonum amphibium*).

Water is an excellent agent for the dispersal of water plants. In running waters fruits, seeds, or vegetative parts of plants are transported in the direction of the stream. In stagnant waters transport of diaspores is less obvious but not less important. Wind often causes slow surface currents which may result in convection currents in deeper water layers. Further, these waters are subjected to the thermal circulation which in the large basins is an annual feature and in small ponds and ditches a daily feature, as a consequence of the diurnal course of temperature. As the specific gravity of the diaspores of water plants is generally lower than or roughly the same as that of water, transport can last a long time and bridge large distances. We may cite here the transport of sea-weeds by the sea currents (DEN HARTOG, 1959 a).

The special features of the aquatic medium are also expressed in the nutritive cycle of the aquatic communities. In fact they do not have a nutritive cycle but are a part of it. A body of water can contain many plant and animal communities, but these are all part of one nutritive cycle, which is characteristic for that water body. Terrestrial communities have an almost closed nutritive cycle, except for the ephemeral pioneer and weed communities on bare soil.

The differences between the terrestrial and the aquatic habitats have also their consequences for the classification of the aquatic plant communities. Criteria other than those used for the classification of the terrestrial communities have to be considered.

We have made use of several criteria for the classification of water-plant communities. Beside the floristic composition of the vegetation we have emphasized some structural characters such as attachment to the substrate and growth-form spectrum of the vegetation. Further, we have taken into account the ecological factors of paramount importance for the aquatic vegetation, such as light, chemical composition of the water, agitation of the water, fluctuations of the water-level and some other physical factors. These criteria are not all of the same importance for the classification. Some are decisive at the level of the classes, while others are only important at the level of the associations.

The most important criterion, from a floristic point of view, is no doubt that the communities of rhizophytes, of haptophytes and of pleustophytes are completely independent of each other; they have not a single species in common.

In places where solid substrates occur on sediment bottoms, e.g. stones mixed with sand on moraine bottoms, mixed vegetations of rhizophytes and haptophytes can develop. The physiognomy may give the impression of homogeneity, but nevertheless the haptophytes in such a vegetation are attached to the solid substrate, while the rhizophytes penetrate with their basal parts into the sediment. Such a mixed vegetation thus consists of 2 separate communities. An example is the *Fuceto-Furcellarietum*, described by KORNAŚ and MEDWECKA-KORNAŚ (1950) from the Bay of Gdansk. Later this unit has been split into the rhizophytic community *Zostero-Furcellarietum* and the haptophytic community *Fuco-Furcellarietum* s.s. (KORNAŚ, 1959).

Vegetations in which rhizophytes and pleustophytes coexist have to be regarded also as mixtures of two vegetation units, even when the vegetation at first glance seems to be homogeneous. Such vegetations may show either a stratification, e.g. a layer of pleustophytes superposed on a rhizophyte layer, or it can be a uniform mixture that can hardly be disentangled. In practice it appears that such mixed vegetations rarely occur. Where pleustophytes form a closed vegetation rhizophytes are sparse or do not occur at all, due to the interception of light by the pleustic layer and to the hampering of the gas exchange at the water surface. In a well-developed vegetation of rhizophytes the pleustophytes generally form only an extremely small portion, mostly having been "trapped" by the standing rhizophytic vegetation and so having become entangled.

The growth-form spectrum of the aquatic vegetation is highly important for the classification. As the diverse vegetation units are each dominated by one special growth form or by a determined combination of growth forms this character is of diagnostic value. The special properties of the aquatic environment increase the importance of the dominance of the growth forms as a criterion for classification, while the value of the floristic composition of the vegetation as a criterion is decreased. The relative homogeneity of the aquatic medium and the very effective dispersal of the water plants have an equalizing effect on the floristic composition of the vegetation units, particularly on those at the level of association. The faithful taxa often have only a limited value and are mostly preferential species, i.e. species which have a clear optimum under well-determined ecological circumstances, but are tolerant to less optimal circumstances to a considerable extent. Species exclusively bound to one association are rare amongst water plants, and their exclusiveness is often a local feature. Therefore, the floristic composition of the vegetation can not be used as a criterion for classification without considering the dominance and the growth-form spectrum of the vegetation, as these cause the differentiation in the vegetation, which enables us to distinguish several units.

Stratification of the terrestrial vegetation is an important criterion for its classification and is incomparable with the stratification found in the aquatic environment. The terrestrial communities are bound to the bottom, which is their only source for nutrition. The layers within these communities usually do not occur as independent vegetation units, but only as structural parts of a greater entirety. The bond between the water plants and the bottom, in contrast, is loose and in a number of cases is even absent, because the nutritive salts are obtained from the water itself. In some places the vegetation layers in the water can be completely independent of each other. This is not difficult to understand where floating vegetation layers are concerned, as these are shifted easily by wind and water currents. It can also happen that in a certain place the vegetation consists of two rhizophytic layers, which are independent or barely dependent on each other. Two examples will be given.

The *Myriophylleto-Nupharetum* KOCH 1926, an association composed of some large nymphaeids, elodeids and myriophyllids, covers the bottom to a very small degree, but at the water surface the percentage of covering is very high, owing to the large floating leaves of the nymphaeids. These intercept a great deal of the light. As a result of the reduced light and of the bareness of the bottom the Characeae, which generally form closed communities in deeper waters, are able to extend under the *Myriophylleto-Nupharetum* and to cover the bottom with a dense mat. Both communities occur also completely separated.

The monospecific community of *Vaucheria dichotoma*, forming extensive carpets on the bottoms of eutrophic fresh-water and oligohaline brackish-water ponds and ditches, is often the sub-layer of a community consisting of small elodeids, the roots of which are anchored in the algal carpet. The elodeid community can occur with exactly the same floristic composition without a sub-layer of *Vaucheria dichotoma*.

It appears that stratification in the aquatic environment generally is caused by the fact that a certain plant community is able to create ecological circumstances, which are favourable for the development of another community. The bond between the two layers of an aquatic vegetation is thus facultative and not obligate as in the terrestrial vegetation. For the aquatic plant communities, therefore, the idea has to be rejected that the diverse vegetation layers, which at a certain place are superposed upon each other, have to belong as a matter of course to one plant community.

From our considerations it appears that the water-plant communities have a very simple structure. They usually consist of one layer and are better characterized by the dominant species and the growth-form spectrum than by their floristic composition only. They do not have a nutritive cycle. They are the initial stages of the succession series. As a consequence of their low degree of organization they have to be classed near the beginning of the phytocoenological system.

6. Classification of water-plant communities

According to our ideas the European aquatic plant communities which are composed of rhizophytes and pleustophytes, have to be arranged in 9 classes. These classes have a wide distribution, as have the orders and alliances. To avoid confusion we have given as examples only associations which occur in the Netherlands. These associations will be described in a separate paper in the near future.

We have not classified the submerged *Vaucheria* communities, as these have not yet been sufficiently studied; their connection with the amphibious and terrestrial *Vaucheria* communities has first to be elucidated. Therefore, the solution proposed by Krausch (1964) to classify the *Vaucheria dichotoma* communities in the *Charetalia* can not be accepted.

Group A: Pleustic water-plant communities.

This group is identical with the order *Hydrocharitetalia* in the system of Rübel (1933).

The units composed of secondary pleustophytes have not been classified.

I. Class: LEMNETEA Koch and Tüxen 1954, apud Oberdorfer 1957.

A. Order: LEMNETALIA Koch and Tüxen 1954, apud Oberdorfer 1957.
Lowly organized water-plant communities consisting of lemnids and ricciellids, which can develop in extremely small bodies of water, and so are able to fill up the small gaps, which are left open in the vegetations of larger pleustophytes and rhizophytes. Two alliances can be distinguished.

1. Lemnion minoris Koch and Tüxen 1954, apud Oberdorfer 1957.
Communities of lemnids and hydrocharids at the surface of the water.
Faithful taxa: *Lemna minor*, *Spirodela*, *Wolffia*, *Azolla*.
The following associations have been recognized in the Netherlands:
a. *Wolffieto-Lemnetum gibbae* (Bennema 1946).
b. *Lemneto-Spirodeletum* Koch 1954.
c. *Ricciocarpeto-Lemnetum* Segal 1964.

2. Lemnion trisulcae all. nov.
Communities of ricciellids, floating freely in the water, often forming dense masses just below the water surface, but also occurring in deeper water layers, where they

may be loosely entangled between other pleustophytes or rhizophytes.
Faithful taxon: *Lemna trisulca.*
To this alliance belong in the Netherlands the following associations:

a. *Lemnetum trisulcae* (Den Hartog 1963).
b. *Riccietum fluitantis* (Slavnić 1956).

II. Class: CERATOPHYLLETEA cl. nov.

A. Order: CERATOPHYLLETALIA ord. nov.

Lowly organized communities of submerged flowering ceratophyllids, which float in the uppermost water layers in spring and summer, but sink to the bottom in the autumn. The plants form by vegetative propagation thick masses, which can fill up a body of water completely from the water surface to the bottom, reaching their optimum in small, stagnant, eutrophic ponds and ditches.
Faithful taxon: *Ceratophyllum.*
Only one alliance:

1. Ceratophyllion all. nov.

In the Netherlands this alliance is represented by two associations:

a. *Ceratophylletum demersi* ass. nov.
b. *Ceratophylletum submersi* ass. nov.

Note: The *Ceratophyllum* species often occur as companion species in other water-plant communities, because these stiff, free floating plants are easily entangled between the standing rhizophytes, and then form with them an almost inextricable whole.

III. Class: UTRICULARIETEA cl. nov.

A. Order: UTRICULARIETALIA ord. nov.

Lowly organized communities of ceratophyllids whose inflorescences rise above the water surface. In spring and summer they float in the uppermost water layers forming by vegetative propagation dense carpets, but in autumn they sink to the bottom. Some species may be loosely stuck in the mud with pale mud sprouts. When the communities consist of more than one species they often occur in separate layers. In stagnant, meso-, oligo- and dystrophic waters, in ponds as well as in depressions in reed- and sedge-marshes. The communities often form a structural entirety together with a carpet of water forms of *Sphagnum.*
Faithful taxon: *Utricularia*[1]), in particular *U. minor.*

---

[1]) In the tropics many terrestrial *Utricularia* species occur.

Only one alliance:

1. Utricularion all. nov.

In the Netherlands the following associations occur:

a. *Utricularietum minoris-intermediae* ass. nov.

b. *Utricularietum neglectae* (Müller and Görs 1960).

Note: For such mixed vegetations of *Utricularia* species and water forms of *Sphagnum* MÜLLER and GÖRS (1960) erected the *Sphagno-Utricularion*, which was placed in the *Littorelletea*. The aquatic *Sphagnum* species have to be regarded more as pleustophytes than as rhizophytes, because they form a layer which may float freely in the water, sometimes close to or at the surface. It also happens that they form a bottom layer on very soft organic mud. As the *Sphagnum* species can not achieve their generative cycle in the aquatic habitat they are not true water plants. Therefore, the *Sphagno-Utricularion* can not be maintained.

IV. Class: STRATIOTETEA cl. nov.

A. Order: STRATIOTETALIA ord. nov.

Closed communities with rather high organization, composed of stratiotids, hydrocharids and ceratophyllids the inflorescences of which rise above the water surface. During spring and summer the plants occur in the uppermost water layer, but in the autumn they sink to the bottom where they decay. Hibernation takes place by means of turions and gemmulae. Forming extensive vegetations at the surface of small, eutrophic stagnant waters and in shallow bights of broads and lakes, sheltered from wind and wave action. As a consequence of the accumulation on the bottom of great quantities of vegetable debris, these pleustophyte communities are able to convert a body of water into a swampy area in a rather short time; this development is often started by the appearance of pleustohelophytes and helophytes.

Faithful taxon: *Stratiotes aloides*.

Only one alliance:

1. Stratiotion all. nov.

In the Netherlands it is represented by one association:

a. *Hydrochareto-Stratiotetum* (Van Langendonck 1935) Westhoff 1942.

Group B: Communities of rhizophytic water plants.

V. Class: CHARETEA Fukarek 1961.

A. Order: CHARETALIA Sauer 1937.

Communities, mainly composed of Charophyta, occurring in stagnant oligo-, meso- and eutrophic fresh water as well as in stagnant oligo- and mesohaline brackish water. Mostly on sandy bottoms, but also on fine, muddy substrates. The depth of occurrence is dependent to a high degree on the clarity of the water, and is in the Netherlands rarely deeper than 4-5 m. Often these communities form a subgrowth under other aquatic plant communities.

Faithful taxa: Charophyta with a few exceptions.

We have distinguished provisionally only one alliance:

1. Charion Rübel 1933.

   The communities belonging to this alliance have been scarcely investigated in the Netherlands. The following units have to be placed in the *Charion*:

   a. Community of *Naias marina* and *Nitellopsis obtusa* Westhoff 1949.
   b. *Chara hispida* sociation Westhoff 1949.

Note: As the *Charetalia* occur in all types of stagnant water ranging from oligotrophic fresh water to mesohaline brackish water it certainly will be possible to recognize more than one alliance. Recently, KRAUSCH (1964) has divided the *Charetalia* into two alliances, viz. the Charion fragilis Krausch 1964 or *Limno-Charion*, which comprises the Charophyceae communities of the fresh water and to which belong the two communities described by WESTHOFF (1949), and the Charion canescentis Krausch 1964 or *Halo-Charion*, in which the Charophyceae associations of the brackish water are taken together.

Krausch regarded several stoneworts as not belonging in the class *Charetea*. So he placed *Nitella translucens*, *N. gracilis*, *N. batrachosperma* and with some doubt a few other species in the *Littorellion*. Although *Nitella* species may occur in associations of the latter alliance their optimum and greatest abundance is in deeper water, where they form closed communities of their own. They represent probably a separate alliance.

VI. Class: ZOSTERETEA (Pignatti 1953).

A. Order: ZOSTERETALIA (Béguinot 1941).

Sea-grass communities, in sea water and the polyhaline section of estuaries along the coasts of the temperate zone, in the northern as well as in the southern hemisphere.

Faithful taxon: *Zostera*.

In the Netherlands only one alliance:

1. Zosterion (Christiansen 1934).

   Boreo-atlantic communities in the marine coastal waters, penetrating into the mesohalinicum in the Baltic Sea.

   Faithful taxon: *Zostera marina*.

   In the Netherlands the alliance is represented by two associations:

   a. *Zosteretum marinae* (Børgesen 1905).
   b. *Zosteretum nano-stenophyllae* Den Hartog 1958.

VII. Class: RUPPIETEA (J. Tüxen 1960).

A. Order: RUPPIETALIA (J. Tüxen 1960).

Communities, poor in species, in poikilohaline salt waters along the coast as well as in continental salt lakes, where the principal salts are sodium chlorine, gypsum or magnesium sulphate. Cosmopolitic distribution.

Faithful taxon: *Ruppia*.

Up to now only one alliance has been recognized:

1. Ruppion maritimae (Braun-Blanquet 1931). Communities of blocked brackish waters (lagoons, saltpans, embanked creeks, "inlagen", ditches and ponds) with a large salinity range, the maximum of which may be well above the salinity of the sea. The ecological circumstances in continental salt waters are comparable with those prevailing in the blocked brackish waters. In large brackish waters with an almost constant salinity they occur only in localities where the hydrographic conditions show a certain instability, for example, in the neighbourhood of river mouths or where upwelling of ground water takes place. In waters subjected to tidal movements communities of this alliance can only develop when the tidal difference is rather small.

   In the Netherlands the *Ruppion* is represented by two associations:

   a. *Ruppietum spiralis* (Iversen 1936).
   b. *Potameto-Zannichellietum pedicellatae* Den Hartog 1958.

Note: We quite agree with the idea of J. Tüxen (1960) that the *Ruppion* and the *Zosterion* can not be classified into one order *Zosteretalia*, but that they have to be placed each in a separate class, on the grounds of their floristic and ecological differences. The *Zosteretea* form a class of marine plant communities which are able to penetrate into the brackish water to some degree. The *Ruppietea*, in contrast, are neither marine nor maritime but are dependent in the first place on the degree of instability of the salt-content, and it is of no consequence to them whether sodium chlorine, sodium sulphate or magnesium sulphate is the principal salt. In the coastal area communities belonging to both classes can show some overlap under certain circumstances, resulting in mixed vegetations. Overlapping between *Ruppia* communities and units of the *Potametea* and the *Charetea* occurs as well. We disagree, however, with J. Tüxen in the delimitation of the *Ruppion maritimae*, *Ruppietalia* and *Ruppietea*, as his concept of these units is obviously based on the circumstances prevailing in the Baltic Sea. There the salinity fluctuations are relatively small, and as a result the *Ruppion* is only locally well-developed. Mostly it is mixed with salt-tolerant fresh-water species, e.g. *Zannichellia palustris* ssp. *pedicellata*, *Ranunculus baudotii*, *Potamogeton pectinatus* and *Myriophyllum spicatum*, sometimes also with the euryhaline *Zostera marina*. It is apparent from the faithful taxa, recorded by J. Tüxen, that his *Ruppion* is indeed a very heterogeneous unit. Beside a true *Ruppion* association, the *Ruppietum spiralis* [1]), he also placed in this alliance a brackish-water association of the *Charion*, the *Chareto-Tolypelletum* Kornaš 1948, and the *Eleocharetum parvulae* (Christiansen 1934) Gillner 1960, an association which because of its life-form spectrum can not be maintained in the *Ruppion*. Further we think that a unit of the *Callitricho-Batrachion* was also included in his *Ruppion* as J. Tüxen gave *Ranunculus baudotii* as a faithful taxon for the latter. Our concept of the *Ruppion* is considerably stricter. It is not used as a collective name for the heterogeneous assemblage of plant communities of the brackish water.

VIII. Class: POTAMETEA Tüxen and Preising 1942.

Communities, mainly consisting of elodeids, myriophyllids, ba-

[1]) It is remarkable, that J. Tüxen did not mention *Ruppia spiralis* as a faithful taxon for the *Ruppion maritimae*.

trachiids and nymphaeids in fresh and slightly brackish water.
Faithful taxa: *Potamogeton pectinatus*, *P. natans*, *Myriophyllum spicatum*.

A. Order: MAGNOPOTAMETALIA ord. nov.

Communities of large elodeids and nymphaeids, rooting in deep, eutrophic and mesotrophic water.

Faithful taxa: *Potamogeton lucens*, *P. perfoliatus*.

Two alliances can be distinguished:

1. Magnopotamion (Vollmar 1947).

   Communities of large species of *Potamogeton* and some other elodeids, rooting at a depth of 1-5 m in open water, exposed to wind and wave action.

   Faithful taxa: *Potamogeton praelongus*, *P. zizii*.

   Not uncommon in the Netherlands, where it occurs with two associations:

   a. *Potametum lucentis* Hueck 1931.
   b. *Potametum pectinato-perfoliati* ass. nov.

2. Nymphaeion albae Oberdorfer 1957.

   Communities of large nymphaeids, in which also large elodeids may play an important part. In water, 1-3 m deep, in canals and bights of broads and lakes, sheltered from wind and wave action.

   Faithful taxa: *Nymphaea alba*, *Nuphar luteum*, *Nymphoides peltata*, *Polygonum amphibium* f. *natans*.

   In the Netherlands this alliance is represented by 2 associations:

   a. *Myriophylleto-Nupharetum* Koch 1926 (inclusive *Potameto-Nupharetum* Müller and Görs 1960).
   b. *Nymphoidetum peltatae* (Allorge 1922) Oberdorfer and Müller 1960.

B. Order: PARVOPOTAMETALIA ord. nov.

Communities of small elodeids, myriophyllids and batrachiids in shallow, meso- and eutrophic and oligohaline waters.

Faithful taxa: *Potamogeton crispus*, *P. pusillus*, *P. berchtoldii*, *Elodea canadensis*, *E. nuttallii*, *Zannichellia palustris*.

Two alliances can be distinguished:

1. Parvopotamion (Vollmar 1947).

   Communities of small elodeids and a few myriophyllids in stagnant, shallow waters of small dimensions, such as ditches and pools.

   Faithful taxa: *Potamogeton* sect. *Graminifolii*, *Ranunculus circinatus*.

Very common in the Netherlands, and represented by several associations:

a. *Ranunculeto-Potametum compressi* Bennema and Westhoff 1943.
b. *Parvopotameto-Zannichellietum* Koch 1926.
c. some still unpublished units.

2. Callitricho-Batrachion all. nov.
Communities composed mainly of batrachiids, some elodeids and some myriophyllids, in very shallow and often temporarily dry water-courses, ditches, drinking pools for cattle, upwellings along dikes and dunes, rivulets, small rivers and high-littoral tidal creeklets in the infrahaline section of estuaries.

Faithful taxa: *Ranunculus* subgen. *Batrachium*, in particular *R. aquatilis*, *Callitriche* sect. *Callitriche*, in particular *C. hamulata*.

In the Netherlands the alliance occurs with several associations:

a. *Callitricheto-Ranunculetum baudotii* Den Hartog 1963.
b. *Hottonietum palustris* Tüxen 1937.
c. *Ranunculetum fluitantis* Allorge 1922.
d. some still unpublished units.

Note: The amphibious water-plant communities show a striking agreement in the occurrence of water crowfeet. *Ranunculus ololeucos* seems to occur in the *Littorellion* (*Eleocharetum multicaulis*). *R. omiophyllus* (= *R. lenormandi*) is the faithful species for a poor association, the *Ranunculetum lenormandii* Braun–Blanquet and Tüxen 1952, which was placed in the *Hypericion elodis* by Müller and Görs (1960), but in fact is an association of the *Potamion polygonifolii*. *R. aquatilis*, *R. baudotii* and *R. fluitans* are characteristic for the *Callitricho-Batrachion*. *R. baudotii* occurs in stagnant to slowly flowing water in the coastal areas, while *R. fluitans* is a leading species in the running water of rivulets and small rivers. *R. hederareus* occurs in the *Ranunculetum hederacei* (Tüxen and Diemont 1936) Libbert 1940, an association usually placed in the *Cardamineto-Montion*, the alliance of the spring and spring-brook communities (Tüxen and Jahns, 1962), but which fits even better in the *Callitricho-Batrachion*.

A second point of agreement exists in the occurrence of water starworts in the amphibious communities. In the *Callitricho-Batrachion*, *Callitriche hamulata*, *C. platycarpa*, *C. obtusangula*, *C. cophocarpa* and *C. stagnalis* occur. The last-mentioned species occurs also in various wet, often disturbed habitats, the vegetations of which show affinity to the *Bidention tripartiti* Nordhagen 1940, and it coexists with *C. palustris* also in the *Montio-Cardaminetalia* and the *Nanocyperion flavescentis*. Moreover, the genera *Montia* and *Callitriche* show a clear resemblance in growth form.

These similarities could be of interest, when we come to consider the place of the *Montio-Cardaminetalia* with regard to the system of the water-plant communities.

The Ranunculion fluitantis Neuhäusl 1959, which comprises the plant communities of fast running waters, fits quite well into the *Callitricho-Batrachion* on the grounds of its floristic composition, life-form spectrum and ecology. Therefore, it can not be maintained as an independent alliance, but must be regarded as a suballiance. A second suballiance, the Hottonion suball. nov. may be distinguished for the vegetations of upwellings along dikes and dunes, which are characterized by the abundant occurrence of *Hottonia palustris* in particular.

C. Order: LURONIO-POTAMETALIA ord. nov.

Communities of elodeids and small nymphaeids, in small to rather extensive, shallow, oligo-, meso- and dystrophic waters. It is noteworthy that these communities contain several facultative nymphaeids, which show a tendency to the batrachiid type (*Potamogeton polygonifolius*, *P. gramineus*, *P. alpinus*).

In the past the communities of this order were often placed in the *Littorelletea*, but on the grounds of the completely different life-form spectrum, as well as the almost total absence of isoetids, they correspond better with the *Potametea*. From a floristic point of view the order is extremely well characterized.

Faithful taxa: *Potamogeton polygonifolius*, *P. gramineus*, *Sparganium minimum*, *Luronium natans*, *Myriophyllum alterniflorum*, *Ranunculus omiophyllus*.

Only one alliance:

1. Potamion polygonifolii all. nov.

   In the Netherlands the following associations belong to this alliance:

   a. *Myriophylletum alterniflori* Lemée 1937.
   b. *Potametum panormitano-graminei* Koch 1926.
   c. *Sparganietum minimi* (Schaaf 1925).

IX. Class: LITTORELLETEA (Braun-Blanquet and Tüxen 1943).

A. Order: LITTORELLETALIA (Koch 1926).

Amphibious plant communities, consisting mainly of isoetids, in oligo-, meso- and dystrophic waters with a considerably fluctuating water-level.

Faithful taxa: *Littorella uniflora*, *Eleocharis acicularis*, *Elatine hexandra*, *Subularia aquatica*, *Isoetes lacustris*, *I. tenella*, *Pilularia globulifera*, *Apium inundatum*.

In the Netherlands only one alliance:

1. Littorellion uniflorae (Koch 1926).

   In the Netherlands the following associations have been recognized:

   a. *Isoeteto-Lobelietum* Tüxen 1937.
   b. *Pilularietum globuliferae* Tüxen 1955.
   c. *Samoleto-Littorelletum* Westhoff 1943.

Note: Some of the species mentioned in the literature as faithful for the *Littorellion* are not true water plants, e.g. *Hypericum elodes*, *Eleocharis multicaulis*. *Echinodorus ranunculoides*, *E. repens*, *Deschampsia setacea*, *Juncus bulbosus* and *Scirpus fluitans*. These species belong to a rather exclusive group of perennials which are limited to the banks of oligo-, meso- and dystrophic waters, where they are subjected to the fluctuations of the water-level. They tolerate submersion for a considerable part of their life, but their generative cycle is achieved during the period of emergence. Although this remarkable species assemblage occurs often intermingled with the amphibious but true aquatic plant communities of the *Littorellion* and the *Potamion polygonifolii*, it has to be regarded as an independent vegetation unit with a very strict ecological range, the Hypericion elodis Müller and Görs 1960. The associations of this rather cryptic alliance have not yet been disentangled from the intricate pattern of vegetation units which coexist with it, viz. aquatic communities at its lower border, the invading terrestrial communities at its upper border and, moreover, the ephemeral communities of summer annuals of the *Nanocyperion* which may develop during the period of emergence.

The *Hypericion elodis* is in several respects the counterpart of the *Agropyro-Rumicion* Nordhagen 1940 (sensu VAN LEEUWEN, 1958) in poor environments. In the first place it inhabits the transition area between the two contrasting regimes of the aquatic and the terrestrial environments. Secondly, it is subjected to the disturbing effect of the changes in the environment, as a consequence of the periodic and episodic fluctuations of the water-level, and thirdly, it occurs more or less disguised between other vegetation units.

MÜLLER and GÖRS (1960) classified the *Hypericion elodis* as an alliance of the *Littorelletalia*, but this seems unjustified, as the alliance consists of amphibious terrestrial plants and not of aquatic plants. We prefer to have the syntaxonomic position of the alliance undecided for the time being, until more is known about its floristic composition and its affinities to other vegetation units.

Group C: Communities of haptophytic water plants.

To this group belong the epilithic algal and lichen communities, the algal communities on the stems and leaves of water plants and helophytes, and some associations of aquatic musci and liverworts.

The epilithic algal communities of the Dutch coast have been described extensively by DEN HARTOG (1959a). The haptophytic communities of the brackish and fresh water in the Netherlands have not been studied so methodically; they have been treated in a few publications (BARKMAN, 1947, 1953; VON HÜBSCHMANN, 1953; DEN HARTOG, 1958b, 1959b), but a general survey of these communities has yet to be carried out.

ACKNOWLEDGEMENT

We are much indebted to Dr. V. Westhoff for his valuable advice and for his help towards a synthesis.

REFERENCES

ALLORGE, P. 1922. Les associations végétales du Vexin français. Thesis, Paris.

ARBER, A. 1920. Water plants, a study of aquatic angiosperms. Cambridge, I–XVI + 436 p.

BARKMAN, J. J. 1947. Mosgezelschappen aan meeroevers. De Levende Natuur **50**: 80–83.

———. 1953. Over de mosvegetatie van onze getijdengrienden. Buxbaumia **7**: 42–49 (mimeographed).

BEEFTINK, W. G. 1962. Conspectus of the phanerogamic salt-plant communities in the Netherlands. Biol. Jb. Dodonaea **30**: 325–362.

BÉGUINOT, A. 1941. La vita della piante vasculari. La Laguna di Venezia **3**, 2: 1–369.

BENNEMA, J., G. SISSINGH and V. WESTHOFF. 1943. Waterplantengemeenschappen in Nederland. 12 p. (mimeographed).

BØRGESEN, F. 1905. The algae vegetation of the Faeröese coasts, with remarks on the phyto-geography. Bot. Faeröes **2**: 683–834.

Braun-Blanquet, J. 1951. Pflanzensoziologie. 2nd ed. Vienna. 631 p.
——— and R. Tüxen. 1943. Übersicht der höheren Vegetationseinheiten Mitteleuropas. Comm. S.I.G.M.A. **84**, Montpellier. 11 p.
——— and ———. 1952. Irische Pflanzengesellschaften. Veröff. Geobot. Inst. Rübel **25**: 224–415.
Carstensen, U. 1955. Laichkrautgesellschaften an Kleingewässern Schleswig-Holsteins. Schrift. naturw. Ver. Schleswig-Holstein **27**: 144–170.
Cederkreutz, C. 1947. Die Gefässpflanzenvegetation der Seen auf Aland. Act. Bot. Fenn. **38**: 1–77.
Christiansen, W. 1934. Das pflanzengeographische und soziologische Verhalten der Salzpflanzen mit besonderer Berücksichtigung von Schleswig-Holstein. Beitr. Biol. Pfl. **22**: 139–154.
Donselaar, J. van, *c.s.* 1961. On the ecology of plant species and plant communities in former river beds. Wentia **5**, 258 p.
Freitag, H., C.-M. Markus and I. Schwippl. 1958. Die Wasser- und Sumpfpflanzengesellschaften in Magdeburger Urstromtal südlich des Fläming (Elbe–Elster Gebiet um Torgau und Herzberg). Wiss. Z. pädagog. Hochsch. Potsdam **4**: 65–92.
Fukarek, F. 1961. Die Vegetation des Darss und ihre Geschichte. Pflanzensoziologie **12**.
Gams, H. 1941. Über neue Beiträge zur Vegetationssystematik unter besonderer Berücksichtigung des floristischen Systems von Braun-Blanquet. Bot. Arch. **42**: 201–238.
Gessner, F. 1955. Hydrobotanik I, 517 p.; 1959, idem II, 701 p. Berlin.
Gillner, V. 1960. Vegetations- und Standortsuntersuchungen in den Strandwiesen der schwedischen Westküste. Act. Phytogeogr. Suec. **43**: 1–198.
Goor, A. C. J. van. 1921. Die Zostera-Assoziation des holländischen Wattenmeeres. Rec. Trav. Bot. Néerl. **18**: 103–123.
Harmsen, G. W. 1936. Systematische Beobachtungen der nordwest-europaeischen Seegrasformen. Ned. Kruidk. Arch. **46**: 852–877.
Hartog, C. den. 1955. A classification system for the epilithic algal communities of the Netherlands' coast. Act. Bot. Neerl. **4**: 126–135.
———. 1958a. De vegetatie van het Balgzand en de oeverterreinen van het Balgkanaal. Wetensch. Meded. K.N.N.V. **27**: 1–28.
———. 1958b. Epilithische algengemeenschappen in Nederland. Hand. Hydrobiol. Ver. **10**: 6–8.
———. 1959a. The epilithic algal communities occurring along the coast of the Netherlands. Wentia **1**: 1–241.
———. 1959b. The Batrachospermeto-Chaetophoretum, a remarkable algal association in the Netherlands. Act. Bot. Neerl. **8**: 247–256.
———. 1963. Enige waterplantengemeenschappen in Zeeland. Gorteria **1**: 155–164.
———. 1964. Typologie des Brackwassers. Helgoländer Wiss. Meeresunt. **10** (in press).
Hejný, S. 1957. Ein Beitrag zur ökologischen Gliederung der Makrophyten der tschechoslowakischen Niederungsgewässer. Preslia **29**: 349–368.
———. 1960. Ökologische Characteristik der Wasser- und Sumpfpflanzen in den slowakischen Tiefebenen (Donau- und Theissgebiet). Bratislava, 487 p.
Hübschmann, A. von. 1953. Einige hygro- und hydrophile Moosgesellschaften Norddeutschlands. Mitt. Flor.-soz. Arbeitsgem. **4**: 15–25.
Hueck, K. 1931. Erläuterungen zur vegetationskundlichen Karte des Endmoränengebietes von Chorin (Uckermark). Beitr. z. Naturdenkmalpflege **14**: 105–214.
Iversen, J. 1936. Biologische Pflanzentypen als Hilfsmittel in der Vegetationsforschung. Thesis, Copenhagen, 224 p.
Kaaret, P. 1953. Wasservegetation der Seen Orlången und Trehörningen. Act. Phytogeogr. Suec. **32**: 1–50.
Kárpáti, V. 1963. Die zönologischen und ökologischen Verhältnisse der Wasservegetation des Donau-Überschwemmungsraumes in Ungarn. Act. Bot. Acad. Sc. Hungar. **9**: 323–385.

KOCH, W. 1926. Die Vegetationseinheiten der Linthebene. Jb. St Gallen Naturw. Ges. **61**, no 2: 1–146.

————. 1954. Pflanzensoziologische Skizzen aus den Reisfeldgebieten des Piemont (Po-Ebene). Vegetatio **5–6**: 487–493.

KORNAŚ, J. 1959. Sea bottom vegetation of the Bay of Gdańsk off Rewa. Bull. Acad. Polon. Sc. Cl. 2, **7**: 5–10.

———— and A. MEDWECKA–KORNAŚ. 1950. Associations végétales sous-marines dans le Golfe de Gdańsk. Vegetatio **2**: 120–127.

————, E. PANCER and B. BRZYSKI. 1960. Studies on sea-bottom vegetation in the Bay of Gdańsk off Rewa. Fragm. Flor. Geobot. **6**: 3–92.

KRAUSCH, H.–D. 1964. Die Pflanzengesellschaften des Stechlinsee-Gebietes I. Die Gesellschaften des offenen Wassers. Limnologica **2**: 145–203.

LANGENDONCK, H. J. VAN. 1935. Étude sur la flore et la végétation des environs de Gand. Bull. Soc. Roy. Bot. Belgique **68**: 117–180.

LEEUWEN, CHR. G. VAN, 1958. Enige opmerkingen over het Agropyro-Rumicion crispi Nordh. 40 in Nederland. Corresp.bl. Flor. Vegetatieonderz. Nederland no. **11**: 117–123 (mimeographed).

LEMÉE, G. 1937. Recherches écologiques sur la végétation du Perche. Thesis, Paris.

LIBBERT, W. 1940. Pflanzensoziologische Beobachtungen während einer Reise durch Schleswig–Holstein in Juli 1939. Feddes Rep. Beih. **121**: 92–130.

LOHMEYER, W., *c.s.* 1962. Contribution à l'unification du système phytosociologique pour l'Europe moyenne et nord-occidentale. Melhoramento **15**: 137–151.

LUTHER, H. 1949. Vorschlag zu einer ökologischen Grundeinteilung der Hydrophyten. Act. Bot. Fenn. **44**: 1–15.

————. 1951. Verbreitung und Ökologie der höheren Wasserpflanzen im Brackwasser der Ekenäs-Gegend in Südfinnland I–II. Act. Bot. Fenn. **49**: 1–231, **50**: 1–370.

MAAS, F. M. 1959. Bronnen, bronbeken en bronbossen van Nederland, in het bijzonder die van de Veluwezoom. Thesis, Wageningen, 166 p.

MIYAWAKI, A. and J. TÜXEN. 1960. Über Lemnetea-Gesellschaften in Europa und Japan. Mitt. Flor.-soz. Arbeitsgem. **8**: 127–135.

MÜLLER, TH. 1962. Die Fluthahnenfussgesellschaften unserer Fliessgewässer. Veröff. Landesstelle f. Naturschutz und Landschaftspflege Baden–Württemberg **30**: 152–163.

———— and S. GÖRS. 1960. Pflanzengesellschaften stehender Gewässer in Baden–Württemberg. Beitr. naturk. Forsch. südwestdeutschl. **19**: 60–100.

NEUHÄUSL, R. 1959. Die Pflanzengesellschaften des südostlichen Teiles des Wittingauer Beckens. Preslia **31**: 115–147.

NORDHAGEN, R. 1940. Studien über die maritime Vegetation Norwegens I. Die Pflanzengesellschaften der Tangwälle. Bergens Mus. Årb. 1939/40 ser. 2, 123 p.

OBERDORFER, E. 1957. Süddeutsche Pflanzengesellschaften. Pflanzensoziologie **10**: 564 p.

————. 1962. Pflanzensoziologische Exkursionsflora für Süddeutschland. 2nd ed. Stuttgart. 987 p.

PIGNATTI, S. 1953. Introduzione allo studio fitosociologico della pianura Veneta orientale con particolare riguardo alla vegetazion litoranea. Atti ser. 5, **11**: 92–258.

POPLAVSKAJA, G. I. 1948. Ekologija rastenij, Sov. nauka, Moscow, 295 p. (in Russian).

RAUNKIAER, C. 1934. The life forms of plants and statistical plant geography. Oxford, 632 p.

RIETZ, E. G. DU. 1921. Zur methodologischen Grundlage der modernen Pflanzensoziologie. Thesis, Uppsala, 272 p.

————. 1930. Vegetationsforschung auf soziationsanalytischer Grundlage. Abderhalden. Handb. biol. Arbeitsmeth. **11**, part 5: 293–480.

————, *c.s.* 1939. Zur Kenntnis der Vegetation des Sees Tåkern. Act. Phytogeogr. Suec. **12**: 1–65.

RÜBEL, E. 1933. Versuch einer Übersicht über die Pflanzengesellschaften der Schweiz. Ber. Geobot. Forsch. inst. Rübel. Zürich, 1932: 19–30.

SAUER, F. 1937. Die Makrophytenvegetation ostholsteinischer Seen und Teiche. Arch. f. Hydrobiol. Suppl. **6**: 431–592.

SCHAAF, G. 1925. Hohenloher Moore. Veröff. staatl. Stelle Naturschutz. **1**.

SCHIMPER, A. F. W. and F. C. VON FABER. 1935. Pflanzengeographie auf physiologischer Grundlage, 3rd ed., vol. 2, 1612 p.

SEGAL, S. 1964. Een vegetatiekundige schets van de moerasvegetaties in de „Landen achter het Singel" te Wanneperveen en Zwartsluis (Noordwest-Overijssel). R.I.V.O.N. report, 27 p. (mimeographed).

SLAVNIĆ, Ž. 1956. Vodena i barska vegetacija Vojvodine. Zbornik Matice Srpske **10**: 5–72.

SOÓ, R. 1957. Systematische Übersicht der pannonischen Pflanzengesellschaften I. Act. Bot. Acad. Sc. Hungar. **3**: 317–373.

TÜXEN, J. 1960. Zur systematischen Stellung des Ruppion-Verbandes. Mitt. Flor.-soz. Arbeitsgem. **8**: 180.

TÜXEN, R. 1937. Die Pflanzengesellschaften Nordwestdeutschlands. Mitt. Flor.-soz. Arbeitsgem. Niedersachsen **3**: 1–170.

————. 1955. Das System der Nordwestdeutschen Pflanzengesellschaften. Mitt. Flor.-soz. Arbeitsgem. **5**: 155–176.

———— and W. JAHNS. 1962. Ranunculus hederaceus und Corydalis claviculata im Gebiet der Mittel-Weser. Mitt. Flor.-soz. Arbeitsgem. **9**: 20–25.

———— and E. OBERDORFER. 1958. Eurosibirische Phanerogamen-Gesellschaften Spaniens. Veröff. Geobot. Inst. Rübel **32**: 1–328.

———— and E. PREISING. 1942. Grundbegriffe und Methoden zum Studium der Wasser- und Sumpfpflanzengesellschaften. Deutsche Wasserwirtschaft **37**: 10–17, 57–69.

VLIEGER, J. and G. KRUSEMAN. 1937. Plantensociologische aanteekeningen in de omgeving van Blokzijl. Ned. Kruidk. Arch. **47**: 374–389.

VOLLMAR, F. 1947. Die Pflanzengesellschaften des Murnauer Moores, Teil I. Ber. Bayerischen Bot. Ges. Erforsch. heim. Flora **27**: 13–97.

WESTHOFF, V. 1943. Plantensociologisch onderzoek, in het bijzonder op de Wadden-eilanden. Hand. 29ste Ned. Natuur-geneesk. Congres: 27–41.

————. 1947. The vegetation of dunes and salt-marshes on the Dutch islands of Terschelling, Vlieland and Texel. Thesis, Utrecht, 131 p.

————. 1949. Landschap, flora en vegetatie van de Botshol nabij Abcoude. Baambrugge, 102 p.

————, *c.s.* 1942. Overzicht der plantengemeenschappen in Nederland. 1st ed. 's-Graveland, 79 p.

————, *c.s.* 1946. Idem, 2nd ed. Amsterdam, 118 p.