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PERIODICITY AND DISTRIBUTION OF BRACKISH VAUCHERIA SPECIES FROM NON-TIDAL COASTAL AREAS IN THE S.W. NETHERLANDS

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SUMMARY

Data are given on periodicity and distribution of fourteen *Vaucheria* species in saline inland areas in the S.W. Netherlands. Periodicity was studied by monthly sampling of permanent sample plots measuring 50 × 50 cm² during the years 1970–1972. Salinity and soil-moisture content of the upper soil layer were measured near the sample plots. Periodicity and distribution of *Vaucheriae* were found to be correlated with soil-moisture and salinity conditions. *Vaucheria* growth as a whole attains optimum development in the colder seasons. Two species occur in all seasons, and two species show optimum summer occurrence. Germination of oospores takes place mainly under low-salinity conditions. The pattern of distribution shows a similar zonation as described earlier for a brackish area in the northern part of the Netherlands.

1. INTRODUCTION

In the S.W. estuarine region of the Netherlands, different types of brackish marshes exist at the landward side of the dikes. In such areas considerable algal vegetations may develop.

The most striking component is formed by the green alga *Rhizoclonium riparium*, especially in relatively open spots in the halophilous vegetation. Besides *Rhizoclonium*, blue-green algae and *Vaucheria* species may form conspicuous aspects of the algal layer, not only in open spots, but also among the vegetation where this is not too dense.

During the last few years the algae of this type of habitat are studied by several Dutch algologists. The study of the present author is focused on the *Vaucheria* species of the Dutch coastal region (SIMONS & VROMAN 1968, 1973; SIMONS 1974a, b, 1975). Data on *Vaucheriae* occurring in inland brackish areas have been given by RAPPARD (1967), SIMONS & VROMAN (1973), DEN HARTOG (1973), POLDERMAN & PRUD'HOMME VAN REINE (1973), POLDERMAN (1974). Periodicity of some *Vaucheria* species in a salt marsh was studied by NIENHUIS & SIMONS (1971), applying nearly the same method as described in this paper.

In the paper by SIMONS & VROMAN (1973) a survey was given of *Vaucheria* species along the shores of the brackish ponds "De Putten" in the northern part of the Netherlands. The data given mainly concern the question whether or not a pattern of zonation exists in the composition of *Vaucheria* species from water level up to the level of surrounding pastures. At one spot the *Vaucheria* growth

within a permanent quadrate (P.Q.) was observed. Within the *Vaucheria* cushions at this locality the species composition showed an interesting periodicity.

The present paper aims to get insight in the dynamics of *Vaucheria* vegetations in relation to environmental factors as salinity and soil-moisture content. Data were mainly gathered in the period between October 1970 and September 1973.

2. AREAS INVESTIGATED; METEOROLOGICAL DATA

The geographic location of the areas dealt with in this paper is shown in *fig. 1;* they can be briefly described as follows:

1. Dijkwater: a deep brackish creek with sandy shores, separated from the Grevelingen sea-arm by a dike in 1954. Salinity of the creek water appeared to be rather constant (mostly 7–8‰ Cl^-). The area is surrounded by pastures and agricultural fields.
2. Guil, Vianen: a shallow pool with muddy and sandy shores, surrounded by small dikes. The salinity of the pool water varied between 4 and 19‰ Cl^- during the period of investigation.
3. Gat van Ouwerkerk: a deep saline water basin (salinity 11–13‰ Cl^-), formed after a breach in the dike bordering the Eastern Scheldt (1953). Between the basin and the surrounding landward dikes sandy soil is found.
4. Susanna Inlaag: a saline basin (observed salinities 3–31‰ Cl^-) behind the dike bordering the Eastern Scheldt, at the landward side surrounded by dikes. Between the water basin and the dikes flat clayish shores with dense halophilous vegetation are found. It originated in the same way as the Gat van Ouwerkerk by a breach-through of the Eastern Scheldt dike in the past.
5. Koudekerksche Inlaag: a brackish area bordering the Eastern Scheldt with shallow pools and ditches between swampy grasslands. The area is enclosed by dikes.
6. Deesche Watergang: relatively low area with shallow pools and ditches. The swampy grassland is intersected by small drainage ditches; it is surrounded by agricultural fields.
7. Inlaag 1887: as Koudekerksche Inlaag; only one large shallow pool is present.

Shallow brackish inland waters in the Netherlands are characterized by a yearly periodicity in salinity. Salinities are relatively low in late autumn, winter and early spring (precipitation surplus), but rather high in the other periods (evapo-transpiration surplus). The waters of the mentioned areas show the same phenomena.

Meteorological data for the S.W. Netherlands which may be of importance to evaluate the observed periodicity are: mean annual precipitation: 706 mm, most precipitation falling from July to November; mean temperature in January 1.9 °C, in July and August 16.8 °C. During the period of investigation several dry periods occurred: the summer of 1971, winter 1971–1972, late summer and autumn 1972. In dry summer periods extremely high salinity values were often recorded. The winters of 1971, 1972 and 1973 were mild with little, if any frost.

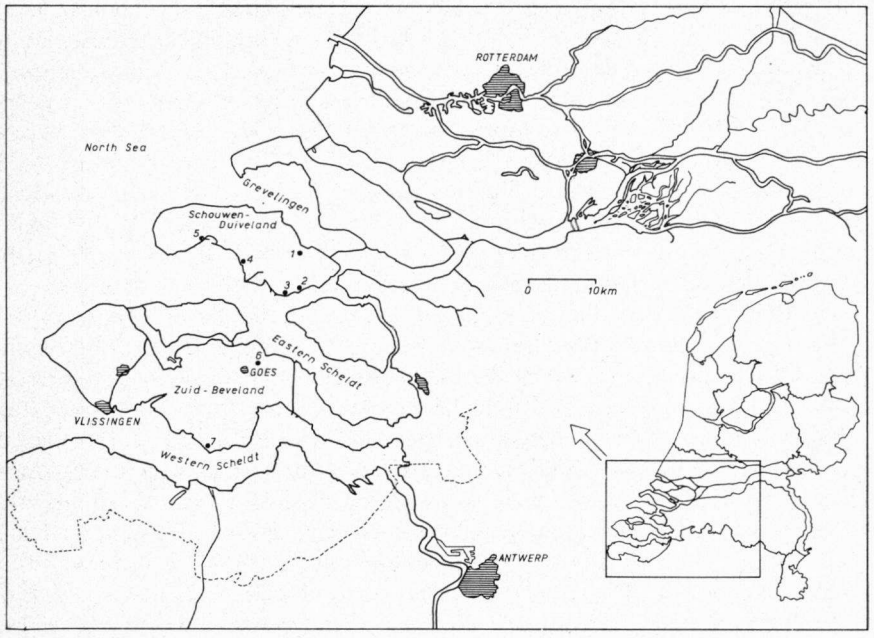

Fig. 1. Map of the S.W. Dutch estuarine region with sample stations indicated: 1. Dijkwater; 2. Guil, Vianen; 3. Gat van Ouwerkerk; 4. Susanna Inlaag; 5. Koudekerksche Inlaag; 6. Deesche Watergang; 7. Inlaag 1887.

3. MATERIAL, METHODS AND NOMENCLATURE

At the start of the investigation in October 1970, *Vaucheria* was richly developed. Permanent sample plots were selected in different vegetations representing as many *Vaucheria* aspects as could be discerned.

The size of each permanent sample plot (PSP) amounted to 50 × 50 cm². With the aid of a lattice an estimate of covering percentages by algal groups and phanerogams was made. The algal groups distinguished in the field were: *Vaucheria* spp., filamentous green algae (mostly *Rhizoclonium riparium*) and blue-green algae.

From each algal group a sample was taken. These samples were taken from outside each PSP in order to keep the situation within the square undisturbed. *Vaucheria* samples measured 4 to 6 × 2 × 1 cm. One part of each *Vaucheria* sample was fixed in formaldehyde 4%, the other part was cultivated for about three weeks in an Erdschreiber medium in petri-dishes to induce maximum development of reproductive structures. Culture conditions involved a temperature of c. 12 °C, a photoperiod L/D 12:12, and light intensities between 1000 and 2000 Lux. The salinity of the medium mostly lied between 3 and $10^0/_{00}$ Cl^-.

The relative quantities of *Vaucheria* species in the sample were estimated by combining the data from the fixed part of the sample with those of the cultivated

part. These quantities were expressed as follows: +: 0–10% of total *Vaucheria*, 1: 10–25%, 2: 25–50%, 3: 50–75%, 4: 75–100%. For graphical representation the maximum obtainable value for each species was used. The relative quantities of the *Vaucheria* species within a sample were assumed to be representative for the whole PSP. At a few occassions this was tested, from which appeared that this may be done at least within the rather broad estimating intervals as used in this investigation. The green and blue-green algae accompanying *Vaucheria* were identified and their quantities were estimated. Only when accompanying algae or algal groups other than *Rhizoclonium* attained 10% or more of the total sample, they were also graphically represented.

The PSP's were visited monthly, during the second decade. At every monthly visit a soil sample near the PSP was taken from the upper 2 cm to determine moisture content and salinity of the soil moisture. These values were expressed as g H_2O/100 g oven-dried soil and g Cl^-/l soil moisture ($^0/_{00}$ Cl^-) respectively.

Nomenclature of the phanerogamic species is in accordance with HEUKELS & VAN OOSTSTROOM (1970). Names of vegetation units are based upon WESTHOFF & DEN HELD (1969). The nomenclature of the coccoid *Cyanophyceae* follows DROUET & DAILY (1956), that of the non-coccoid forms is based upon GEITLER (1932). The following taxa of the filamentous blue-green algae however, were named according to DROUET (1968): *Spirulina subsalsa*, *Microcoleus lyngbyaceus* (some of the synonyms are *Hydrocoleum lyngbyaceum* Kütz., *Lyngbya aestuarii* (Mert.) Lyngb., *L. semiplena* (Ag.) J. Ag.), *Schizothrix calcicola* and *Microcoleus vaginatus*.

The morphology and nomenclature of *Vaucheria* species are dealt with by RIETH (1956), CHRISTENSEN (1952, 1956, 1969, 1973), and BLUM (1972). The nomenclatoral changes as proposed by CHRISTENSEN (1969, 1973) have been followed. This means a.o. that *Vaucheria subsimplex* = *V. sphaerospora* and *V. velutina* = *V. thuretii*.

4. RESULTS

From 12 PSP's data are presented on occurrence and periodicity of *Vaucheria* species and other algae. In *table 1* a survey is given of the higher plants and *Vaucheria* species occurring at these PSP's. The results will be dealt with in 3 sections respectively: a group of PSP's with open vegetations (4.1: PSP 1, 2, 10, 13), a group of PSP's in rather dense grassy vegetations (4.2: PSP 8, 6, 5, 12, 9) and some PSP's with large *Vaucheria* masses situated at the edges of pools and ditches (4.3: PSP 11, 4, 15).

4.1. PSP's in open vegetations belonging to the Puccinellio-Spergularion salinae, Saginion maritimae, Agropyro-Rumicion crispi

4.1.1. Description of PSP 1, 2, 10 and 13

PSP 1 (Dijkwater) was situated relatively high compared to the surrounding

Table 1. Survey of higher plants, one moss, and Vaucheria species at the PSP's dealt with. Figures relate to covering percentages; +: present; ⊗: dominant or codominant species; v.: only seen in vegetative state. Covering percentages apply to the situation in summer.

	PSP 1	PSP 2	PSP 10	PSP 13	PSP 8	PSP 6	PSP 5	PSP 12	PSP 9	PSP 11	PSP 4	PSP 15
Matricaria maritima (spp. *indora* var. *salina*)	40	–	–	–	–	–	–	–	–	–	–	–
Chenopodium rubrum	<5	–	–	–	–	–	–	–	–	–	–	–
Agrostis stolonifera	10	5	5	–	–	–	–	10	<5	–	–	–
Juncus bufonius (ssp. *ambiguus*)	5	25	–	10	–	–	–	–	–	–	–	–
Centaurium pulchellum	<5	–	–	–	–	–	–	–	–	–	–	–
Centaurium littorale	–	<5	–	–	–	–	–	–	–	–	–	–
Taraxacum sp.	<5	–	–	–	–	–	–	–	–	–	–	–
Plantago major	5	–	–	–	–	–	–	–	–	–	–	–
Trifolium repens	<5	–	–	–	–	–	–	–	–	–	–	–
Spergularia marina	–	20	<5	<5	–	–	–	<5	–	<5	–	–
Spergularia media	–	–	<5	–	<5	5	5	–	–	–	–	–
Salicornia europaea	–	<5(v)	⩽5(v)	–	<5(v)	5	<5(v)	<5(v)	–	10	+	–
Puccinellia distans	–	10	20	5	–	–	–	–	–	5	–	–
Aster tripolium	–	10(v)	15(v)	<5(v)	–	–	<5(v)	5(v)	–	30	–	–
Juncus gerardii	–	–	10	–	65	–	65	75	75	–	+	–
Parapholis strigosa	–	–	<5	–	–	–	5	5	5	–	–	–
Hordeum marinum	–	–	<5	–	–	–	–	–	–	–	–	–
Sagina maritima	–	–	–	15	–	–	–	–	–	–	–	–
Plantago coronopus	–	–	–	<5	–	–	–	–	<5	–	–	–
Glaux maritima	–	–	–	<5	–	–	–	<5	<5	–	–	–
Puccinellia maritima	–	–	–	–	20	20	15	–	5	–	+	70
Suaeda maritima	–	–	–	–	<5(v)	–	–	–	–	–	+	–
Triglochin maritima	–	–	–	–	–	40	–	–	–	–	–	–
Cochlearia danica	–	–	–	–	–	–	5	<5	–	–	–	–
Puccinellia fasciculata	–	–	–	–	–	–	–	–	–	–	–	5
Puccinellia capillaris	–	–	–	–	–	–	–	–	–	–	–	5
Pottia heimii	<5	–	–	–	–	–	–	–	5	–	–	–
Vaucheria canalicularis	⊗	–	–	–	–	–	–	–	+	–	–	–
Vaucheria synandra	⊗	+	+	–	+	–	–	⊗	⊗	–	–	–
Vaucheria intermedia	+	⊗	–	–	+	⊗	⊗	+	+	–	–	–
Vaucheria sescuplicaria	–	–	⊗	–	⊗	⊗	⊗	+	+	⊗	+	–
Vaucheria erythrospora	–	+	⊗	⊗	⊗	+	⊗	+	+	–	–	–
Vaucheria arcassonensis	–	–	+	–	+	+	+	+	–	–	–	–
Vaucheria coronata	–	–	+	–	+	+	+	+	–	–	–	–
Vaucheria velutina	–	–	–	–	–	–	–	–	–	+	⊗	⊗
Vaucheria subsimplex	–	–	–	–	–	–	–	–	–	+	⊗	⊗
Vaucheria litorea	–	–	–	–	–	–	–	–	–	–	–	+
Vaucheria compacta	–	–	–	–	–	–	–	–	–	+	–	–

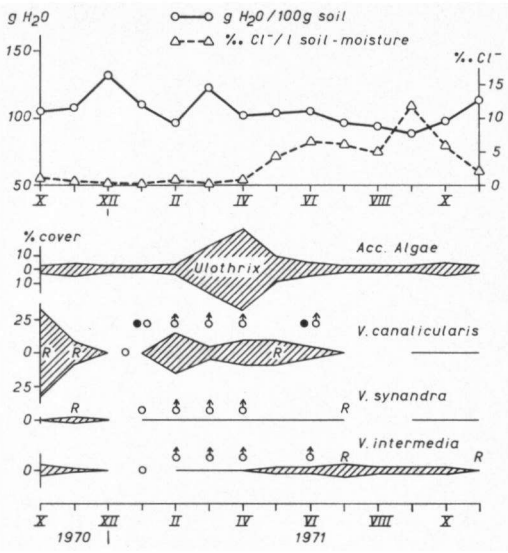

Fig. 2. Periodicity of *Vaucheria* spp. and other algae together with fluctuations of soil-moisture content and salinity of soil-moisture at PSP 1. Acc.: accompanying, R: reproductive structures, o: loose oospores, ♂: germinating oospores, ●: aplanospores

area, on clayish soil bearing a rather open vegetation. The phanerogamic species (*table 1*) could not be assigned to one vegetational unit, but belonged partly to the *Agropyro-Rumicion crispi* and partly to the *Puccinellio-Spergularion salinae*. Total covering of the phanerogams varied between less than 10% in winter and 60% in summer. Total covering of algae appeared not to be correlated with the phanerogamic covering, as was also the case in most PSP's studied.

PSP 1 was sampled from October 1970 until December 1971. In *fig. 2* observations on the algal vegetation are depicted. The main *Vaucheria* species was *V. canalicularis*, a limnic species penetrating into the brackish biotope (SIMONS 1975). *V. canalicularis* was accompanied by the brackish species *V. synandra* and *V. intermedia*. *V. intermedia* disappeared in winter, reappearing in summer at the onset of dry weather with relatively high salinities in the upper soil layer. The replacement, in summer, of other *Vaucheria* species by *V. intermedia* is a general phenomenon in the Netherlands. The high salinities in the summer of 1971 may be responsible for the disappearance of *V. canalicularis* and *V. synandra* in summer and for the fact that *Vaucheria* did not resume the high covering percentage as at the beginning of the observations.

The green and blue-green algae were of minor importance on this spot. A remarkable peak occurrence of *Ulothrix* was found between February and May, chiefly caused by *Ulothrix pseudoflacca*. A similar *Ulothrix* peak was observed by POLDERMAN (1974).

PSP 2 (Dijkwater) was located in a relatively low flat sandy area bordered by a vegetation comparable to that of PSP 1. The vegetation at PSP 2 (see *table 1*)

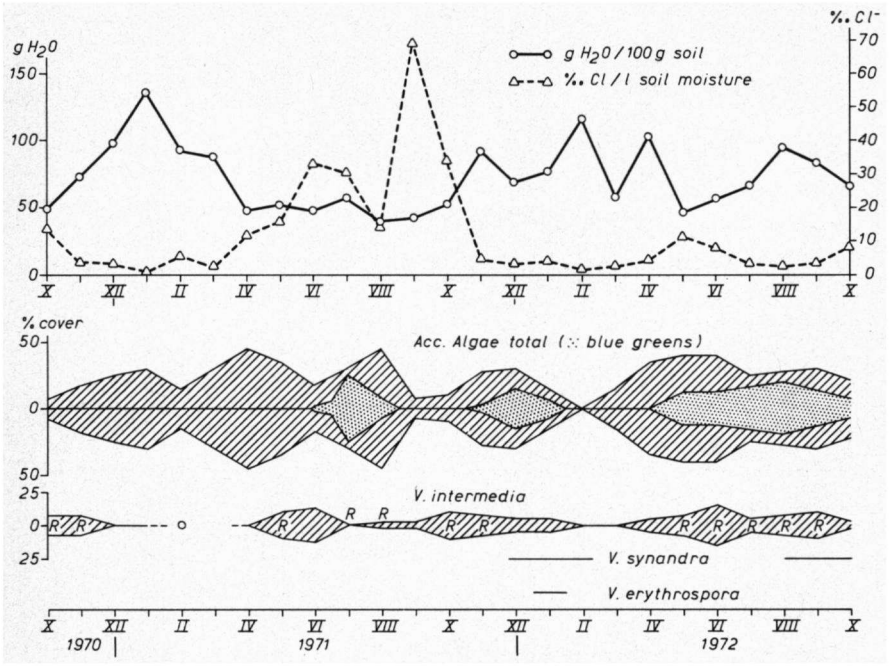

Fig. 3. Periodicity of *Vaucheria* spp. and other algae together with fluctuations of soil-moisture content and salinity of soil-moisture at PSP 2.

may be classified as *Puccinellietum distantis* which belongs to the *Puccinellio-Spergularion salinae*. Total covering of higher plants varied between 5 and 70%. The upper soil showed black sulfide layers. *Fig. 3* shows that salinity of the soil moisture was generally less than $10^0/_{00}$ Cl^-; extremely high values were recorded in the dry summer of 1971 (maximum of $69^0/_{00}$ Cl^-!). Total *Vaucheria* covering was rather constant, varying between 0 and 30%. The covering of green and blue-greens was generally higher and strongly fluctuating (< 5%–90%). The aspect of the algae, other than *Vaucheria*, was dominated by *Rhizoclonium riparium*. The main *Vaucheria* species appeared to be *V. intermedia;* it was conspicuously absent in winter, when only oospores of this species could be found. The decrease of *V. intermedia* and the maximum development of the blue-green algae in the months June, July and September 1971 coincided with extremely high salinities in this period. At the end of 1971 *V. erythrospora* and *V. synandra* appeared as new elements in the algal vegetation, presumably penetrating into the PSP from the adjoining *Agrostis* vegetation in which these species were often recorded. In summer blue-greens formed a conspicuous aspect of the algal mat, often overgrowing the *Vaucheria* cushions. Quantitatively the most important blue-greens were *Microcoleus lyngbyaceus*, *M. chthonoplastes* and *Symploca funicularis*.

PSP 10 (Guil, Vianen) was situated on sandy soil which contained some silt

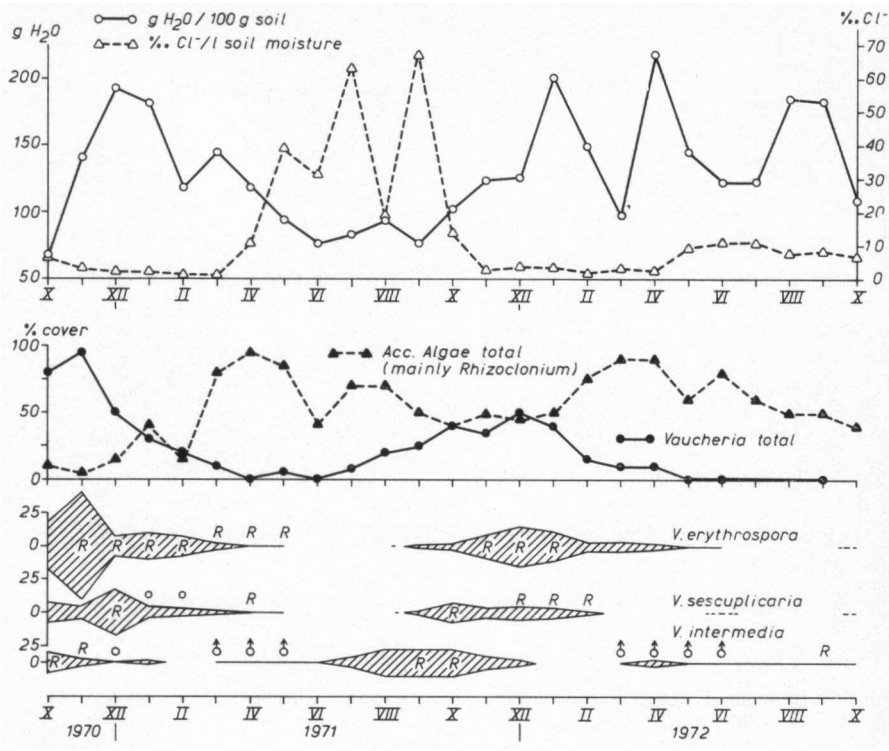

Fig. 4. Periodicity of *Vaucheria* spp. and other algae together with fluctuations of soil-moisture content and salinity of soil-moisture at PSP 10.

in the upper cm's. Its open vegetation may at best be classified as belonging to a *Puccinellietum distantis*. The adjacent vegetation consisted of large patches of *Agrostis stolonifera* with *Hordeum marinum* and *Juncus gerardii*.

The algal vegetation was recorded in detail until May 1972 (*fig. 4*). Thereafter *Vaucheria* hardly played any role in the algal vegetation until autumn 1973. *Fig. 4* shows the main *Vaucheria* species to be *V. erythrospora* and *V. sescuplicaria*, both with maximum development in the cold and wet seasons. *V. intermedia* came to considerable development in summer 1971 despite the high salinity. Species of minor importance were *V. synandra*, *V. coronata* and *V. arcassonensis* (not shown in *fig. 4*). During 1971 there was a striking alternation between the maximum development of green and blue-green algae in spring and summer and the optimum development of *Vaucheria* in winter and autumn. Similar alternations were frequently observed at other PSP's.

PSP 13 (Gat van Ouwerkerk) was situated on a flat sandy area with a very open vegetation containing many small therophytes as *Sagina maritima*, *Spergularia marina* and *Juncus bufonius* (see *table 1*). Total covering varied between 5 and 40%. Outside the PSP in the same sandy area the following species were re-

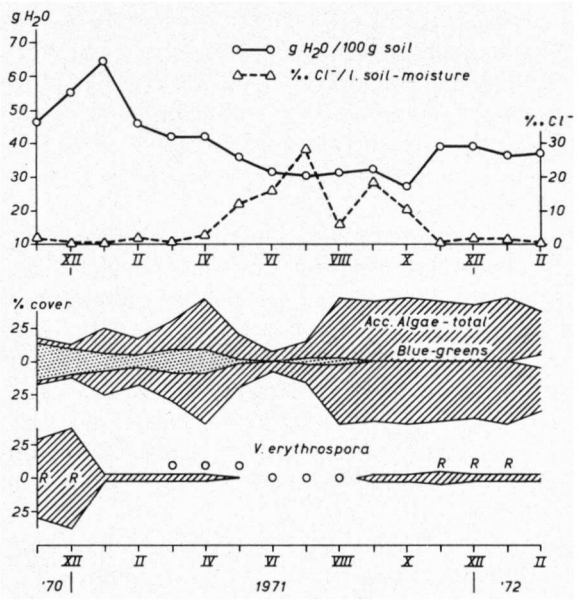

Fig. 5. Periodicity of *Vaucheria erythrospora* and other algae together with fluctuations of soil moisture content and salinity of soil-moisture at PSP 13.

corded: *Agrostis stolonifera, Plantago major, Cirsium vulgare, Carex distans, Leontodon autumnalis, Centaurium pulchellum* and *Samolus valerandi.* The vegetation at PSP 13 may be classified as belonging to the *Saginion maritimae* with elements of the *Agropyro-Rumicion crispi* and the *Puccinellio-Spergularion salinae.*

Soil moisture content was lower than at PSP 1, 2 and 10. Except for the high values recorded in the summer of 1971, salinities were generally very low. The algae at PSP 13 were sampled until March 1972 (*fig. 5*). Since that time *Vaucheria* was absent until it reappeared in autumn 1972. *Vaucheria* was only represented by *V. erythrospora.* This species has its optimum development in the colder seasons. Very often it occurs at open sandy localities on high salt marshes and also in beach plains. The aspect of the accompanying green and blue-green algee was determined by *Rhizoclonium riparium* and *Nostoc* sp. *Nostoc* often forms a striking component of the algal vegetation of beach plain habitats. *Fig. 5* shows that due to desiccation not only *V. erythrospora* disappeared in summer, but also for the greater part the companion algae. Maximum development of *V. erythrospora* coincided with the highest soil moisture values which were recorded in autumn and winter 1970/1971.

4.1.2. Concluding remarks

Resuming the data from PSP 1, 2, 10 and 13, the following general statements can be made:

In brackish inland vegetations belonging to the *Puccinellio-Spergularion salinae*, *Saginion maritimae* and *Agropyro-Rumicion crispi*, which have in common a large degree of instability in factors as soil moisture and salinity, the *Vaucheria* species *V. canalicularis*, *V. erythrospora*, *V. synandra*, *V. intermedia*, *V. coronata*, *V. arcassonensis* and *V. sescuplicaria* were recorded. Which combination of species occurs at a certain locality is clearly influenced by the local constitution of soil moisture and soil salinity.

PSP 1 and 13 have in common very low salinities during the cold seasons. Moisture content of the clayish PSP 1 was mostly higher than at the sandy PSP 13. This may account for the difference in species composition (*V. canalicularis* and *V. synandra* at PSP 1, *V. erythrospora* at PSP 13). This assumption is supported by data from the brackish ponds "De Putten" (SIMONS & VROMAN 1973) where *V. erythrospora* showed a larger tolerance towards dry conditions than *V. canalicularis* and *V. synandra*. In summer, under relatively high salinity conditions, *V. intermedia* penetrated into PSP 1 presumably from the adjacent sandy plain where this species richly occurred. Near PSP 13 *V. intermedia* was not recorded.

PSP 2 and 10, both in *Puccinellietum distantis* vegetations (PSP 2 with *Juncus bufonius* and PSP 10 with *Parapholis strigosa*) also contain different combinations of *Vaucheria* species. At PSP 2 *V. intermedia* was the main species and at PSP 10 *V. erythrospora*, *V. sescuplicaria* and *V. intermedia* were recorded, sometimes accompanied by *V. synandra*, *V. coronata* and *V. arcassonensis*. The occurrence of *V. sescuplicaria* at PSP 10 and not at PSP 2 can be explained by the fact that soil moisture content at PSP 10 was considerably higher than at PSP 2. Salinities at PSP 2 and 10 were generally higher than at PSP 1 and 13, especially in summer. This may account for the rather rich occurrence of *V. intermedia* at PSP 2 and 10 in summer, and the occurrence of *V. coronata* and *V. arcassonensis* at PSP 10. The latter assumption is supported by the fact that *V. arcassonensis*, *V. coronata* and *V. intermedia* belong to a polyhalobe group of species and *V. synandra*, and *V. erythrospora* to a meso-oligohalobe group in estuarine environments (SIMONS 1975).

4.2. PSP's in grassy vegetations with Puccinellia maritima and/or Juncus gerardii

4.2.1. Description of PSP 8, 6, 5, 12 and 9

PSP 8 (Deesche Watergang) was situated in a grassy vegetation on clayish soil (2 à 3 cm clay on sand). The aspect of the vegetation was determined by *Juncus gerardii* and *Puccinellia maritima* (max. height 6 cm). For total composition of species see *table 1*. Total covering of higher plants varied between 70 and 95 %.

Despite the rather dense vegetation, the algal mat was well developed, its total covering varying between 35 and 95 %. The algal vegetation has been studied in detail until July 1972 (*fig. 6*). After that time the phanerogamic vegetation, probably due to long absence of grazing, had grown too dense for the algae to develop.

Fig. 6 shows a striking interaction between *Vaucheria* and the other algae (predominantly *Rhizoclonium*). When *Vaucheria* was well developed in winter and autumn, the covering of the accompanying algae was considerably lower than in spring and summer when *Vaucheria* was rather poorly developed. At the onset of dry weather in spring 1971 *Vaucheria* sharply decreased in covering, while *Rhizoclonium* increased. At the end of the summer 1971 in which extremely high salinities were measured, the blue-green algae were well developed. The most important blue-greens were *Microcoleus lyngbyaceus*, *M. chthonoplastes*, *Anacystis montana*, *Coccochloris stagnina* and *Spirulina subsalsa*.

When regarding the different *Vaucheria* species, it appears that each one shows its own pattern of periodicity. The three main species were *V. sescuplicaria*, *V. intermedia* and *V. erythrospora;* of minor importance were *V. coronata* and especially *V. arcassonensis* and *V. synandra*. The last two species may often have escaped detection. During the first year of observation the growth pattern of *V.*

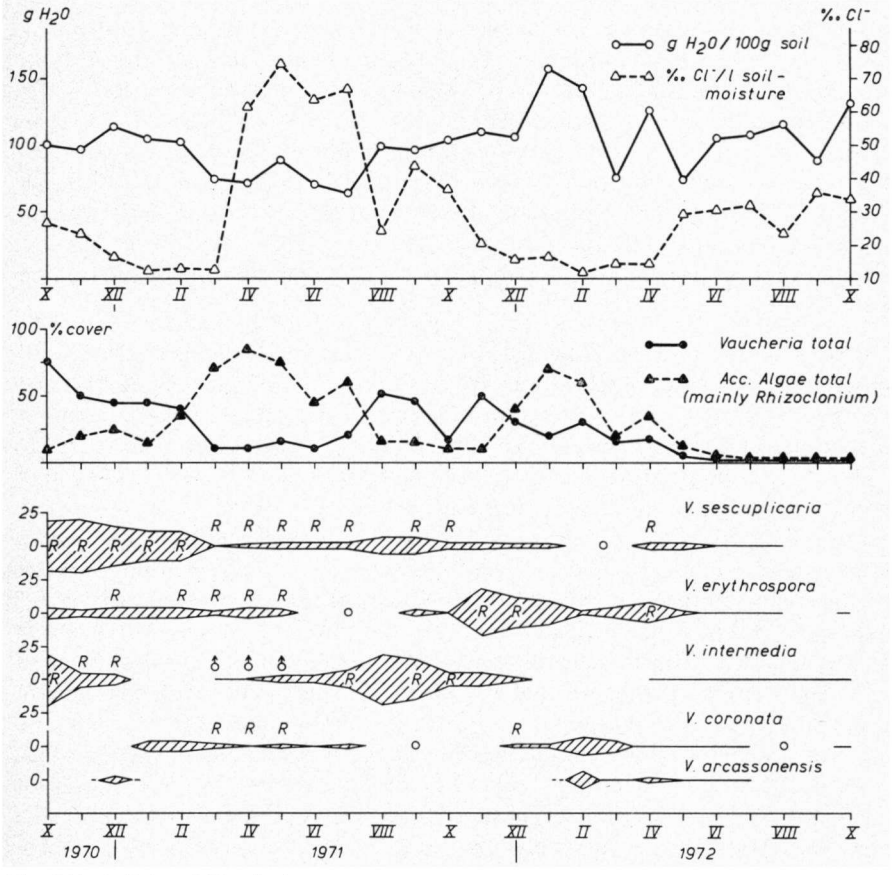

Fig. 6. Periodicity of *Vaucheria* spp. and other algae together with fluctuations of soil-moisture content and salinity of soil-moisture at PSP 8.

sescuplicaria proved to be correlated with the course of the soil moisture content. The decrease of this species after February 1971 presumably is caused by the strongly increasing salinity and by the, be it only slightly, decreasing moisture content. The latter assumption is supported by the fact that the increasing quantity of *V. sescuplicaria* during August 1971 was correlated with increasing soil moisture, while salinity during that period remained very high. When soil moisture content rose and salinity decreased in autumn and winter 1971/1972, *V. sescuplicaria* did not recover. A probable explanation for this could be that many of the thin-walled oospores died during the high salinity conditions. *V. intermedia* again shows its optimum summer occurrence, being the main *Vaucheria* component in summer 1971. Optimum occurrence of *V. erythrospora* was in autumn and winter as was the case at PSP 13 and 10. *V. coronata* showed maximum growth in winter, a well known feature for this species in the Netherlands.

PSP 6 (Inlaag 1887) was situated in a *Puccinellietum maritimae* vegetation. The species composition is given in *table 1*.

The most important *Vaucheria* species were *V. sescuplicaria*, *V. coronata*, *V. arcassonensis* and *V. intermedia*. *V. erythrospora* was of minor importance at this locality. Moisture content and salinity were generally higher than at PSP 8. The author is of the opinion that, in comparing this PSP with PSP 8, the higher salinity (always $> 5^{o}/_{oo}$ Cl^{-}) accounts for the minor role of *V. erythrospora* and the rather rich occurrence of *V. arcassonensis*, *V. coronata* and *V. intermedia*. At PSP 6, during 1972, hardly any *Vaucheria* spp. were found until autumn, while other algae (mainly *Rhizoclonium*) were always richly developed. The long absence of *Vaucheria* may be due to the extremely high salinities of the summer 1971.

PSP 5 (Koudekerksche Inlaag) was located in a grassy, occasionally grazed, vegetation, the aspect of which was determined by *Juncus gerardii* and *Puccinellia maritima* (max. height 4 cm). For other species see *table 1*. Total covering of higher plants varied between 60 and 95%. Soil: 2 to 3 cm clay on sand.

Total covering of algae varied between 40 and 90%. *Fig. 7* only shows algal periodicity, not the covering percentages. As at PSP 8, the most important *Vaucheria* species were *V. sescuplicaria*, *V. erythrospora* and *V. intermedia*. Other species: *V. coronata* and *V. arcassonensis*. The periodicity of these species is also similar to that observed at PSP 8. One of the differences between PSP 5 and PSP 8 is that *V. sescuplicaria* was more constantly present in PSP 5, and in greater quantity. This may be due to the considerably higher moisture content of the upper soil layer, as compared with PSP 8. The higher moisture content presumably is also the reason for the more constant presence of the accompanying algae, even during the summer 1971 under extremely high salinity conditions.

At PSP 5 special attention was paid to the occurrence and germination of oospores. *Fig. 7* shows that sexual reproduction of *Vaucheria* species can take place over large periods of time. *V. sescuplicaria* nearly always showed reproductive structures. Germination of oospores however, generally appeared to be restricted to those periods directly preceding the vegetative appearance of spe-

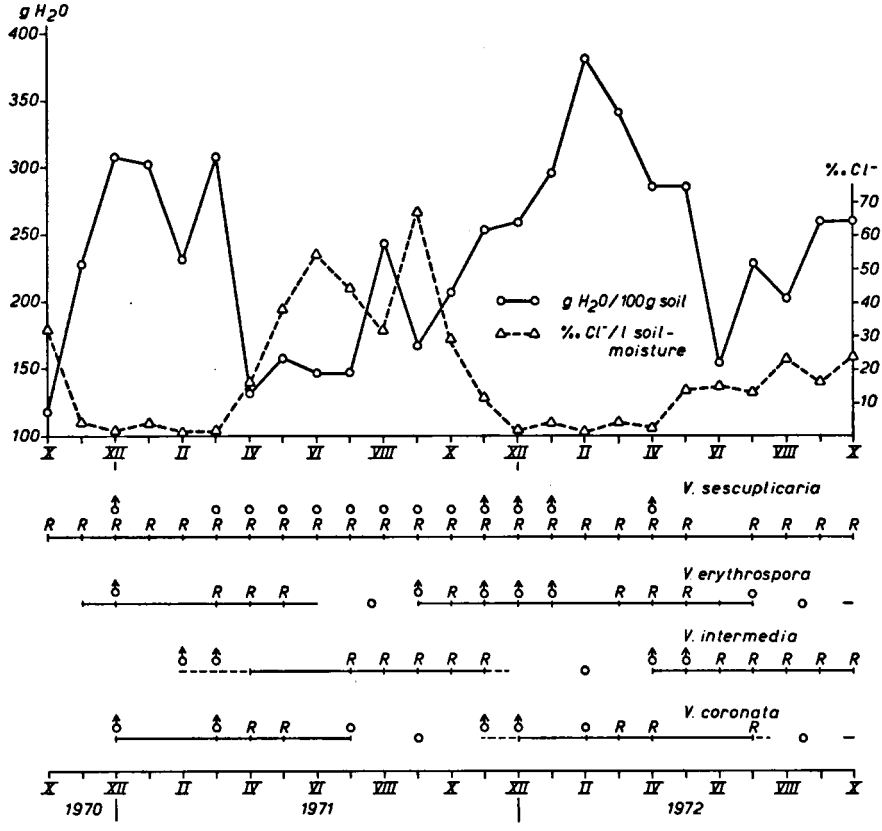

Fig. 7. Periodicity of *Vaucheria* spp. together with fluctuations of soil-moisture content and salinity of soil-moisture at PSP 5.

cies. Even in the case of *V. sescuplicaria* which was present during all seasons, germination of oospores was restricted to winter and spring. When considering salinity conditions during germination of oospores, the fact emerges that during these periods salinities were always relatively low. This is in accordance with the finding that the great majority of salt marsh plants shows optimum germination of seeds under fresh or nearly freshwater conditions (CHAPMAN 1964).

PSP 12 (Koudekerksche Inlaag) was situated at slightly higher level than the before-mentioned PSP's. The vegetational aspect of PSP 12 was determined by *Juncus gerardii* (height about 10 cm). The soil was clayish. For other species see *table 1.* Moisture content was rather high, and salinity relatively low (moisture contents: 140–377 g H_2O/100 g soil; salinities between November and May: 0.78–6.10‰ Cl^-, between May and November: 9.60–36.40‰ Cl^-).

Total *Vaucheria* covering varied between 10 and 90%. *Vaucheria synandra* was the main species, occurring in all seasons with reproductive organs. Mini-

mum development was in summer 1971 under extremely high salinities. Other *Vaucheriae* recorded were *V. sescuplicaria* (only in winter and spring), *V. intermedia* (optimum occurrence in summer), *V. erythrospora*, *V. arcassonensis* and *V. coronata* (only in early spring).

PSP 9 (Susanna Inlaag) was also located in a *Juncus gerardii* vegetation. For other species see *table 1*. Near PSP 9 *Carex distans* occurred. Moisture and salinity conditions were nearly the same as at PSP 12.

Vaucheria synandra also was the main *Vaucheria* species. Other *Vaucheriae: V. intermedia*, *V. erythrospora*, *V. sescuplicaria* and *V. canalicularis*. The last species was recorded only once namely in March 1971 (salinity $0.40^0/_{00}$ Cl^-). The occurrence of *V. canalicularis* and the absence of *V. coronata* and *V. arcassonensis* at this PSP may be due to the bordering of the PSP to a non-saline vegetation. PSP 12 on the other hand was wholly surrounded by saline vegetation.

4.2.2. Concluding remarks

Resuming the data from PSP 8, 6, 5, 12 and 9, the following statements can be made: in saline, grassy, inland vegetations *Vaucheria* is a widespread algal component, especially in the cold seasons. The most consistently present alga is *Rhizoclonium riparium*, while in late summer and autumn blue-greens show a rather rich development.

On clayish soils with high moisture contents, in vegetations belonging to the *Puccinellietum maritimae* and/or *Juncetum gerardii* the following *Vaucheria* species were recorded: *V. sescuplicaria*, *V. erythrospora*, *V. coronata*, *V. arcassonensis*, *V. intermedia* and *V. synandra*. In vegetations dominated by *Juncus gerardii*, *Vaucheria synandra* is the dominant *Vaucheria* species. *V. coronata* and *V. arcassonensis* are more abundant in *Puccinellietum maritimae* vegetations than in the higher *Juncetum gerardii*. *V. sescuplicaria* occurs from the *Puccinellietum maritimae* onwards to *Juncus gerardii* vegetations, its optimum occurrence being at levels below the *Juncetum gerardii* under high soil moisture conditions. *V. erythrospora* shows a wide range of occurrence, its optimum development situated at levels higher than the *Puccinellietum maritimae*.

Most species can be found in the cold seasons. The optimum occurrence of *V. intermedia* however is in summer, while *V. synandra* and *V. sescuplicaria* can be found in all seasons (cf. SIMONS & VROMAN 1973). Germination of oospores has only been observed under low salinity conditions.

4.3. Swampy shores of pools and ditches with mass growth of Vaucheria

4.3.1. Description of PSP 11, 4 and 15

PSP 11 (Guil, Vianen) was located at a distance of about 5 m from a shallow brackish pool in a vegetation dominated by a luxurious growth of *Aster tripolium*. Other species: see *table 1*. The covering of higher plants varied between 20 and 80%.

On the swampy sandy soil with silty black sulfide layers at some distance be-

low surface, *Vaucheria* formed a thick dense mat. *Fig. 8* gives a survey of the algal observations. The aspect of the algal mat was wholly determined by *Vaucheria*. The most important accompanying algae especially in summer were the green alga *Percursaria percursa* and the blue-greens *Microcoleus lyngbyaceus* and *M. chthonoplastes*. The covering of the algal mat varied between 5 and 100 %. The dominant *Vaucheria* species was *V. sescuplicaria*. This species sharply decreased in presence after April 1971 when salinity sharply increased; it recovered rather quickly after decrease of salinity in August 1971. In 1972 *V. sescuplicaria* again showed a decrease but not as strong as in 1971, presumably because salinity did not reach values as high as in 1971. The rise in salinity rather than the decrease in moisture content must have been the cause for the observed growth reduction of *V. sescuplicaria*, because moisture content at this PSP never fell below critical values for this species. This view is supported by the fact that *V. sescuplicaria* was present at other PSP's under much lower moisture conditions.

Besides *V. sescuplicaria*, also *V. velutina*, *V. subsimplex* and *V. compacta* were found in this habitat. *V. velutina* showed optimum occurrence in summer under high salinity conditions while *V. subsimplex* was encountered less frequently.

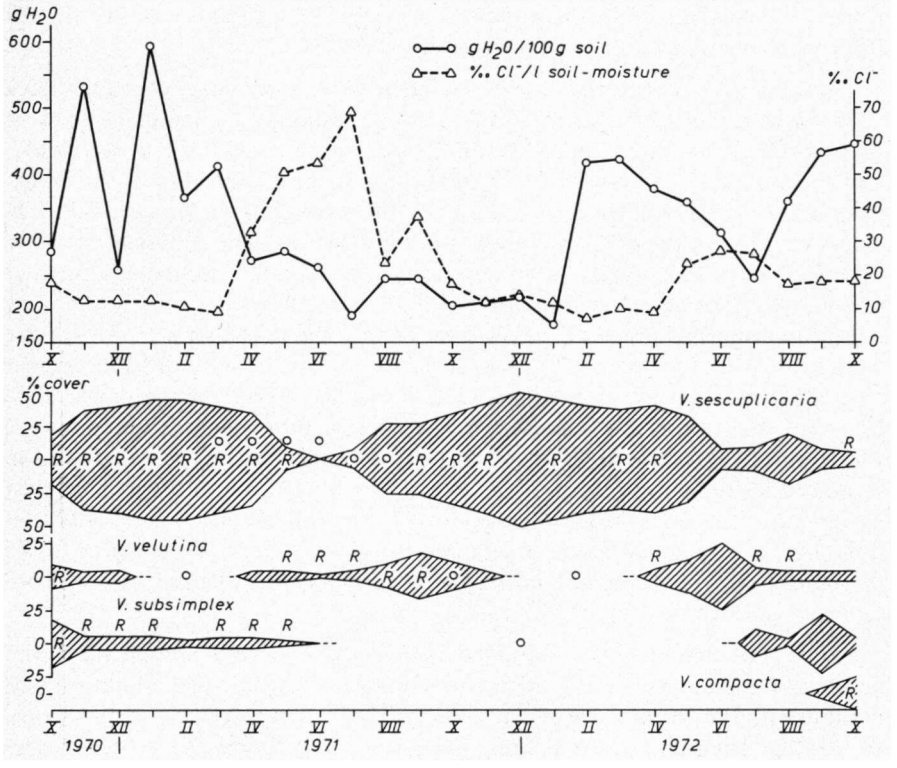

Fig. 8. Periodicity of *Vaucheria* spp. together with fluctuations of soil-moisture content and salinity of soil moisture at PSP 11.

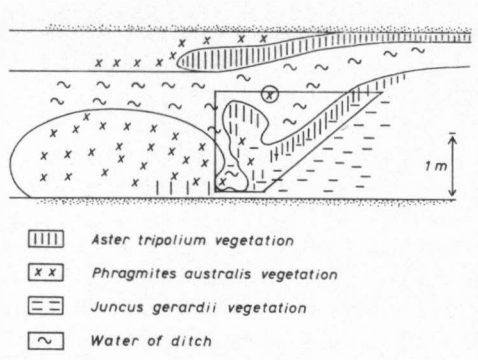

Fig. 9. Sketch of situation at PSP 4. The *Vaucheria* cushions were sampled and mapped within the trapeziform figure.

V. compacta has not often been recorded in inland environments, it behaves as a true estuarine species (SIMONS 1975). The occurrence of *V. velutina* and *V. subsimplex* at PSP 11 may be the result of the rather high salinity and very high moisture content throughout the year. The appearance of *V. compacta* in October 1972 coincides with the optimum period of growth and reproduction of this species in estuarine environments (SIMONS 1974b).

PSP 4 (Koudekerksche Inlaag). See sketch in *fig. 9*. At the edges of a ditch thick dark-green *Vaucheria* cushions could be found, especially in summer, growing on black H_2S containing mud. Dominant species appeared to be *V. subsimplex* and *V. velutina*. This habitat is comparable to a ditch, described from the brackish ponds "De Putten" (SIMONS & VROMAN 1973), where *V. velutina* and *V. subsimplex* also were the dominant species in the cushions. The combination of *V. velutina* – *V. subsimplex* has been described as a sociation occurring along eupolyhaline estuarine waters (NIENHUIS 1970, SIMONS 1975).

Within a marked area (*fig. 9*) observations on the development of the algae were made from October 1970 to October 1973. From January until December 1973 algal covering within the marked area was followed by mapping the algal cushions. The results are shown in *fig. 10*. This picture which is representative for the three years of observation, shows an enormous "bloom" of *V. velutina* in summer. The rapid increase of *V. velutina* during May and June may be achieved by the ample production of aplanospores. *V. subsimplex* may occur in all seasons, but in summer it has been suppressed by *V. velutina* at this locality; *V. subsimplex* also produces aplanospores. *V. sescuplicaria* was only seldom observed at this habitat.

PSP 15 (Susanna Inlaag) was situated on the bumpy shore of a ditch which ran paralell to the dike bordering the Eastern Scheldt. This seepage habitat is comparable with the "bumpy shore" as described for "De Putten" (SIMONS & VROMAN 1973). The bumps were densely overgrown with *Puccinellia maritima*. Occasionally also *Puccinellia capillaris* and *P. fasciculata* were found. *Vaucheria* cushions grew at the edges of the *Puccinellia* clumps on black mud.

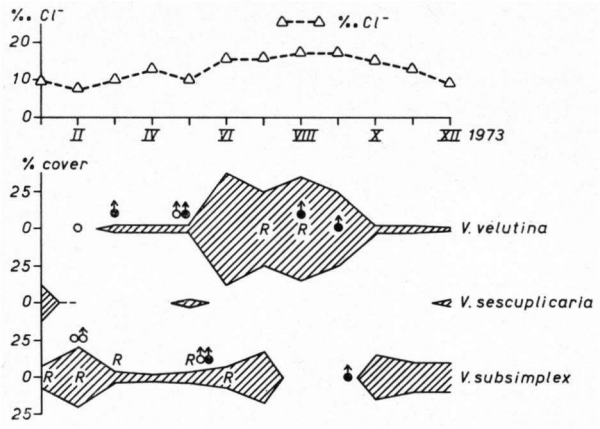

Fig. 10. Periodicity of *Vaucheria* spp. together with salinity variation of ditch water at PSP 4. ↕ : germinating aplanospores.

The *Vaucheria* cushions contained *V. subsimplex*, *V. velutina* and *V. litorea*. Salinity values of the water around the clumps were nearly similar to those at PSP 4. Contrary to the comparable PSP 4, *Vaucheria* did not show a maximum summer development; *V. velutina* and *V. subsimplex* appeared to have the same periodicity behaviour as at PSP 4, however. Consequently, the maximum development of the algal cushions in autumn, winter and spring was mainly caused by *V. subsimplex*. In summer the *Vaucheria* cushions, mainly consisting of *V. velutina*, presumably were suppressed by the luxuriously growing *Puccinellia* shoots. In spring *V. litorea* occurred at the lower parts of the cushions where they touched the water surface.

4.3.2. Concluding remarks

Resuming the results from PSP 11, 4 and 15, it can be concluded that mass *Vaucheria* growth on moisture-saturated brackish substrata is achieved by *V. velutina*, *V. subsimplex* and/or *V. sescuplicaria*. The ability of producing great numbers of aplanospores may contribute to mass development of these three species.

V. velutina and *V. subsimplex* were found together on black H_2S containing mud. *V. velutina* is able to form summer blooms. The salinity values at which the two species were found were constantly rather high (mostly 10–15‰ Cl^-). Mass occurrence of *V. sescuplicaria* seems to be correlated with less reduced soil-conditions, as was the case at the sandy PSP 11. Under extremely high salinities *V. sescuplicaria* was replaced by *V. velutina* and *V. subsimplex*.

The minimum winter development of the *Vaucheria* cushions at PSP 4 contrary to PSP 15 and 11 might be caused by the fact that in winter PSP 4 was frequently flooded by ditch water. The summer minimum at PSP 15 may be caused by overgrowing *Puccinellia* plants.

Table 2. Survey of Vaucheria-accompanying green and blue-green algae at the PSP's dealt with.

Chlorophyceae:
Enteromorpha prolifera (O. F. Müller) J.Ag.
Enteromorpha torta (Mertens) Reinb.
Percursaria percursa (C. Ag.) Bory
Rhizoclonium riparium (Roth) Harvey
Ulothrix pseudoflacca Wille
Ulothrix subflaccida Wille

Cyanophyceae (non-coccoid forms):
Anabaena variabilis Kütz.
Anabaena torulosa (Carm.) Lagerh.
Calothrix aeruginea (Kütz.) Thuret
Microcoleus chthonoplastes (Mert.) Zanard.
Microcoleus lyngbyaceus (Kütz.) Crouan
Microcoleus vaginatus (Vauch.) Gom.
Nodularia harveyana (Thwaites) Thuret
Nostoc sp.
Oscillatoria brevis (Kütz.) Crouan
Oscillatoria laetevirens Crouan
Oscillatoria margaritifera Kütz.
Oscillatoria nigro-viridis (Thwaites) Gom.
Oscillatoria tenuis Ag.
Phormidium corium Gom.
Schizothrix calcicola (Ag.) Gom.
Spirulina subsalsa Oerst.
Symploca funicularis Setch. & Gardner

Cyanophyceae (coccoid forms):
Agmenellum quadruplicatum (Menegh.) Bréb.
Anacystis dimidiata (Kütz.) Dr. & Daily
Anacystis montana (Lightf.) Dr. & Daily
Coccochloris stagnina Spreng.
Entophysalis deusta (Menegh.) Dr. & Daily

5. ACCOMPANYING ALGAE

The accompanying green and blue-green algae found at the different PSP's (*table 2*) showed no clear pattern of distribution. A few tendencies were observed however: *Microcoleus lyngbyaceus* and *M. chthonoplastes* were nearly the only companion species of *Vaucheria* at low levels (e.g. PSP 4, 11, 15); at higher levels *Rhizoclonium riparium* most frequently occurred, together with the other accompanying algae. At some occasions, peak occurrences of blue-green algae were observed, caused by the coccoid species *Anacystis montana* (f. *minor*) or *Coccochloris stagnina* (PSP 10, 12). In non-saline vegetations *Microcoleus vaginatus* was in most cases the only algal species accompanying *Vaucheria.*

6. PATTERN OF DISTRIBUTION AND DISCUSSION

Vaucheria samples were not only taken at the PSP's but also at numerous other places where *Vaucheria* growth was observed, in order to gather as much information as possible on the distribution of the different species.

Data on distribution of *Vaucheria* species in inland brackish areas are given by SIMONS & VROMAN (1973) and by POLDERMAN (1974). In the former paper four combinations of species were discerned in "De Putten" from water level up to pasture level respectively:

a: *V. sescuplicaria, V. litorea, V. subsimplex, V. velutina;*
b: *V. synandra, V. erythrospora, V. sescuplicaria;*
c: *V. synandra, V. erythrospora, V. canalicularis, V. cruciata;*
d: *V. dillwynii, V. frigida, V. terrestris, V. prona.*

Polderman found a rather similar sequence for *Vaucheria* species at different inland saline areas. As to group b, this author wants to include *V. coronata* and *V. intermedia* besides *V. sescuplicaria.* The combination with *V. coronata/intermedia* would be a variant of group b occurring in relatively dry areas and the combination with *V. sescuplicaria* the variant of moist areas. According to the present author however, *V. coronata* and *V. intermedia* do not necessarily prefer relatively dry conditions; they are found under very moist to rather dry circumstances.

The zonation pattern found in De Putten applies to a rather steep transition from water level up to pasture level. In the areas investigated in the S.W. Netherlands this transition is of a more gradual nature.

The general pattern in the sequence of *Vaucheria* species as described for "De Putten" however, was also found in the S.W. Netherlands. From water level of pools and ditches towards the non-saline terrestrial environment the following groups can be discerned:

1: *V. sescuplicaria, V. litorea, V. subsimplex, V. velutina;*
2: *V. sescuplicaria, V. erythrospora;*
3: *V. synandra, V. erythrospora, V. sescuplicaria;*
4: *V. canalicularis, V. cruciata, V. erythrospora, V. terrestris, V. dillwynii;*
5: *V. dillwynii, V. terrestris.*

The species *V. arcassonensis, V. coronata* and *V. intermedia* may sometimes be found among group 1, but more frequently in group 2 and 3. Groups 1, 3, 4 and 5 are nearly similar to the groups a, b, c, and d from De Putten.

Group 1 occurs at the lowest levels with vegetations dominated by *Puccinellia maritima* and/or *Salicornia europaea; V. velutina* and *V. subsimplex* under relatively high salinity conditions and on blackish FeS and H_2S containing substrata. Group 2 is mostly found at the level between vegetations dominated by *Puccinellia maritima* and/or *Salicornia europaea* and vegetations dominated by *Juncus gerardii. V. synandra* often is the dominating species of group 3 in *Juncus gerardii* vegetations. Group 3, sometimes extended with *V. canalicularis,* is often found in *Puccinellio-Spergularion salinae* vegetations in which *V. erythrospora* may occur at open sandy spots, while *V. synandra* is always found in grassy habitats. In summer *V. intermedia* is an important algal component in the *Puccinellio-Spergularion salinae.* Group 4 is found on bare patches in Juncus gerardii vegetations and in non-saline vegetations, often accompanied by *Agrostis stolonifera.* Species of group 4 also occur at localities within the *Juncetum gerardii* strongly influenced by freshwater (cf. POLDERMAN 1974). Group 5

always occurs in non-saline vegetations, such as the *Lolio-Cynosuretum* and the *Lolio-Plantaginetum*, often on dikes bordering the saline areas.

Except *V. dillwynii*, *V. terrestris*, *V. canalicularis* and *V. cruciata*, all species mentioned are genuine brackish algae. *V. canalicularis* and *V. cruciata* are salt-tolerant freshwater species. Based on the distribution pattern in estuarine environments, two groups have been discerned within the brackish group namely a polyhalobe and a meso-oligohalobe group (SIMONS 1975).

V. velutina, *V. subsimplex*, *V. arcassonensis*, *V. coronata*, and *V. intermedia* belong to the polyhalobe group. During the present investigation, *V. velutina*, *V. sumbsimplex* and *V. intermedia* were indeed found under predominantly polyhaline (10–15$^0/_{00}$ Cl^-) and even more saline circumstances. However, *V. arcassonensis* and especially *V. coronata*, were found under less saline conditions, be it never in great quantities. In estuarine environments *V. arcassonensis*, *V. coronata* and *V. intermedia* show a rather euryhaline character as the species often occur at high tidal levels being exposed to large salinity fluctuations.

V. litorea, *V. synandra* and *V. erythrospora* belong to the meso-oligohalobe group. The optimum development of *V. litorea* in the areas in question occurred in isolated pools or ditches strongly influenced by rainwater. Salinity mostly varied between 3 and 10$^0/_{00}$ Cl^-. In such habitats this species reaches mass appearance and shows abundant sexual reproduction in spring, while in more saline situations (as at PSP 15) sexual reproduction was not observed. *V. synandra* and *V. erythrospora* were mostly found under oligohaline and slightly mesohaline conditions.

V. sescuplicaria being one of the most important *Vaucheria* species in moist inland saline areas, is far more common in inland areas than in estuarine environments (SIMONS 1975). This brackish species shows a broad range of occurrence at different salinities, varying from oligohaline towards polyhaline, perhaps reflecting its adaption to this kind of environment.

Since the species of groups 2, 3 and partly those of group 4 belong to the meso-oligohalobe group or are very euryhaline in the case or *V. sescuplicaria*, the sequence of these species combinations from low to high rather reflects differences in moisture preferences than different salinity preferences. This assumption is supported by data from the PSP's. For instance, *V. sescuplicaria* clearly shows its preference for high moisture conditions (e.g. PSP 11) and *V. erythrospora* is more able to grow under low moisture conditions than *V. synandra* (cf. PSP 1 and 13).

The periodicity phenomena as observed at the different PSP's strongly suggest that the factors moisture and salinity are both involved in the wax and wane of *Vaucheria* species.

Vaucheria as a whole prefers the high moisture and low salinity conditions as found in autumn, winter and early spring, 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. Many blue-green algae showed optimum development in late summer and autumn, a feature well-known from many other habitats.

Regarding the periodicity of individual *Vaucheria* species, the following general statements can be made:

V. sescuplicaria may be present throughout the year under relatively high moisture conditions. *V. synandra* too is able to grow throughout the year. Both species show reproductive organs in all seasons suggesting that many generations succeed each other within a year.

V. velutina and *V. subsimplex* likewise occur in all seasons, the optimum period of growth and reproduction of *V. velutina* being in summer. *V. intermedia* also is a species showing optimum occurrence in summer.

All other species mentioned were restricted to autumn, winter and spring. Which species occurred in these periods and in which quantity was mainly determined by the local constitution of moisture and salinity in the upper soil layer.

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REFERENCES

BLUM, J. L. (1972): North American Flora, Series II, Part 8: *Vaucheriaceae*. New York Botanical Garden, New York, 63 pp.

CHAPMAN, V. J. (1964): Coastal Vegetation. London, New York, 245 pp.

CHRISTENSEN, T. (1952): Studies on the genus Vaucheria. I. A list of finds from Denmark and England with notes on some submarine species. *Bot. Tidsskr.* **49**: 171–188.

— (1956): Studies on the genus Vaucheria. III. Remarks on some species from brackish water. *Bot. Notiser* **109**: 275–280.

— (1969): Vaucheria collections from Vaucher's region. *Biol. skr.* **16**: 1–36.

— (1973): Some early Vaucheria descriptions. *Bot. Notiser* **126**: 513–518.

DROUET, F. (1968): Revision of the classification of the Oscillatoriaceae. *Nat. Ac. Sc. Philad.* **15**: 1–370.

DROUET, F. & W. A. DAILY (1956): Revision of the coccoid Myxophyceae. *Butler Univ. Bot. Stud.* **12**: 1–222.

GEITLER, L. (1932): *Cyanophyceae*. In: RABENHORST's Kryptogamen-flora. Leipzig, 6 + 1196 pp.

HARTOG, C. DEN (1973): Preliminary survey of the algal vegetation of salt-marshes, a littoral border environment. *Hydrobiol. Bull.* **7** (1): 3–14.

HEUKELS, H. & S. J. VAN OOSTSTROOM (1970): *Flora van Nederland*. Noordhoff, Groningen.

NIENHUIS, P. H. (1970): The benthic algal communities of flats and salt marshes in the Grevelingen, a sea-arm in the south-western Netherlands. *Neth. J. Sea Res.* **5** (1): 20–49.

NIENHUIS, P. H. & J. SIMONS (1971): Vaucheria species and some other algae on a Dutch salt marsh, with ecological notes on their periodicity. *Acta Bot. Neerl.* **20** (1): 107–118.

POLDERMAN, P. J. G. (1974): The algae of saline areas near Vlissingen (the Netherlands). *Acta Bot. Neerl.* **23** (2): 65–79.

POLDERMAN, P. J. G. & W. F. PRUD'HOMME VAN REINE (1973): Chrysomeris ramosa (Chrysophyceae) in Denmark and in the Netherlands. *Acta Bot. Neerl.* **22** (2): 81–91.

RAPPARD, F. W. (1967): Zout wierveen bij Breede Gooi? *De Levende Natuur* **70**: 49–55.

RIETH, A. (1956): Zur Kenntnis halophiler Vaucherien. I & II. *Flora* **143**: 127–160; 281–294.

SIMONS, J. (1974a): Vaucheria birostris n. sp. and some further remarks on the genus Vaucheria in the Netherlands. *Acta Bot. Neerl.* **23** (4): 399–413.

— (1974b): Vaucheria compacta: a euryhaline, estuarine algal species. *Acta Bot. Neerl.* **23** (5, 6): 613–626.

— (1975): *Vaucheria* species from estuarine areas in the Netherlands. *Neth. J. Sea Res.* **9** (2): 1–23.

SIMONS, J. & M. VROMAN (1968): Some remarks on the genus Vaucheria in the Netherlands. *Acta Bot. Neerl.* **17** (6): 461–466.

— (1973): Vaucheria species from the Dutch brackish inland ponds "De Putten". *Acta Bot. Neerl.*, **22** (3): 177–192.

WESTHOFF, V. & A. J. DEN HELD (1969): *Plantengemeenschappen in Nederland.* Thieme, Zutphen, 324 pp.