# VAUCHERIA SPECIES AND SOME OTHER ALGAE ON A DUTCH SALT MARSH, WITH ECOLOGICAL NOTES ON THEIR PERIODICITY

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SUMMARY

A survey of the distribution and the periodicity of eight *Vaucheria* species (*V. arcassonensis*, *V. compacta*, *V. coronata*, *V. intermedia*, *V. minuta*, *V. sphaerospora*, *V. thuretii* and *V. vipera*) on the Dutch salt marsh Springersgors in relation to environment and vegetation pattern of algae and higher plants is given. The quantitative changes occurring in the algal vegetation (green algae, blue-green algae and *Vaucheria* spp.) on two permanent quadrates, checked monthly algae and higher plants is given over a period of two years, are given in relation to some important ecological factors. Both sample plots, situated at MHWS level on the tidal marsh, constitute an instable habitat with large changes in soil moisture content (42–165 g $H_2O$/100 g soil) and in salinity of the soil moisture (0.8–72.4‰ $Cl^-$). The periodicity of five *Vaucheria* species could be correlated with the action of extreme environmental conditions (desiccation, high salinities, frost).

## 1. INTRODUCTION

In the literature the ecology of benthic algae living on salt marshes received only little attention. Important work in this field was done by CHAPMAN (1934, 1937, 1960, 1964) who included the higher plants as well as the algae in his investigations, CARTER (1932, 1933), and WEBBER (1968). A number of smaller contributions was reviewed by NIENHUIS (1970).

Many algal species on the salt marsh present great taxonomic problems, and this accounts for much of the lack of knowledge in this field. The greater part of the algal stock belongs to the *Chlorophyceae*, the *Xanthophyceae*, and the *Cyanophyceae*. A number of recent taxonomic revisions, however, made it possible to study some of the larger salt marsh algae from an ecological point of view. BLIDING (1963) revised, *i.a.*, the genera *Enteromorpha* and *Blidingia*, both frequently occurring on the marshes.

DROUET (1968) and DROUET & DAILY (1956) rigorously remodelled some large groups of blue-green algae.

The genus *Vaucheria* plays an important part in the salt marsh algal flora. The material collected in the field is often wholly or partly sterile, making it necessary to cultivate the material until reproductive structures, indispensable for identi-

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fication, appear. Identification of the samples, moreover, is hampered by the fact that very often two or more species grow together in inextricable cushions. The second author of this paper succeeded so far in isolating fourteen species of *Vaucheria* from Dutch salt marshes and beach plains. Some remarks on a number of these species were published previously (SIMONS & VROMAN 1968).

The first author is engaged in an ecological and biosystematic study of a number of benthic algae living in brackish habitats. The second author is working on the distribution, periodicity, and morphology of *Vaucheria* spp. Their separate results will be published in the future. At this stage, however, it seemed useful to publish some data in a joint effort to study the quantitative changes of the *Vaucheria* spp. and other algae occurring on two permanent plots in correlation with some important environmental factors.

## 2. MATERIALS AND METHODS

For the quantitative research two permanent plots (or permanent quadrats = P.Q.'s) measuring 0.5 × 0.5 m each were used. These P.Q.'s were checked every month from March 1968 till March 1970. The percentage of covering of both the halophytes and the algae was estimated, and in the same procedure the percentage of covering of each algal species or group of species was noted. From every species or species-group distinguished in the P.Q. a sample was taken outside the P.Q., supposing the proportions in the sample to be representative for the proportions in the quadrat. The quantity of every species in the permanent plots was converted into a percentage of covering and expressed in the following scale: R = individuals rare; O = individuals occasional; F = individuals frequent, in all three cases covering less than 5%; C = individuals (mostly) common, covering 5–30%; A = individuals (mostly) abundant, covering 30–60%; D = individuals dominant, covering more than 60%. It should be noted that the estimation of the covering-percentage of the *Vaucheria* species is liable to cause great errors, because it is always necessary to cultivate them, resulting in a possible distortion of the original proportions in the sample.

The *Vaucheria* samples from the field were cultivated in the Botanical Laboratory of the Free University, in an Erdschreiber medium in petri dishes, until a stage of maximal development of the reproductive structures was reached. The culture conditions involved a temperature of c. 12 °C, a photoperiod L/D 14:10 or L/D 12:12, and a light intensity of 1500–2000 lux.

The physio-chemical data are based on analyses of the Delta Institute. Every month a sample was taken next to the P.Q.'s from the uppermost cm of the soil, the layer upon which and in which the algae live. The moisture content of these soil samples and the salinity of the soil moisture were estimated and expressed as g $H_2O$/100 g oven dried soil (105 °C) and g NaCl/l soil moisture ($^0/_{00}$ $Cl^-$), respectively. The meteorological data were derived from the Monthly Surveys, published by the Royal Netherlands Meteorological Institute (KNMI).

## 3. ENVIRONMENT AND VEGETATION ON THE SPRINGERSGORS

### 3.1. The environment

The Grevelingen, a sea-arm in the SW. Netherlands, was a part of the complicated Rhine-Meuse estuary before 1964. In that year the Grevelingen was cut off from the direct river influence by a dam, as a preliminary to the future damming of the mouth of this sea-arm.

The tidal difference in the Grevelingen amounts to about 2.5 to 3 m. The salinity of the water fluctuates between about 8 and 16‰ $Cl^-$, whereas the temperature – dependent on the season – varies between 2° and 20°C. On the banks extensive salt marshes and sand and mud flats occur.

The Springersgors is a salt marsh area situated in the mouth of the Grevelingen in the westernmost part of the island of Goeree-Overflakkee. For the greater part the marsh is bordered by dune ridges. The area is intersected by deep creeks supplied by water from the Grevelingen. Most of the salt marsh lies between MHW and MHWS. It is not grazed by cattle and hardly trodden by man.

### 3.2. The vegetation pattern

The vegetation of halophytes on the Springersgors was investigated by ADRIANI (1945) and BEEFTINK (1965). The lower levels of the marsh are dominated by a dense *Spartina townsendii* vegetation. On the gently sloping creek banks *Aster tripolium* frequently occurs. Higher on the marsh *Halimione portulacoides* is found in quantity, near the dunes superseded by *Limonium vulgare*; these two dominant species grow intermingled with *Puccinellia maritima, Salicornia europaea, Suaeda maritima, Triglochin maritima,* and *Spergularia marginata.* Still higher areas are overgrown with *Festuca rubra, Elytrigia pungens, Artemisia maritima,* and other species. The dunes proper are covered with a dense *Hippophaë rhamnoides* brushwood.

The algal vegetation on the Springersgors is rich and varied (NIENHUIS 1970). On the lower marsh, especially among *Spartina townsendii* plants, a *Fucus vesiculosus* f. *volubilis* sociation can be distinguished. In slightly higher spots among *Halimione, Puccinellia,* and *Limonium* the *Bostrychia scorpioides* sociation occurs. A third community is formed by some *Vaucheria* spp. (*V. sphaerospora* and *V. thuretii*), growing on the lower creek banks. The *Blidingia minima* sociation, furthermore, is an epiphytic community on the woody stems of phanerogams. In early spring the *Ulothrix* sociation develops on the wet spots of the marsh. Blue-green algae are as a whole an important component of the algal vegetation; the most striking constituent is *Microcoleus lyngbyaceus,* especially in the summer months. In the general *Chlorophyceae* community a number of facies are combined in which *Enteromorpha, Rhizoclonium,* and *Vaucheria* locally dominate. Finally, NIENHUIS (1970) distinguished an algal vegetation in salt-marsh pools as well.

## 4. DISTRIBUTION AND PERIODICITY OF VAUCHERIA SPECIES

Since 1967 eight *Vaucheria* species have been found on the Springersgors: *V. arcassonensis* Dangeard, *V. compacta* (Collins) Collins, *V. coronata* Nordst., *V. intermedia* Nordst., *V. minuta* Blum & Conover, *V. sphaerospora* Nordst., *V. thuretii* Wor. and *V. vipera* Blum. These species may cover considerable areas of the tidal marsh, thus being both qualitatively and quantitatively very important components of the algal vegetation.

Below MHW level *V. sphaerospora* and *V. thuretii* form a relatively homogeneous mat, especially on the higher parts of the mud flats and on the slopes of the creeks, growing on rather firm, silty sand. The accompanying halophyte is usually *Salicornia europaea*. Among *Spartina townsendii*, where the soil is very soft and muddy, the community does not occur. At the mouth of gently sloping creeks *V. vipera* was found, growing together with *V. sphaerospora* and *V. thuretii* (SIMONS & VROMAN 1968). This was the second record in Europe after the observation of *V. vipera* on a British salt marsh at Canvey by CARTER (1933; *sub nomine V. woroniniana*).

The blue-green mats of the interwoven *V. sphaerospora* and *V. thuretii* become visible in April or May and disappear around December. *V. sphaerospora* bears reproductive bodies from about July till December, *V. thuretii* from about May till December, and *V. vipera* from August till October.

*V. sphaerospora* and *V. vipera* were not found above MHW level. However, all other species under discussion may occur on higher levels; they often grow together, suggesting a widely overlapping ecological amplitude.

Higher up the marsh, between MHW and MHWS, dominated by the phanerogamic communities *Halimionetum portulacoidis* and *Puccinellietum maritimae* (*cf.* BEEFTINK 1965), some *Vaucheria* patterns can be discerned. On creek banks, especially those overgrown with *Halimione portulacoides*, *V. coronata* may be found, sometimes together with *V. intermedia* and, less frequently, with *V. arcassonensis*.

On still higher parts, about MHWS level, the marsh changes into a beach plain sparsely overgrown with halophytes (*e.g.*, *Salicornia europaea*, *Puccinellia maritima*). Throughout the year the soil is covered with a dense algal mat. The *Vaucheria* species in this algal vegetation are *V. coronata*, *V. intermedia*, *V. arcassonensis*, *V. compacta*, and *V. thuretii* (*cf.* P.Q. 13 and P.Q. 16).

Very remarkable was the observation in February 1968 of *V. minuta* growing together with *V. coronata* at the edge of the beach plain, among withered *Suaeda maritima* and the grasses *Festuca rubra* and *Puccinellia maritima*. This was the first European record for this species (SIMONS & VROMAN 1968). It is apparently a rare species, since so far only a few observations from the Netherlands are known.

*V. coronata* has its growing and fructificating period mainly in the colder seasons, with an optimum in early spring (April, May). *V. arcassonensis* seems to have the same periodicity as *V. coronata*, except for a much shorter fruiting period. *V. intermedia*, on the contrary, has its main growing period in late sum-

mer and autumn and its fruiting time chiefly during the period from September till November. In spots becoming bare in autumn after the degeneration of the halophytes (*Limonium vulgare*, *Triglochin maritima*) *V. intermedia* is able to overgrow the soil within some weeks.

*V. compacta* is a species with a wide distribution in the upper littoral part of the fresh and brackish water tidal area in the estuaries in the SW. Netherlands. On the Springersgors *V. compacta* has only been found at about MHWS level in very small quantities. As yet no fructification of *V. compacta* has been observed on this marsh.

## 5. QUANTITATIVE INVESTIGATIONS ON PERMANENT PLOTS

### 5.1. General remarks

The periodicity of a number of dominant algae, correlated with several environmental factors, was studied by the first author (unpublished) in a series of permanent plots. Two of these plots are important in the present study owing to the role of the *Vaucheria* species: P.Q. 13 and P.Q. 16. The two sample plots are situated on the beach plain, at the foot of the dunes, at the upper salt marsh, about 500 m from each other. In both cases the soil profile consists of a very thin layer of silt on sand.

The soil in P.Q. 13 is permanently covered with a closed algal mat. The phanerogam vegetation is a very open one, every year dominated by *Salicornia europaea*. The covering of algae in P.Q. 16 is much smaller; *Salicornia europaea* is the most striking halophyte. Furthermore a number of higher plants play a very subordinate role in both quadrats: *Suaeda maritima*, *Spergularia marginata*, *Puccinellia maritima*, *Festuca rubra*, *Glaux maritima*, *Halimione portulacoides*, *Limonium vulgare*, *Spartina townsendii*.

### 5.2. Environmental factors

Algae living on salt marshes, bedded in the soil, are exposed to a complex of environmental factors. Within the scope of this paper we cannot deal with these phenomena in detail. They form the subject of a comprehensive study by the first author (unpublished).

The permanent quadrats P.Q. 13 and P.Q. 16 are situated at mean high water-level at springtide; they are submerged by thirty percent of all high tides, during a short time. A prominent habitat-factor for the semi-terrestrial algae living on this level is the moisture condition of the soil. When the soil desiccates, the decrease of the moisture content, whether or not in combination with an increase of the concentration of the dissolved salts, may inhibit the growth of the algae or even damage the plants. The concentration of sodium chloride may rise to very high values owing to the desiccating action of the atmosphere, or to very low values owing to the influence of precipitation.

The fluctuations in the two master factors, moisture content and chlorinity of the upper cm of the soil of P.Q. 13 and P.Q. 16, were plotted over the period March 1968 to February 1970 (*figs. 1* and *2*). The highest salinity concentrations

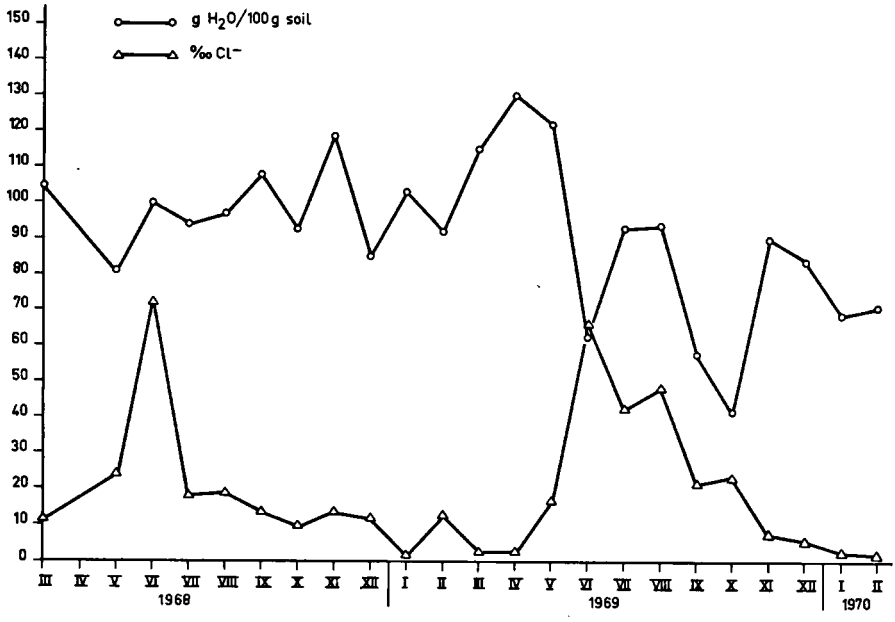


Fig. 1. Moisture content and salinity of the soil moisture in P.Q. 13 (Springersgors).

were measured during the months in which the precipitation is smaller than the evapo-transpiration (March-August 1968; April-October 1969, except second half of August). Maximal chlorinity in P.Q. 13 was estimated on 14-VI-1968 (72.4°/$_{oo}$ $Cl^-$; *fig. 1*) and in P.Q. 16 on 20-VI-1969 (54.2°/$_{oo}$ $Cl^-$; *fig. 2*). In the period with a surplus of precipitation (rest of the year) the salinity often dropped far below the value of the open water of the Grevelingen: minimum P.Q. 13 on 20-II-1970, 1.6°/$_{oo}$ $Cl^-$ (*fig. 1*); minimum P.Q. 16 on 20-II-1970 0.8°/$_{oo}$ $Cl^-$ (*fig. 2*). The wet late summer months of 1968 show low salinity values as a result of the dilution of the brackish soil moisture with rainwater. The dry late summer period of 1969, on the contrary, shows very high salinities, owing to the desiccation of the soil.

A high salinity value is usually correlated with a low moisture content of the soil: P.Q. 13 in June 1969 (*fig. 1*), P.Q. 16 in June 1968 (*fig. 2*). The salinity, however, may increase strongly, while the moisture condition of the topsoil stands at a "normal" level: P.Q. 13 in June 1968 (*fig. 1*); also the opposite takes place: P.Q. 13 in October 1969 (*fig. 1*). Which influence predominates depends wholly on the complicated interaction between flooding, precipitation, and evapo-transpiration.

Another factor of importance for the semi-terrestrial algae is the temperature of the topsoil. Extreme temperatures dropping to low values in winter (—2.5 °C on 19-II-1969 in P.Q. 13 and P.Q. 16) have a notable influence on the vitality of the algal mat.

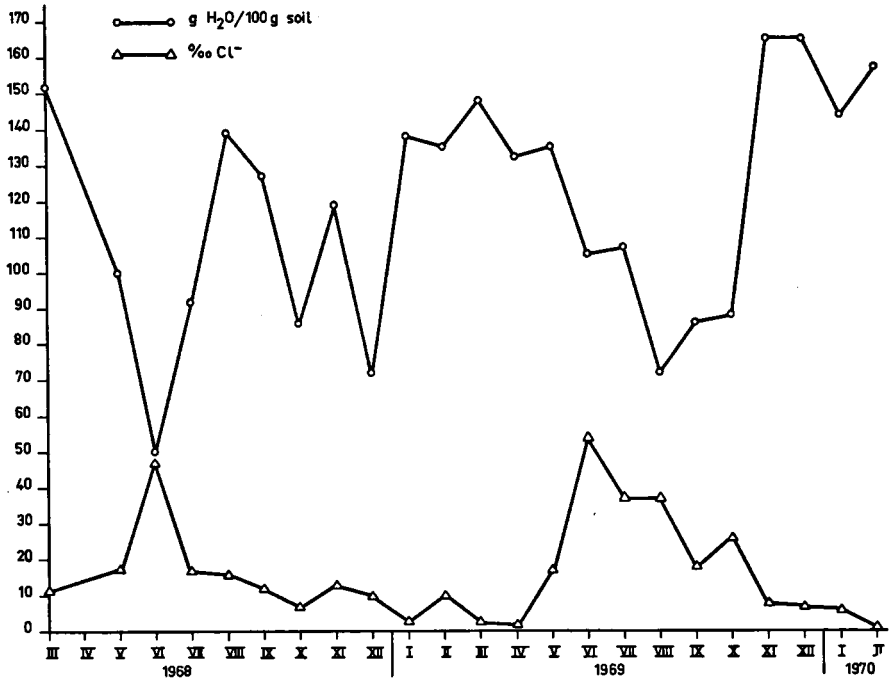


Fig. 2. Moisture content and salinity of the soil moisture in P.Q. 16 (Springersgors).

Summing up: moisture content, salinity, and temperature of the topsoil fluctuate greatly in P.Q. 13 and P.Q. 16, thus creating a very unstable environment.

Beside the chemical and physical factors a biotic factor, *viz.* competition for space, should be mentioned. Both quadrats are almost entirely overgrown with algae. When a species dies off, whatever the reason may be, and its percentage of covering decreases, the empty space is quickly taken by another species.

## 5.3. The algal vegetation

In the course of the investigations a number of algal species was found in P.Q. 13 and P.Q. 16 (*table 1*). Only a few of them play, quantitatively spoken, an important role; the periodicity of these species is depicted in *fig. 3*. Owing to the low covering percentages of the phanerogams no correlation with the total covering percentages of the algae exists. The vegetation of halophytes is an open one and obviously does not hamper the growth of the algae.

In the field the only changes observed were fluctuations in the covering percentages in the P.Q.'s and in the vitality of the algal mat. The individual species of green algae and *Vaucheria* species could not be recognized. Yet a species may be replaced by another in the same spot in the course of the seasons. Next to the changes occurring as a result of the action of the environmental factors, this

Table 1. List of species in P.Q. 13 and P.Q. 16 on the Springersgors

*Vaucheria arcassonensis* Dangeard
*Vaucheria compacta* (Collins) Collins
*Vaucheria coronata* Nordst.
*Vaucheria intermedia* Nordst.
*Vaucheria thuretii* Wor.
*Blidingia minima* (Näg. ex Kütz.) Kylin
var. *ramifera* Blid.
*Chaetomorpha capillaris* (Kütz.) Børg.
*Enteromorpha flexuosa* (Wulfen ex Roth)
J. Ag. subsp. *pilifera* (Kütz.) Blid.
*Enteromorpha intestinalis* (L.) Link
var. *intestinalis*
*Enteromorpha prolifera* (O. F. Müller) J. Ag.
subsp. *prolifera*
*Enteromorpha torta* (Mertens) Reinb.
*Monostroma* spec.
*Percursaria percursa* (C. Ag.) Rosenv.
*Rhizoclonium riparium* (Roth) Harv.
syn.: *Rhizoclonium implexum* (Dillw.) Kütz.
*Ulothrix flacca* (Dillw.) Thur.
*Ulothrix pseudoflacca* Wille
*Ulothrix subflaccida* Wille
*Anacystis montana* (Lightf.) Dr. & Daily
*Anacystis aeruginosa* Dr. & Daily
*Coccochloris stagnina* Sprengel
*Anabaena torulosa* Born. & Flah.
*Nodularia harveyana* Born. & Flah.
*Microcoleus lyngbyaceus* (Kütz.) Crouan
syn.: *Lyngbya aestuarii* (Mert.) Liebm.
*Lyngbya confervoides* Gom.
*Lyngbya semiplena* (C. Ag.) J. G. Ag.
*Hydrocoleum lyngbyaceum* Kütz.
*Schizothrix arenaria* (Berk.) Gomont
syn.: *Microcoleus chthonoplastes* (Mert.)
Thur.
*Schizothrix calcicola* (Ag.) Gom.
syn.: *Lyngbya* spp. ø 1–3 μ
*Phormidium fragile* (Menegh.) Gom.
*Plectonema norvegicum* Gom.
*Oscillatoria* spec.
*Spirulina subsalsa* Oersted
syn.: *Spirulina subtilissima* Kütz.

succession suggests a competition for space, with expansion of one species at the expense of another.

In March 1968 *Rhizoclonium riparium* dominated in P.Q. 13 and *Vaucheria coronata* in P.Q. 16. The rather dry spring-weather brought about a gradual desiccation of the soil. In June the highest salinity value of 1968 was measured in both sample plots. In P.Q. 16 this phenomenon was attended by strong desiccation of the soil. This combination proved to be fatal for the *Vaucheria* mat. The vegetation dried up and lost its colour and the covering decreased. The *Rhizoclonium* vegetation in P.Q. 13 dried up and turned pale as well.

Notwithstanding the relatively dry summer months the covering of *Vaucheria* spp. in P.Q. 13 increased after June 1968, as contrasted with the situation in P.Q. 16. A comparison between *fig. 1* and *fig. 2* shows that in P.Q. 13 an increase of the salinity of the soil in June is not coupled with a strong decrease of the moisture content; the contrary is the case in P.Q. 16. This suggests that in this habitat, within the limits measured, the moisture content of the soil is a limiting factor and not the salinity of the soil moisture, for the life of *Vaucheria* spp.

After June 1968 the salinity and the moisture content did not reach extremely high, or extremely low, values again. In P.Q. 13 an explosive development of *Vaucheria* species (particularly *V. thuretii*) occurred on those spots becoming available after the deterioration of *Rhizoclonium riparium*. In P.Q. 16 as well *V. thuretii* began to flourish in August. For the rest of the year *Vaucheria* spp. remained the dominating algae in P.Q. 13. The competition for space, suggested by the large changes in P.Q. 13, was lost by *Rhizoclonium riparium*.

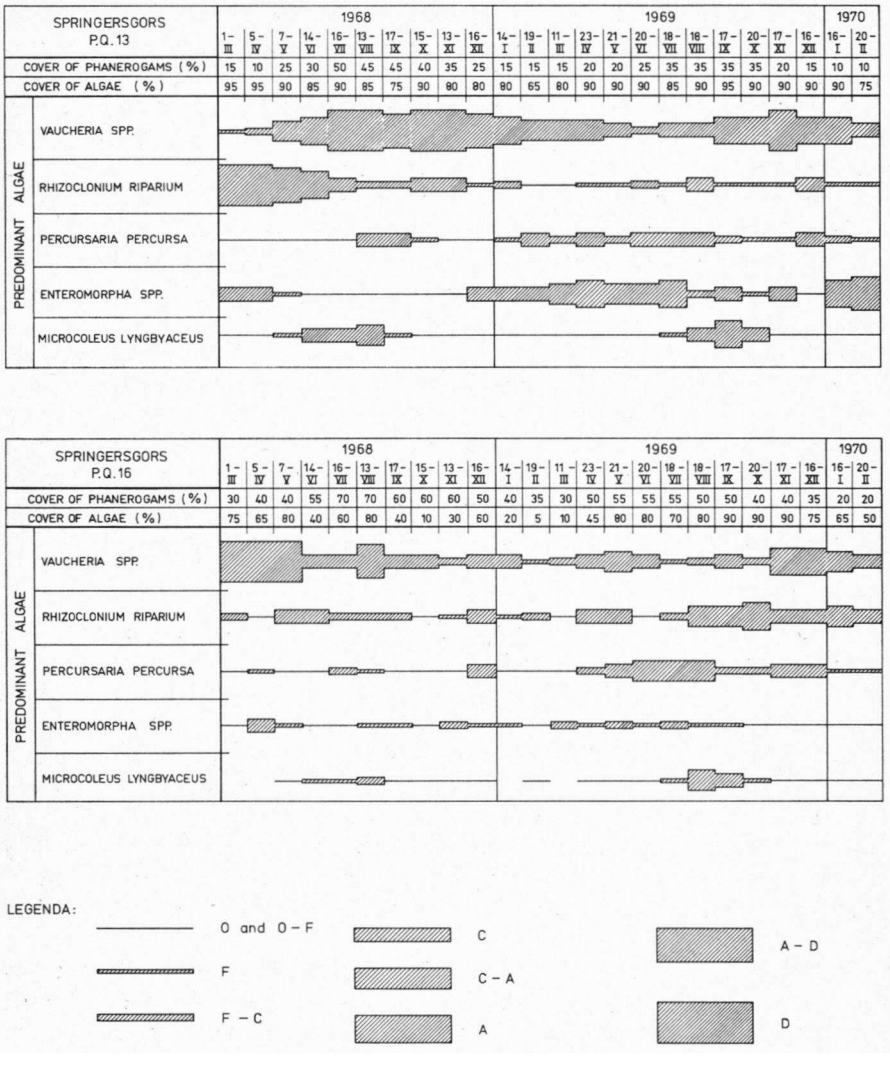


Fig. 3. Periodicity of dominant algae in two permanent quadrats on the Springersgors.

Februari 1969 was characterized by some weeks of frosty weather. On February 19th the soil in both P.Q.'s was frozen. (T −2.5 °C). The algal vegetation suffered from these extreme temperatures. In P.Q. 13 a marked decrease of the total covering percentage occurred: bare spots in the vegetation could be observed. Especially *Vaucheria* spp. were in a moribund state. In P.Q. 16 the effect of freezing was even better marked. *Rhizoclonium riparium* was the only alga still alive in quantity.

After the frost period a gradual development of several species followed. In P.Q. 13 *Vaucheria coronata* became overgrown by green algae (*Enteromorpha* spp., *Percursaria percursa*). In P.Q. 16 a temporary flourishing of *V. coronata* and an irregular growth of *Percursaria* and *Rhizoclonium* could be observed, without clear-cut correlation with changes in the salt and water table. In P.Q. 13 *Vaucheria* reached its lowest point in June, the soil being extremely desiccated and the salinity high. In P.Q. 16 a rather homologous development occurred.

*Enteromorpha* maintained itself during the dry summer months, although the vitality of the thalli decreased considerably. The *Enteromorpha* complex reached its lowest point in the last months of the year. In January 1970 these green algae began to flourish again in P.Q. 13.

During the whole year *Cyanophyceae* were present in small quantities (esp. *Microcoleus lyngbyaceus*). The proper development took place in summer. The optimum was reached in August, and in 1969 also in the dry September month. As blue-green algae grow very rapidly, they will form thin layers over the green algae and over *Vaucheria* species, within a short period partially suffocating the underlying algal mat. In the wet autumn period the blue-green algae died off and were washed away; they hardly occurred in winter and spring.

### 5.4. Periodicity of Vaucheria species

In the period March 1968–December 1968 *Vaucheria* samples of the two P.Q.'s were examined in preserved state. It appeared that in P.Q. 13 from March to May *V. coronata* dominated. This species was quickly replaced by the explosively expanding *V. thuretii*, probably as a result of the production of aplanospores (aplanospores could be observed from May till September). From September onwards the latter species was accompanied by *V. intermedia*. *V. thuretii* was for the greater part responsible for the summer maximum in 1968 in P.Q. 13 (*fig. 3*). The *Vaucheria* maximum in P.Q. 16 (*fig. 3*) in March, April, and May was especially caused by *V. coronata* and to a lesser extent by *V. arcassonensis*. In the summer months *V. thuretii* dominated with aplanospores in P.Q. 16 as well.

From December 1968 till February 1970 the *Vaucheria* vegetation in the two P.Q.'s was carefully analysed. The monthly *Vaucheria* samples were cultivated and with the aid of fructifications the composition of the samples could be established. The quantitative results, obtained as described in 5.3, are depicted in *fig. 4*.

In both P.Q.'s *V. coronata* was present in quantity in winter and spring and disappeared entirely in summer. The disappearance of the species in June coincided with very high salinities of the soil moisture (max. $67.4^0/_{00}$ $Cl^-$ in P.Q. 13) and with desiccation of the top soil (P.Q. 13). The flourishing in autumn (November) coincided with an increase of the moisture content and a decrease of the salinity (minimum $0.8^0/_{00}$ $Cl^-$ in P.Q. 16 in February 1970).

In both sample plots *V. intermedia* was hardly present in spring, a period in which *V. coronata* was still very common. *V. intermedia* flourished in late summer and autumn and the development went on into winter. *V. coronata* and *V.*

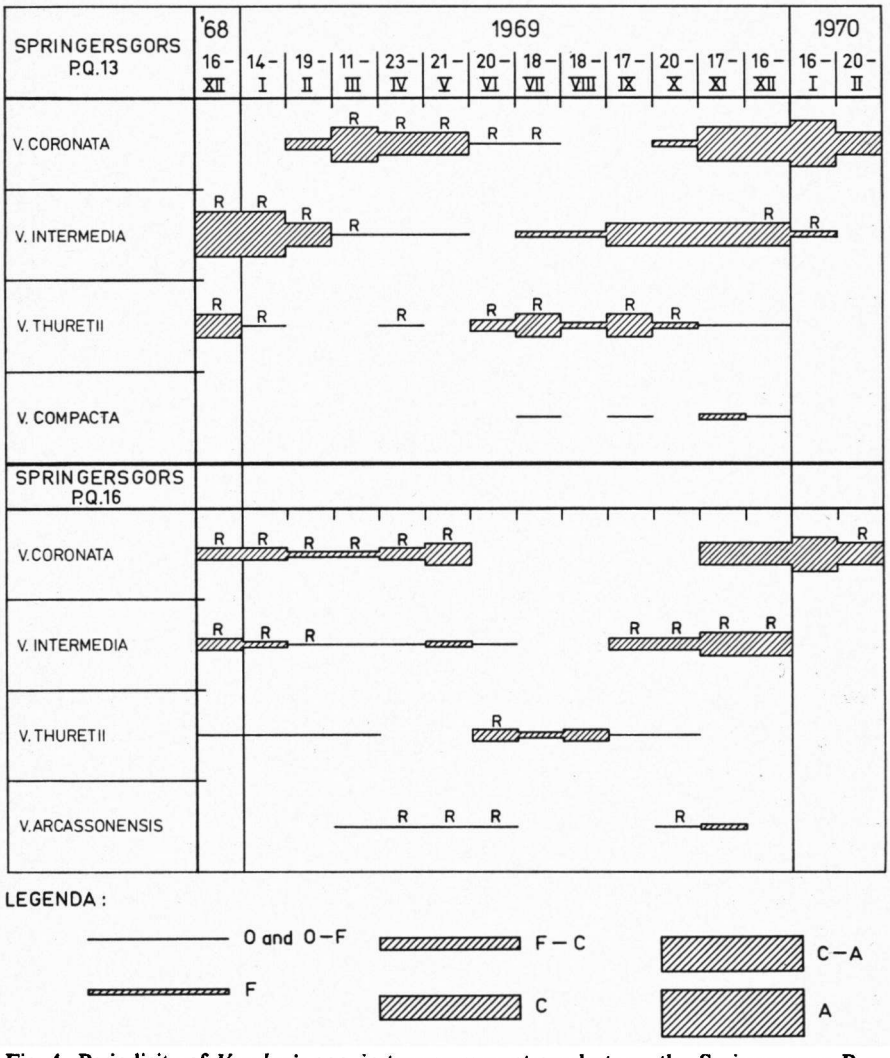


Fig. 4. Periodicity of *Vaucheria* spp. in two permanent quadrats on the Springersgors. R = with reproductive structures

*intermedia* replaced one another in spring 1969, whereas they were found together in autumn and early winter.

Almost the whole year *V. thuretii* was met with; the maximum development in both sample plots was in summer, in contrast with *V. coronata* and *V. intermedia*. *V. arcassonensis* and *V. compacta* played a very subordinate part in the permanent quadrats. *V. arcassonensis* was found in spring and autumn in P.Q. 16 and *V. compacta* in P.Q. 13 in the second half of the year.

In the periodicity of the *Vaucheria* species the largest changes occurred after

the action of extreme environmental conditions. During the frost period or February 1969 *V. intermedia* almost completely disappeared in both P.Q.'s. Afterwards in the same spot, *V. coronata* began to flourish. In June 1969 the soil desiccated and salinities rose ro high values, and probably as a consequence of these extreme conditions *V. coronata* vanished in both quadrats. In the following summer months, with high temperatures, high salinities and low moisture contents of the soil, a fluctuating growth of *V. thuretii* could be observed, in late summer dominated by renewed flourishing of *V. intermedia.* In November, when salinities of the soil water dropped sharply and moisture contents of the soil strongly increased, *V. coronata* quickly overgrew the other species and dominated in early winter.

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## ERRATA

*Acta bot. neerl. 20 (1)*

p. 107, line 6 of the summary: *delete* the words 'algae and higher plants is given'

p. 118, first line : last word should read: of
fourth line: 6th word should read: to
REFERENCES: In the titles of the two papers by N. CARTER 'algal' should read: alga