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OLIGOTROPHICATION AND EUTROPHICATION TENDENCIES IN SOME DUTCH MOORLAND POOLS, AS REFLECTED IN THEIR DESMID FLORA

Peter F. M. COESEL, Rita KWAKKESTEIN & Annemarie VERSCHOOR

Hugo de Vries Laboratory, University of Amsterdam, Plantage Middenlaan 2A, 1018 DD Amsterdam, The Netherlands

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Abstract

An inventory of the desmid flora in a number of forest and moorland pools, carried out in 1975, revealed that an appreciable impoverishment has occurred since the turn of the century. In those pools which are immediately surrounded by arable land and pastures or are connected with cultivated areas by small streams, the deterioration is caused by eutrophication and pollution of the aquatic environment. In hydrologically isolated pools, situated within nature reserves, the decline must be attributed to an acidification and oligotrophication of the site. The latter phenomenon may be associated with a much increased acid deposition in the atmospheric precipitation owing to air pollution, as recorded in the Netherlands especially in the last decennia.

Introduction

In the Dutch province of N. Brabant, to the SE of the little town of Oisterwijk, there is a complex of shallow moorland lakes and pools (Dutch: 'vennen') situated in an area of forest and heath country and of an exceptional biological importance for the Netherlands (compare Van Dijk, 1960). The hydrobiological interest in these small lakes consists mainly of an extensive survey of the desmid flora carried out in the period 1916-1925 by Professor J. Heimans. This thorough investigation revealed the exceptional abundance of this group of algae, over 250 species having been recorded among which taxa never recorded before from any other Dutch locality (Heimans, 1925). Already during the course of his studies Heimans observed a gradual deterioration of the desmid flora initiated by the disappearance of the most exclusive species. A repeated inventory during the years 1950-1955 showed that the tendency had been progressive in spite of the prolonged conservancy protection of the area in question (Heimans, 1960). The decline could partly be explained by the illicit drainage of sewage into the biologically richest series of lakes from a tea-garden situated nearby. In an attempt to regain the previous biological opulence, large-scale cleaning operations were carried out in 1950, during which the saprobic mud deposit on the lake bottoms was removed. As a result of this action the macrophytes indicative of eutrophic to saprobic conditions, became replaced by more mesotrophic forms in the course of a few years (Van Dijk & Westhoff, 1960b). Whether the control measures had achieved the desired results, also as far as the desmid flora is concerned, could not be ascertained after a time-span of five years, because the desmid vegetation seemed to be still in a pioneer stage (Heimans, 1960). The present authors deemed it interesting to draw up a new balance so as to get some insight into the long-term biological development of the best-known heathland pool landscape of the Netherlands.

The area studied

Fig. 1 shows the topographical situation of the pools studied, which lie in a Pleistocene cover sand area, partly surrounded and partly drained by the rivulets 'Rosep' and 'Achterste Stroom'. The lakelets presumably originated during the Pleniglacial by the blowing out of the sand cover until the underlying till layers became exposed. According as the pools were isolated and surrounded by nutrient-poor cover sands, or fed by nutrients seeping in

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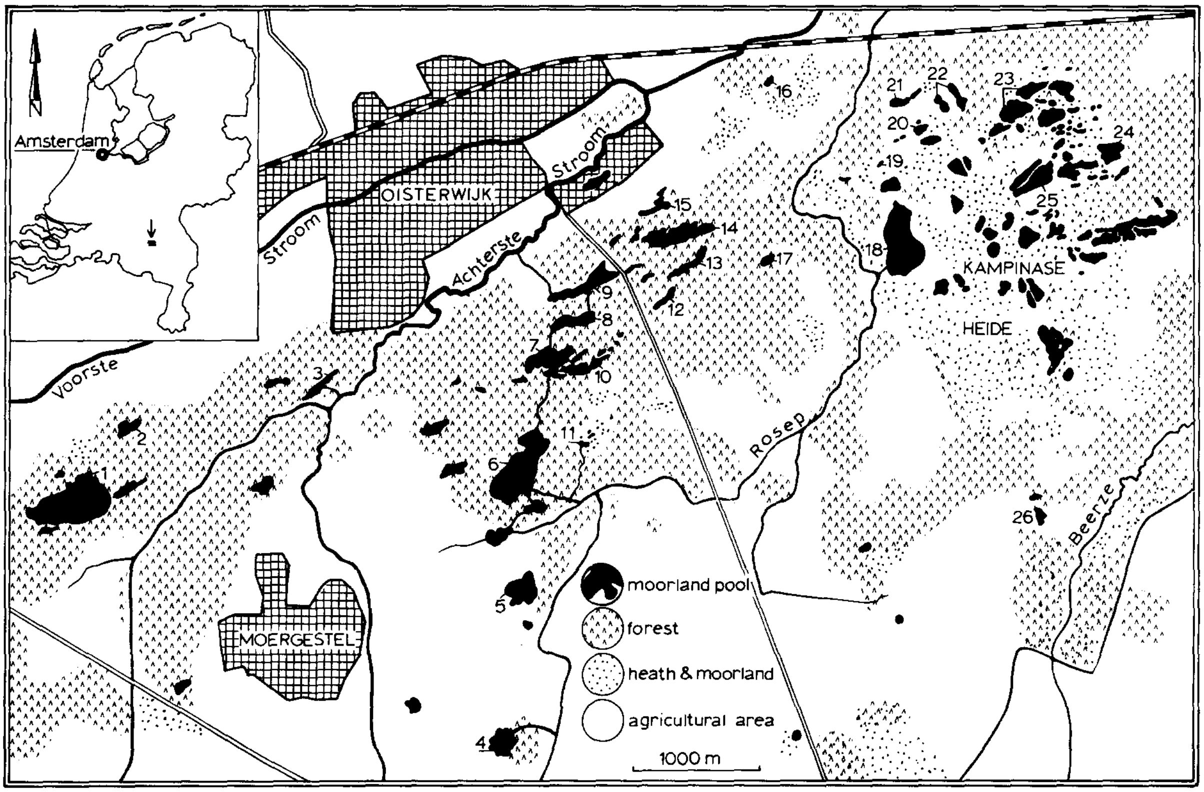

Fig. 1. Situation of the moorland pools near Oisterwijk. The pools studied for their desmid flora are numbered as follows:
1) Galgenven. 2) Schaapsven. 3) Rietven. 4) Hildsven. 5) Allemansven. 6) Kolkven. 7) Voorste Goorven. 8) Witven. 9) Van Esschenven. 10) Achterste Goorven. 11) Lammerven. 12) Klein Aderven. 13) Groot Aderven. 14) Staalbergven. 15) Wolfsputven. 16) Beeldven. 17) Duinven. 18) Belversven. 19) Belversputven. 20) Palingven. 21) Langeven. 22) Tongbergvennen. 23) Noordelijke Huisvennen. 24) Kogelvangersven. 25) Landmetersven. 26) Winkelsven.

from nearby streamlets, they originally had either an oligotrophic or a mesotrophic character. Up to about the middle of the last century the fen lakes under discussion were surrounded by vast moor- en heathlands, but since that time a large part of the country was afforested with Scotch pines, both as a prevention to shifting of the sand and for the production of pit-props. Especially by the beginning of the 20th century the development of the country side for agricultural purposes increased progressively. In spite of the protection of a considerable part of the area under the nature conservancy acts since about 1913, the deterioration of the biological quality of the richest lakes, situated in the southernmost part, could not be prevented, owing to the exploitation of the area due south of these lakes for agricultural purposes and directly or indirectly draining off towards these lakes. The ensuing eutrophication and pollution of the rivulet Rosep ultimately became so strong that the biological richness of the so-called 'Centrale Vennen', which had a direct connection with the Rosep (see Fig. 1, lakelets nos. 7-9), seemed to be threatened with complete obliteration. For this reason it was decided to close the connection radically in 1950.

Sampling

At the beginning of the month of September, 1975. samples for an analysis of the desmid flora were collected from about 30 lakes and pools by means of a plankton net, and by sequeezing out suitable submerged substrates such as mosses, higher aquatics, filamentous algae, etc. According as a lake or pool exhibited a greater internal, geomorphological and vegetational diversity, more samples were taken. Altogether the desmid flora was investigated in about 100 samples preserved in formalin.

To this end individual slides were microscopically examined until in three successive slides no additional taxa were encountered. Although the relative abundance of the various species was also recorded by means of a simple code, this information is not reported in the present paper because it cannot be used to compare the present situation with the records of the older relevant literature in which only presence-absence data are given. The records of relative abundance, in addition to much detailed information concerning the sampling sites, are to be found in Kwakkestein (1977) and Verschoor (1977). At each sampling site pH and conductivity were measured electrometrically in the field and from most lakes a water sample for chemical analysis (according to methods described in De Lange & De Ruiter, 1977) was taken.

The development of the desmid flora in the first half of this century

In former years the richest desmid locality was the so-called 'Centrale Vennenreeks' consisting of Voorste Goorven (lake no. 7 in Fig. 1), Witven (no. 8), and Van Esschenven (no. 9). They received water from the rivulet Rosep arising in the southeasternly situated bog- and heathland complex 'Moergestelse Broek', via the Kolkven (no. 6), notably during the cold season. From these Centrale Vennen an eventual excess of water drained off towards the NE on the Achterste Stroom. In this way there was a more or less steady flow of water provided by the Rosep. Since this water was most probably fairly nutrient-rich owing to small-scale farming, mesotrophic conditions developed in these lakes situated in poor sandy soils. This mesotrophic character was manifest from the occurrence of such macrophytes as *Nitella translucens, Scirpus fluitans, Potamogeton gramineus, Luronium natans, Utricularia intermedia, Hypericum elodes, Carex lasiocarpa, Eriophorum gracile,* and *Anagallis tenella.* The desmid flora was decidedly rich by the beginning of this century, and was represented by about 150 species belonging to some 20 genera (compare Table 1). Other, comparable lakelets in the drainage area with a similar, albeit somewhat poorer, well-developed mesotrophic desmid community were, at that time, *e.g.*, the Hildsven (no. 4 in Fig. 1), the Allemansven (no. 5), the Kolkven (no. 6), and the Rietven (no. 3), A totally different situation prevailed in somewhat more elevated and hydrologically isolated ones in the area towards the NE of the Centrale Vennen, where oligotrophic conditions were evident from the occurrence of such macrophytes as *Isoëtes lacustris, Lobelia dortmanna, Carex rostrata, Narthecium ossifragum, Oxycoccus palustris, Andromeda polifolia,* and *Erica tetralix.* The desmid flora of these oligotrophic pools, although rather poor in species, was of a very characteristic composition and contained as most exclusive species: *Docidium undulatum, Staurastrum elongatum, Cosmarium ralfsii* and *Micrasterias oscitans.* A transitional character, intermediate between these oligotrophic pools and the mesotrophic complex of the Centrale Vennen, was exhibited by the Achterste Goorven (No. 10). Although the Voorste and the Achterste Goorven (Nos. 7 and 10, respectively) are only separated by a low and locally hardly one metre broad dam, their respective desmid floras differed considerably. Heimans (1969) reports that of the over 100 species of the Achterste Goorven and the about 150 ones recorded from the adjacent Voorste Goorven only some 50 occur in both lakes, the differentiating species representing nearly all genera. Of the genus *Euastrum,* for instance, the species *E. oblongum* and *E. verrucosum* were exclusively found in the Voorste, and the species *E. affinis, E. ampullaceum, E. crassum, E. inerme, E. pinnatum,* and *E. validum* only in the Achterste Goorven. The genus *Micrasterias* was mostly restricted to the Voorste Goorven (13 of the 15 species recorded for both lakes). The comparative list of species (Table 1, column '1916-'25') clearly demonstrates the more nutrient-rich nature of the Voorste Goorven indirectly fed by the rivulet Rosep, as opposed to the more acid and hydrologically more isolated Achterste Goorven.

The nutrient-enriching action of the water from the Rosep on the Centrale Vennen increased progressively in the course of the 20th Century as more land draining upon that area was developed for agriculture and more fertilisers came into use on the arable fields. Thus mesotrophic conditions progressively tended to become eutrophic. The eutrophication became alarming by the late 'forties, especially the Voorste Goorven becoming almost clogged with stands of marshland and quivering bog species such as *Carex acutiformis, Alisma plantago-aquatica, Cicuta virosa, Lysimachia vulgaris, Lycopus europaeus,* and *Rumex hydrolapathum.* It was at that time that the clandestine discharge of sewage water from a nearby tea-garden was discovered, which source of pollution was manifest from a concentration of such indicator species as *Glyceria fluitans, Polygonum hydropiper, Epilobium hirsutum, Rorippa amphibia,* and

Table 1. List of desmid species from Centrale Vennenserie, Voorste Goorven (separately), and Achterste Goorven in, successively, the periods 1916-1925, 1950-1955 (data after Heimans, 1960) and 1975. Arrangement of the desmid species in such a way that a distinct shifting in species composition is demonstrated.

	Centrale Vennen			Voorste Goorven			Achterste Goorven		
	'16 - '25	'50 - '55	'75	'16 - '25	'52 - '55	'75	'16 - '25	'50 - '55	'75
Closterium aciculare	x			x					
C. cynthia	x			x					
C. limneticum	x			x					
C. malinvernianum	x			x					
C. moniliferum	x			x					
C. praelongum	x			x					
Cosmarium bioculatum	x			x					
C. conspersum (latum)	x			x					
C. debaryi	x			x					
C. fontigenum	x			x					
C. meneghinii	x			x					
C. moniliforme	x			x					
C. pachydermum	x			x					
C. pygmaeum	x			x					
C. quadrum	x			x					
C. retusiforme	x			x					
C. subprotumidum	x			x					
C. taxichondriforme	x			x					
C. triplicatum	x			x					
C. turgidum	x			x					
Staurastrum arctison	x			x					
S. avicula	x			x					
S. bieneanum	x			x					
S. brebissonii	x			x					
S. brevispinum	x			x					
S. cristatum	x			x					
S. cyrtocerum	x			x					
S. gracile (cyathiforme)	x			x					
S. johnsonii	x			x					
S. oligacanthum	x			x					
S. orbiculare	x			x					
S. sebaldi (ornatum)	x			x					
Micrasterias apiculata	x			x					
M. brachyptera	x			x					
M. fimbriata	x			x					
M. mahabuleshwarensis	x			x					
M. pinnatifida	x			x					
Cosmocladium saxonicum	x			x					
C. pusillum	x			x					
Gonatozygon monotaenium	x			x					
Onychonema filiforme	x			x					
Desmidium aptogonum	x			x					
Spondylosium pulchellum	x			x					
Xanthidium fasciculatum	x			x					
Closterium attenuatum	x	x		x					
C. costatum	x	x		x					
C. incurvum	x	x		x					
Cosmarium depressum	x	x		x					
C. formosulum	x	x		x					
C. granatum	x	x		x					
C. ovale	x	x		x					
C. perforatum	x	x		x					
C. tesselatum	x	x		x					
Micrasterias angulosa	x	x		x					
M. crux-melitensis	x	x		x					
M. radiata	x	x		x					
M. sol (ornata)	x	x		x					
Staurastrum furcigerum	x	x		x					
S. polytrichum	x	x		x					
Netrium interruptum	x	x		x					
Arthrodesmus octocornis	x	x		x	x				
Cosmarium boeckii	x	x		x	x				
C. botrytis	x	x		x	x				
C. contractum (ellipsoideum)	x	x		x	x				
C. humile	x	x		x	x				
C. phaseolus	x	x		x	x				
Pleurotaenium coronatum	x	x		x	x				
Xanthidium cristatum	x	x		x	x				
Micrasterias rotata	x	x	x	x					
Euastrum oblongum	x	x	x	x					
Sphaerozosma granulatum	x		x	x					
Staurastrum dickiei	x		x	x					
Gonatozygon brebissonii	x		x	x					
Cosmarium punctulatum	x	x	x	x	x				
Euastrum verrucosum	x	x	x	x	x	x			
Closterium lineatum	x	x	x	x		x			
Pleurotaenium trabecula	x		x	x		x			
Desmidium cylindricum		x			x				
Micrasterias americana		x							
M. papillifera		x							
Spondylosium planum	x			x			x		
Staurastrum dilatatum	x			x			x		
Sphaerozosma excavatum	x			x			x		
Euastrum insulare	x			x			x		
E. bidentatum	x			x			x		
Cosmarium portianum	x			x			x		
C. diplosporum	x			x			x		
C. tetraophthalmum	x			x			x		
C. sulcatum	x	x		x			x		
C. connatum	x	x		x			x		
Arthrodesmus convergens	x	x		x			x		
Closterium angustatum	x	x		x			x		
Euastrum elegans	x	x		x	x		x		
Cosmarium subcrenatum	x	x		x	x		x		
Staurastrum hystrix	x			x			x	x	
Cosmarium variolatum	x			x			x	x	
C. tumidum	x			x			x	x	
C. subtumidum	x			x			x	x	
C. ocellatum	x			x			x	x	
C. monomazum (polymazum)	x			x			x	x	
Closterium libellula	x			x			x	x	
C. jenneri	x			x			x	x	
C. turgidum	x			x			x	x	
Cosmarium blyttii		x			x		x	x	
Staurastrum polymorphum		x	x				x	x	
S. vestitum	x	x		x			x	x	
Cosmarium quadratum	x	x		x			x	x	
Closterium pseudodianae	x	x		x			x	x	
C. venus	x	x		x	x			x	
Desmidium swartzii	x	x		x	x			x	
Staurastrum alternans	x	x		x	x		x	x	
Hyalotheca mucosa	x	x		x	x		x	x	
Cosmarium reniforme	x	x		x	x		x	x	
C. margaritatum	x	x		x	x		x	x	
Closterium ralfsii (hybridum)	x	x	x	x			x		
Staurastrum tetracerum	x	x	x	x			x		
Xanthidium antilopaeum	x	x	x	x	x		x	x	
Hyalotheca dissiliens	x	x	x	x	x		x	x	
Closterium lunula	x	x	x	x	x		x	x	
C. kuetzingii	x	x	x	x	x		x	x	
C. dianae	x	x	x	x	x		x	x	
Staurastrum paradoxum	x		x	x		x	x		
Arthrodesmus incus	x		x	x			x	x	
Cosmarium ornatum	x		x	x		x	x	x	
C. angulosum (concinnum)	x		x	x		x	x	x	
C. subcostatum	x	x	x	x	x	x	x		
Closterium baillyanum	x	x	x	x	x	x	x	x	
C. setaceum	x	x	x	x	x	x	x	x	
Euastrum ansatum	x	x	x	x	x	x	x	x	
E. binale	x	x	x	x	x	x	x	x	
Staurastrum teliferum	x	x	x	x	x	x	x	x	
S. dejectum	x		x	x				x	x
Closterium acutum (linea)	x	x	x	x		x			x
Cosmarium impressulum	x	x	x	x	x				x
Cylindrocystis brebissonii	x		x	x		x			x
Tetmemorus granulatus	x		x	x		x	x	x	x
Cosmarium pyramidatum	x		x	x		x	x	x	x
Bambusina borreri	x	x	x	x	x		x	x	x
Staurastrum anatinum	x	x	x	x		x	x	x	x
Netrium digitus	x	x	x	x		x	x	x	x
Micrasterias truncata	x	x	x	x		x	x	x	x
M. denticulata (incl. thom.)	x	x	x	x		x	x	x	x
Closterium striolatum	x	x	x	x		x	x	x	x
C. intermedium	x	x	x	x	x	x	x	x	x
C. parvulum	x	x	x	x	x	x	x	x	x
Cosmarium margaritiferum	x	x	x	x	x	x	x	x	x
Euastrum denticulatum	x	x	x	x	x	x	x	x	x
E. pectinatum	x	x	x	x	x	x	x	x	x
Cosmarium venustum		x			x		x		
Closterium gracile (elongatum)			x			x		x	
C. juncidum			x		x	x	x	x	x
Euastrum ampullaceum			x				x	x	x
E. affine			x			x	x	x	x
E. crassum			x			x	x	x	x
Closterium ulna			x			x	x	x	x
Cosmarium cucurbita			x			x	x	x	x
Pleurotaenium minutum			x			x	x	x	x
Xanthidium armatum			x			x	x	x	x
Tetmorus laevis			x			x	x	x	x
T. brebissonii			x			x	x		x
Cosmarium quinarium			x			x	x	x	
C. pseudopyramidatum			x			x	x	x	
C. pseudoconnatum			x			x	x	x	
Arthrodesmus bulnheimii			x			x	x	x	
Pleurotaenium ehrenbergii			x			x	x	x	
Penium spirostriolatum			x			x	x	x	
Cosmarium tinctum			x				x	x	
Euastrum pinnatum			x				x	x	
Staurastrum brachiatum			x				x	x	
Penium cylindrus			x			x	x		
P. exiguum			x				x		
Staurastrum glabrum			x				x		
Euastrum inerme							x	x	x
Cosmarium difficile							x	x	
C. obsoletum							x	x	
C. orthostichum							x	x	
C. amoenum							x	x	
C. cucurbitinum							x	x	
C. pseudonitidulum							x	x	
Docidium baculum							x	x	
Euastrum validum							x	x	
Staurastrum cuspidatum							x	x	
Xanthidium variabile							x	x	
Closterium navicula							x	x	
Netrium oblongum							x	x	
Cosmarium orbiculatum							x		
C. zonatum							x		
C. exiguum							x		
C. globosum							x		
C. isthmochondrum							x		
C. quadrifarium							x		
C. sphaeroideum							x		
C. taxichondrum							x		
C. undulatum							x		
Closterium archerianum							x		
Docidium undulatum							x		
Staurastrum aristiferum							x		
S. elongatum							x		
S. furcatum							x		
S. inconspicuum							x		
Xanthidium smithii							x		
no. of ssp.	143	76	67	143	40	43	114	79	28

Bidens cernuus. The Dutch Conservancy Society (Vereniging tot Behoud van Natuurmonumenten in Nederland) decided, as mentioned before, to start a large cleaning operation. In the autumn of 1950 the sources of eutrophication and saprobication, viz., the connecting ditch between Kolkven and Voorste Goorven, and the sewer of the tea room, were blocked off, and the lake was pumped dry so as to enable the removal of the mud, the profile of the sandy bottom being left intact (Van Dijk & Westhoff 1960a). In the same way the adjacent but less polluted Witven was dredged. In a short while the lakes filled up again with seepage- and rainwater. Although in the first few years after the cleaning the eutrophic macrophytes remained plentiful, from the very beginning the arrival and extension of mesotrophic species (such as *Hypericum elodes, Scirpus fluitans, Carex lasiocarpa, Sparganium minimum,* and *Nitella translucens*) was signalised. These species could easily establish themselves from stands surrounding some small, marginal pools which had escaped from the process of eutrophication because they had no open connection with the principal lake. By 1955 the eutrophy indicators had almost completely disappeared, while the appearance of the species *Utricularia intermedia* and *Baldellia repens* marked the progressive increase of mesotrophic elements (Van Dijk & Westhoff, 1960b). In order to accelerate the recovery of the microfauna and -flora, a considerable amount of the water pumped out of the cleaned lakes had been kept in reserve in the Van Esschenven. This water was pumped back into the Voorste Goorven as a kind of 'inoculation' agent, but nevertheless this lake was still very poor in desmids by 1955 (compare Table I). The occurrence of very large numbers of some of the species present (such as *Desmidium cylindricum*) may be interpreted as an indication of the pioneer nature of the desmid vegetation (Heimans, 1960). As far as the Achterste Goorven is concerned, the comparative list of species covering the periods 1916-1925 and 1950-1955 (Table 1) clearly indicates that owing to its isolated situation it was not or hardly affected by the eutrophication process.

The present investigation

For the sake of an appropriate comparison only those lakes will be included in the discussion whose desmid flora was most thoroughly investigated by Heimans, namely the Centrale Vennen and some other lakes and pools in the immediate vicinity.

A glance at the records relating to the complex of Centrale Vennen plus Achterste Goorven (the nos. 7-10) in Table 1 shows that:

(1) The total amount of species recorded from the complex has decreased from 195 species in 1925 through 123 in 1955 to 68 in 1975.

(2) The decline during the first half of the present century is more evident in the Centrale Vennen, the decrease in the number of species in the Achterste Goorven only becoming manifest somewhat later (from 79 in 1955 to a mere 28 in 1975).

(3) The appreciable difference between the specific composition of the desmid floras of the Voorste and the Achterste Goorven during the period 1916-1925 (81 and 52 'innate' species, respectively) had become far less pronounced in 1975 (with 20 and 5 'innate' species, respectively). The Achterste Goorven, properly speaking, hardly possesses any characteristic species any longer, partly because many of the original species have simply disappeared, and partly because a number of its formerly 'typical' taxa are now shared with the Voorste Goorven.

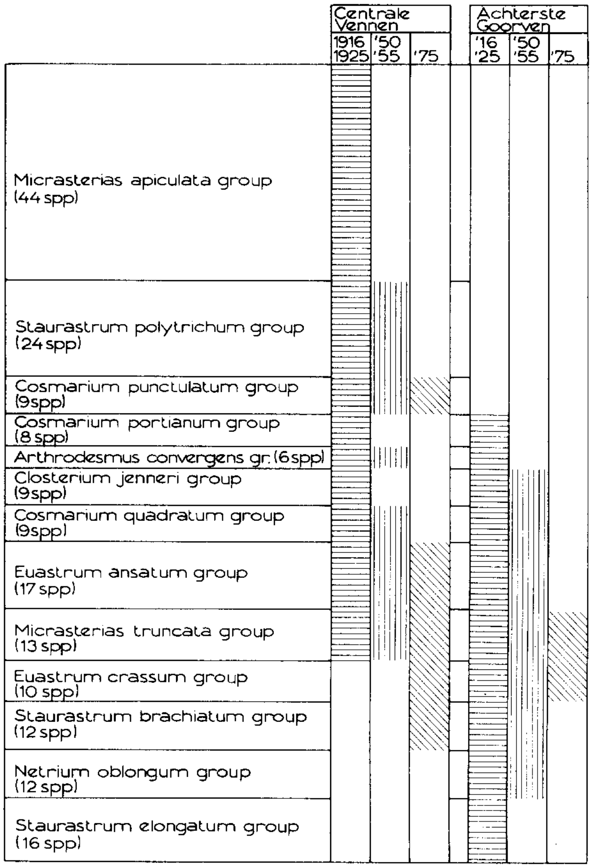

Fig. 2. Representation of various desmid species groups in Centrale Vennen and Achterste Goorven during the three periods of investigation. Composition of the species groups derived from Table I. Species groups situated in the upper part of the figure are characteristic of eutrophic to mesotrophic conditions, those in the lower part of the figure of oligotrophic conditions.

If the specific composition of the Centrale Vennenreeks is followed in time as a whole, not only an absolute decrease in numbers but also a kind of 'shift' of the components becomes evident: a large amount of typically mesotrophic forms disappears to become replaced by a smaller number of typically oligotrophic ones. Especially during the last two decades a fair amount of species originally characteristic of the Achterste Goorven established themselves in the Centrale Vennen, such as *Closterium ulna, C. juncidum, Pleurotaenium minutum, Tetmemorus brebissonii, Euastrum affine, E. crassum, Cosmarium cucurbita,* and *Xanthidium armatum* (united in the '*Euastrum crassum* group' in Fig. 2). These species are accepted as characteristic of an oligotrophic environment (compare Coesel, 1975). Even some species at one time exclusively recorded from the Achterste Goorven but since disappeared from there, such as *Cosmarium quinarium, C. pseudoconnatum, Arthrodesmus bulnheimii* and *Staurastrum brachiatum* (forming the '*Staurastrum brachiatum* group' in Fig. 2), have recently (in 1975) been found in the Centrale Vennen. This may indicate that the Centrale Vennen are now in a stage of trophism in the meantime already 'left behind' in the Achterste Goorven. In brief, a total shift towards a more oligotrophic situation seems to be manifest, the Centrale Vennen turning from mesotrophy to oligo-mesotrophy, and the Achterste Goorven, with a limited and trivial species assortment, at present being in a typically oligotrophic phase. This general oligotrophication of the environment can also be deduced from other parameters: specifically mesotrophic species (such as *Utricularia intermedia, Nitella translucens, Scirpus fluitans,* and *Sparganium minimum*) have disappeared from the stands of higher plants in the Centrale Vennen, and the pH in the Voorste en Achterste Goorven, recorded as about 7.2 and 6.7, respectively, in the period between 1916 and 1925 (Heimans, 1960), fell off through 5.7 and 5.5, respectively, in the 'fifties' (Glass, 1957) to 4.7 and 3.9, respectively, in 1975.

Since the initially mesotrophic lakes of the Centrale Vennen gradually became more acid after the supply of nutrients was cut off, one may raise the question whether – and to what extent – such a trend towards acidification also prevailed in the of old isolated, oligotrophic pools situated to the NE. As a representative example of a body of water of this kind the Wolfsputven (no. 15) may be taken: it was characterised in the period 1916-1925 by some twenty species of desmids (see Table 2), among which very specific forms such as *Micrasterias oscitans,*

Table 2. List of desmid species from Wolfsputven in the period 1916-1925, after data in Heimans (1925).

Closterium intermedium	Micrasterias jenneri
C. lunula	M. oscitans var.
C. parvulum	mucronata
C. striolatum	M. truncata
Cosmarium cucurbita	Netrium digitus
C. nymannianum	Pleurotaenium minutum
C. pyramidatum	Staurastrum brachiatum
C. ralfsii	S. elongatum
C. tumidum	S. hystrix
Docidium undulatum	S. punctulatum
	Tetmemorus granulatus

M. jenneri, Cosmarium ralfsii, Docidium undulatum, and *Staurastrum elongatum* known to be characteristic of weakly oligotrophic conditions (Coesel, 1975). In 1975 however, only two species were collected, viz. *Staurastrum punctulatum* and *S. arnellii,* which both occur in the Netherlands regularly in extremely acid milieus poor in species. The pH of this Wolfsputven was 5.5 when recorded by Glas (1957) in the 'fifties', but appeared to be extremely low in 1975, viz., 3.3. Also in this case an unmistakable acidification took place associated with a marked impoverishment of the desmid flora. It is highly probable, however, that this decline of the desmid flora also had something to do with the disapperance of a former opulent *Sphagnum* zone encroaching upon the open water, resulting in the loss of an important habitat for desmids. The appreciable decline of the stands of bryophytes and higher plants in this pool is most probably to be ascribed to the increasing overshading of the water by the forest immediately surrounding the pool. It is certain that other oligotrophic pools at more open sites in the heathlands mostly contain a better developed desmid flora. In how far acidification and oligotrophication processes have acted adversely on the diversity of the desmid communities in these pools in the course of this century, cannot easily be ascertained, because but little detailed information concerning previously prevailing conditions is available. In some cases the answering of this question is even more hampered because the possible effects of more recently started recreational activities such as fishing and swimming, must be taken into account.

In the Centrale Vennen, the formerly rich, mesotrophic desmid flora is threatened with extinction, after having become hydrologically isolated owing to a progressive oligotrophication of the environment. However, in the lakes and pools situated towards the W and S, where the effect of drain-off from cultivated land persisted, the initially mesotrophic flora has already been replaced by clearly eutrophic elements for a considerable

Table 3. List of desmid species from Allemansven in the period 1916-1925, after data in Heimans (1925).

Arthrodesmus convergens	Euastrum bidentatum
A. octocornis	E. elegans
Bambusina brebissonii	E. insulare
Closterium dianae	E. oblongum
C. didymotocum	E. pectinatum
C. ehrenbergii	E. verrucosum
C. gracile	Gonatozygon monotaenium
C. intermedium	Hyalotheca dissiliens
C. juncidum	H. mucosa
C. kuetzingii	Micrasterias apiculata
C. lunula	M. crux-melitensis
C. setaceum	M. denticulata (incl. thom.)
Cosmarium amoenum	M. fimbriata
C. bioculatum	M. mahabuleshwarensis
C. boeckii	M. pinnatifida
C. botrytis	M. radiata
C. clepsydra	M. rotata
C. connatum	M. sol var. ornata
C. conspersum	M. truncata
C. contractum var.	Netrium digitus
ellipsoideum	Onychonema filiforme
C. diplosporum	Pleurotaenium coronatum
C. elfvingii	var. nodulosum
C. formosulum	P. ehrenbergii
C. granatum	P. truncatum
C. margaritatum	Spondylosium planum
C. margaritiferum	Staurastrum arctison
C. meneghinii	S. brevispinum
C. moniliforme	S. cristatum
C. obtusatum	S. cuspidatum
C. ocellatum	S. dejectum
C. pachydermum	S. furcigerum
C. perforatum	S. gracile
C. phaseolus	S. gracile var. cyathiforme
C. portianum	S. oligacanthum
C. quadratum	S. orbiculare
C. reniforme	S. polytrichum
C. retusiforme	S. sebaldi var. ornatum
C. subprotumidum	S. tetracerum
C. subtumidum	Xanthidium antilopaeum
C. sulcatum	X. antilopaeum var.
C. tetraophthalmum	hebridarum
C. triplicatum	X. antilopaeum var.
C. tumidum	polymazum
Desmidium aptogonum	X. cristatum
D. swartzii	

time. As examples the Allemansven (no. 5) may be mentioned. This pool was still typically mesotrophic between 1916 and 1925, as shown in Table 3, with such specifically mesotrophic desmidiaceous indicators as *Closterium lunula, C. dianae, Pleurotaenium ehrenbergii, Euastrum oblongum, E. elegans, Micrasterias rotata, Cosmarium connatum, C. margaritatum, Arthrodesmus convergens,* and *Staurastrum polytrichum.* There are no records from the 'fifties' known to us, but Glas (1957) reported from that time an appreciable increase of eutrophic macrophytes, such as *Myriophyllum spicatum, Phragmites australis* and *Typha angustifolia,* to the detriment of the species of the original *Littorellion.* The water was still clear at that time, but in 1975 an excessive development of the blue-green alga *Oscillatoria redekei* was immediately noticed. Proper aquatics were conspicuous by their absence, only some reed growing along the edges. This privately owned lakelet, surrounded by a narrow belt of woodland in its turn adjoining pastures all around, is at present very badly polluted by pisciculture and duck-farming, carried out by the owner. The desmid flora, as may be expected, now consists of a few typically eutrophic species such as *Staurastrum chaetoceras* and *S. tetracerum.* The pH, according to Van Heusden & Meyer (1947) 6.9 in 1947, was 8.4 when sampled in 1975, and the other physico-chemical data recorded by us all point unmistakably to eutrophic conditions (Fig. 3).

Discussion

The above-mentioned findings render it perfectly clear that the rich desmid flora present in the Oisterwijk lake area by the turn of the century has declined appreciably. As far as this deterioration can be attributed to an increase in eutrophy and/or saproby of the aquatic environment, this development is not at all surprising in the densely populated Netherlands. Lakes and pools of the eutrophied type, in their overall aspect characterised by an opulence of blue-green algae and the almost complete absence of aquatic macrophytes, exhibit a relatively high pH and conductivity, a relatively high calcium and magnesium hardness, and a relatively high total-P content (Fig. 3, category I).

More striking is the conclusion that the tendencies towards an oligotrophication are largely responsible for the impoverishment. This change is almost certainly to be ascribed to a lowering of the pH by polluted atmospheric precipitation in strongly industrialised and densely populated areas, as the result of a high emission of sulphur dioxide and nitrogen oxides as signalised in many countries. Vermeulen (1977) draws the attention to the situation of the Netherlands in the very centre of the European acid precipitation region. Especially during the last 15 to 20 years the pH fell off by 2 units in most observation points. In the years 1966 and 1967 pH values were measured in the Netherlands which on a yearly base were under 4. The atmospheric acid deposition (consisting of a mixture of nitric and sulphuric acid) originally not exceeding 1 kg per hectare, increased from 8 kg in 1957 to about 75 kg in 1967 (Vermeulen, *l.c.*). It was particularly in Scandinavia that alarming reports were issued concerning the detrimental effects of acid deposition on the fauna and the flora (see, *e.g.*, Almer *et al.*, 1974). The stocks of fish become decimated or totally eliminated, whilst various groups of evertebrate animals and algae become much reduced, both as far as their biomass and their specific diversity are concerned. Even the primary production of such a recognised oligotrophic macrophyte as *Lobelia dortmanna* was experimentally shown to be reduced by 75% at pH 4.0 as compared to the controls grown at pH 4.3-5.5 (Hendrey *et al.*, 1976). In addition an abnormal accumulation of coarse organic detritus and a lowered bacterial activity was noted concomitant with an opulent growth of fungi on the bottom (Hendrey *et al.*, *op. cit.*). Grahn *et al.* (1974) signalised the replacement of communities of macrophytes dominated by *Lobelia* and *Isoëtes*, by stands of mainly species of *Sphagnum*. Rather similar phenomena could also be noticed in a number of lakes studied during the present investigation. Waters formerly characterised by their *Littorellion* communities rich in species, at present contain mostly extensive submerged stands of *Sphagnum cuspidatum* and *Juncus bulbosus*. This concerns hydrologically isolated lakes and pools situated in protected nature reserves and not or hardly subjected to recreational pollution. Their pH values, at present usually below 4 (Fig. 3, category III), were in a number of such lakes and pools several units higher some decades ago according to earlier records. The relatively high sulphate content in some of these acid bodies of water is also conspicuous (see Fig. 3). Almer *et al.* (1974) also reported an increasing sulphate concentration in lakes as the result of a high sulphuric acid content of the precipitation. That the lowering of the pH also leads to an oligotrophication of the water, as indicated by the desmid composition analyses, can be explained by the increased growth of *Sphagnum*, which taxon can remove ions as nutrients from the ecosystem for a long time by absorption, in addition to the incomplete mineralisation of the organic detritus, by the inhibition of bacterial activity, the screening off of the water from the mineral subsoil by dense mats of fungal growth, and the inhibition of nitrogen fixation and the precipitation of phosphates (Almer *et al.*, 1974, Hendrey *et al.*, 1976).

The decline of the desmid flora is even more accelerated in our area of study by a progressively increasing effect of overshadowing by developing forests planted during the last century, which influence is particularly

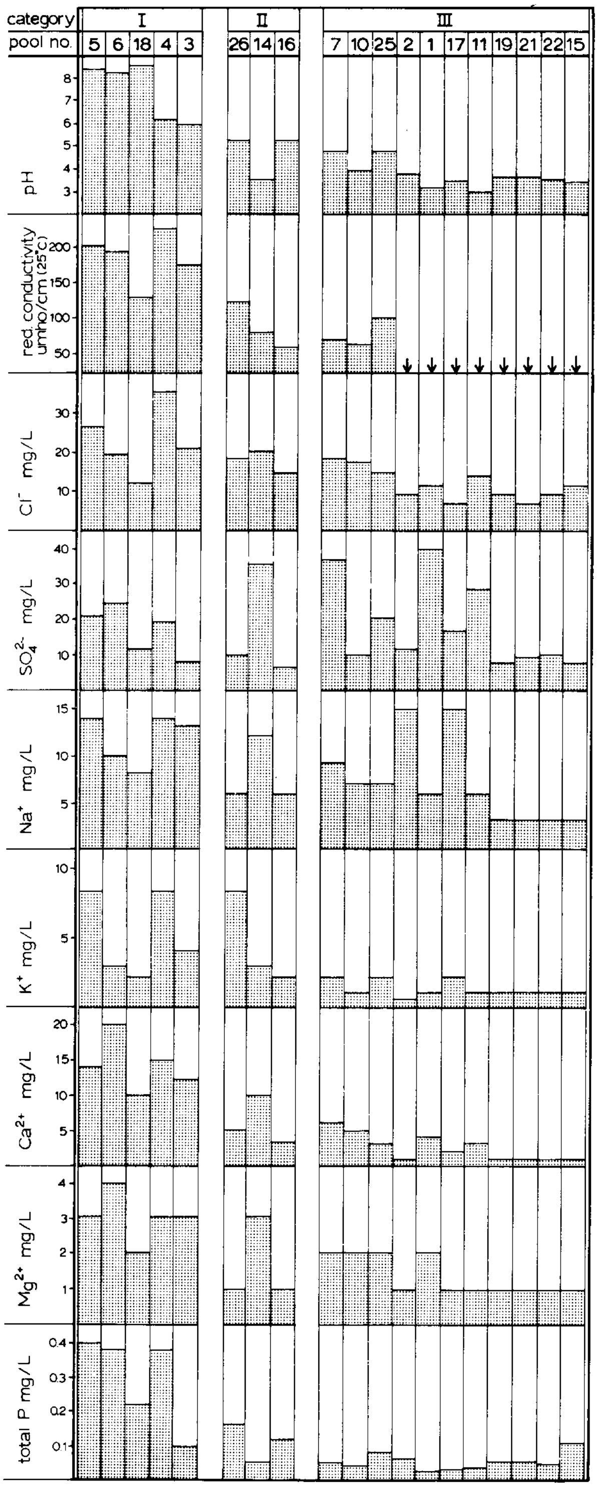

Fig. 3. Some chemical data (after a single sampling) of various lake types. The categories I, II and III include lakes that can be qualified, on the basis of the biocoenoses, as eutrophic, meso- or metatrophic, and oligotrophic, respectively. The conductivity is reduced by substracting the contribution of the hydrogen ions. The arrow symbol is used here to indicate that at low pH values a reduced conductivity lower than 25 μmho could not be accurately determined.

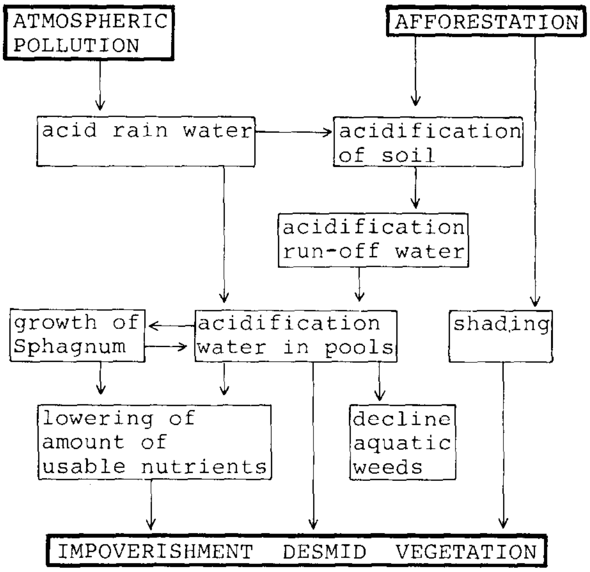

Fig. 4. Effects of air pollution and afforestation upon the desmid flora.

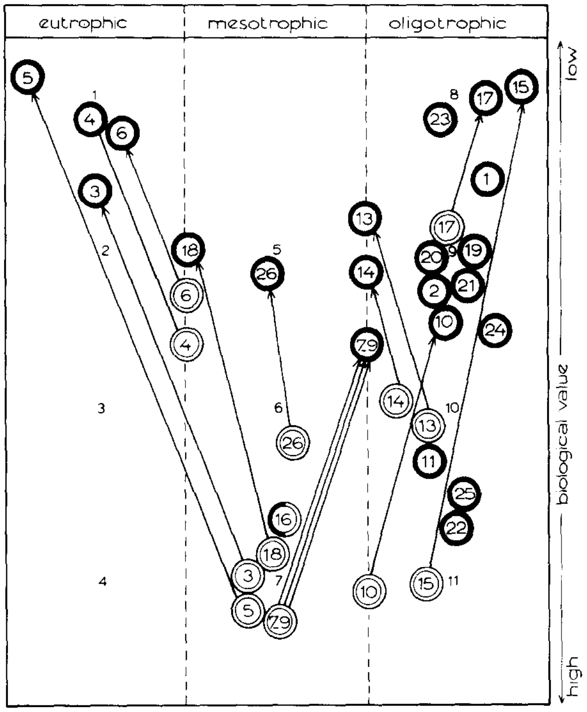

Fig. 5. Arrangement of the pools studied - indicated by encircled numbers in a typological scheme. Thin-lined circles represent the situation during the period 1916-1925; heavily lined ones that in 1975. Numbering of the pools as mentioned in Fig. 1. Further explanation in the text.

noticeable in the smaller pools by their quantitatively and qualitatively scanty desmid vegetation. The lack of sufficient light does not only directly threatens the possibility of existence of these algae but also indirectly, because submerged macrophytes providing an important substratum for the benthic and tychoplanktonic forms, are also hardly represented. The deleterious effects of atmospheric pollution and afforestation on the desmid flora are diagrammatically shown, with their interrelations, in Fig. 4. Fig. 5, finally, gives an idea of the process of biological impoverishment in the Oisterwijk lake complex during the last half century, as reflected in the desmid flora. All lakes and pools studied during the present investigation are included in the diagram, and also those whose desmid flora had been recorded at the beginning of this century. The position of the individual lakes and pools in the diagram is determined according to the specific composition of their desmid flora by means of which they can be fitted into a typological diagram designed by the senior author. This diagram (see Coesel, 1975, Fig. 1) shows the typological arrangement of 11 desmid communities on the basis of the degree of trophism and the degree of structural complexity of the environment. Generally speaking, the number of species of the desmid communities increases in this diagram from top to bottom, which increase is correlated with a higher stability and internal diversity of the environment. In the derived diagram of Fig. 5 the biological value of the habitat also increases from top to bottom. It appears that the bodies of water we recently surveyed mostly find a place in the upper (*i.e.*, biologically not so valuable) half of the scheme, but that they – as far as older records are available – would have had to be placed in the lower half of the diagram if the previous situation would have persisted to the present. The lines in the diagrams connecting the former and the present situation clearly show a divergent development, starting from a mesotrophic environment rich in species, either in the direction of much poorer eutrophic to saprobic conditions, or towards a poorer oligotrophic situation. In only two of the lakes, *viz.*, in the Staalbergven (no. 14) and the Groot Aderven (no. 13), the development proceeds in a different direction; the originally oligotrophic conditions changed, owing to recreational activities causing a moderate increase in nutrients, into a situation best characterised as 'metatrophic' (a term introduced by Leentvaar, 1958, to describe an unstable, transitional stage between oligotrophy and eutrophy not so much typified by mesotrophic organisms but rather by a combination of oligotrophic and eutrophic ones). There is every reason to conclude that the signalised divergent development will be progressive unless adequate control measures can be taken in due time.

Summary

Summarising the recorded data one may decide that the appreciable opulence of desmids in the Oisterwijk lake district, as present by the turn of the century, can be explained by the then prevailing wide range of degrees of trophism. Especially the mesotrophic waters were teeming with a great diversity of species. The truly alarming deterioration of the desmid flora since that time must be mainly attributed to the disappearance of the formerly mesotrophic conditions.

During the first few decades of this century it was mainly agricultural activities, such as the use of fertilisers in the hinterland and pollution by waste water, that caused a change from mesotrophic to more eutrophic conditions or even to saprobic ones. Examples of lakes and pools of this kind are the Kolkven (no. 6), Allemansven (no. 5), Belversven (no. 18), Hildsven (no. 4) and Rietven (no. 3).

During the last decennia the mesotrophic bodies of water hitherto remaining unaffected by the above-mentioned eutrophication through human activities (*e.g.*, because they were situated in protected areas), gradually became more oligotrophic. This oligotrophication can be explained by an appreciable lowering of the pH of the atmospheric precipitation as the result of a much increased emission of sulphur dioxide and nitrogen oxides in the densely populated and industrialised Netherlands. As typical examples of such oligotrophied lakes the Centrale Vennen (nos. 7-9) and the Achterste Goorven (no. 10) may be mentioned.

An increasing overshadowing, as a result of the growing pine plantations, must have had an additional deleterious effect especially on the flora of the smaller pools surrounded by forest. Not only is algal development directly hampered owing to the lack of light, but also indirectly as the result of the disappearance of higher submerged macrophytes serving as a substratum (most species of desmids being benthic or tychoplanktonic). The Wolfsputven (no. 15) is a typical example of a pool still in a fairly open situation and fringed by a broad zone of growing *Sphagnum* vegetation by the beginning of the century but now completely surrounded by tall trees and without a trace of encroaching marsh vegetation.

Only in exceptional cases did a development take place from oligotrophy to mesotrophy, namely as the result of recreational pollution. Nevertheless the desmid flora deteriorated, which is attributable to the greater instability of the habitat. Such situations can therefore better be described as metatrophic rather than mesotrophic. Examples are the Staalbergven (no. 14) and the Groot Adersven (no. 13).

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