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VAUCHERIA SPECIES FROM THE DUTCH BRACKISH INLAND PONDS "DE PUTTEN"

J. SIMONS and M. VROMAN

Botanisch Laboratorium, afd. Plantensystematiek, Vrije Universiteit, Amsterdam

SUMMARY

Data are given on the distribution and periodicity of fifteen *Vaucheria* species in three main types of habitat: a ditch, drainage ditches, and pond banks. At five stations a detailed analysis of *Vaucheria* growth was made. On the shores of the ponds from mean water level upwards, four groups of species can be discerned. The occurrence of most *Vaucheria* species shows a seasonal periodicity.

1. INTRODUCTION

Field data of brackish-water *Vaucheria* species are very sparse, in spite of the fact that *Vaucheria* species are important and constant components of the algal vegetation on soft, brackish substrata. The reason for this lack of knowledge is that *Vaucheria* species are often found without reproductive organs, and these organs are indispensable for the identification of the species. Reproduction, however, can easily be induced by culturing the algae in an Erdschreiber medium. Combining sampling in the field with this culture method, the authors are studying the brackish-water *Vaucheria* species from the Dutch coastal region (Simons & Vroman 1968; Nienhuis & Simons 1971).

For general considerations on brackish-water algae see Den Hartog (1967). The area dealt with in this publication, "De Putten", comprises ponds situated at the landward side of the North Sea dike named "Hondsbossche Zeewering". The late F. Boxem was the first person who called attention to the luxurious growth of *Vaucheria* in this locality (unpublished). From autumn 1968 until autumn 1969 regular observations on the occurrence of *Vaucheria* species were made at a series of sampling stations in this area by Hamer (1969) and Van der Spelt (1969).

On the basis of their data some stations were selected for seasonal observation during the years 1970–1972 in order to obtain an overall picture of the distribution and periodicity of the *Vaucheria* species in this habitat.

Originally "De Putten" consisted of two groups of ponds, a northern one and at a distance of about 1 km a southern one. During the year 1970 the northern ponds were disturbed for the greater part due to the construction of a road. The map (*fig. 1*) shows the southern part of the area where our samples were taken. Recently (1972) the southern group also was for the greater part destroyed by the construction of the above mentioned road.

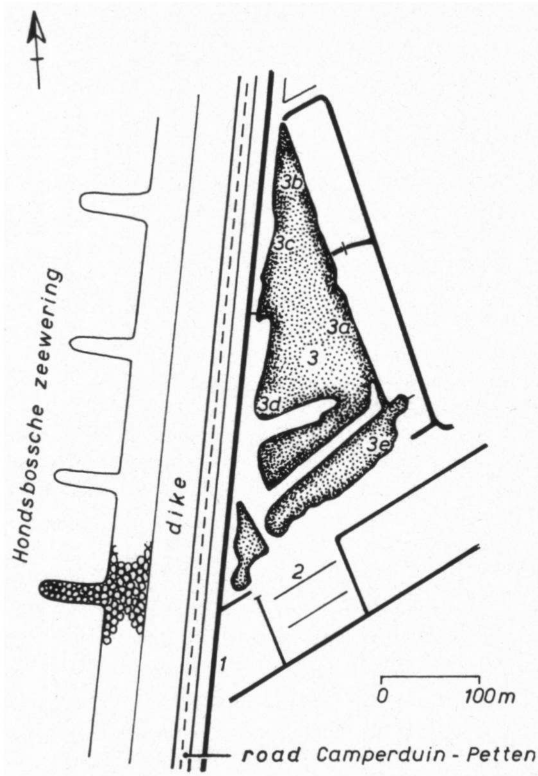

Fig. 1. Map showing the southern ponds where samples were taken from autumn 1968 until spring 1972. 1: ditch, 2: drainage ditches, 3: pond, 3a: station 3a etc. (see text and *fig.* 2).

2. MATERIAL AND METHODS

Algal samples were taken by cutting away a piece of soil measuring about 4–6 × 2 × 1 cm. One part of each sample was fixed in formaldehyde 4%, the other part was cultivated in an Erdschreiber medium in petri-dishes until, after about three weeks, a stage of maximal development of the reproductive structures was reached. The culture conditions involved a temperature of c. 13 °C, a photoperiod L/D 12:12, and light intensities between 1000 and 2000 Lux. Moisture content of soil and salinity of the soil moisture were estimated from soil samples of the upper 2 cm and expressed as g H_2O/100 g oven-dried soil and g Cl^-/l soil moisture (‰ Cl^-), respectively. The relative quantities of *Vaucheria* species in the total mass of *Vaucheria* were estimated by combining the data from the fixed part of the sample with those of the cultivated part. These quantities were expressed in the following scale: +: 0–10% of total *Vaucheria*-mass, 1: 10–25%, 2: 25–50%, 3: 50–75%, 4: 75–100%. For graphical representation the maximum obtainable value for each species was used. In some cases estimations were made of whole algal groups namely: *Vaucheria* spp., *Chlorophyceae*, *Cyanophyceae*. In one place a permanent quadrate (P.Q.), measuring 50 × 50 cm was kept under observation. The method of sampling and estimating at this P.Q. was as described by NIENHUIS & SIMONS (1971). The covering percentages of *Vaucheria* spp., green and blue-green algae in this sampling place were estimated by combining field data with data from microscopical investigation of the fixed and the cultivated sample parts. It should be noted that for non-P.Q. samples the relative quantities of the total sampled algal mass are given.

3. ENVIRONMENT AND VEGETATION

3.1. Topography

The ponds are man-made; they were dug in the second half of the last century during construction works on the sea dike. The maximum depth of the ponds was about 1.50 m. The water level was kept fairly constant, at about 50–100 cm under the level of the surrounding pastures. The soil was predominantly clayey. Parallel to the dike ran a ditch (*fig. 1,1* and *2,1*), its water depth varying between 0 and 10 cm. In some places in the pastures there were narrow drainage ditches (*figs. 1,2* and *2,2*), which were often without water in summer. The banks of the ponds vary considerably in structure. At the wind-exposed eastern side the shores were in general as shown in *fig. 2,3a* or *3b* (see also *fig. 1*). Maximum water level (*fig. 2,3b*) was reached only for brief periods with much precipitation. At the sheltered western side the shores were often as shown in *fig. 2,3d* (see also *fig. 1*).

At one spot there was a situation (*fig. 1,3c*), where a flat bank was found with a marshy vegetation dominated by *Aster tripolium* and *Phragmites australis*.

Ditch, drainage ditches and pond shores (*1,2* and *3*, resp. in *figs. 1* and *2*) represent three distinctly different situations. Above the water level of the ditch a thick belt of *Vaucheria* on a blackish sandy mud was of constant appearance at least during the summer. The algal vegetation of the drainage ditches was of a very unstable nature, reflecting the unstable moisture and salinity conditions in this type of habitat. The algal vegetation of the pond shores may be expected to react upon the increasing instability of factors as salinity and soil moisture going from water level to pasture level. Consequently in the algal vegetation of the pond shores, zonation phenomena could be expected and indeed were found in the species composition of *Vaucheria* growth from low to high level.

3.2. Water salinities

Shallow brackish inland waters in the Netherlands are characterized by a yearly periodicity in salinity (DEN HARTOG 1970). Salinities are low in late autumn, winter and early spring (precipitation surplus), but rather high in the other periods (evapo-transpiration surplus). "De Putten" fitted well in this scheme. The ponds were brackish due to seepage of water from the North Sea. The salinities fluctuated from 4–21 (–25) ‰ Cl^-. The water of the earlier mentioned

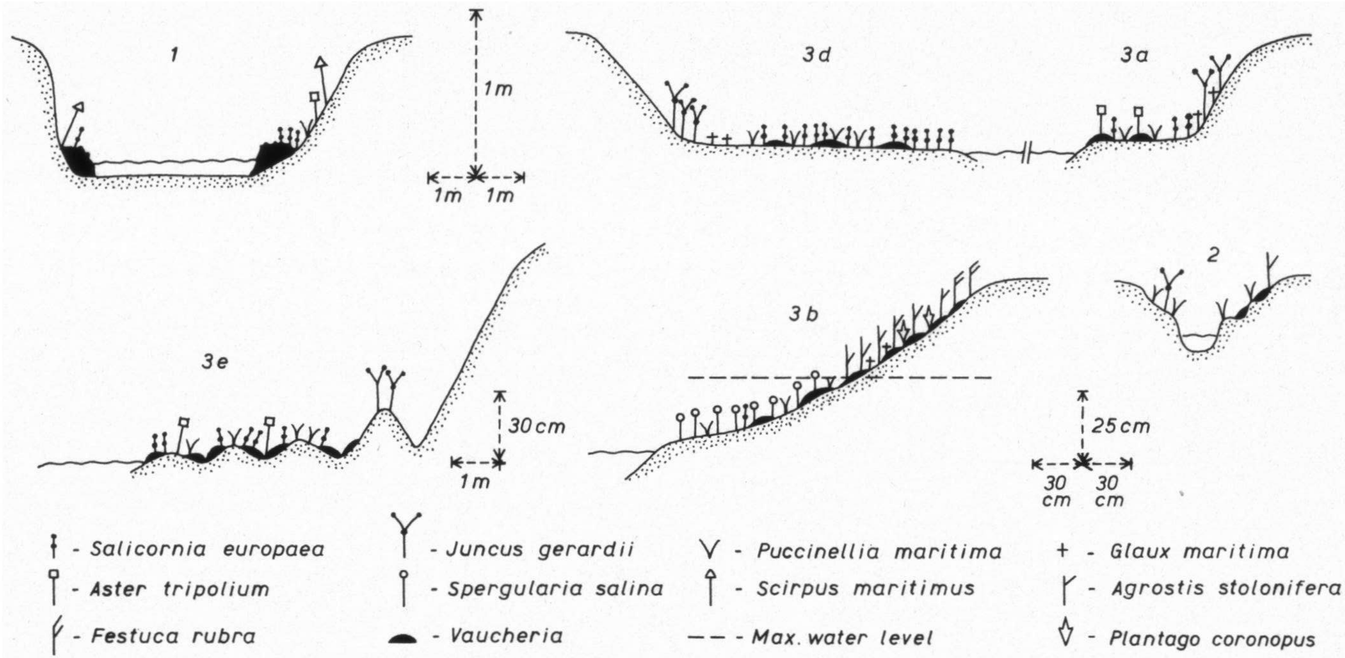

Fig. 2. Structure of various stations dealt with. 1: ditch, 2: drainage ditch, 3a: part of eastern pond shore, 3b: other part of eastern pond shore, 3d: part of western pond shore, 3e: "bumpy" pond shore.
Note *Spergularia salina* J. & C. Presl = *Spergularva marina* (L.) Grisel.!

ditch varied between 4 and 16 (-26) $^0/_{00}$ Cl^-, while the drainage ditch water varied between 2 and 11 $^0/_{00}$ Cl^- in salinity.

3.3. Description of the vegetation

Paragraphs 3.3.1.–3.3.6. sum up broadly our observations from autumn 1968 until spring 1972. The topic of these paragraphs is: which *Vaucheria* species grow in which places along the pond banks.

In the paragraphs 4.1.–4.3. some stations are dealt with where the *Vaucheria* growth was striking and richly developed. Such stations were suited to a more quantitative approach. Most of these observations were made during the years 1970–1972.

The names of the phanerogams are in accordance with HEUKELS & VAN OOSTSTROOM (1970). A list of algal species dealt with, is given in *table 1*.

3.3.1. Station 3a (*figs. 1* and *2*)

On the horizontal parts a vegetation dominated by *Salicornia europaea* and *Puccinellia maritima* was found, accompanied by, in sequence of decreasing quantities, *Aster tripolium*, *Spergularia media*, *Triglochin maritima*, *Spergularia marina*, *Juncus gerardii*, *Glaux maritima*. This vegetation was rather open, yet *Vaucheria* spp. were not very common in this type of habitat. The species *V. coronata*, *V. intermedia*, *V. arcassonensis*, *V. sescuplicaria*, and *V. erythrospora* were found especially in the colder seasons when soil-moisture content was high and salinities rather low (4–8 $^0/_{00}$ Cl^-). In summer other species occurred, namely *V. sphaerospora* and *V. thuretii*, sometimes accompanied by *V. intermedia*. The blackish-green tufts of *V. thuretii* and *V. sphaerospora* grew mainly on the outermost edges of shores or in small depressions where soil-moisture content and especially salinity were high. Three measurements during dry periods showed moisture contents of 78.2–108.3 g H_2O/100 g soil and soil-moisture salinities of 19.6–39 $^0/_{00}$ Cl^-.

The optimal occurrence of *V. thuretii* in summer and (to a lesser extent) of *V. sphaerospora* and *V. intermedia* is a common phenomenon in the Netherlands, as is the optimal winter occurrence of *V. coronata* (NIENHUIS & SIMONS 1971).

Other algae at this level on station 3a were predominantly *Chlorophyceae* like *Blidingia minima*, *Enteromorpha prolifera*, *E. torta*, *Rhizoclonium riparium*, *Percursaria percursa*, *Ulothrix pseudoflacca*, *U. subflaccida*. These *Chlorophyceae* were especially abundant in the colder seasons. The horizontal part of the shore was bordered by a belt in which *Juncus gerardii* was dominant. On bare spots in this dense vegetation the following *Vaucheria* spp. could be found growing intermingled: *V. arcassonensis*, *V. coronata*, *V. erythrospora* (especially in winter), *V. intermedia* (especially in summer), *V. sescuplicaria* and *V. synandra*. Between the *Juncus gerardii* belt and the pasture, a dense vegetation was found dominated by *Elytrigia pungens* and/or *Cochlearia danica*. Here hardly any algae could be found.

Table 1. List of species of *Chlorophyceae*, *Cyanophyceae* and *Vaucheria* spp. dealt with. The nomenclature of coccoid *Cyanophyceae* is in accordance with DROUET & DAILY (1956). The nomenclature of non-coccoid *Cyanophyceae* follows GEITLER (1932). The morphology and nomenclature of *Vaucheria* spp. are dealt with by RIETH (1956) and CHRISTENSEN (1952, 1956, 1969).

Chlorophyceae:
Blidingia minima (Näg. ex Kütz.) Kylin
Enteromorpha intestinalis (L.) Link
E. prolifera (O. F. Müller) J. Ag.
E. torta (Mertens) Reinb.
Percursaria percursa (C. Ag.) Rosenv.
Rhizoclonium riparium (Roth) Harv.
Ulothrix flacca (Dillw.) Thur.
U. pseudoflacca Wille
U. subflaccida Wille

Cyanophyceae:
Agmenellum quadruplicatum Brébisson
Anacystis dimidiata Dr. & Daily
Anacystis montana (Lightf.) Dr. & Daily
Hydrocoleum lyngbyaceum Kütz.
Lyngbya aestuarii (Mert.) Liebm.
L. semiplena (C. Ag.) J. G. Ag.
Microcoleus vaginatus (Vauch.) Gom.
Nodularia harveyana Born. & Flah.
Oscillatoria cf. *amphibia* Ag.
O. brevis (Kütz.) Gom.
O. nigro-viridis Thwaites
Phormidium corium Kütz.
P. autumnale (Ag.) Trevis
Schizothrix calcicola (Ag.) Gom.
Spirulina subsalsa Oersted
Symploca funicularis Setch. & Gard.

Vaucheria spp.:
V. arcassonensis Dangeard
V. canalicularis (L.) Christensen (syn.: *V. woroniniana* Heering)
V. compacta (Coll.) Coll. ex Taylor
V. coronata Nordtstedt
V. cruciata (Vauch.) DC. (syn.: *V. debaryana* Wor.)
V. dillwynii (Web. et Mohr) C. Ag. (syn.: *V. pachyderma* Walz)
V. erythrospora Christensen
V. frigida (Roth) C. Ag. (syn.: *V. terrestris* sensu Götz)
V. intermedia Nordtstedt
V. litorea Hofm. ex C. Ag.
V. prona Christensen (syn.: *V. hamata* sensu Götz)
V. sescuplicaria Christensen
V. sphaerospora Nordtstedt
V. synandra Wor.
V. terrestris (Vauch.) DC.
V. thuretii Wor. (revised name: *V. velutina* C. Ag.)

3.3.2. Station 3b (*figs. 1* and *2*)

This type of shore showed a more or less continuous slope from water level to pasture level. Here the lowest parts in summer were dominated by *Spergularia marina*, together with *Puccinellia maritima*, *Salicornia europaea*, *Spergularia media*, *Triglochin maritima*, and *Juncus gerardii*. Above this level *Agrostis stolonifera* was the dominant species accompanied by *Glaux maritima* and still higher species like *Plantago coronopus*, *Leontodon autumnalis*, *Plantago major*, *Potentilla anserina*, *Cirsium arvense* were found, together with species of the horizontal pasture vegetation. We assume that the lowest level, with *Spergularia* *marina*, is of too unstable a nature for *Vaucheria* to grow. The algal vegetation here consisted predominantly of the *Chlorophyceae* as mentioned for station 3a. Desiccation may be strong at this locality. Two measurements on October 5, 1971 (very dry conditions) yielded 59.5 g H_2O/100 g soil and 74.9$^0/_{00}$ Cl^-/l soil moisture at the lower level and 69.2 g H_2O and 73–1$^0/_{00}$ Cl^- at the middle level. Under these circumstances only a poor algal growth of *Rhizoclonium riparium* was observed.

Above the level with *Spergularia marina* a rich growth of *Vaucheria* was observed in autumn and winter, with *V. sescuplicaria*, *V. erythrospora*, and *V. synandra* as the most important species. In the "zone" with *Plantago coronopus* several mosses were found, showing luxurious growth in autumn and winter. The following species were encountered: *Oxyrrhynchium praelongum* (Hedw.) Kindb., *O. swartzii* (Turn.)Warnst., *Brachythecium albicans* (Hedw.)B.S.G., and *Pottia heimii* (Hedw.)Hampe.

3.3.3. Station 3c (*fig. 1*)

At this station a belt, consisting of a marshy vegetation dominated by *Aster tripolium* and *Phragmites australis* was found. In the undergrowth *Puccinellia maritima*, *Triglochin maritima*, and *Juncus gerardii* were the most important species. At bottom-level, under circumstances of very low light intensities, often a dense *Vaucheria* felt was found. During the colder seasons this felt consisted of a mixture of the following species: *V. synandra*, *V. litorea*, *V. sescuplicaria*, *V. sphaerospora*, *V. coronata*, and less often *V. intermedia*. In summer another species-combination was obvious: *V. synandra*, *V. sescuplicaria*, *V. intermedia*, and *V. thuretii*.

3.3.4. Station 3d (*figs. 1* and *2*)

This station showed a flat border with a blackish muddy substratum dominated by *Salicornia europaea*. Other halophytes at this locality were: *Puccinellia maritima*, *Triglochin maritima*, *Spergularia media*. On this moisture-saturated substratum a thick cushion-like growth of *Vaucheria* could be found in every season consisting of the following species: *V. sphaerospora* (especially at the lower *Salicornia* level), *V. thuretii*, *V. sescuplicaria*, *V. litorea* (see under 4.1.3.). This flat level was bordered again by a *Juncus gerardii* zone as described for station 3a. During the colder seasons the *Vaucheria* species were: *V. arcassonensis*, *V. coronata*, *V. intermedia*, *V. synandra*, *V. erythrospora*, and *V. sescuplicaria*. In summer hardly any *Vaucheria* could be found; they were replaced by a growth of *Rhizoclonium*.

3.3.5. Station 3e (*figs. 1* and *2*)

At this locality a border of a bumpy appearance was found. The lower bumps bore a vegetation dominated by *Puccinellia maritima* and/or *Salicornia europaea*. The vegetation of the higher ones was dominated by *Juncus gerardii*. Among the bumps and on their lower edges, blackish cushions of *Vaucheria thuretii* and *V. sphaerospora* were found which were richly developed in summer.

These cushions were accompanied by *Puccinellia maritima*, *Aster tripolium*, and *Salicornia europaea*.

3.3.6. The ponds

In the water of the ponds a rich growth of *Ruppia spiralis* occurred. *Vaucheria* was never observed here.

4. DETAILED ANALYSIS OF SOME VAUCHERIA-RICH SITUATIONS

4.1. Cushion-like growth on black mud

4.1.1. Ditch situation (*figs. 1,1* and *2,1*)

Parallel to the road ran a ditch, its water-depth varying between 0 and about 10 cm, the salinity fluctuating between 4 and 16 (26) $^0/_{00}$ Cl^-. On the banks of this ditch at water level a thick blackish-green, more or less continuous belt of *Vaucheria* was found. This belt was accompanied mainly by *Salicornia europaea*. In the water *Ruppia maritima* and loose, floating masses of *Enteromorpha intestinalis* did occur. The substratum of the *Vaucheria* mass was a black, FeS containing sandy mud. Such *Vaucheria* cushions are continuously growing at the top and dying off and turning black at their bases. The *Vaucheria* belt had its maximum development during summer. In winter only here and there a *Vaucheria* tuft was found. Flooding and frost caused suffocation of this *Vaucheria* growth. The *Vaucheria* mass was formed by the following species: *V. thuretii*, *V. sphaerospora*, and *V. litorea* in varying relative quantities, the most important component being *V. thuretii*. This species has its maximum development in summer and early autumn. Reproductive structures were found only during that period. Asexual reproduction by means of aplanospores was often observed. This is apparently one of the causes of the rapid expansion of *V. thuretii* in summer. The occurrence of *V. sphaerospora* in this case could not be correlated with the season (reproductive organs mostly in summer and autumn, but also in winter and spring). *V. litorea* was present only in autumn and winter. This species prefers the colder seasons. It has short reproductive periods (not observed at this station). Contrary to *V. thuretii* and *V. sphaerospora*, *V. litorea* in general has its optimum occurrence under purely aquatic conditions like little pools, creeks, ditches, etc. The accompanying algae (predominantly Cyanophyceae) at this station were in order of decreasing quantity and frequency: *Lyngbya aestuarii*, *Oscillatoria* cf. *amphibia*, *Schizothrix calcicola*, *Enteromorpha intestinalis*, *E. prolifera*, *Percursaria percursa*, *Hydrocoleum lyngbyaceum*, *Anacystis dimidiata*. In summer *Lyngbya aestuarii* may form calcareous crusts on the *Vaucheria* masses.

4.1.2. Bumpy shore (*figs. 1,3* and *2,3e*)

For description of this locality see 3.3.5. Especially in late spring, summer and early autumn a growth of thick blackish *Vaucheria* cushions occurred on the edges of the bumps on a FeS and H_2S containing blackish mud. Purple bacteria were often visible. In winter, when the cushions were often flooded, the *Vauche-*

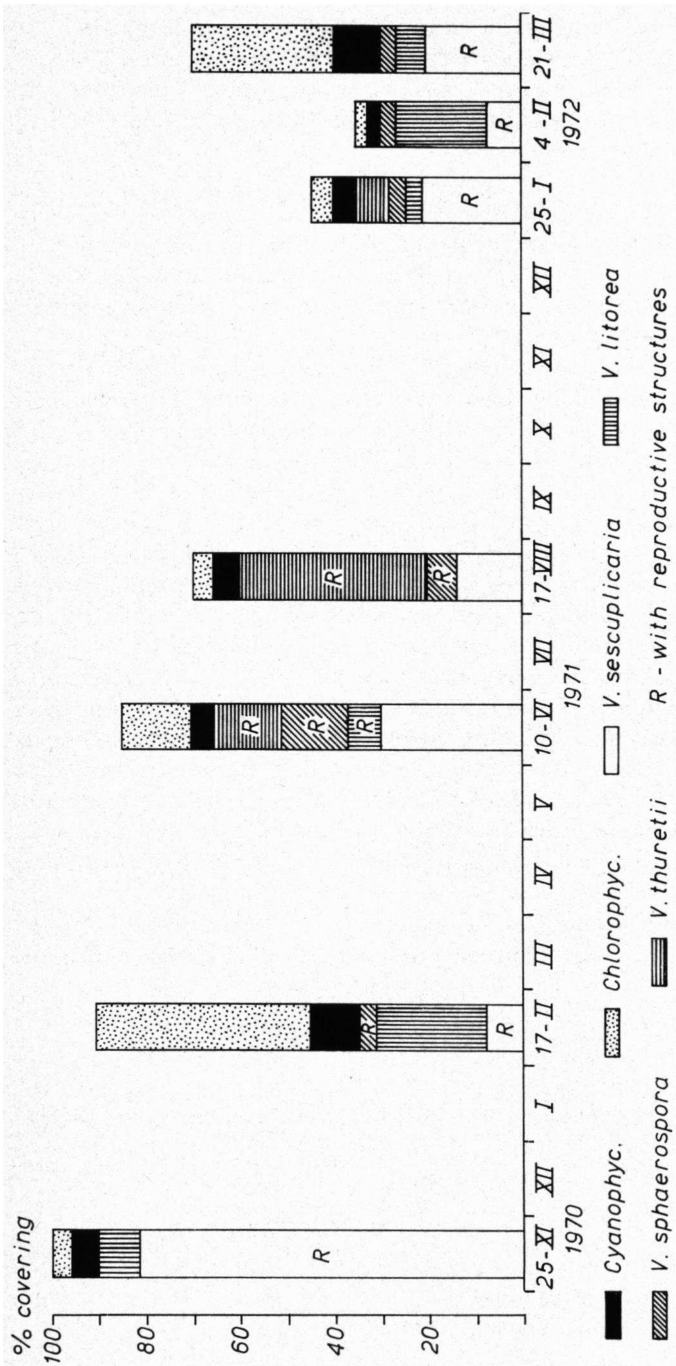

Fig. 3. Seasonal variation in species composition and covering of the *Vaucheria* mat on the P. Q. at station 3d.

ria aspect disappeared. The salinities during the growing period of *Vaucheria* varied between 8 and 15 °/₀₀ Cl. *V. thuretii* was the dominant species (75–90% of the sampled mass). Reproductive structures were found from June until October. The other *Vaucheria* species was *V. sphaerospora* (reproductive structures from August until October).

4.1.3. The permanent quadrate (*figs. 1,3d* and *2,3d*)

The aim of this P.Q. was to gain insight into the dynamics of variation in species composition in the course of at least one year. Apart from variations in quantity, the cushions always had the same aspect to the naked eye, yet internally there was a remarkable variability.

The P.Q. (50 × 50 cm) was situated on that part of the flat border where *Salicornia europaea* was accompanied by *Puccinellia maritima*, *Triglochin maritima* and *Spergularia media*. The covering percentages of phanerogams varied between 25 and 75%. A correlation between the covering of phanerogams and algae could not be found. Seven algal samples from the border of the P.Q. were, as far as possible, quantitatively analysed. The results are shown in *fig. 3*.

As is clearly visible from this figure, samples from different seasons have a different species composition. Here again *V. thuretii* had its optimum development in summer. *V. sphaerospora* flourished in late spring and summer, but was also present, albeit not in large quantities, during the other seasons. *V. sescuplicaria* had its maximum development in autumn 1970 and was present in all seasons with a minimum in winter. *V. litorea* had its maximum development in winter (compare 4.1.1) and was not present in the summer sample. Quite remarkable is the similarity of the *Vaucheria* species combination between February 1971 and February 1972. Each of these time spans was preceded by a period of frosty weather. Attention must also be paid to the coincidence of the optimum occurrence of *V. thuretii* and *V. sphaerospora* with the relatively high salinities in July and August. See *table 2*.

In *fig. 3* the first four columns show a competition for space between *Vaucheria* and the other algae. Evidently there is also competition for space among the *Vaucheria* species.

Table 2. Salinities of neighbouring pond water or of stagnant water on the P.Q. (+) on the 7 observation dates.

date	salinity (°/₀₀ Cl^-)
25– XI–1970	13.30
17– II–1971	8.10
10– VI–1971	14.00; 25.00 (+)
17–VIII–1971	16.30; 18.40 (+)
25– I–1972	9.60
4– II–1972	4.20
21– III–1972	10.70

The above mentioned phenomena, together with other observations (e.g. NIENHUIS & SIMONS 1971), support the idea that there exists a more or less cyclic variation in species composition, but not (at least not in general) a cyclic variation in total quantity of *Vaucheria.*

To check to what extent one sample is representative for the whole P.Q., six samples were taken within the quadrate on the last observation date. Four out of the six samples had a species composition as shown in the last column in *fig. 3.* The other two samples contained the same three species but in more or less different proportions. Thus we can state that the columns give a fairly correct picture of what really happened within the quadrate.

It must be kept in mind that the two winters in the observation period were of a mild nature with little frost, and that during the summer some extremely dry periods occurred.

The most important accompanying algae from the P.Q. were: Chlorophyceae: *Enteromorpha prolifera, Percursaria percursa, Rhizoclonium riparium, Ulothrix pseudoflacca, U. subflaccida;* Cyanophyceae: *Anacystis dimidiata, A. montana, Hydrocoleum lyngbyaceum, Lyngbya aestuarii, Nodularia harveyana, Oscillatoria* cf. *amphibia, O.* sp., *O. nigro-viridis, Phormidium corium, Schizothrix calcicola, Spirulina subsalsa.*

4.2. Drainage ditch situation (*figs. 1,2* and *2,2*)

The water and bank of a drainage ditch in one of the pastures appeared to provide a good habitat for *Vaucheria.* In summer the drain was mostly without water. When in other seasons the drain contained water, often a luxurious growth of *Vaucheria* (*V. litorea, V. sescuplicaria* and – less – *V. synandra*) could be observed in the water. The eastern bank of the drain, with a growth of *Puccinellia maritima, Agrostis stolonifera, Juncus gerardii, Festuca rubra,* and other halophytes like *Glaux maritima, Spergularia media,* and *Cochlearia danica* contained many small depressions caused by cattle tread. In these depressions *Vaucheria* was mostly present as small, bright green mats. Apparently these *Vaucheria* species often grow under circumstances of very reduced light intensities. The *Vaucheria* species encountered here were: *V. erythrospora, V. coronata, V. intermedia, V. sescuplicaria,* and *V. synandra.* Above the level of these brackish-water species we found several terrestrial species (especially in winter): *V. frigida, V. prona, V. dillwynii.* This last species group (+ *V. terrestris*) was of general occurrence on open spots in the surrounding pastures. *Fig. 4* gives an impression of the enormous qualitative as well as quantitative variation in the course of the seasons. These diagrams are the result of an analysis of four different samples from the same spot on the above-mentioned eastern drain bank.

We suppose that this enormous variation reflects the great variation in salinity of soil moisture on this spot. See *table 3.*

From these diagrams the following facts, which are generally valid, can be deduced: *V. intermedia* seldom occurs in winter. *V. erythrospora* and *V. coronata* occur rarely or never in summer, and the best growing period for many *Vaucheria* species is autumn and/or spring.

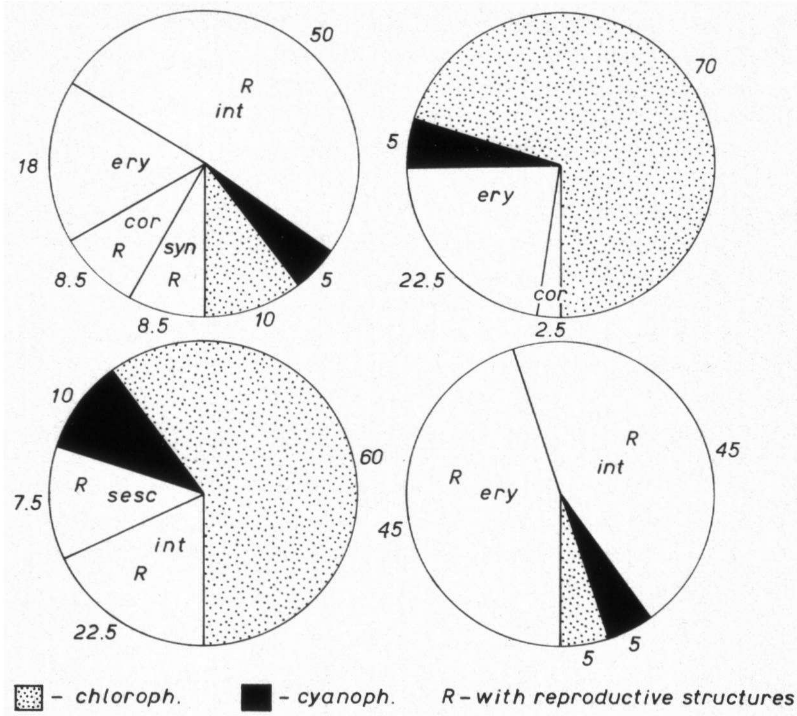

Fig. 4. Seasonal variation in algal composition at one spot on the eastern bank of drainage ditch. Upper diagram left: observation on 25–XI–1970, upper right: on 17–II–1971, lower right: on 10–VI–1971, lower left: on 17–VIII–1971. cor: *Vaucheria coronata*, ery: *V. erythrospora*, int: *V. intermedia*, sesc: *V. sescuplicaria*, syn: *V. synandra*. Figures relate to estimated percentages.

Table 3. Moisture and salinity values expressed as g H_2O/100 g soil and ‰ Cl^-/l soil-moisture resp. on the eastern drain bank on the four observation data.

date	moisture	salinity
25– XI–1970	71.1	5.32
17– II–1971	123.4	0.74
10– VI–1971	62.2	20.90
17–VIII–1971	62.3	16.30

Accompanying algae in this locality were: Chlorophyceae: *Percursaria percursa*, *Rhizoclonium riparium*, *Ulothrix subflaccida;* Cyanophyceae: *Anabaena* cf. *variabilis*, *Hydrocoleum lyngbyaceum*, *Lyngbya aestuarii*, *L. semiplena*, *Microcoleus vaginatus*, *Nodularia harveyana*, *Nostoc* sp., *Oscillatoria brevis*, *Phormidium autumnale*, *Symploca funicularis*, *Schizothrix calcicola*.

4.3. Transition from pond to pasture (*figs. 1,3b* and *2,3b*)

On this rather steep and continuous transition from pond to pasture a relatively clear pattern of zonation (if there were to be any) could be expected.

At a marked spot a series of samples were taken from the lowest occurring growth of *Vaucheria* up to the highest at intervals of about 5 cm. The sample spots were related to a standard level (about 23 cm above mean water level). Maximum water level can reach this point. In some spots on the line of samples moisture content and salinity of soil were determined. One observation was made in autumn, the other in winter. In summer hardly any *Vaucheria* could be observed. The result of the sample analysis is shown in *fig. 5*. It appeared that in

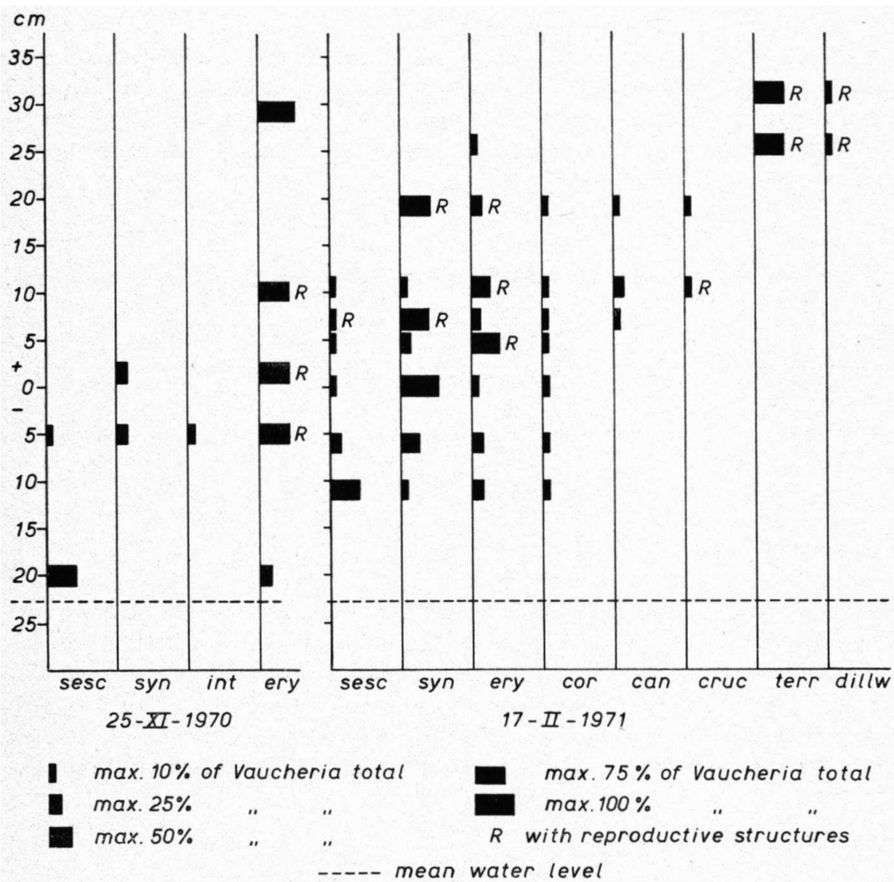

Fig. 5. Species composition of *Vaucheria* growth from pond water level upwards to pasture level (+ 30 cm). sesc: *Vaucheria sescuplicaria*, syn: *V. synandra*, int. *V. intermedia*, ery: *V. erythrospora*, cor: *V. coronata*, can: *V. canalicularis*, cruc: *V. cruciata*, terr: *V. terrestris*, dillw: *V. dillwynii*.

autumn the lowest level of *Vaucheria* growth was lower than in winter (*Vaucheria* apparently did not like flooding). In autumn there were only four species as compared to eight in winter. Another remarkable fact to be pointed out is the vertical migration of species. *V. sescuplicaria*, for example, grows at higher levels and over a wider range in winter than in autumn. *V. synandra* too extends its range in winter. Presumably this was caused by the higher winter moisture values at higher levels. In winter the terrestrial species *V. terrestris* (in this case an intermediate form between *V. terrestris* and *V. frigida*) and *V. dillwynii* grow on the upper level. There they replace the autumn occurrence of *V. erythrospora*. The winter occurrence of *V. coronata* and *V. cruciata* is more or less inherent to these species. Concerning the zonation pattern: in autumn this figured from low to high: *V. sescuplicaria* → *V. synandra* → *V. erythrospora;* in winter: *V. sescuplicaria* → *V. synandra* + *V. coronata* + *V. erythrospora* → *V. canalicularis* + *V. cruciata* → *V. terrestris* + *V. dillwynii.*

It should be noted that the species have more or less overlapping vertical ranges and that they quantitatively affect each other, causing a zonation pattern without definite boundaries. In this situation the mixture of species gradually changes in composition along a gradient of moisture and salinity in the upper soil layer, as shown in *table 4*.

Table 4. Moisture and salinity values on different spots along the shore transect (expressed as in *table* 3).

date	level + or – 0	moisture	salinity
25–XI–1970	– 12 cm	123.2	5.84
	+ 30 cm	39.5	1.85
17– II–1971	– 10 cm	173.8	2.90
	+ 5 cm	166.3	1.50
	+ 30 cm	41.4	0.01

The zonation tendencies as observed here are in agreement with observations from other brackish inland localities (to be published). The distribution pattern of accompanying algae showed no clear zonation, except that *Enteromorpha prolifera*, *E. torta* and *Percursaria percursa* were restricted to the lowest level. Six species, namely *Rhizoclonium riparium*, *Ulothrix flacca*, *U. pseudoflacca*, *U. subflaccida*, *Nostoc* sp. and *Schizothrix calcicola* occurred over the whole transect.

5. CONCLUDING REMARKS

Four groups of *Vaucheria* spp. may be discerned. The group on the lowest levels with optimum development under relatively high soil-moisture conditions consists of *V. sescuplicaria*, *V. litorea*, *V. sphaerospora* and *V. thuretii* (group a). The halophytes accompanying this group mostly belong to vegetations in which

Puccinellia maritima and/or *Salicornia europaea* play a dominant role. *V. sphaerospora* and *V. thuretii* tolerate high salinities and are adapted to growing on blackish mud.

The aspect of *Vaucheria* cushions on black mud is not uncommon in the Netherlands. A very typical locality, for example, is "Breede Gooi", a brackish creek at Herkingen on Goeree-Overflakkee in the S.W. part of the country (RAPPARD 1967). At Breede Gooi we found that the most important species are *V. thuretii* and *V. sphaerospora,* while *V. sescuplicaria* is present in very small quantities within the cushions. Another species which may form thick cushions is *V. compacta,* presumably under circumstances of relatively low average salinities (examples: "De Bol" on the isle of Texel; ditches directly behind the dikes of the Westerschelde near Terneuzen and Bath in the S.W. estuarine region of the Netherlands). *V. thuretii, V. sphaerospora* and *V. compacta* are often found together in salt marshes, forming a zone on the high littoral part of creek banks, on blackish, often sandy silt (SIMONS & VROMAN 1968; NIENHUIS 1970; NIENHUIS & SIMONS 1971). This zone has its optimum development in summer and autumn. Apparently these species prefer (or tolerate in the case of *V. compacta*) rather high salinities and high moisture conditions and endure an oxygen-poor, H_2S containing substratum.

At "De Putten" on the succeedingly higher levels where *Juncus gerardii* often is the dominant species, the following *Vaucheria* species are mostly met with: *V. synandra, V. erythrospora* and *V. sescuplicaria* (group b). In the transition zone between this level and the terrestrial pasture vegetation *V. synandra* and *V. erythrospora* may be accompanied by *V. canalicularis* and *V. cruciata* (group c). In pasture- (and dike-) vegetations the terrestrial species *V. dillwynii, V. frigida, V. terrestris* and *V. prona* find their optimum habitat (group d). The distinction between *V. frigida* and *V. terrestris* as made by CHRISTENSEN (1969) is not a clear one. Intermediate forms occur, suggesting that one species is involved rather than two (*V. frigida*).

The species *V. coronata, V. intermedia,* and *V. arcassonensis* which have great ecological affinities to each other, do not fit very well into the groups mentioned above. They can be found in group a as well as in group b and occasionally also in group c. Probably this group of species is better adapted to salt marsh situations than to inland brackish localities. They often are the only three *Vaucheria* species in the supra-littoral zone of salt marshes (NIENHUIS & SIMONS 1971).

It should be noted that this is a generalized scheme. There are many exceptional situations caused by small local variations. Apart from this restriction the species have overlapping ecological amplitudes, and as they mostly grow together, they strongly affect each other.

As to periodicity the following generalizations can be made: Species with optimum development during autumn, winter and spring are: *V. arcassonensis, V. coronata, V. erythrospora, V. litorea, V. dillwynii, V. terrestris, V. frigida, V. prona, V. canalicularis, V. cruciata.* Species with optimum development in summer are: *V. thuretii, V. sphaerospora* and *V. intermedia. V. sescuplicaria* and *V. synandra* show no clear seasonal periodicity.

Periodicity phenomena of *Vaucheria* species and other algae, based on a quantitative approach by monthly observations at some P.Q.'s in different brackish inland localities in the S.W. part of the Netherlands, will be dealt with in a next publication.

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