Acta Bot. Neerl. 25(1), February 1976, p. 117–123

MEETINGS OF THE ROYAL BOTANICAL SOCIETY OF THE NETHERLANDS

MEETING OF THE SECTION FOR VEGETATION RESEARCH ON SEPTEMBER 30, 1975

Theme: Dynamics of algal vegetations in the Netherlands

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Periodicity of multicellular green algae

The scale of temporal patterns (periodicity, succession, colonization) of multicellular green algae differs considerably from comparable patterns of higher plants. This gives a possibility to study these patterns under favourable conditions.

A phycologist can be compared with a vegetation ecologist, trying to describe a vegetation from a balloon with aid of a telescope: it is not possible to sit down beside an algal growth, sorting and investigating the organisms by simple hand movements. On the other hand, when an algal ecologist waits a few weeks, processes have evolved that take several years in higher plants. Algal growths can be collected in the field and can be kept during long periods after fixation. Only little material is collected, since the "minimum area" often is very small. Within a few decimeters, zonation patterns occur, resembling higher plant patterns which are of a much greater scale (metres, kilometres). Complete colonization of a bare area with algae is effectuated in a short time (1–3 months, including several successional stages). The same process in higher plants requires several years. The algal growth has stabilized within one or two years, higher plants need many more (5–20) years.

In algal ecology, periodicity phenomena have drawn much attention. Periodicity is a cyclic alternation of communities of organisms, present whenever important ecological factors show long range fluctuations. Algae show an annual periodicity, related to climate fluctuations. At the beginning of the 20-th century, algal periodicity was described extensively by COMÈRE (1906), BROWN (1908), FRITSCH & RICH (1913), TRANSEAU (1916) and many others. Since a few years, it is possible to use multivariate techniques (principal component analysis, factor analysis, cluster analysis) to describe periodicity phenomena. This gives the opportunity to describe these phenomena in a less subjective manner (ALLEN & SKAGEN, 1973).

The application of factor analysis (in this case Principal Component analysis with Varimax rotation with Kaiser normalization) gave interesting results. The factor analyses were applied to observations of multicellular green algae from two lake areas in the Netherlands (Botshol and Hol) during two subsequent years (june 1968–june 1970). The resulting factor patterns resemble the graphs of TRANSEAU (1916), both giving the periodicity of a number of seasonal species groups.

It is difficult, to fit the temporal patterns of algae to the terminology of vegetation ecologists. In future, it will be necessary to do so, for both are biological temporal phenomena, which possibly are subject to highly comparable rules.

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Succession of desmid communities in the broads area of NW Overijssel

The ecology of the chlorophycean group of the Desmidiaceae has often been misunderstood owing to the introduction of the so-called plankton quotients by Thunmark and Nygaard in the "fourties". In several of such quotients – intended as a measure for the degree of trophism of the water – the desmids are considered to be indicative of an oligotrophic environment, and thus the occurrence of these algae became in the eyes of most hydrobiologists synonymous with an oligotrophic habitat, which idea is at least not sufficiently discriminating. The optimum conditions for most species of desmids in fact appear to be as follows:

(1) mesotrophy (characterised by such higher plants as *Pilularia globulifera, Hypericum elodes, Carex lasiocarpa, Utricularia intermedia, Scorpidium scorpioides*),
(2) a lush stand of aquatic vegetation (in connection with their tychoplanktonic or benthic way of life), and
(3) a high degree of structural diversity and stability (COESEL 1975a).

A habitat fulfilling these conditions is found in, e.g., quivering bogs exploited for haymaking in the holocene broads in the NW corner of the province of Overijssel. Such bogs, developed out of filled-in peat pits, are very suitable for studies of the succession in desmid communities on account of their often marked trophic gradients. The floating bog vegetation becomes more solid as the succession of higher plant communities progresses, and the shallow superficial gullies between them become better isolated from the eutrophic bodies of open water infiltrating the plots of quivering bog. An absolute isolation is never attained, however. There is no stagnation of rain water so characteristic of the ombrotrophic type of peat bog, so that several species of desmids known from fens and bogs of pleistocene origin (such as *Tetmemorus brebissonii, Pleurotaenium minutum, Closterium ulna, Cosmarium pyramidatum*) are absent. The well surveyable spatial separation of trophic levels in NW Overijssel – eutrophic conditions in the open water of lakes, peat pits, and ditches, against mesotrophic gradients in the quivering bogs – and the absence of truly oligotrophic water enables us to obtain a good insight into the trophic preference of Dutch species of desmids. It appears, for instance, that the biocoenosis indicated by BEIJERINCK (1926) at "type A" contains species preferring eutrophic waters as well as species with a local distribution in mesotrophic habitats. From a series of investigations dating back from 1970, in which the composition of the desmid flora of the various environments was recorded, the following preliminary, overall pattern of succession could be deduced.

In the larger, eutrophic lakes in which veritable plankton communities may develop, the desmids are only represented by a few but characteristic species, namely some acicular species of *Closterium* (such as *Cl. aciculare*) and long-armed *Staurastrum* species (such as *S. chaetoceras*). In the smaller bodies of water, with a comparable trophic level but a much denser stand of aquatic vegetation, these euplankters are replaced by tychoplanktonic forms. Species of common occurrence in this type of water are, e.g., *Closterium moniliferum* and *Cosmarium obtusatum*. They constitute a part of the basic assembly which is supplemented by some ecologically more particular taxa according as the environment is less polluted and more differentiated internally. *Stratiotes* vegetation, for instance, usually harbours a quantitatively and qualitatively rich desmid flora (with sometimes more than 50 species) including such characteristic taxa as *Cosmarium insigne* and *Staurastrum gladiosum* var. *delicatulum* (see COESEL 1975b). The zone of transition to the quivering bog with an initial electric conductivity about equalling that of the open water (500–800 μmho) but with a lower pH (a little below 7), is characterised by the appearance of a few additional species such as *Netrium digitus* and *Cosmarium quadratum*. They contribute to the basic assembly in the mesotrophic quivering bog habitat comparable with the *Closterium moniliferum – Cosmarium obtusatum* – community in the eutrophic open water which is also encountered at sites where extensive grazing has led to an enrichment of nutrients. Where a careful management of the haymaking on quivering bogs is maintained, the common basic assembly is supplemented by an appreciable

number of characteristic taxa, the composition of the desmid flora in the shallow gullies appearing to have a close relation with the stage of succession in the surrounding, higher stands of vegetation. In the beginning there is especially an increase in the number of species of *Cosmarium*. Characteristic taxa of a relatively early successional phase with *Chara vulgaris* and an optimum development of *Scorpidium scorpioides*, a conductivity of about 600 μmho, and a pH 6.5–7.0. are e.g., *Cosmarium turgidum* and *C. conspersum*.
When the succession in the floating vegetation proceeds, the conductivity and pH become lower, the number of desmid taxa reaching its optimum when the conductivity is about 350 μmho and the pH 6. In gullies exhibiting these conditions (which are usually filled with *Utricularia intermedia* stands), up to about one hundred species of desmids belonging to more than ten genera may be present, including representatives of the genera *Euastrum* and *Micrasterias* which attain their optimum development in this stage of vegetational succession. A progressive solidification of the soil and oligotrophiation of the habitat results in a decrease in the number of species. In gullies in which the *Scorpidium* belt is undeveloped and the surrounding zone of *Sphagnum* borders immediately on the open water, the large and relatively eutrophic genus *Cosmarium* has almost disappeared when the conductivity falls to about 200 μmho and the pH to about 5.5; the desmid flora present at such sites is characterised by a marked dominance of *Tetmemorus granulatus* and *Closterium costatum*. As stated before, the isolation of the bog water from the larger open water bodies is insufficient in this region of broads and bogs to allow veritably oligotrophic conditions (conductivity below 100 μmho, pH below 5) to develop. The conductivity and pH values only fall below these limits in the capillary rain water retained in the raised clumps of *Spagnum* where the conditions are suitable only for such atmophytic genera as *Cylindrocystis* and *Mesotaenium*. The above-mentioned successional changes clearly confirm the author's opinion that the richest desmid flora is found in more mesotrophic rather than in oligotrophic environments.

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Dynamics of algal vegetations dominated by Vaucheria species

During the years 1967–1974 investigations on the *Vaucheria* species from the Dutch coastal region were carried out in the northern Wadden Sea area and in the southwestern estuarine area.

Methods: a part of each sample was cultivated in an Erdschreiber medium at 12 °C, L/D: 12/12, 1000–2000 Lux, until after about 3 weeks enough reproductive structures were obtained to allow identification of all species present in the sample.

Results: as yet thirty *Vaucheria* species were found in the Netherlands, among which one new to science: *V. birostris* Simons. Fifteen species live in the saline environment of salt-marshes, beach plains, seepage areas and so on, where they form bright to dark velvet green patches or tufted mats. The apically growing coenocytic filaments are more or less firmly attached to the substratum by means of rhizoidal outgrowths.

Above MHW in the phanerogamic vegetation of marine salt-marshes, a group of species occurs consisting of *V. arcassonensis*, *V. coronata*, *V. intermedia*, and *V. minuta*. This group may be found throughout the year, but the four species show differences in periodicity.

In the mesohaline traject of the estuaries this supra-littoral group is gradually replaced by a group consisting of *V. synandra*, *V. canalicularis*, *V. cruciata*, and *V. erythrospora*, which are in turn replaced by limnic species in the freshwater tidal area.

At high tidal levels in the marine marshes, mostly in *Juncetum gerardii* vegetations, the species of the former group often grow intermixed with species of the latter group, presumably reflecting the generally less saline conditions as compared to the lower tidal levels, at least in the colder seasons. In summer *Vaucheria* disappears at the high levels or only *V. intermedia* may be present.

At MHW and below on the silty slopes of creeks or levees along eu-polyhaline waters the species *V. velutina* and *V. subsimplex* may form extensive mats in summer and autumn. This algal community is replaced by *V. compacta* in the mesohaline traject. *V. compacta* likewise forms extensive mats along the estuaries as far as the upstream limit of the tidal wave reaches. All three pioneering species are capable of asexual reproduction by means of aplanospores.

A comprehensive diagram of all data from estuarine areas is shown in SIMONS (1975a).

The species from estuarine habitats also occur in inland brackish seepage areas. In such non-tidal habitats there is a yearly periodicity in variation of moisture and salinity content of the upper soil layer: high salinities and relatively low moisture values in summer and low salinities and high moisture values in the colder seasons.

From low levels like shores of pools and ditches towards high levels like dikes or pastures a distinct shifting is found in the combination of *Vaucheria* spp. present: *V. velutina*, *V. subsimplex*, *V. litorea* and *V. sescuplicaria* often form mass aspects at the lowest levels, while at the higher levels in grassy vegetations patches occur consisting of combinations of *V. sescuplicaria*, *V. arcassonensis*, *V. coronata*, *V. intermedia*, *V. erythrospora* and *V. synandra*. *V. synandra* is the dominant *Vaucheria* species in *Juncus gerardii* vegetations.

The dynamics of the *Vaucheria* mats in this environment were studied using the Permanent Quadrate method, by monthly estimates on covering of algal species and measuring of moisture content and soil-moisture salinity of the upper layer near the PQ's.

Several examples were given (SIMONS 1975b) which show that periodicity phenomena of the *Vaucheria* species are correlated with fluctuations in factors as soil-moisture and salinity.

The genus *Vaucheria* as a whole prefers the high moisture and low salinity conditions in the colder seasons, except at the lowest levels where it often shows mass appearance in summer under relatively high salinity values.

When *Vaucheria* growth was present in summer at the higher levels under high salinity conditions, in most cases only one species, viz. *V. intermedia* was present. The accompanying green alga *Rhizoclonium riparium* was of more constant appearance being apparently better adapted to desiccation than *Vaucheria* as a whole.

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Dynamics of environment and algal vegetation in salt marshes in the S.W.-Netherlands

Knowledge of the spatial structure of benthic algal vegetations in salt marshes, consisting of about 100 species of blue-green, green, brown and red algae, formed the basis of a detailed study into the dynamics of the algal mat.

The temporal changes in algal vegetations and concomitant processes in their environments were studied in 29 parmanent quadrats (PQs), plotted in tidal salt marshes and along brackish inland waters in the S.W.-Netherlands. Once a month vegetation and environment of the PQs were examined over the period March 1968–February 1971 (NIENHUIS 1972, 1973, 1975).

From the Spearman rank-correlation between vegetational and environmental parameters it appeared that in semi-terrestrial and terrestrial environments the average number of algal species in a relevé and the average similarity between the species composition of successive relevés have a significant positive correlation with the stability of the substrate, and hardly any correlation with fluctuations in soil moisture content and salinity of the soil moisture and with the maximum cover percentage of the phanerogams.

Stable substrates tend to bear stable algal mats, as appeared from quantitative data. Small and moderate fluctuations in soil moisture content and salinity of the soil moisture have no limiting influence on the algal cover degree. During periods of extreme high salinities and concomitant extreme low soil moisture contents that coincide with evaporation surpluses, the green algal mat bleaches and decreases in cover in semi-terrestrial and terrestrial environments. Below 20% soil moisture content this factor is limiting for the expansion of a mat of green algae (*Rhizoclonium riparium, Percursaria percursa. Enteromorpha torta, E. prolifera*) and *Vaucheria* species. The mat desiccates and bleaches but recovers after increase of the soil moisture content above 20% within one month. Two weeks of severe frost (temperature down to –10 °C) do not influence the cover degree of the algal mat in aquatic brackish PQs but the cover degree in semi-terrestrial PQs decreases. Short lasting soil moisture salinities of 130–190 ‰ Cl^- have no limiting effect on the expansion of the algal mat.

The ecological role of the filamentous green alga *Rhizoclonium riparium*, one of the characteristic species in the salt-marsh ecosystem, has been studied.

Rhizoclonium riparium is present in green algal mats all year round, although in changing quantities. The wax and wane of the populations is irregular and no marked seasonal periodicity can be observed, unless the soil moisture content acts as a limiting factor in summer. A *Rhizoclonium* mat is also able to bear short lasting desiccation and frost very well, recovering quickly after an unfavourable period. *Rhizoclonium* populations can stand both dry hyperhaline conditions (over 150 ‰ Cl^-) as well as wet, slightly brackish conditions (less than 0.5 ‰ Cl^-) in one and the same PQ in the course of one year. Dry summer weather and consequent decrease of the soil moisture content to less than 5% is fatal for *Rhizoclonium:* it dries up and disappears.

Rhizoclonium riparium only forms mats that occur throughout the year on a relatively stable substrate. It does never occur in quantity on weak miry soils. The settlement and the expansion of a *Rhizoclonium* population takes several months, as could be observed from artificially cleaned PQs. *Rhizoclonium riparium* does not act as a colonist like *Ulothrix* species or certain Cyanophyceae, overgrowing a bare soil within one or two weeks and vanishing equally quick. Moderate grazing by cattle and consequent treading and manuring do not influence the *Rhizoclonium* mat negatively.

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Dynamics of the algal vegetation of saltmarshes in the Wadden Sea

In the Wadden area, the littoral border environment is often formed by saltmarshes. The saltmarshes of the islands generally have a rich algal vegetation; those on the mainland generally a poorly developed one. In most Wadden Sea saltmarshes, three groups of species constitute the majority of algal mats: 1. *Vaucheria* (Xanthophyceae), siphonal algae growing upright; 2. filamentous Chlorophyceae, with a multicellular structure and growing parallel to their substratum; and 3. some filamentous Cyanophyceae (Oscillatoriaceae), possessing a mucous sheath. The cold and wet seasons favour the growth of the first two groups. Of these the Chlorophyceae are better able to withstand periods of drought. During the warm and dry periods of the year, the filamentous Cyanophyceae survive best.

This general phenomenon can be influenced in various ways by environmental factors, such as seepage and the flooding regime, which influence the salinity regime, the water regime and silting up. Accretion, for example, which is an important factor in the salt-marshes along the Frisian and Groningen mainland, causes a silt cover over the algal mat. When the silt deposition is little several algae, *Vaucheria* and Oscillatoriaceae species, are still capable of growing through the silt, but on thick layers of silt the algal vegetation has to germinate anew. Silting up is thus a factor in reducing the richness in species of an area.

Animal life and the human presence also influence the algal vegetation. Invertebrates destroy an algal mat by feeding on it, birds by digging for food and nesting, and cattle by grazing and trampling. On the other hand, treading by man and animal and also grazing may be beneficial to an algal vegetation. Grazing keeps the phanerogam vegetation low, thus protecting the algae from too much competition for light and space, whereas a certain shelter by the higher plants is maintained. Treading sometimes destroys the phanerogam vegetation and creates open spots, in which, under certain conditions, algae can still grow. The kind of substratum, the moisture regime and most of all the seasonal factors determine whether *Vaucheria*, filamentous Chlorophyceae or Oscillatoriaceae will be dominant.

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Distribution and seasonal periodicity of sediment inhabiting diatoms in the Waddensea and the Ems-Dollard estuary

The separation of benthic diatoms from their original substratum (sediment, organic debris) has made quantitative work nearly impossible. Two new methods have been recently developed, which have solved this problem. Altogether, three different methods can be used which have their specific applications. They will be discussed shortly:

1. Convential method. Sediment containing diatoms is sampled by scraping. The cells are cleaned by chemical methods and mounted in a highly refractive medium such as clearax.

In this case a distinction between dead and living cells can not be made. This method is adequate for floristic studies only.

2. Lens-tissue technique. With this method only motile cells can be sampled whose positive phototaxis is used to collect them in lens tissues spread over the sediment. The method is not quantitative, but all cells harvested are alive.
3. Density-gradient method. This new method developed by de Jonge is quantitative; moreover harvested cells are still alive.

A comparison of these three methods is given in *table 1*. The results must be considered as preliminary, because this analysis has sofar been made only once.

Table 1.

	Cells/cm² sediment	Number of species
Conventional method, dead + living cells	274.10^4	39
Lens-tissue method, living cells	111.10^4	17
Density gradient method, living cells	238.10^4	36

Nearly all species found with the conventional method were also observed in the density gradient samples. The same holds true for the cell number: apparently the overwhelming majority of cells in the used sediment sample was alive. The lens-tissue technique gives both less than half the cell number and the number of species. The vegetation analyses which have been made till now are: part of the Groninger wad (three permanent plots) using the lens-tissue technique (COLIJN 1974), part of the Hohe Knechtsand in the German part of the Waddensea (COLIJN & KOEMAN 1975) with the conventional method, another part of the Groninger wad (seven permanent plots) (DIJKEMA 1975) using the lens-tissue technique, and the epipsammic (fixed to sandgrains) flora of four permanent plots in the Ems-Dollard estuary (NIENHUIS 1975). Several methods have been used to analyse these vegetations: principal component analysis (Q-type analysis), ordination techniques (Bray and Curtiss) and simple centroid clustering methods.

It is impossible to give all results obtained but some general trends can be given: for the Knechtsand material circumstantial evidence was found for a relation between type of sediment and diatom vegetation, material investigated by Dijkema leads to the same conclusion, though seasonal periodicity complicates the picture. This seasonal periodicity was also found on the Groninger wad. Samples analysed by Nienhuis showed a spatial variation inside the estuary. Further analysis of diatom vegetations over longer periods with permanent plots is needed to establish the occurrence of vegetational units as described by BROCKMANN (1950).

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