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ON THE CLASSIFICATION OF AQUATIC PLANT COMMUNITIES

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It is probably generally recognised that the classification of aquatic, and to a less degree of marsh, plant communities, is at present in a most confused condition, due partly to our ignorance of the factors controlling them, and partly to the variability and number of the conditions which affect aquatic vegetation. Many of the latter are, indeed, still under debate, and until they have been decided, any classification must remain, in parts at least, provisional.

TYPES OF CLASSIFICATION

At present, three chief methods of classification have been put forward.

(a) Warming (**24**, p. 180) classifies aquatic plants in accordance with their *growth form*. He distinguishes, among others, such vegetative types as the Elodioid (e.g., *Elodea canadensis, Potamogeton pusillus*), the Rosette (e.g., *Isoetes lacustris, Litorella lacustris*), and the Nymphaea (e.g., *Castalia alba, Nymphaea lutea*) types. The recognition this classification gives to the importance of life form is of great value, but at the same time it fails to take into account the wide range of habitats in which different members of the same growth form may be found.

(b) In *Types of British Vegetation* (**21**, p. 188) emphasis is laid on the importance of the *habitat* factor—to the partial exclusion of the life form—as a basis of classification. The sub-formation of waters relatively poor in mineral salts is provisionally distinguished from that of waters relatively rich in mineral salts. It is by no means certain, however, that variation in the amount of dissolved salts is the chief factor controlling aquatic vegetation. This point may be left for further discussion.

(c) Lastly, in the account of the Norfolk Broads contributed by Miss Marietta Pallis to the same work (**12**, p. 214), where the relation between successive plant communities is described—the method of regarding aquatic and fen communities as part of one succession has been applied to British vegetation. A similar method has been adopted by Matthews (**9**) for the vegetation of a small Scottish loch, which affords good examples of biotic succession. In both these cases the developmental point of view is emphasised as a basis of classification, and the successional nature of floating-leaved, reedswamp, and

fen communities is clearly recognised. An examination of the vegetation of the English Lakes[1] confirms the validity of this view, and also shews that the *submerged* communities occur in definite successions, controlled chiefly by the rate at which inorganic silt is deposited. The fen and marsh communities round these lakes succeed the aquatic vegetation, and depend in a similar manner upon the rate of sedimentation. As the peat underlying these communities is raised above the flood level, silting ceases, and "acid" peat is developed, dominated by moor vegetation. *Thus, starting from bare stones and finishing in moor, we have typically one long succession, in the varied development of which, the rate of sedimentation is the principal factor.*

The abundance of moors of lacustrine and estuarine origin in and around the English Lake District, shows that this succession is here the rule rather than the exception. In the case of the larger lakes, however, a more primitive condition is retained on account of their size and depth. While the absence of similar lakes in other parts of England makes it less easy to apply this generalisation to all British lake vegetation, yet the Cheshire meres, the Somerset region (Moss, **10**), the Norfolk Fens and Broads (**21**), seem all to fall in with such a general classification. The Scottish lakes certainly agree with it. The Welsh lakes have not yet been investigated ecologically. The most notable difference in the Fens is, that local conditions (low rainfall and rich soil waters) extend the importance of the *carr* stage, while cultivation, drainage and especially climate limit the development of moor. In this case, also, calcareous waters are, in a certain degree, equivalent in effect to abundant silt.

Since there is one master factor running throughout the development of the above succession, any attempt to divide it must clearly be of an arbitrary nature. Though Moss (**11**, p. 37) makes such an attempt, he recognises the difficulty of deciding at what point a *habitat* division should be made. A distinction is usually drawn (**9, 11, 12**) between *aquatic* and *fen* formations—reed-swamps being included in the former. From actual observation, I have concluded that no such line of demarcation is possible. Not only does reed-swamp dominate large areas of land (e.g., Woodwalton Fen in Huntingdonshire), but the type of reedswamp bears a definite relation to the type of fen or marsh succeeding it, both in habitat and floristic (e.g., Esthwaite). The reedswamp must, in short, be regarded both as the *climax aquatic community*, and as *the pioneer fen community*.

In the parallel case of the transition of fen to moor, the *Molinia caerulea* community occupies an exactly similar position. While the life form of the dominant plant is apparently adapted to a *fen* condition—gentle silting—(**19**), the subordinate members of the community are heathy, and the occurrence of *Molinia* "grass moors," with similar floristic composition, points rather to the inclusion of this community in the *moor* stage of the

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[1] For a detailed account of one of these lakes, the reader is referred to the writer's paper on Esthwaite Water in this JOURNAL, **5**, p. 180 and **6**, p. 53.

succession. There is, moreover, no clear habitat factor indicating the position of the *Molinia* community. While the presence of silting (altogether lacking in moors), should include it among fens, its type of undecayed peat, with low ash content, indicates undoubtedly a close approach to the edaphic conditions of moor[1]. Here again, therefore, we cannot distinguish a clear line of division.

The aquatic, fen, and moor successions should therefore be regarded as together forming a unit, for the following reasons: (1) There is a single biotic succession. (2) There is a single controlling physical factor—silt or soil waters rich in bases. (3) There are no outstanding habitat variations subdividing the succession. Though the so-called aquatic, fen, and moor formations (**9, 11, 12**) have hence little right to be considered as separate entities, they constitute well marked *phases* of the unit as a whole.

<center>NOMENCLATURE</center>

The recent publication of Prof. Clements' *Plant Succession* (1916), has given us a comprehensive terminology, likely to prove of considerable value in classifying such successional plant communities as are dealt with in this paper. In this volume, a complete succession is divided into two types of communities, the *climax* units and the *seral* or developmental units, the latter being distinguished by distinctive name-forms. Thus an *association* is considered as the *climax* equivalent of the *seral associes*. In this way, the nomenclature is designed to indicate whether or not, a community is developmental.

Now the aquatic, fen, and moor succession may most conveniently be regarded as leading up to one *formation*—moor—uniform with those described by Clements, and lending itself admirably to his nomenclature of plant communities. In agreement with Clements' views, this moor formation is apparently primarily conditioned by *climate,* since it is independent of the strata, calcareous or siliceous, underlying it. The causes of its initiation, are both *topographic* and *biotic*, and this also agrees with Clements' conception. There is, however, one difference, due to the fact that these moors are essentially *valley* formations, and not therefore, entirely climatic. With this variation, I propose to adopt Clements' conception of the formation, for the aquatic and fen succession leading up to moor. All the aquatic and fen communities thus become seral units, since they belong to the developmental stages of the formation. For more detailed proof of the seral nature of the communities mentioned below, the reader is referred to the paper on Esthwaite Water (**13**).

I propose now to take further examples indicating the value and application of Clements' nomenclature, but altering his arrangement of aquatic

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[1] All the Lake District fens—while often bearing a close floristic resemblance to those of East Anglia—have *acid* soil waters. Acidity of soil is not, therefore, a distinction between fen and moor.

communities. In the hydrarch succession, he distinguishes (**2**, p. 137) "three well marked associes, namely, *submerged* plants, *floating* plants and *swamp* plants." This classification agrees essentially with that of Miss Pallis (**12**), of *submerged leaf, floating leaf*, and open and closed *reedswamp* "associations." Miss Pallis, however, remarks on the probability that these are, in reality, groups of "associations," and from my observations, this seems actually to be the case. Taking reedswamp first, as an example we can contrast the community of *Typha latifolia*, characterised by the rapid deposition of inorganic silt, with the community of *Carex inflata* in habitats where inorganic silt is quite or nearly absent. These are seral communities of definite floristic and habitat, each having one dominant; each therefore ranks as a *consocies* (agreeing with Matthews, **9**). The more typical reedswamp of *Phragmites communis* and *Scirpus lacustris*—the latter toward the open water—occupies an intermediate position between these two, and, having two dominants, ranks as an *associes*, in which each of the two zones is a *consocies*. Thus the reedswamp growth form includes a series of consocies, much as a climax forest formation may include a group of consociations (see Clements, *loc. cit.*).

A further illustration may be found among floating leaved plants, where the growth form also includes several seral communities. We can here distinguish, as one example, the *Castalia (Nymphaea) alba* consocies of moderately rapid sedimentation, from the *Castalia (Nymphaea) minor* consocies of very slight inorganic sedimentation.

Lastly, we find that submerged plants include several growth-forms, and also occur on a great variety of habitats, in characteristic communities. Taking the Elodioid first, my observations on the English Lakes shew that three main types of habitat communities exist within this life-type. These are classified in the following summary, and it will be also noticed that these habitat variations coincide with minor variations in life form. All are communities covering large areas, not small or scattered clumps.

1. *The linear leaved associes* is characteristic of relatively rapid inorganic silting, and includes consocies dominated by one of the following: *Naias flexilis, Callitriche autumnalis, Potamogeton pusillus*, or *Scirpus fluitans* (deep water form).

2. *The associes of Potamogete of P. praelongus type* is apparently typical of rather rapid silting. Consocies are dominated by *P. praelongus, P. lucens, P. Zizii* (deep water form) or *P. perfoliatus*. (This does not compete with 1.)

3. *The Nitella associes* occurs where silting is moderate, and often succeeds 1 and 2, as the habitat gets more organic. It includes the following consocies, usually in different lakes: consocies of *Nitella opaca* or *Nitella flexilis* or *Chara fragilis*[1].

In each of these associes, there are a number of consocies which approach

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[1] **Warming (24)** includes *Characeae* in the Rosette life form!

one another in ecological equivalence. It is probable that the *invasional* factor may partly determine which consocies dominates a particular water, for the migration of submerged water plants from lake to lake, must be fortuitous to some degree, If, however, two or more equivalent consocies occur in one lake they fuse, and reflect the associes in miniature.

Secondly, the Rosette type of submerged plants is as a whole characteristic of silt-free localities. Nevertheless, there are distinct habitat communities within the growth-form, and these communities are in no way equivalent. We can, in illustration, distinguish: (i) The *Isoetes lacustris consocies* of deep water and no silt, from (ii) the *Litorella-Lobelia associes* of shallow, coarse, unstable habitats. The former passes into the *Nitella* associes if silt accumulates, the latter into floating leaved or reedswamp communities.

Now in the larger lakes the slowness of silting coupled with the depth of the water often make it impossible for the *Isoetes* consocies and the *Nitella* associes to go through the normal seral development, and hence one community is kept on for a long period without changing, the succession being thus fixed in a subclimax stage. In this condition the above communities rank respectively as the *Isoetes* consociation and the *Nitella* association. It would thus seem that Clements' division of the water seres into submerged, floating, and swamp associes fails to take account of the wide habitat variations existing within the range of these major growth forms. Since varying communities included in these life forms exist under different conditions and are severally arranged, they are fully entitled to the higher rank I give them.

Other communities occur, however, which lack the characters distinguishing the above associes and consocies.

In Derwentwater, for example, the typical reedswamps are open, with *Phragmites communis*, *Scirpus lacustris*, and *Equisetum limosum* almost equally abundant. Developed at first on a thick *Litorella-Lobelia* carpet, they may also include *Potamogeton natans*, *P. Zizii*, *P. perfoliatus*, *Castalia minor*, *Nymphaea intermedia*, *Myriophyllum spicatum* and *Juncus fluitans*. At any one place from three to six species of differing life form may be equally abundant. Such a community is a mixture of differing stages of a succession; and these stages happen to be approximately equivalent under the conditions in which these open reedswamps are found. Probably the open reedswamps of the Broads (**12**) are of a similar nature. Such a mixed community may be called a *mictium*, in the sense suggested by Tansley (**22**, footnote, p. 199), and defined as "a transitional mixture of successive seral dominants."

In moderately shallow waters, e.g. the Broads (**12**), small clumps of *Scirpus lacustris* may appear far in advance of the open or closed community in which this plant normally occurs. Among unrelated life-forms, and bearing no fixed relation to the habitat, these clumps can only be regarded as detached initial stages of a later seral dominant. Such small groups of one species, characteristic of bare areas and initial stages, Clements terms *families*.

Litorella lacustris also forms families on exposed, unstable gravel, long in advance of the *Litorella-Lobelia* associes. *Sparganium natans* almost confines itself to this type of vegetative unit. It grows on bare stones, or on mud where other factors (e.g.; very turbid water) inhibit the development of submerged vegetation, and then shews nothing in common with other floating-leaved communities, except a need for shelter.

<div align="center">HABITAT FACTORS</div>

After these brief indications of the value and application of Clements' nomenclature, we may pass on to. consider the habitat factors governing the earlier stages of water seres. This phase of the subject involves the discussion of two questions: (1) What constitute habitat differences among water plants? (2) How are aquatic plants related to these differences?

The provisional distinction of "waters poor in mineral salts" from those "rich in mineral salts" was an attempt to answer the first of these two questions. But though this distinction coincides with Graebner's classification (**7**) of the fundamental habitat factors, it does not appear to be truly applicable to all aquatic vegetation.

A water, poor in mineral salts, may yet, especially in flood, bring down vast quantities of sediment. While this sediment may have no effect upon the mineral residue of the water, it may, even if chemically inert, have an enormous effect upon the aquatic communities, primarily because of its intimate relation with the physical nature of the substratum. This condition is very well marked at Esthwaite, especially in contrast with larger lakes, and adjacent upland tarns. Still more important in this country is the fact that waters rich in mineral salts lie in areas geologically stable, and overlaid by finely divided superficial layers, easily transported by water. Such waters will contain, in flood, if not normally, a large proportion of suspended matter. In consequence, lakes, pools, and broads tend to be silted up, and as a result, few of these richer waters shew primitive features (e.g., irregular or coarse substrata). Particularly is this the case in calcareous areas.

The distribution of waters poor in mineral salts corresponds, on the whole, with that of mountainous regions and hard rocks, where the majority of the lakes are in a comparatively primitive condition. As a result, the marginal slopes of such lakes are often steep, and their composition is normally coarse. These regions are also characterised by relatively great surface change, and therefore they shew many unstable habitats. Thus the plant communities of waters poor in mineral salts are developed under a series of conditions which usually occur together in this country, but are not *necessarily* related. They may be summarised as follows: (i) Waters poor in mineral salts, (ii) Waters usually rather poor in inorganic silt, (iii) Substrata either (*a*) coarse and primitive, (*b*) under erosion and unstable, or (*c*) only slightly and recently sedimented.

Such substrata may support plants of widely diverse types, not necessarily depending primarily on the paucity of salts in the water. Prominent among them will be plants with a *colonising* rôle. There will be also plants of *inorganic* silts, and perhaps true *silicicole* plants. On the other hand, as the absence of inorganic bases prevents the decay of humus, we shall also find plants of *undecayed peat*, a condition akin to that of terrestrial moors.

There is obviously, therefore, a danger of confusing plants characteristic of waters poor in mineral salts, with those found colonising the products of recent erosion, or sedimentation. In old, silted up waters the silting factor becomes of little importance; and since the colonising stages are quickly passed over, colonising plants are less typical. The paucity of species in many primitive lakes is certainly due primarily to the absence of sediments (i.e., suitable substrata), rather than to the paucity of their waters in mineral salts.

The *Litorella lacustris* community is one of the most characteristic of the colonising stages, and it typically develops on barely stable gravel. West (**25**) records it in Lindores and Lochmill Lochs, and also as forming bottom carpets in Carlingwark Loch. All these are calcareous waters. He observes further that it is less abundant in the calcareous Lismore area than in the Loch Ness region. His list of species indicates, however, an advanced state of sedimentation in the Lismore lakes, and therefore. few coarse substrata. Crampton (**3**) also records this plant in calcareous waters in Caithness. Thus the Litorella community does not appear to be conditioned primarily by waters poor in mineral salts.

Sparganium natans is a similar colonising plant. It occurs in two calcareous waters in the Furness district—Urswick Tarn and a pool by the railway near Barrow. In each case the water has a dissolved mineral residue of over ·2 gm. per litre, but has no submerged plants, their absence being due to the extreme turbidity of the water. The consequent lack of competition on abundant silt, is accompanied by the growth of this colonising plant, usually confined to waters poor in mineral salts. The *Naias flexilis* consocies of Esthwaite Water also appears to be a colonising community, but a study of its habitat elsewhere is needed, before we can accept this definitely.

The chief habitat factors governing the distribution of aquatic vegetation in lakes seem to be: (i) Large variations in the dissolved mineral and organic contents of the water, (ii) Variations in the amount and type of sediments deposited and the effect of these on the substratum, (iii) The physical and chemical nature of the primitive lake floor—if exposed.

There is probably a certain degree of equivalence between dissolved and suspended matters. There are probably also *calcicole* and *calcifuge* aquatic plants, and we may, in addition, expect aquatic plants to shew affinities with regional floristic variations[1]. On the other hand, just as there are

[1] Cf. **Magnin** (**8**).

terrestrial plant communities of organic and inorganic soils, there are also aquatic communities of these habitat types. In the same manner as we can distinguish terrestrial organic soils according as their rate of decay is rapid (e.g. *fens*), or slow (e.g. *moors*), so we can distinguish sub-aquatic soils of these types, with their corresponding floristic variations.

The future classification of aquatic plant communities may perhaps proceed, therefore, on lines closely analogous to those of terrestrial communities, and the conditions indicated above should control the starting points. In view of the great number of variations possible in these conditions, emphasis laid on the successional nature of the communities would seem to give the only unified method of treatment possible. Especially would unity be achieved if the final development of moor from water seres were found to be general throughout the British Isles, which I believe to be probable.

We will now turn to the second question raised in this section, viz. how are aquatic plants related to the substratum? Three prevalent views bearing directly on this point must be considered. It is stated by some authors that aquatic plants have roots which lack root-hairs, and whose only function is fixative. Others declare these plants to be normal in this respect. Brown(1) suggests that the relation of *Elodea* (and probably other plants) to organic soils is possibly due to the local concentrations of carbon dioxide over such substrata. He found that free floating *Elodea* was apparently independent of the substratum, if supplied with abundance of carbon dioxide. It is doubtful however, how far such experiments can be related to the conditions of plant life in lakes. From Delebecque's (5) experiments on the French lakes where 38–40 c.c. of carbon dioxide per litre were present, at temperatures ranging from $4 \cdot 5°$ to $20 \cdot 5°$ C., and from a few personal observations on English lakes, which agree remarkably with his results, it is found that the normal variation possible is so slight ($\cdot 2$ %), as to be negligible. Brown's assumption is further negatived by the fact of the known and continual movements of lake waters, even in sheltered places[1]; these would inevitably prevent such assumed local concentrations of dissolved matters. Thus we are driven to conclude that aquatic plants are related to their substrata through their roots.

Schenk (18), Sachs (17), Vines (23), and Warming (24) consider that aquatic plants absorb nutrient salts throughout their entire surface, their roots being purely fixative, but they do not support their contention by experimental evidence. Pfeffer (14), after reviewing the literature in 1897, concluded that no decisive experiments had been made to confirm either view. Since then (1905), Snell (20) and Pond (16) found independently, that *Elodea canadensis, Myriophyllum spicatum, Potamogeton obtusifolius, P. perfoliatus, Ranunculus trichophyllus* and *Vallisneria spiralis* grew more vigorously when rooted in the substratum than when anchored over it, and

[1] **Gilbert (6)**, and numerous authors in *Proc. Roy. Soc. Edin.*

especially when rooted in *soil* not *sand*. Hence they concluded that the roots have an absorptive as well as a fixative function.

The known differences in aquatic plant communities on different substrata[1] agree with this conclusion. These differences are especially marked in the English Lakes.

Further it seems highly probable that most aquatic plants develop root hairs. I have observed these structures in the following species: *Naias flexilis, Hydrilla verticillata, Elodea canadensis, Scirpus fluitans, Potamogeton pusillus* (agg.), *P. obtusifolius, P. praelongus, P. lucens, P. perfoliatus, P. heterophyllus, P. Zizii,* while Pond (**16**) also records them in *Potamogeton pectinatus, P. pauciflorus, P. natans, P. zosterifolius, Ranunculus trichophyllus, Vallisneria spiralis.*

This necessarily brief review of the evidence points toward the conclusion that aquatic plants bear a relation·to the substratum not markedly dissimilar from that of terrestrial plants, in absorbing nutrient salts through their roots. If this indeed be the case, there is all the less reason for considering aquatic communities as a separate ecological unit, and we may further conclude that their correlation with terrestrial communities into one succession, is as justifiable in this sense, as it is from the point of view of development.

Finally, I may point out that the system of classification adopted here coordinates, to a great extent, the conceptions underlying the previous classifications here reviewed. While the basis of the vegetational unit is the development of a biotic succession, growth form and habitat become factors of fundamental importance in considering the distribution of individual component communities, and in determining their status. The difficulty of deciding which of these two factors is the more important in assigning formational rank to types of vegetation, is thus avoided. The further difficulty of securing agreement as to what constitutes fundamental identity of habitat does not apply to the unit of vegetation here defined. Moreover, this unit is exceedingly flexible, since it allows the inclusion of the most diverse starting points in the successions composing it.

I must, in conclusion, express my indebtedness to Mr A. G. Tansley, for his valuable suggestions on nomenclature.

[1] **Pieters (15), Brown (1).**

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