

VAUCHERIA COMPACTA: A EURYHALINE ESTUARINE ALGAL SPECIES

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SUMMARY

Data are presented on distribution and ecology of *Vaucheria compacta* in the Netherlands. A description is given of a sociation of *V. compacta*, an estuarine community, often showing mass occurrence. From culture experiments in salinity ranges it is concluded that there are no "salinity races" but that a non-modificative morphological variation is present in some antheridial characters. As a consequence of this, a new variety is described: *Vaucheria compacta* var. *dulcis*. At some occasions monoecious filaments were observed within this dioecious species.

1. INTRODUCTION

Investigating the brackish *Vaucheria* species in the Netherlands, it appeared that *V. compacta* is one of the most common and widespread species in the Dutch coastal region, especially in estuarine habitats (SIMONS & VROMAN 1968).

From the few records on its geographical distribution, it seems that the species is restricted to the Atlantic coasts of Europe and N. America. European records are a.o. from France (DANGEARD 1939); Denmark and England (CHRISTENSEN 1952); Germany (RIETH 1956, BEHRE 1961). American records are from Massachusetts (BLUM & CONOVER 1953, WEBBER 1968) and Quebec (BLUM & WILCE 1958).

CHRISTENSEN (1952) gives information about the nomenclatural history. So the species has been described first by ROSENVINGE (1879) as *V. sphaerospora* var. *dioica*. and later by COLLINS (1900) as *V. piloboloides* var. *compacta*. After his description Collins considered it to be a distinct species and so in TAYLOR (1937) it is named *V. compacta*. Although not strictly correct, Christensen prefers to quote the name as *V. compacta* (Collins) Collins ex Taylor.

In the same paper Christensen also drew attention to morphological variation within this dioecious species, especially in form and size of the antheridia. He states: "It is to be hoped that further research will decide whether the different types can be arranged in mutually distinct groups or not, but at present one must, in any case, treat the complex as a whole".

The present paper deals with variation in form and arrangement of antheridia, and based on these data a new variety is described named *V. compacta* var. *dulcis*. Another variety has been distinguished by BLUM & WILCE (1958) named *V. compacta* var. *koksoakensis*. This variety, characterized by extremely long oogonia, has not been recorded in the Netherlands so far.

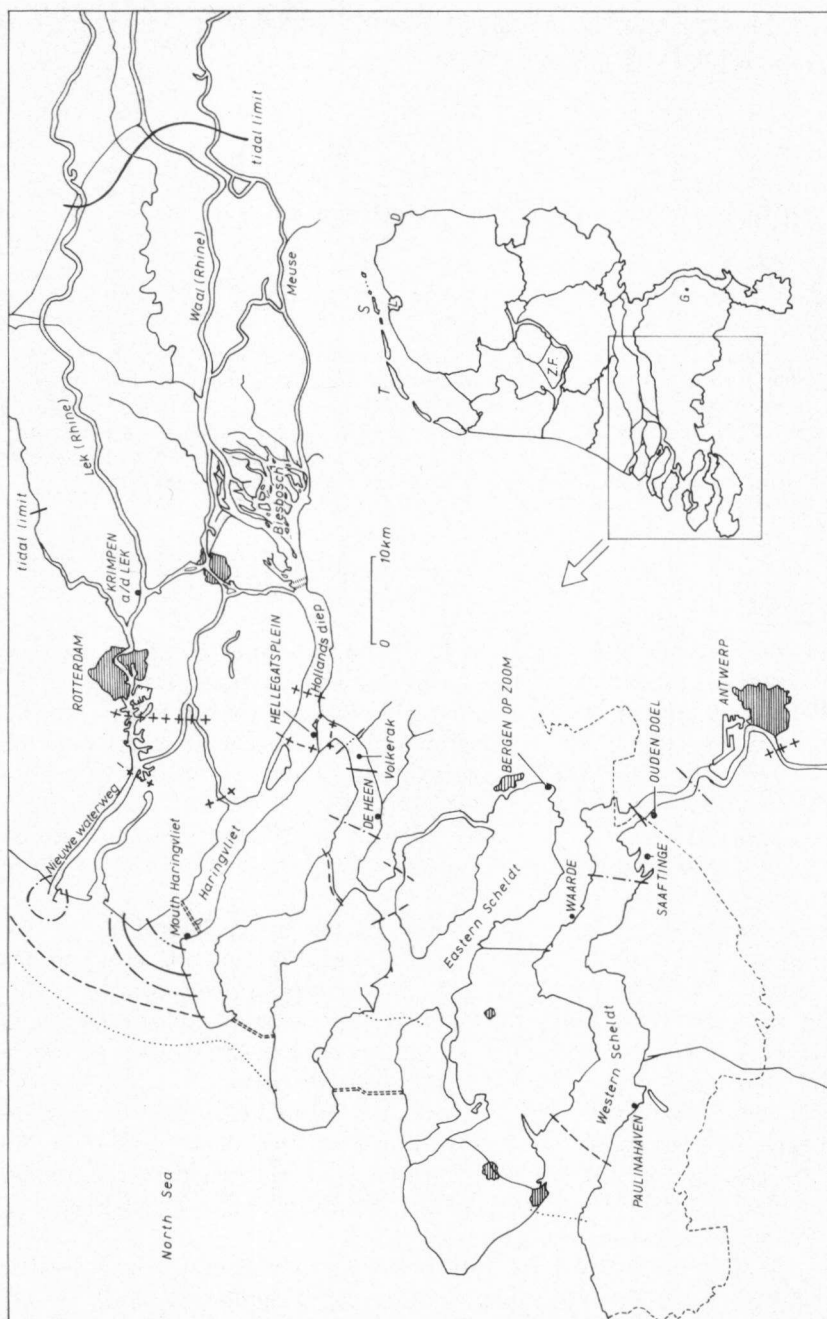


Fig. 1. Survey of the S.W. Dutch estuarine region. The position of isohalines and tidal limit relate to the situation before the dams in the Haringvliet (1970) and Volkerak (1969). Isohalines are drawn according to data from PEELEN (1967). The isohalines were measured at surface, midtide, and average river discharge.

.....: isohaline 16.5‰ Cl⁻, ----: 15‰, -.-.-: 10‰, ———: 5.5‰, -...-...: 3‰, +-+-+: 1‰, +++: 0.3‰. ===: designed construction of dams.

On the map of the Netherlands: T: Terschelling, S: Schiermonnikoog, L: Lauwerszeepolder, D: Dollard, Z.F.: polder Z. Flevoland, G: Grathem.

2. DISTRIBUTION AND PERIODICITY OF *V. COMPACTA* IN THE NETHERLANDS

The distributional pattern of *V. compacta* in the Netherlands includes a great variety of habitats (for local geographic names see the map in *fig. 1*).

The vertical range of *V. compacta* extends from either about 2 m. below MHW in freshwater tidal areas or about 1 m. below MHW in brackish and marine localities towards about 30 cm. above MHW. Along euhalinic and polyhalinic waters *V. compacta* grows intermixed with the species *V. subsimplex* (= *V. sphaerospora*, and *V. velutina* (= *V. thuretii*). In such habitats *V. subsimplex* and *V. velutina* make up the greater part of a dark green *Vaucheria* mat often carpeting the high littoral part of creek banks in salt marshes (NIENHUIS 1970, NIENHUIS & SIMONS 1971). Along mesohalinic and oligohalinic tidal waters and in freshwater tidal areas *V. compacta* is the most important *Vaucheria* species in the littoral zone, often forming extensive algal mats especially on flats consisting of muddy sand (*figs. 2 and 3*). These algal mats often show a tufted appearance (*figs. 3 and 4*). The function of these tufts may be to provide a mode of aeration of the otherwise compact algal felts. In the freshwater tidal area the Biesbosch the Dutch name "nopjeswier" has been derived from this typical tufted aspect. Luxurious occurrence of *V. compacta* upstreams of the rivers Rhine and Meuse reaches as far as the tidal influence is measurable.



Fig. 2. Mass occurrence of *V. compacta* on a sandy flat at Hellegatsplein (Haringvliet).

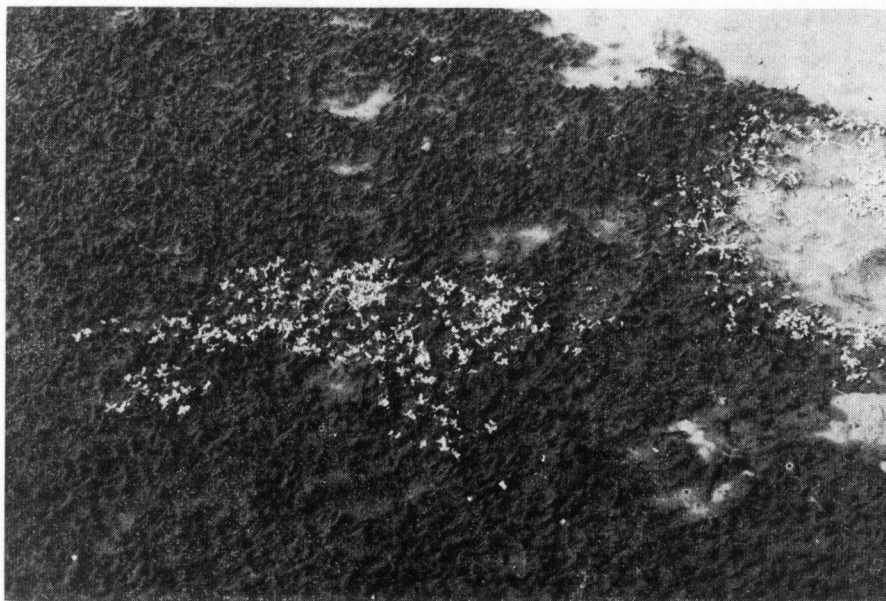


Fig. 3. Close up of *V. compacta* mat at Krimpen a/d Lek, with *Callitriche stagnalis* as accompanying phanerogamic species.

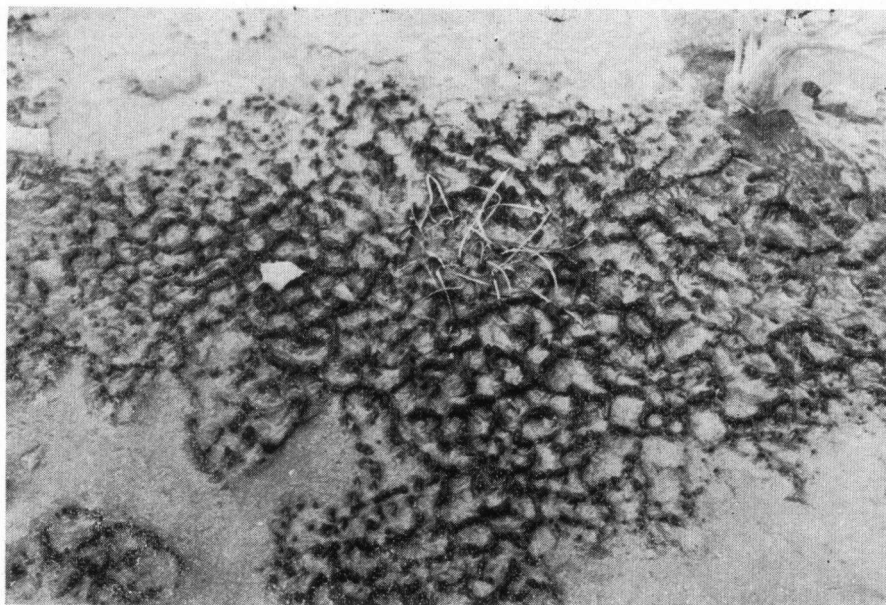


Fig. 4. Net-like appearance of tufted *V. compacta* mat in Lauwerszee polder.



Fig. 5. Parts of displaced *V. compacta* mats, one of the mats has been rolled up behind a *Salicornia* plant.

Farther upstream, only a few records exist. The most distant record is from the province of Limburg (about 200 km. inland).

Recently the tidal influence in the greater part of the Rhine-Meuse estuary has disappeared due to the construction of dams in the mouth of the Haringvliet (1970) and in the Volkerak (1969). With the vanishing of the tides in the streams called Haringvliet, Hollands Diep and Biesbosch, *V. compacta* no longer is one of the most prominent algal species along these river systems. Mass occurrence of *V. compacta* is nowadays restricted to only a few remaining freshwater tidal areas. The tidal influence at these places comes via the Nieuwe Waterweg canal near Rotterdam. For example, one freshwater tidal locality with much *V. compacta* is left at Krimpen a/d Lek East of Rotterdam.

In the southern part of the Dutch S.W. estuarine region rich occurrence of *V. compacta* can be observed from the brackish (mesohalinic) marshes called Saaftinge towards beyond Antwerp along the river Western Scheldt.

Apparently the species can withstand heavy pollution. This is in accordance with other European records from towns as Bremen (BEHRE 1961), Bordeaux and Paris (DANGEARD 1939). The present author has observed *V. compacta* in Paris in 1969 along the river Seine forming a more or less continuous belt above water level where the stones of the quays were covered with some silt. The upper limit of this belt was determined by the splash zone.

In the northern part of the Netherlands, *V. compacta* occurs in the Wadden

Sea region in salt marshes, beach plains, and also in the Dollard (part of the Eems estuary). In the salt marshes of the Wadden isles *V. compacta* shows its optimum growth along creek systems in a transitional zone between salt marshes and dunes (meso-oligohaline). Closer to the sea *V. compacta* is again mixed up with *V. subsimplex* and *V. velutina*. In the mesohalinic and oligohalinic parts of the Dollard marshes, *V. compacta* does not show the mass appearance that could be expected on account of salinity. This may be explained by the nature of the substratum. The soil of the Dollard marshes contains a very large lutum fraction, causing too unstable an environment for algae to develop in mass. This influence of substratum composition is also shown in the mesohalinic marshes of Saaftinge (Western Scheldt), where the most richly developed *V. compacta* mats can be found in relatively sandy places.

A mass aspect of *V. compacta* as mentioned here has also been described by BEHRE (1961) from the tidal part of the river Weser and by KÖTTER (1961) from a comparable habitat in the river Elbe. Kötter does not mention any species, but it can safely be assumed that this *Vaucheria* growth contains *V. compacta* as dominant species. Kötter described this *Vaucheria* aspect as an association named "*Vaucherietum*". This community consisting of one dominant species should actually be called a sociation: *Vaucheria compacta* sociation. This sociation is presumed to be common in the N.W. European estuaries.

V. compacta not only occurs in tidal environments, but also in non-tidal environments. Examples are: a beach plain on Schiermonnikoog (SIMONS 1974), shores of brackish inland pools, brackish ditches. Newly reclaimed polders appear to be an ideal environment. Two cases could be studied namely the polder Z. Flevoiland (fig. 1), reclaimed in May 1968 from the freshwater lake IJsselmeer, and the polder Lauwerszee reclaimed in May 1969 from the Wadden Sea. In these polders the *Vaucheria* aspect was present within a year after the draining of the water. Especially in the Lauwerszee polder *V. compacta* showed an abundant development over vast sandy areas along the relatively moist, gently sloping edges of creeks. During a visit to this polder it was observed that the *Vaucheria* mass is really a mat which can be lifted from the bottom by the water during stormy and rainy weather. In fig. 5 it can be seen that such a mat can be rolled up. Similar rolling up of mats has also been mentioned by KÖTTER (1961).

One of the explanations for the mass occurrence of this pioneering algal species is the well-developed capacity of asexual propagation by means of aplanospores. The production of aplanospores takes place at the filament tips. After liberation of an aplanospore the walls of the terminal part of the filament are left behind as an empty envelope. The filament can grow out either through this envelope (fig. 6a) or laterally (fig. 6c). Shortly after growing out a new aplanospore can be formed and so on (fig. 6a). A similar way of aplanospore production has been observed in *V. sescuplicaria*, *V. subsimplex* and *V. velutina*. Immediately after liberation, the aplanospore germinates into one or more new filaments (fig. 6d-g). Sometimes aplanospores are observed to germinate even before being liberated.

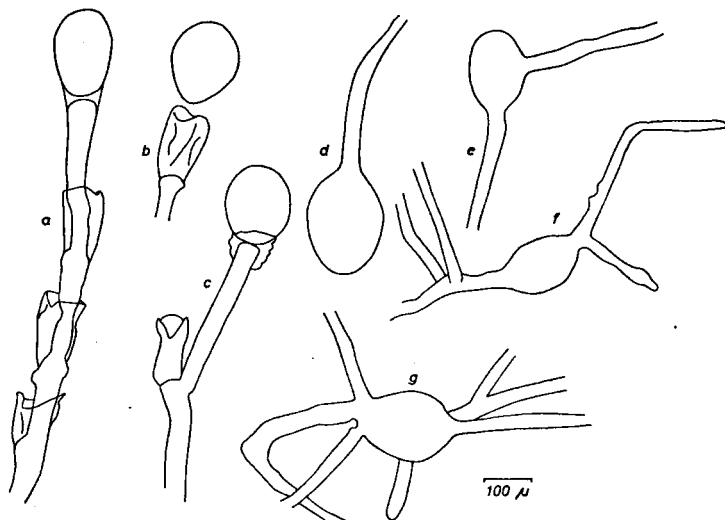


Fig. 6. Aplanospore production and germination of aplanospores. a-c: aplanospore production; d-g: different modes of germination of aplanospores.

Sexual reproduction was observed also, be it on a much smaller scale. It takes place over the whole salinity range from sea to freshwater, with an optimum in the mesohalinic areas.

As to the periodicity of *V. compacta*, it can be stated that the optimum occurrence is in summer and autumn, but in other periods of the year the species can be found as well, although never in great quantities, and more often in brackish than in non-brackish situations. Sexual propagation is restricted to summer and autumn with an optimum in September and October.

3. THE EURYHALINE CHARACTER AND MORPHOLOGICAL VARIATION

3.1. The euryhaline character

The field data presented in this paper clearly demonstrate the euryhaline character of *V. compacta* as it does occur over the whole salinity trajectory of the estuaries, from sea to freshwater.

In order to make out to which extent there exists morphological or physiological variation within this species, which could be correlated with the salinity of the environment, the alga was cultivated many times in salinity ranges. Salinity values in the cultures were situated between 0 and 25‰ Cl^- . Culture conditions involved a temperature of 12°C., a photoperiod L/D: 12/12, and light intensities between 1000 and 2000 Lux. Media used were Erdschreiber solutions with either a freshwater basis or a seawater basis. Salinity was varied in different ways: a: mixing Erdschr./freshwater with Erdschr./seawater, b: adding NaCl to Erdschr./freshwater and c: dilution of Erdschr./seawater with distilled water.

Within each range the number of salinity steps varied from four to ten. Each test lasted about one month. Small quantities were taken from a freshly collected sample (after about two weeks of acclimatization in the laboratory) or from clonal material, cultivated from aplanospores. In this way we have tested material of *V. compacta* from the brackish locality Waarde on the Western Scheldt (salinity of about 11‰ Cl⁻) and from several freshwater localities (mostly Biesbosch and Krimpen a/d Lek).

From these culture experiments it could be concluded that there are no different physiological races with respect to salinity: the brackish *V. compacta* showed a similar behaviour towards salinity as the freshwater *V. compacta*. Vegetative growth occurs between 0 and 16‰ Cl⁻; an optimum was often found between 1 and 5‰ Cl⁻. Growth stops between 16 and 20‰ Cl⁻. Thus optimum growth was found in the oligohalinic and mesohalinic part of the salinity range. Sexual reproduction occurs only between 0.5 and about 10‰ Cl⁻, and is again similar for both the brackish and the freshwater material. Aplanospores are produced under all salinity conditions tested, without any apparent regularity.

Resuming it can be stated that *V. compacta* is a true brackish species, which penetrates into marine and especially into freshwater environments.

3.2. Morphological variation

3.2.1. Variation in antheridium characters

In material from different localities over the whole salinity range, no discontinuities could be found in size of filaments, oogonia, oospores and antheridia. OGGEL (1971) measured these organs in material from ten different localities in the whole salinity range. Each sample was cultivated in a medium with a salinity value corresponding to the mean salinity value of the habitat, until sufficient reproductive structures appeared. For each character at least fifty measurements were taken. The characters showed considerable overlap in variation. Summing up all his measurements the following figures were obtained: oogonia: 140 – 364 (mean 226) × 98 – 168 (mean 128) μ; length of antheridia: 72 – 224 (mean 135) μ; diameter of filaments: 25 – 70 (mean 40) μ. All sizes given in literature for the greater part lie within these ranges.

When considering the form and arrangement of the antheridia however, some interesting features were observed. In an earlier paper (SIMONS & VROMAN 1968) attention was drawn to the sympodial clustering of antheridia in brackish material. A few examples of this phenomenon are shown in *fig. 7*. In freshwater material such abundant clustering was never observed; only occasionally two and sometimes three antheridia are implanted together on relatively short lateral branches (*fig. 7e*). Clusters of more than three antheridia are formed only terminally in freshwater material (*fig. 7d*). This way of antheridium implantation in both the brackish and freshwater material was observed to remain constant while culturing the two forms in different salinities. Therefore the conclusion must be drawn that this is a non-modificative character.

Another important feature to be pointed at is the form of the antheridium, especially the number of pores. An antheridium is always provided with one terminal pore and mostly one or two lateral pores on conical papillae. However, the number of lateral pores can amount to five (fig. 8g) in brackish material. For morphological variation in antheridia see figs. 7 and 8. In brackish material of *V. compacta* the number of lateral pores is mostly two or sometimes more than two, while in freshwater material there is usually only one lateral pore, or none at all. On the basis of the number of lateral pores the following antheridial classes can be discerned: 1.0:0 lateral pores, 1.1:1 lateral pore, 1.2:2 lateral pores and 1.3:3 (or more) lateral pores. In cultivated samples, from localities along the whole salinity range, 50–100 antheridia from each sample were investigated and grouped in the above mentioned pore classes. The result is shown in fig. 9. This diagram shows that in material from freshwater localities the classes 1.0 and 1.1 taken together, are clearly larger (mostly twice or more) than 1.2, and that in brackish/marine localities the classes 1.0 and 1.1 together are clearly smaller than 1.2 and 1.3 together. In freshwater material, for example

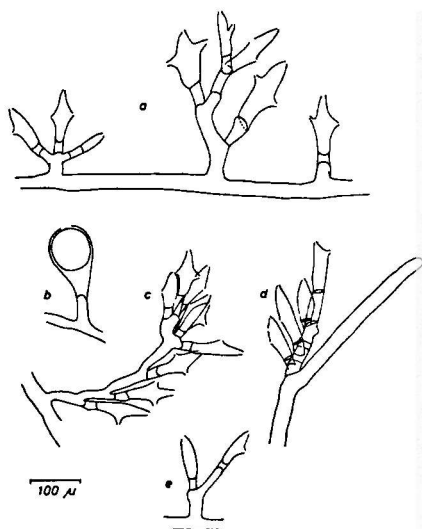


Fig. 7. Clustering of antheridia and form of oogonium. a–c: clustering of antheridia in brackish material; d: terminal cluster of antheridia in freshwater material; e: sympodium with two antheridia from a freshwater sample; b: general form of oogonium.

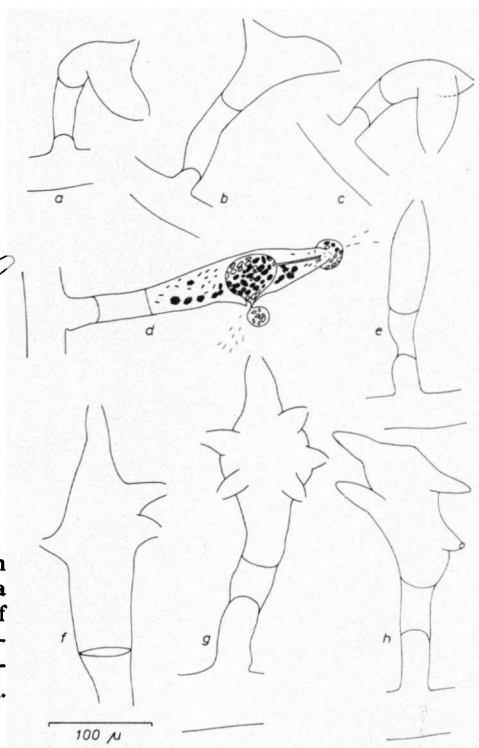


Fig. 8. Form variation of antheridia. a–e: antheridia of freshwater material; d: liberation of spermatozoids accompanied by plasma-expulsion; f–h: antheridia of brackish material with more than two lateral pores.

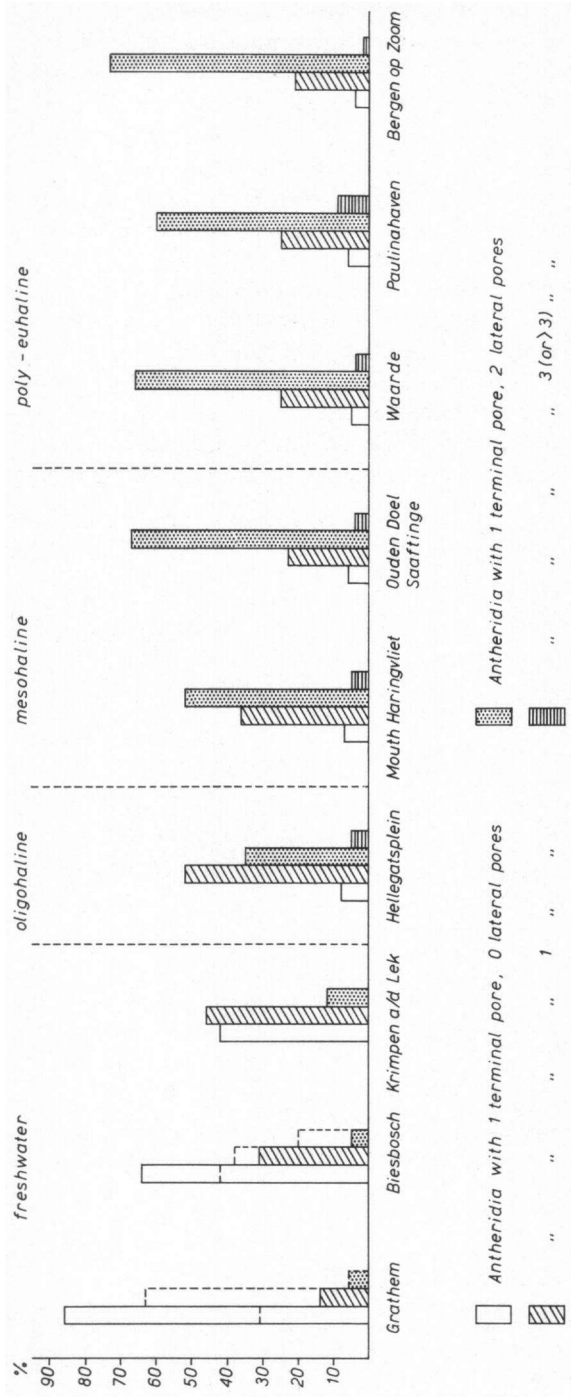


Fig. 9. Diagram with frequency distribution of antheridial classes from samples along the whole salinity range of the estuaries. The dotted lines in the Grathem and Biesbosch blocks apply to the frequency distribution when samples of these localities were cultivated under brackish conditions.

from Grathem (non-tidal freshwater) or the Biesbosch, the number of antheridia belonging in class 1.0 can be lowered by culturing the material under brackish conditions, but not to such an extent as to change the typical freshwater pattern into a brackish one (*fig. 9*).

There does not seem to be a quantitative relation between these antheridial characters and salinity of the environment, although the oligohalinic material shows some transition between the freshwater and the brackish situation (*fig. 9*). In this case the classes 1.0 + 1.1 are less than twice as large as 1.2 + 1.3.

3.2.2. Variation of antheridial characters in salinity ranges

To answer the question whether implantation and form of antheridia is a matter of environmental modification or not, these characters were studied in cultures with different salinities. This has been done both with freshly collected (wild) material and with clonal material from aplanospores of the localities Waarde (brackish) and Krimpen a/d Lek (tidal freshwater). Variation in salinity was obtained by the three methods a, b and c as mentioned in 3.1. Five salinity values were tested: 0.5, 5, 8, 12 and 16‰ Cl⁻. The experiments lasted from 2½ months for the Waarde material to 4½ months for the Krimpen material.

The results of these experiments are summed up in *tables 1* and *2*. As to the Waarde material the following remarks can be made: sexual reproduction in the clonal material occurs from 5 – 12‰ Cl⁻, contrary to wild material where sexual reproduction takes place over a broader range of salinity (0.5 – 16‰ Cl⁻). In the clonal aplanospore material vegetative growth is optimal under salinities from 5 – 12‰ Cl⁻, which is in accordance with the wild material. The composition of the antheridium classes (*table 2*) does not vary much under all circumstances tested, and clearly shows the brackish pattern: the classes 1.0 + 1.1 are much smaller than 1.2 + 1.3. The values mentioned in *table 2* of the wild Waarde material are compiled from fifteen records (five salinity values in three different media), while the values of the aplanospore material are based upon two records (at 5 and 8‰ Cl⁻).

In the same *tables 1* and *2* the results of the freshwater Krimpen a/d Lek material are presented. Growth and reproduction rates are almost similar to those of the Waarde material, the only difference being the rate of sexual reproduction of the wild material, which is lower under seawater conditions. The composition of the antheridial classes does again remain constant under all salinity values tested, and clearly shows the freshwater pattern: the classes 1.0 + 1.1 are much larger than 1.2 + 1.3. This was not only the case with the fifteen values obtained from the wild material, but also with the one value (at 8‰ Cl⁻) from the aplanospore material, which is a very strong indication for the constancy of this character in the freshwater *V. compacta*.

3.2.3. Description of variety *dulcis*

On account of the above mentioned data the conclusion must be drawn that there are no different salinity "races" within *V. compacta*, but that there are two morphological entities which differ from each other in two antheridium char-

Table 1. Summary of results from salinity test series of the brackish *V. compacta* from Waarde and of the freshwater *V. compacta* from Krimpen a/d Lek. Salinities are expressed as ‰ Cl⁻. The results are compiled from the data obtained in three different media (a, b, c). Explanation of symbols: ++: poor growth, +: good, +++: very good, ++++: rich.

♀: presence of male and female reproductive organs. One symbol: some organs, two: numerous, three: very numerous, four: abundant. ♂: the same, but only antheridia. o: some aplanospores and so on.

	0.5‰	5‰	8‰	12‰	16‰
Waarde					
wild material:					
vegetative growth	+++	++++	++++	+++	+++
sexual reproduction	♀	♀♀♀	♀♀♀	♀♀♀	♀♀♀
aplanospores	ooo	o	oo	o	o
clonal material:					
vegetative growth	+	+++	+++	+++	++
sexual reproduction	-	♂♂	♂♂	♂	-
aplanospores	o	oo	oo	oo	o
Krimpen a/d Lek					
wild material:					
vegetative growth	++	+++	++	+++	++
sexual reproduction	♀	♀♀♀	♀♀♀	♀♀♀	♀
aplanospores	oo	o	o	o	o
clonal material:					
vegetative growth	+	++	++++	+++	++
sexual reproduction	-	♂	♂♂♂	♂♂	♂
aplanospores	o	o	ooo	ooo	o

Table 2. Frequency distribution of antheridium classes at different salinity values of culture medium. The figures between brackets relate to the number of records from which the values were compiled.

	Antheridium classes			
	1.0	1.1	1.2	1.3
Waarde				
wild material:	4%	20%	71%	5%
clonal material:	1%	24%	70%	5%
Krimpen a/d Lek				
wild material:	42%	46%	12%	(15)
clonal material:	42%	44%	14%	(1)

acters namely the sympodial arrangement and the number of lateral pores.

The type material of which antheridia are shown by CHRISTENSEN (1952), belongs to the brackish form, so that the freshwater form can be named as a distinct entity. As taxonomic rank of this entity the rank of variety is proposed. On account of its occurrence in freshwater this variety is named: *Vaucheria compacta* var. *dulcis* var. nov. (fig. 7b, d, e; fig. 8a-e). Latin diagnosis: A type

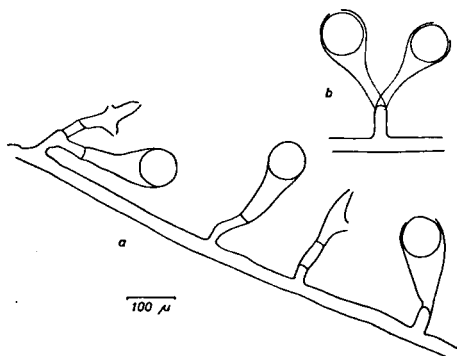


Fig. 10. Morphological aberrations. a: a monoecious filament; b: two oogonia on one common lateral branch.

differt in antheridiis poris lateralibus plerumque 0 aut 1 vice 2 aut plusquam 2, antheridia non disposita in sympodiis lateralibus aut interdum disposita in sympodiis brevibus lateralibus antheridiis non plus quam 3.

V. compacta var. *dulcis* prefers freshwater habitats, either tidal or non-tidal. It can be found in oligohalinic waters as well, be it in a less pronounced form. Non-tidal records for the Netherlands are among others: Grathem, Molenbeek (brook with slowly running water), polder Z. Flevoland. It is interesting to note that in the polder Z. Flevoland which has been reclaimed from freshwater the variety *dulcis* was recorded, while in the polder Lauwerszee, with a brackish character, the normal brackish form was recorded as a pioneering alga.

It is assumed that var. *dulcis* occurs outside the Netherlands as well, as for example the Paris record clearly showed the antheridial characters of var. *dulcis* (1.0: 50%, 1.1: 44%, 1.2: 6%).

3.2.4. Aberrations

At some occasions monoecious filaments were observed within a dioecious sample. This phenomenon has so far been observed from three brackish localities: Saaftinge, De Heen and Terschelling (see map, *fig. 1*). At De Heen this aberration was first seen in 1968 and, curiously, also in 1973. On such monoecious filaments the antheridia and oogonia mostly stand apart, but occasionally an antheridium and oogonium originate on the same sympodial lateral branch (*fig. 10a*).

Another abnormality to be pointed at is the occurrence of two oogonia on one lateral branch (*fig. 10b*) suggesting that the single oogonia are in fact implanted on reduced sympodia.

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