

Light climate and its impact on *Potamogeton pectinatus* L. in
a shallow eutrophic lake



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*Promotoren: dr W.J. Wolff,
hoogleraar in de Aquatische Ecologie
dr C.W. Stortenbeker,
emeritus hoogleraar in Natuurbeheer en -behoud*

**Light climate and its impact on *Potamogeton pectinatus* L. in
a shallow eutrophic lake**

G.M. van Dijk

Proefschrift
ter verkrijging van de graad van doctor
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BIBLIOTHEEK
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WAGENINGEN

Voor mijn ouders

Stellingen

- 1 De rol van opwerveling van bodemmateriaal voor het lichtklimaat van de ondergedoken waterplant, zoals aangetoond in het Veluwemeer, is onvoldoende onderkend.
Dit proefschrift
- 2 Beheersmaatregelen die de opwerveling van bodemmateriaal verminderen hebben in het Veluwemeer op korte termijn een hoger rendement in termen van herstel van de begroeiing met waterplanten, dan beheersmaatregelen die een verlaging van het nutriëtniveau beogen.
Dit proefschrift
- 3 Het begin van de tuberproductie van *Potamogeton pectinatus* L. wordt bepaald door de fotoperiode; het aantal tubers hangt af van de fotosynthetische periode.
Dit proefschrift
- 4 In het Veluwemeer hangt de vegetatieontwikkeling van *Potamogeton pectinatus* L. niet alleen af van de waterkwaliteit in het groeiseizoen maar ook, via de tuberbank, van de waterkwaliteit in de voorgaande groeiperiode(n).
Dit proefschrift
- 5 Er is niets bekend over de ecologische gevolgen van een normstelling voor stoffen die 95% van de soorten veiligstelt.
n.a.v. Kooijman (1987), Van Straalen & Denneman (1989), Aldenberg & Slob (1991)
- 6 Bij experimenteel veldonderzoek in grootschalige systemen (meren, rivieren, etc.) is replicatie vaak onmogelijk. Past men toch replicatie toe, dan dient men niet in de val van pseudoreplicatie te lopen.
Hurlbert, 1984
- 7 De invasie van *Corophium curvispinum* in de Rijn illustreert dat restauratie van aangetaste ecosystemen op soortniveau niet voorspelbaar is.
n.a.v. Van den Brink, Van der Velde & Bij de Vaate (1991)
- 8 'Zorg ervoor dat je natuurlijk speelt - tast die grenzen af. Aan die grenzen voorbijgaan is voorbijgaan aan de essentie van het toneel.'
W. Shakespeare: Hamlet (Vertaling: J. Boonen)
- 9 blauwte x geelte = groente
Pierre Thielen, titel van een vijfluik
- 10 Ter verhoging van de effectiviteit van een staking bij het openbaar vervoer verdient het aanbeveling de treinen op spoorwegovergangen te parkeren.
- 11 Wie altijd met beide benen op de grond blijft staan, komt slechts langzaam vooruit.

11 december 1991

Gerda van Dijk

Voorwoord

Dit proefschrift is tot stand gekomen dankzij de inzet en inbreng van vele betrokkenen. Graag wil ik iedereen die op enigerlei wijze een bijdrage aan dit proefschrift heeft geleverd bedanken. Daarbij wil ik de volgende instanties en personen graag met name noemen.

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General introduction

It is widely recognized that submerged macrophytes play an important role in a variety of aquatic ecosystems (e.g. Hutchinson, 1975; Wetzel, 1983). Submerged macrophytes affect the physical environment (light climate, water temperature, water movement and wave action, substrate, etc.), the chemical environment (oxygen, inorganic and organic carbon, nutrients, etc.) and biotic interactions. The latter involve the use of macrophytes as habitat or food by other organisms both aquatic and terrestrial (e.g. epiphytes, grazers, detritivores, fish, waterfowl) (see also review by Carpenter and Lodge, 1986).

Eutrophication threatens many macrophyte dominated aquatic ecosystems all over the world. As a result of severe eutrophication a marked decline in abundance of the submerged vegetation has been recorded in many freshwaters as well as lacustrine and marine waters in Europe (e.g. Schiemer and Prosser, 1976; Phillips *et al.*, 1978; Ozimek and Kowalczewski, 1984; Lachavanne, 1985, De Nie, 1987), North-America (e.g. Jones *et al.*, 1983; Kemp *et al.*, 1983; Twilley *et al.*, 1985), Australia (e.g. Congdon and McComb, 1979; Bulthuis and Woelkerling, 1983) and Asia (e.g. Kunii and Maeda, 1982). Considerable reductions in submerged macrophyte abundance have been reported for various eutrophicated freshwater lakes in The Netherlands also (e.g. Best *et al.*, 1984; Van Liere, 1986; Best, 1987).

The observed dwindling in the submerged vegetation with gradual nutrient additions has been explained by an associated promotion of phytoplanktonic (Jupp and Spence, 1977) and epiphytic growth (Sand-Jensen and Søndergaard, 1981; Sand-Jensen and Borum, 1984) resulting in reduced light availability to the macrophytes. Additionally, the molecular transport between the leaves and the ambient water may be inhibited by the presence of a dense periphytic layer giving a noticeable reduction in photosynthetic rate of the macrophytes (Sand-Jensen, 1977; Sand-Jensen *et al.*, 1985). Allelopathic interactions between macrophytes and phytoplanktonic algae may be involved as well (Phillips *et al.*, 1978; Wium-Andersen *et al.*, 1982). More recently, it is argued that a poisoning of the community of cladocerans by organochlorine insecticides likely caused the switch from macrophyte to phytoplankton dominance. These insecticides were widely used in the 1950s and 1960s and cladocerans are particularly sensitive to organochlorines. Poisoning of the cladocerans allows phytoplankton to take advantage of the increased nutrient load because of reduced

grazing (Stansfield *et al.*, 1989).

Apparently, various mechanisms may be involved in the replacement of macrophyte dominance by that of phytoplankton in case of eutrophication. However, it is generally accepted that unfavourable light climate conditions play a key role through reduced photosynthesis in the observed macrophyte declines. When the amount of photosynthetically active radiation (PAR) exceeds the light compensation point (LCP), net growth may be expected to occur, but the population dynamics of aquatic macrophytes do not depend on growth rates only. Many species have to survive periods unsuitable for vegetative growth each year. The life cycle of many macrophytes is characterized by the annual production of either generative (seeds) or vegetative (tubers or turions) propagules or both, to survive such periods. The unfavourable period in the temperate zone is usually the winter season. Therefore, the annual regeneration of the vegetation largely depends on the number and quality of the propagules being produced (Van Vierssen, 1990). Hence, to consider the life cycle and survival mechanisms of aquatic macrophytes is also important in evaluating the causes of their decline.

The present studies aim at making a contribution to a better understanding of the role of light climate on the dynamics of a submerged vegetation dominated by *Potamogeton pectinatus* L. in a shallow eutrophic lake (Lake Veluwe) in the temperate zone.

Study site

Lake Veluwe is one of the manmade lakes formed along with land reclamation in the IJsselmeer district between the dikes of the Flevoland polders and the former coastline of the 'old land' in 1957. Some selected morphometric and physical characteristics of Lake Veluwe are presented in Table 1.

Lake Veluwe was characterized by a high transparency of the water and a dense submerged vegetation with *Chara* sp. and *Potamogeton perfoliatus* L. as the dominant macrophytes and with locally a dense vegetation of *Myriophyllum spicatum* L., *Elodea canadensis* Rich., *Ranunculus circinatum* Sibth. and *Alisma gramineum* Gmel. in its early years (Leentvaar, 1961). The system gradually changed into a cyanobacteria dominated system due to severe anthropogenic eutrophication starting in the early sixties. *Oscillatoria agardhii* Gomont was the dominant species during the 1970s (Brinkman and Van Raaphorst, 1986). Probably, light became limiting for growth of the submerged macrophytes and consequently, the submerged vegetation disappeared almost completely. Only monospecific stands of *Potamogeton pectinatus* L. remained, with *P. perfoliatus* stands less frequent at certain sites (Bick and Van Schaik, 1980).

Table 1: Summary of some selected morphometric and physical characteristics of Lake Veluwe after Hosper (1983) and Brinkman and Van Raaphorst (1986).

Characteristic	Lake
Area	32.4 km ²
Volume	41.5 * 10 ⁶ m ³
Direction of major axis	NE - SW
Mean depth	1.15 m (summer) - 1.40 m (winter)
ca. 70% of total area	depth <0.90 m
ca. 24% of total area	depth 0.90 m - 2.00 m
ca. 6% of total area	depth >3.70 m
Primary inflow sources	streams, precipitation, seepage (from the 'old' land, sewage plants, sluices)
Primary outflow mechanisms	pumping, seepage (to the polders), evaporation, sluices
Sediment characteristics	
more deeper parts	silty and clayish
more shallow parts	sandy

Light penetration increased considerably in the 1980s because of lower phytoplankton due to a reduction in the external phosphorus loading and through regularly flushing of the lake (Hosper, 1984). As a result the underwater light climate improved and the macrophyte vegetation slowly recovered. *P. pectinatus* became the dominant macrophyte. However, a complete recovery was not established and Lake Veluwe was still characterized as a turbid eutrophic lake with low macrophyte biomass at the time of the present studies. Some chemical characteristics of Lake Veluwe at that time are summarized in Table 2.

The present studies

Various studies have described effects of eutrophication on algal and vascular plant growth or abundance, but few have examined interactive mechanisms directly under field conditions. In the present studies, the impact of light climate on submerged macrophytes has been investigated under controlled field conditions. The hypothesis is tested that the low macrophyte biomass in Lake Veluwe can be explained in terms of high phytoplanktonic and epiphytic algal biomass, which decreases the available light to leaves for macrophyte productivity.

Main objectives of the present studies are:

- to elucidate quantitative and qualitative aspects of the light climate for the submerged macrophytes,
- to gain insight into the factors governing light climate for the submerged macrophytes,
- to elucidate the impact of light climate on growth and survival of a *P. pectinatus* population in Lake Veluwe.

In Chapter 2, the underwater light climate is characterized in terms of amount and spectral composition of PAR during the growing season of *P. pectinatus* in 1986 and 1987. Furthermore, the relative contribution of water itself, gilvin (defined as the filtrate passing through a filter of 0.22 μm), phytoplankton and tripton (detrital and inorganic particulate matter) to the attenuation of irradiance by the water column are determined. Special attention is paid to the impact of wind-induced resuspension of sediment particles.

Table 2: Mean, minimum and maximum value of some chemical parameters of Lake Veluwe measured fortnightly (around noon) in 1986 (from 2 April until 27 October) and 1987 (from 15 April until 30 September), respectively.

Parameter	mean	min	max
1986			
Total nitrogen (mg.l^{-1})	1.48	0.82	3.04
Total phosphorus (mg.l^{-1})	0.12	0.01	0.32
Carbonate (mg.l^{-1})	4.5	0	18
Bicarbonate (mg.l^{-1})	101	17	154
Ph	8.5	7.9	9.5
1987			
Total nitrogen (mg.l^{-1})	-	-	-
Total phosphorus (mg.l^{-1})	-	-	-
Carbonate (mg.l^{-1})	5.2	0	13
Bicarbonate (mg.l^{-1})	107	60	140
pH	8.8	8.4	9.1

- not measured

In Chapter 3, mass dynamics and attenuation characteristics of periphyton upon artificial substrate are studied during two subsequent growing seasons (1986 and 1987) under four experimental light conditions. Concurrently, additional observations are made on periphyton upon leaves of *P. pectinatus*. Insight is given in the potential impact of periphyton on light climate of submerged macrophytes during the growing season and the impact of light climate in the water column on the attenuation characteristics of the periphytic layer.

Chapters 4 and 5 deal with the impact of light climate on the growth and survival of a *P. pectinatus* population. In Lake Veluwe, *P. pectinatus* performs an annual life cycle and survives the winter period unfavourable for growth by means of vegetative propagules: tubers. The annual reestablishment of the vegetation depends almost completely on tubers (Van Wijk, 1988).

In the present studies, the photon flux density is experimentally manipulated by creating three levels of shading and one control situation in a more or less homogeneous *P. pectinatus* vegetation in Lake Veluwe. Chapter 4 provides information on the impact of light climate on the seasonal dynamics of *P. pectinatus* biomass during the growing season of 1986. Insight is given in the impact of light climate on the biomass dynamics, tuber induction and production, and size of the tuber bank.

Chapter 5 discusses the results concerning the biomass development and survival of *P. pectinatus* in various experimental areas varying in light climate and light climate history during three growing seasons (1986-1988). Main objective of this Chapter is assessing the impact of light climate history on biomass dynamics and survival of a *P. pectinatus* population. Furthermore, the regeneration potential of a *P. pectinatus* population which had been shaded in the previous season(s) has been studied under Lake Veluwe conditions. Insight is gained in the importance of the hibernated tuber bank as a controlling factor for biomass dynamics and survival of a *P. pectinatus* population.

In the final chapter, Chapter 6, an overview is given of the role of macrophytes in some well-documented restoration projects of eutrophic lakes in The Netherlands. Taking into account the conclusions of Chapters 2 and 3, expectations for large scale restoration projects and the potential role of submerged macrophytes before and after biomanipulation are discussed.

References

- Best E.P.H., D. de Vries and A. Reins, 1984. The macrophytes in the Loosdrecht Lakes: A story of their decline in the course of eutrophication. Verh. Internat. Verein. Limnol. 22: 868-875.
- Best E.P.H., 1987. The submerged macrophytes in Lake Maarsseveen I: Changes in species composition and biomass over a six year period. Hydrobiol. Bull. 21: 55-60.
- Bick H. and A.W.J. van Schaik, 1980. Oecologische visie randmeren. Advies van de Natuurwetenschappelijke Commissie van de Natuurbeschermingsraad, 291 pp. (in Dutch).
- Brinkman A.G. and W. van Raaphorst, 1986. De fosfaathuishouding in het Veluwemeer. Thesis, Technical University Twente, The Netherlands, 481 pp. (in Dutch with English summary).
- Bulthuis D.A. and W.J. Woelkerling, 1983. Biomass accumulation and shading effects of epiphytes on leaves of seagrass, *Heterozostera tasmanica*, in Victoria, Australia. Aquat. Bot. 16: 137-148.
- Carpenter S.R. and D.M. Lodge, 1986. Effects of submerged macrophytes on ecosystem processes. Aquat. Bot. 26: 341-370.
- Congdon R.A. and A.J. McComb, 1979. Productivity of *Ruppia*: seasonal changes and dependence on light in an Australian estuary. Aquat. Bot. 6: 121-132.
- De Nie H.W., 1987. The decrease in aquatic vegetation in Europe and its consequences for fish population. EIFAC, Occasional Paper no. 19, FAO, Rome, 52 pp.
- Hosper S.H., 1983. Herstel van het Veluwemeer en het Drontermeer door aanpak van fosfaatbelasting en doorspoeling met polderwater. H₂O 16: 172-177 (in Dutch with English summary).
- Hosper S.H., 1984. Restoration of Lake Veluwe, The Netherlands, by reduction of phosphorus loading and flushing. Wat. Sci. Tech. 17: 757-768.
- Hutchinson G.E., 1975. A treatise on limnology, vol. III, limnological botany. John Wiley, New York, 660 pp.
- Jones R.C., K. Walti and M.S. Adams, 1983. Phytoplankton as a factor in decline of submerged macrophyte *Myriophyllum spicatum* L. in Lake Wingra, Wisconsin. Hydrobiologia 107: 213-219.
- Jupp B.P. and D.H.N. Spence, 1977. Limitations on macrophytes in a eutrophic lake, Loch Leven. I. Effects of phytoplankton. J. Ecol. 65: 175-186.
- Kemp W.M., W.R. Boynton, R.R. Twilley, J.C. Stevenson and J. Means, 1983. The decline of submersed vascular plants in Upper Cheasapeake Bay: Summary of results concerning possible causes. Mar. Sci. Tech. 17: 78-89.
- Kunii H. and K. Maeda, 1982. Seasonal and long-term changes in surface cover of aquatic plants in a shallow pond, Ojaga-ike, Chiba, Japan. Hydrobiologia 87: 45-55.
- Leentvaar P., 1961. Hydrobiologische waarnemingen in het Veluwemeer. De Levende Natuur 64: 273-279 (in Dutch).
- Lachavanne J.B., 1985. The influence of accelerated eutrophication on the macrophytes of Swiss lakes: Abundances and distribution. Verh. Internat. Verein. Limnol. 22: 2950-2955.

- Ozimek T. and A. Kowalczewski, 1984. Long-term changes of the submerged macrophytes in eutrophic lake Mikolajskie (North Poland). *Aquat. Bot.* 19: 1-11.
- Phillips G.L., D. Eminson and B. Moss, 1978. A mechanism to account for macrophyte decline in progressively eutrophicated freshwaters. *Aquat. Bot.* 4: 103-126.
- Sand-Jensen K., 1977. Effect of epiphytes on eelgrass photosynthesis. *Aquat. Bot.* 3: 55-63.
- Sand-Jensen K. and M. Søndergaard, 1981. Phytoplankton and epiphyte development and their shading effect on submerged macrophytes in lakes of different nutrient status. *Int. Revue Ges. Hydrobiol.* 66: 529-552.
- Sand-Jensen K. and J. Borum, 1984. Epiphyte shading and its effect on photosynthesis and diel metabolism of *Lobelia dortmanna* L. during the spring bloom in a Danish lake. *Aquat. Bot.* 20: 109-119.
- Sand-Jensen K., N.P. Revsbech and B.B. Jørgensen, 1985. Microprofiles of oxygen in epiphyte communities on submerged macrophytes. *Mar. Biol.* 89: 55-62.
- Schiemer F. and M. Prosser, 1976. Distribution and biomass of submerged macrophytes in Neusiedlersee. *Aquat. Bot.* 2: 289-307.
- Stansfield J., B. Moss and K. Irvine, 1989. The loss of submerged plants with eutrophication III. Potential role of organochlorine pesticides: a palaeoecological study. *Freshw. Biol.* 22: 109-132.
- Twilley R.R., W.M. Kemp, K.W. Staver, J.C. Stevenson and W.R. Boynton, 1985. Nutrient enrichment of estuarine submersed vascular plant communities. I. Algal growth and effects on production of plant and associated communities. *Mar. Ecol. Prog. Ser.* 23: 179-191.
- Van Liere L., 1986. Loosdrecht lakes, origin, eutrophication, restoration and research programme. *Hydrobiol. Bull.* 20: 9-15.
- Van Vierssen W., 1990. Relationships between survival strategies of aquatic weeds and control measures. In A.H. Pieterse and K.J. Murphy (eds.): *Aquatic Weeds*. Oxford University Press, Oxford, p. 238-253.
- Van Wijk R.J., 1988. Ecological studies on *Potamogeton pectinatus* L. I. General characteristics, biomass production and life cycles under field conditions. *Aquat. Bot.* 31: 211-258.
- Wetzel R.G., 1983. *Limnology*. CBS College publishing, Philadelphia, 767 pp.
- Wium-Andersen S., U. Anthoni, C. Christophersen and G. Houen, 1982. Allelopathic effects on phytoplankton by substances isolated from aquatic macrophytes (Charales). *Oikos* 39: 187-190.

Light climate in the water column of a shallow eutrophic lake (Lake Veluwe) in The Netherlands

with Eric P. Achterberg

Abstract

In situ irradiance measurements were performed during 1986 and 1987, to obtain information on the nature of the light climate and on factors governing the absorption (*a*), scattering (*b*) and beam attenuation coefficient (*c*) in the water column of a shallow eutrophic lake (Lake Veluwe).

Phytoplankton chlorophyll-*a* concentration ranged from 2 to 85 mg.m⁻³, the seston concentration from 8 to 148 mg dry weight.l⁻¹ and gilvin concentration from 0.79 to 1.11 m⁻¹ (*g₄₄₀*).

The vertical attenuation coefficient (*K_d*) varied between 1.56 and 6.76 m⁻¹. The relative effects of water itself, gilvin, phytoplankton, and tripton on *a*, *b* and *c* showed relatively small seasonal variation. The relative effects of water and gilvin on *c* were of minor importance (less than 10%). Phytoplankton attributed 6 to 20% to *a*, 3 to 33% (with a peak value of 55%) to *b* and less than 30% to *c*. Tripton was the dominant factor determining the diminution of irradiance penetrating the water column in Lake Veluwe. Irradiance was strongly scattered which was mainly due to tripton.

The spectral distribution of the photosynthetically active radiation was progressively compressed with depth into a region between 550 and 700 nm. Water absorbed strongly in the red regions of the spectrum, and gilvin and seston in the blue regions. The seston concentration was positively correlated with wind-induced resuspension of bottom material.

It was concluded that an improvement of the underwater light climate requires a reduction in resuspension of bottom particles.

Introduction

The growth of submerged macrophytes is limited by the nature of the light climate in the water column in many eutrophic waters. The underwater light climate in aquatic ecosystems is the result of incident solar radiance, reflectance properties of the water surface, and absorption and scattering properties of components comprising the water column. The absorption and scattering of irradiance within natural waters is attributable to the water itself, gilvin (defined as the filtrate passing through a filter of $0.22\ \mu\text{m}$), phytoplankton and tripton (detrital and inorganic particulate matter) (Kirk, 1983).

The optical properties of natural waters can usefully be separated into inherent and apparent optical properties. The inherent properties are those whose operational value at a given point in a given medium are independent of changes in the radiance distribution. These are the absorption coefficient, the scattering coefficient, the beam attenuation coefficient (being equal to the sum of the absorption and the scattering coefficient), and the volume scattering function which describes the angular distribution of scattering. All these properties are defined in terms of the behaviour of a hypothetical parallel beam of irradiance incident on a thin layer of the medium and can so be regarded as properties belonging to the water itself, regardless of the light regime to which the water might be exposed in nature. In principle, all these properties can be measured in water samples from the field under laboratory conditions. The apparent optical properties are those whose operational value at a given point in a given medium are not independent of changes in the radiance distribution. Vertical attenuation coefficient and reflectance (ratio of upward to downward irradiance) are apparent optical properties. The apparent optical properties can only be measured in the water body itself. The apparent properties define the light climate within the water column and these very properties are routinely measured by limnologists who deal with photosynthesis or underwater visibility. However, to understand the impact of the various absorbing and scattering components of the aquatic medium on the underwater light climate, their effect on the inherent optical properties must be considered.

Recently, progress has been made in analyzing in situ irradiance measurements to obtain information on the scattering and absorption properties of the water column (e.g. Kirk, 1983). Furthermore, both field and laboratory studies derived predictive relationships between concentrations of the constituents in the water column and absorption and scattering properties (Vant and Davies-Colley, 1984; Weidemann and Bannister, 1986; Morel, 1987; Effler *et al.*, 1988; Oliver and Ganf, 1988). These results seem to open the way to simple, theoretically sound, examinations of the light climate in an aquatic medium. In the present Chapter light climate in the water column of

Lake Veluwe is studied during two years (1986-1987).

Wind-induced resuspension of sediment particles plays an important role in Lake Veluwe (Brinkman and Van Raaphorst, 1986). Consequently, wind-induced turbulence may increase the attenuation of penetrating irradiance considerably in Lake Veluwe. Main purpose of the present Chapter is to describe the underwater light climate in terms of amount and spectral composition of photosynthetically active radiation (PAR). The relative effects of pure water, gilvin, phytoplankton, and tripton on irradiance quantity and quality are examined as well as the extent to which wind-induced resuspension of sediment particles affects the underwater light climate in Lake Veluwe.

Materials and methods

Seston

Water samples were taken fortnightly at the water surface at a fixed location in Lake Veluwe, during the periods April-October 1986 and 1987. Lake water (200 to 1000 ml) was filtered (precombusted and preweighted Whatman GF/C filters) in fourfold for mass determination of the seston. The filters with seston were dried (105 °C, 24 h), weighted (dry weight; DW) and subsequently ashed (510 °C, 4 h) and weighted again (ash weight; AW). Ash-free dry weight (AFDW) was calculated by subtracting AW from DW.

For seston chlorophyll-a content determinations, lake water (200 to 1000 ml) was filtered (Whatman GF/C filters) in fourfold. These filters with collected matter were deep frozen until they were treated according to the method of Vernon (1960), modified following Moed and Hallegraeff (1978) to control post-acidification Ph in the sample.

Generally, the variation in procedure of seston mass and chlorophyll-a content was less than 10%.

Dominant phytoplankton genera were determined by counting at random 100 to 200 individual algae in a concentrated water sample using a phase-contrast microscope.

Light climate

Upwelling and downwelling PAR (400-700 nm) were measured during the periods from May until September 1986 and 1987. Three Bottemanne RA 200 A Quantum Sensors (flat-plate, cosine-law) were clamped to a floating device, in such a way that the sensors were positioned at fixed depths relative to the water surface, independent of wave motion or changes in water level. The downwelling irradiance was measured at depths of 0.15 and 0.30 m; the upwelling irradiance at a depth of 0.35 m. The

upward irradiance was assumed to be unaffected by bottom reflection at the depth of measurements. The maximum depth of the lake at the location was only about 0.70 m but the bottom was relatively dark brown coloured. PAR was measured every minute simultaneously with water temperature. Mean PAR of the last 15 measurements was recorded digitally every 15 minutes.

The spectral distribution of downwelling PAR was measured at different depths in Lake Veluwe using a submersible spectroradiometer (Tectum QSM 2500).

Changeable incident irradiance due to variable meteorological conditions during the measurements was corrected by referencing the spectral distribution measurements to the incident PAR measured simultaneously by a Bottemanne quantum sensor placed in open air.

Absorption spectra for gilvin were obtained from irradiance spectra of filtered lake water (Millipore filters 0.22 μm) relative to distilled water. An experimental setup was used, consisting of the Tectum spectroradiometer placed underneath a vertically placed long tube (height: 2.00 m, diameter: 0.085 m) with a silver coating on the inside and a bottom of glass. The irradiance source was a 500 W halogen lamp.

Wind

Wind velocity and direction were measured continuously using an anemometer. Mean daily values were calculated.

Sedimentation

Sedimentation rate was determined by using cylindrical sediment traps having a height:diameter ratio of 10 and a diameter of 0.015 m. Cylindrical traps give the most reliable estimations for sedimentation (Brinkman and Van Raaphorst, 1986). The used traps were deep and narrow enough to prevent resuspension (Blomqvist and Kofoed, 1981). The traps were placed vertically in a frame on a fixed location nearby the experimental setup for irradiance measurements with the opening at a depth of ca. 0.50 m (ca. 0.20 m above the bottom).

The traps were emptied fortnightly (3 to 5 replicates). The overlying water was decanted carefully. Settled matter was collected in preweighted porcelain cups and dried to constant weight (24h, 105°C). AFDW was calculated after combustion at 550°C (4h).

The attenuation spectra of the settled matter were determined on 4 and 18 August, 1986. Trapped matter was resuspended (3 traps) in distilled water (4 l) and was measured against distilled water (4 l) in the same experimental setup described above.

Calculations and statistical analyses

The daily mean downwelling vertical attenuation coefficient (K_d) and the daily mean reflectance (R) were calculated from the PAR values registered every 15 minutes, in case the irradiance reaching the lowest sensor exceeded $10 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. K_d was calculated according Lambert-Beer's law and R as the ratio of upwelling to downwelling PAR (Kirk, 1977). The data for the upwelling PAR measured at 0.35 m were extrapolated to a depth of 0.30 m in calculating R , assuming the mean upwelling vertical attenuation coefficient (K_u) and K_d had the same value. This is a sound assumption at depths near or below the euphotic depth (the depth at which the irradiance has been reduced to 1% of the subsurface value) (Tyler and Preisendorfer, 1962; Kirk, 1983). It was assumed that the error involved would be of minor importance although the euphotic depth was much deeper (in case $K_d=2.5$, the euphotic depth is 1.8 m).

The ratios of scattering to absorption coefficient ($b:a$) were derived from the nomograms of Kirk (1981), relating the calculated R and K_d to μ (= the average cosine of the radiance distribution) and $b:a$ ratio. The nomograms for a zenith angle of 45° were used, which is a fair approximation for all zenith angles from 0° to 60° (Weidemann and Bannister, 1986). These nomograms were calculated for the depth at which the irradiance has been reduced to 10% of subsurface value (= $Z_{0.1}$) (Kirk, 1981). It was practically impossible to conduct irradiance measurements at $Z_{0.1}$ in Lake Veluwe because of its shallowness ($Z_{0.1}$ corresponds to a depth of about 0.9 m, in case $K_d = 2.5 \text{ m}^{-1}$). The error introduced cannot be ruled out, but is assumed to be of minor importance, since in quite turbid lakes (*i.e.* Lake Veluwe) the asymptotic radiance distribution will be established at small depths (Kirk, 1981). Furthermore, R never varies more than 0.01 m^{-1} with increasing depth (Weidemann and Bannister, 1986; Oliver and Ganf, 1988) implying that Kirk's functions are scarcely affected by depth.

The value of the absorption coefficient was obtained from the Gershun-Jerlov equation (Jerlov, 1976):

$$(1) \quad a = \mu * K_d$$

where a is the absorption coefficient, μ is the average cosine of the radiance distribution and K_d is the vertical attenuation coefficient for net downward irradiance. K_d was used instead of K_e in equation (1) in calculating the absorption coefficient because K_e was not measured. The difference between K_d and K_e is about 1% for a homogeneous water column (Weidemann and Bannister, 1986) and the water column of Lake Veluwe can be assumed to be homogeneous given its shallowness.

Furthermore, K_d provides a reliable estimate for K_e (Kirk, 1981).

The scattering coefficient was calculated from the estimated value of a and the $b:a$ ratio. The beam attenuation coefficient was derived by summing the absorption and scattering coefficients.

The optical contributions of gilvin, phytoplankton and tripton in terms of absorption, scattering and beam attenuation coefficients are proportional to their concentration (e.g. Vant and Davies-Colley, 1984):

$$(2) \quad a = a_w + a_g + a_{ph} + a_t$$

with a_w , a_g , a_{ph} and a_t representing the absorption coefficients due to water itself, dissolved gilvin, phytoplankton, and tripton, respectively. Similar equations can be derived for b and c . A value of 0.23 m^{-1} was used for a_w (Weidemann and Bannister, 1986) and a value of $< 10^{-2} \text{ m}^{-1}$ for b_w (Jerlov, 1976) in the present Chapter. Gilvin concentration is expressed in absorption coefficient at 440 nm due to dissolved colour ($G_{440} \text{ m}^{-1}$, base e; Kirk, 1976). Empirically derived relationships between gilvin concentrations and a_g (Kirk, 1976) were used to obtain a_g . The value of b_g is negligible (Kirk, 1976). The phytoplankton contributions to a and b (a_{ph} and b_{ph} , respectively) can be expressed in terms of chlorophyll-specific coefficients and their chlorophyll concentration:

$$(3) \quad a_{ph} = k_a * chl$$

and

$$(4) \quad b_{ph} = k_b * chl$$

Values of k_a and k_b presented by several workers are listed in Table 1. k_a was estimated in the high range of these values: $0.0100 \text{ m}^2.\text{mg}^{-1} \text{ chl}$ in order not to underestimate the actual a_{ph} for Lake Veluwe. A range of $0.05\text{-}0.15 \text{ m}^2.\text{mg}^{-1} \text{ chl}$ was assumed for k_b .

No attempts were made to measure the values of a , b , and c , directly. Similar estimates of the absorption coefficient are obtained from R and K_d by Kirk's nomograms and by summing the separately determined absorption contributions (Weidemann and Bannister, 1986). Therefore, it is reasonable to calculate a , by subtracting the sum of a_{ph} , a_g and a_w from a derived by Kirk's nomograms. The same applies to b and c .

Approximate estimates of in situ attenuation spectra were calculated at 10 nm intervals from the underwater irradiance spectra following Kirk (1979). This involved correcting the measured vertical attenuation coefficient for monochromatic downward

Table 1: Summary of chlorophyll-specific absorption (k_a , $\text{m}^2.\text{mg}^{-1}$ chl) and chlorophyll-specific scattering coefficient (k_b , $\text{m}^2.\text{mg}^{-1}$ chl) values presented in the literature.

k_a	k_b	water type	reference(s)
0.009	0.09-0.60	marine phytoplankton multiple linear regression analysis for 27 New Zealand lakes	Bricaud <i>et al.</i> (1983) Vant and Davies-Colley (1984)
0.008 0.010	0.16	Lake Otisco cultured freshwater phytoplankton	Weidemann <i>et al.</i> (1985) Davies-Colley <i>et al.</i> (1986)
0.008-0.010 0.005-0.007	0.05-0.10 0.05-0.09	eutrophic hard-water lake South Australian lake	Weidemann and Bannister (1986) Oliver and Ganf (1988)

irradiance for solar altitude and for refraction at the water surface.

The contribution of seston (tripton plus phytoplankton) to the attenuation spectra was calculated as the difference between the attenuation spectra measured in the field and the sum of the attenuation spectra for gilvin (measured in the laboratory) and pure water (Smith and Baker, 1981).

The SAS statistical package was used for statistical analyses (SAS Institute Inc., 1985). In all cases $p < 0.05$ has been taken to indicate statistical significance.

Results

Seston

The organic content of the seston varied from 5 to 25 mg.l^{-1} with a peak value at 1 September of 48 mg.l^{-1} , during the sampling period in 1986. It varied from 7 to 28 mg.l^{-1} during the sampling period in 1987 (Fig. 1). The inorganic fraction seston (represented by fraction AW of DW) averaged about 40% in both years with some peak values at the end and at the beginning of the sampling periods (Fig. 1). Chlorophyll-a content of seston displayed a range of 2-85 mg.m^{-3} during the sampling periods in 1986 and 1987 (Fig. 1). Chlorophyll-a content expressed in seston AFDW ranged from ca. 0.5 to 4 mg chl-a.g^{-1} AFDW, in both years.

The seasonal variation in AFDW, DW, inorganic attribution to DW and chlorophyll-a content showed no obvious trends. Generally, AFDW, ash and chlorophyll-a content were higher in 1987 than in 1986 at the beginning of the sampling periods.

Phytoplankton was dominated by diatoms (Fig. 2) with *Nitzschia* and *Diatoma elongatum* Agardh. as the most abundant genera in spring, in both years. From May

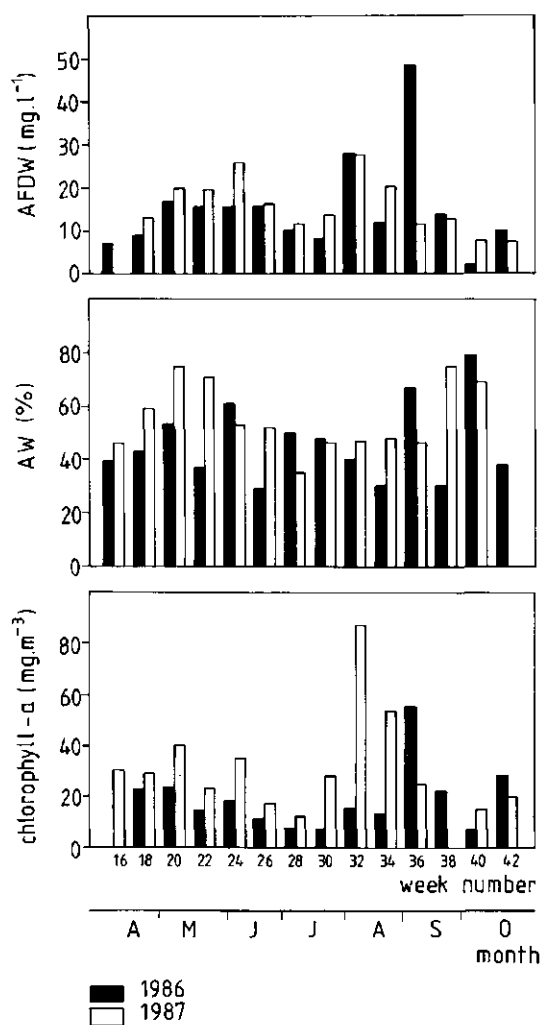


Fig. 1: Seasonal variation in the mean organic content (top), ash content (AW as a percentage of DW; middle) and chlorophyll-a concentration (bottom) of seston in Lake Veluwe during the sampling periods in 1986 and 1987, respectively.

onwards, green algae became the dominant group with highest abundances of *Botryococcus*, *Scenedesmus* and *Monoraphidium*. In May 1986, cyanobacteria became more abundant and contributed for a maximum of 20% to the total number of phytoplanktonic algae during the rest of the sampling period. Most abundant cyanobacteria genera were *Oscillatoria* during spring and autumn and *Microcystis*

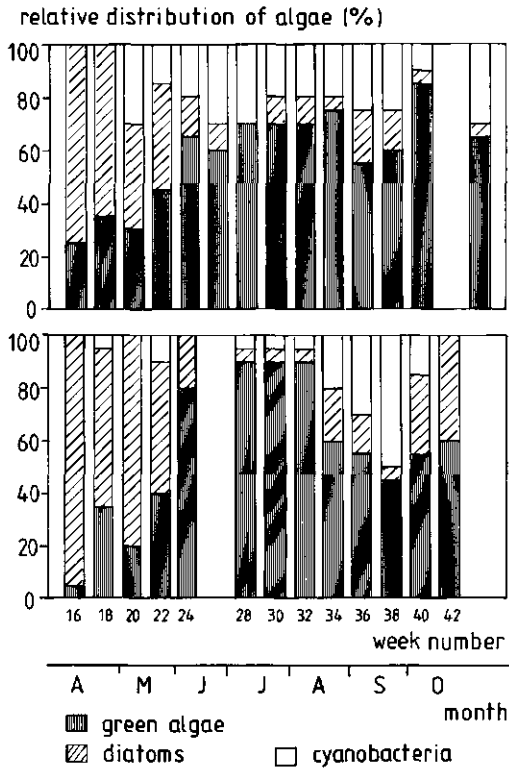


Fig. 2: Seasonal variation in relative distribution of phytoplankton over various algae groups in Lake Veluwe during the sampling periods in 1986 (top) and 1987 (bottom), respectively.

during summer. Cyanobacteria contributed for less than 10% to the total number of phytoplanktonic algae with *Lyngbya contorta* Lemm. and *Oscillatoria* as the dominant genera until mid August in 1987. *Oscillatoria agardhii* Gomont was only scarcely observed in both years. Substantial amounts of tripton were observed in the concentrated water samples.

Light climate and factors affecting it

The K_d varied between 1.56 m^{-1} and 6.76 m^{-1} with a mean of *ca.* 2 m^{-1} in 1986 and *ca.* 3 m^{-1} in 1987. K_d was strikingly high on 1 September, 1986 and on 4 August, 1987 (6.76 and 6.74 m^{-1} respectively) (Table 2). These high values coincided with stormy weather conditions.

The variance in K_d was significantly explained for 77%, 92%, 92%, 59% and 60% by variance in seston AFDW, DW, AW and chlorophyll-a content, respectively in 1986.

Table 2: Aspects of the light climate in the water column of Lake Veluwe for various sampling dates in 1986 and 1987. The abbreviations used are the vertical attenuation coefficient (K_d), reflectance (R), absorption coefficient (a), scattering coefficient (b), beam attenuation coefficient (c), chlorophyll concentration (g_{440}) and the relative contribution of water, gilvin, phytoplankton and tripton to a , b and c (a_w , b_w , c_w , a_g , b_g , c_g , a_{pt} , b_{pt} , c_{pt} , a_t , b_t , c_t respectively).

Date	K_d (m^{-1})	R	a (m^{-1})	b (m^{-1})	g_{440} (m^{-1})	a_w (%)	c_w (%)	a_g (%)	c_g (%)	a_{pt} (%)	b_{pt} (%)	c_{pt} (%)	a_t (%)	b_t (%)	c_t (%)
13-May-86	2.83														
26-May-86	2.50				0.79										
09-Jun-86	1.95				0.88 ⁺										
23-Jun-86	2.08	0.08	1.14	9.72	0.88 ⁺	20	2	32	3	10	6-11	6-11	38	89-94	84-89
07-Jul-86	2.37	0.08	1.30	11.08	0.88 ⁺	18	2	28	3	6	3-7	4-6	48	93-97	89-91
21-Jul-86	2.09	0.08	1.15	9.77	0.95	20	2	33	3	6	3-7	4-7	41	93-97	88-91
04-Aug-86	2.09	0.07	1.21	8.49	0.81	19	2	29	4	12	9-18	9-17	40	82-91	77-85
18-Aug-86	2.17	0.06	1.28	7.55	0.73	18	3	27	4	10	9-18	9-16	46	82-91	77-83
01-Sep-86	6.76	0.08	3.72	31.60	1.11	6	1	11	1	15	9-18	9-17	68	82-91	81-89
15-Sep-86	1.95	0.06	1.15	6.79	0.88 ⁺	20	3	34	5	19	16-33	17-31	27	67-84	61-75
30-Sep-86	1.56	0.04	0.97	3.97	0.88 ⁺	24	5	40	8	7	8-17	8-15	29	83-92	72-79
28-Apr-87	2.51	0.06	1.48	8.74	0.88 ⁺	16	2	26	4	20	17-33	17-31	38	67-83	63-77
13-May-87	4.29	0.05	2.57	12.87	0.88 ⁺	9	1	15	3	15	15-31	15-28	61	69-85	68-81
27-May-87	3.39	0.05	2.03	10.17	0.88 ⁺	11	2	19	3	11	11-22	11-21	59	78-89	74-84
11-Jun-87	5.84	0.05	3.50	17.52	0.88 ⁺	7	1	11	2	10	10-20	10-18	72	80-90	79-87
24-Jun-87	3.48	0.05	2.09	10.44	0.88 ⁺	11	2	19	3	8	8-16	8-15	62	84-94	80-87
08-Jul-87	3.21	0.05	1.93	9.63	0.88 ⁺	12	2	20	3	6	6-12	6-11	62	88-94	84-89
04-Aug-87	6.74	0.03	4.52	14.00	0.88 ⁺	5	1	9	2	19	31-62	28-52	67	38-69	45-69
18-Aug-87	4.71	0.03	3.16	9.78	0.88 ⁺	7	2	12	3	17	28-55	25-46	64	45-72	49-70
01-Sep-87	4.58	0.05	2.75	13.74	0.88 ⁺	8	1	14	2	9	9-18	9-17	69	82-91	80-88

⁺ not measured though, calculated as a seasonal mean (see text)

Table 3: Results of correlation analyses (coefficient of determination: r^2 and significance: p) of attenuation coefficient (K_d) and AFDW, AW, DW, chlorophyll-a content (chl-a) of seston in the water column for the dataset of 1986 (11 Degrees of Freedom) and 1987 (9 Degrees of Freedom), respectively.

Independent variable	Dependent variable			
	1986		1987	
	r^2	p	r^2	p
K_d (m^{-1})				
AFDW ($mg.l^{-1}$)	0.77	0.0002	0.65	0.0088
DW ($mg.l^{-1}$)	0.92	0.0001	0.16	0.2805
AW ($mg.l^{-1}$)	0.92	0.0001	0.06	0.5367
chl-a ($mg.m^{-3}$)	0.59	0.0036	0.61	0.0126
AFDW ($mg.l^{-1}$)				
DW ($mg.l^{-1}$)	0.88	0.0001	0.56	0.0199
AW ($mg.l^{-1}$)	0.76	0.0002	0.36	0.0896
chl-a ($mg.m^{-3}$)	0.65	0.0016	0.55	0.0214
DW ($mg.l^{-1}$)				
AW ($mg.l^{-1}$)	0.96	0.0001	0.96	0.0001

In 1987, the variance in K_d was explained significantly for 65% and 61% by variance in AFDW and chlorophyll-a content, respectively. Variances in DW and AW did not explain the variance in K_d in that year. The explained variance in AFDW by variance in DW and AW was much lower in 1987 than in 1986. The explained variance in DW by variance in AW was high (96%) in both years (Table 3).

Irradiance penetrating the water column was considerably scattered (Table 2). b was about one order of magnitude higher than a on all sampling dates.

Consequently, variations in proportional contributions of various components in the water column to b have a more pronounced effect on c than on a .

Gilvin concentration was determined on only a restricted number of sampling dates and varied from 0.73 to 1.11 m^{-1} . Mean gilvin concentration was used as an estimate for gilvin concentration for sampling dates on which no gilvin concentrations were measured, since the seasonal variation in gilvin is generally small (Weidemann and Bannister, 1986). The relative contribution of gilvin to a (a_g) was slightly higher than the relative contribution of pure water to a (a_w).

The relative contribution of water to a ranged from 5 to 24%. The relatively high contributions were observed on sampling dates on which Lake Veluwe was relatively clear ($K_d = 1.56 m^{-1}$; 30 September, 1986). The relatively low contributions (5-10%) were observed in more turbid situations ($K_d > 2.5 m^{-1}$). The relative contribution of

water to c was small (ranging from 1% to 5%). The relative contribution of gilvin to c ranged from 1% to 8%. The maximum relative contribution of gilvin to a was 40% ($K_d = 1.56 \text{ m}^{-1}$; 30 September, 1986). The contribution to a ranged from 9% to 20% in situations the lake was more turbid ($K_d > 2.5 \text{ m}^{-1}$).

Due to the wide range of estimated k_b ($0.05\text{--}0.10 \text{ m}^2\text{.mg chl-a}^{-1}$), the derived b_{ph} and c_{ph} showed a wide range as well and thus did the derived b_i and c_i values. However, obviously, tripton contributed mostly to the beam attenuation coefficient of the water column of Lake Veluwe during both sampling periods.

The spectral distribution of downward PAR showed a similar pattern on all dates measured, notably, a plateau from 550–700 nm and often a dip at about 670–680 nm. Irradiance was also diminished at the red end of the spectrum although not to the same extent as at the blue end. Only a small amount of PAR was available at wavelengths below 500 nm at depth 0.40–0.50 m (Fig. 3).

The estimated contribution of gilvin, pure water and seston (tripton plus phytoplankton) to the attenuation spectrum have been calculated for those sampling dates on which gilvin spectra were determined. Water was always the strongest attenuating component in the red regions of the spectrum, gilvin and seston played no part there. Both gilvin and seston attenuated strongly in the blue regions of the spectrum (Fig. 3) considering water itself hardly attenuates in these regions (Smith and Baker, 1981). Apparently, seston played a dominant role in attenuation on most sampling dates. This observation is in accordance with results presented in Table 2. The attenuation spectra for seston showed a similar shape on sampling dates with relatively low seston DW concentrations; attenuation at wavelengths below 450 nm was primarily due to gilvin, whereas seston attenuated strongly in the 450–650 nm region of the spectrum. This is illustrated by sampling date 18 August (Fig. 3). Attenuation was relatively high at all wavelengths on 1 September. This was also reflected in the relative high K_d of 6.76 m^{-1} (Table 3). The contributions of water and gilvin to the attenuation spectra were of minor interest, seston (DW: 148 mg.l^{-1}) was the major attenuating factor at that time.

Effects of wind field on seston concentration

Wind velocity showed no apparent seasonal trends nor apparent differences between the two years. No data were available on 1 September due to malfunctioning of the registration system. Stormy weather conditions occurred on that date all over the Netherlands (wind velocity $> 9 \text{ m.s}^{-1}$ at the climatological station at Den Bilt).

The variance in AFDW, AW and DW of seston was explained by wind velocity for 51%, 61%, and 63% respectively, in case the data-pairs of two periods measured were pooled (Table 4). Apparently, both inorganic and organic matter were stirred up by wind-induced turbulence. Chlorophyll- a content of the seston was not significantly

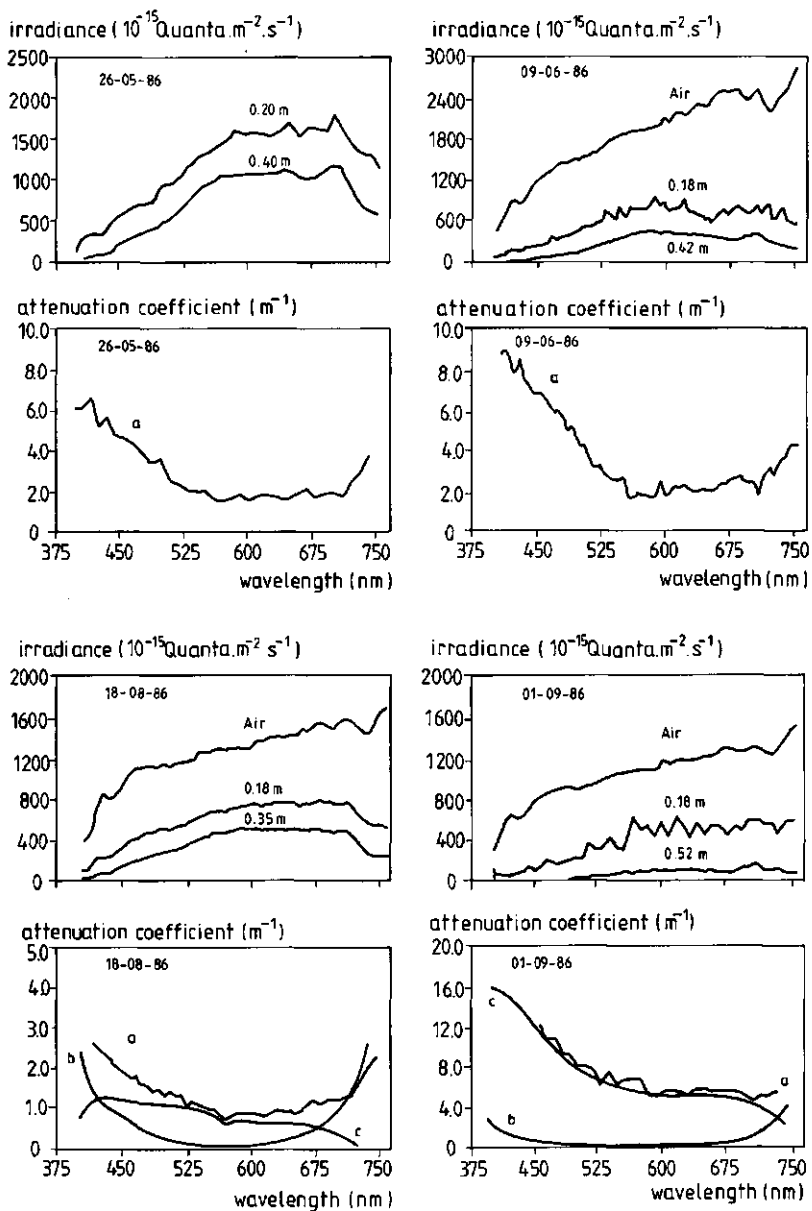


Fig. 3: The spectral distribution of PAR at various depths in Lake Veluwe for some selected sampling dates in 1986. The corresponding attenuation spectra are given for each date. Beside the total attenuation spectra (a), the attenuation spectra for water plus gilvin (b) and seston (c) are shown as well when available.

Table 4: Results of correlation analyses (coefficient of determination: r^2 and significance: p) on AFDW, AW, DW and chlorophyll-a content of seston in the water column with wind velocity (11 Degrees of Freedom).

Dependent variable	Independent variable	
	r^2	p
	wind velocity (m.s^{-1})	
AFDW (mg.l^{-1})	0.51	0.0087
AW (mg.l^{-1})	0.61	0.0028
DW (mg.l^{-1})	0.63	0.0020
chl-a (mg.m^{-3})	0.07	0.4092

affected by wind velocity. This result indicates that the resuspension of living benthic algae was negligible.

Beside wind velocity, fetch is another major factor determining resuspension of bottom material. Fetch is the distance the wind has travelled over open water to reach the point of interest (Smith, 1979). The prevailing wind direction was south-west implying that the fetch corresponded with the length axis of the lake and was maximum. The data-pairs are indicated by an arrow in case the wind direction was north-west which corresponded with a fetch of only about 200 m. This is probably why two data-pairs did not fit very well in the observed pattern (Fig. 4).

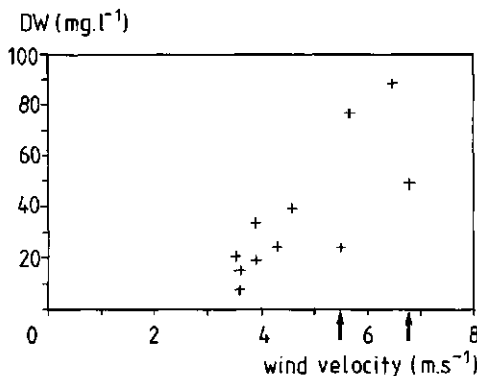


Fig. 4: Seston concentration against wind velocity in Lake Veluwe for the data of 1986 and 1987 pooled. The fetch was about 200 m in cases the data-pairs are indicated by an arrow, otherwise the fetch varied from 5 to 14 km.

Sedimentation

Settled matter consisted mainly of inorganic matter (Fig. 5). Generally, AW contributed more than 80% to DW. The composition of settled matter was different from the composition of the seston which showed an inorganic content in range of 20-75%.

The sedimentation rates showed highest values in May and June and in the second half of August and September during both sampling periods. On the whole, the sedimentation rates were about one order of magnitude higher in 1987 than in 1986. There was no parallel trend nor any correlation between sedimentation rates and wind velocity during the periods sampled. Apparently, wind effects, if any, were masked by the length of the periods over which sedimentation was measured. Resuspended settled matter mainly scattered PAR. Absorption was restricted only to the blue regions of the spectrum (Fig. 6).

Discussion

Seston

The inorganic particulate matter made only a relatively small contribution to total seston weight in Lake Veluwe. The inorganic fractions of seston were almost similar in Lake Veluwe and in a natural water column of a pond in The Netherlands, relatively rich in detritus (about 40% read from Figs. 38 and 39, Roijackers, 1985). The organic fraction of seston consisted of considerable amounts of detrital matter considering its relatively low chlorophyll-a content ($0.5-4.0 \text{ mg chl-a.g}^{-1} \text{ AFDW}$). Chlorophyll-a content ranged from 1.8 to $8 \text{ mg chl-a.g}^{-1} \text{ AFDW}$ in a natural water column a pond in The Netherlands, relatively rich in detritus (read from Figs. 39 and 42, Roijackers, 1985). It was about $25 \text{ mg chl-a.g}^{-1} \text{ AFDW}$ in a Minnesota lake low in detritus (Megard and Smith, 1974) assuming an AFDW:C ratio of 2.5. A chlorophyll-a content of about $20 \text{ mg chl-a.g}^{-1} \text{ AFDW}$ is considered as typical for waters with low chlorophyll-a content and of about $83 \text{ mg chl-a.g}^{-1} \text{ AFDW}$ for waters with relatively high chlorophyll-a content both low in detritus (Lorenzen, 1968).

Light climate and factors affecting it

Lake Veluwe can be characterized as a moderately turbid lake. Changes in the concentration of tripton were the major cause of variation in the beam attenuation coefficient; other components had only additional effects. The relative contributions of water and gilvin to the beam attenuation coefficient were low: maximally 5% and 8%, respectively. The gilvin concentration in Lake Veluwe was relatively low compared with values reported for other lakes (Table 3.2 in Kirk, 1983; Davies-Colley and Vant,

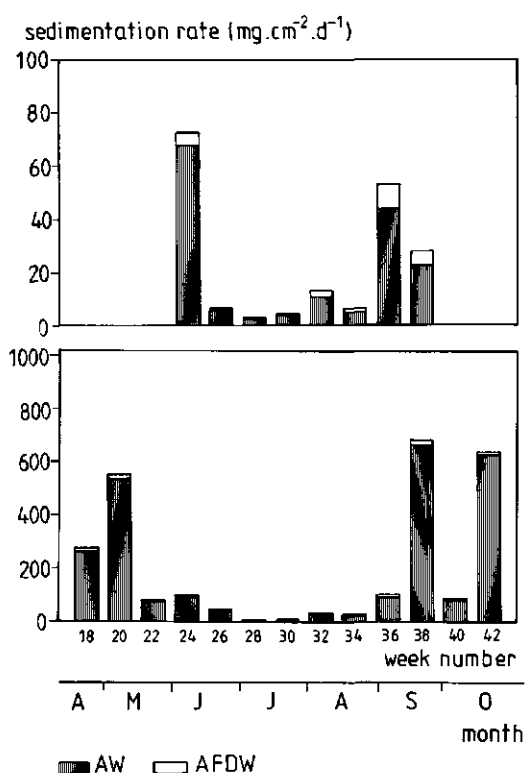


Fig. 5: Seasonal variation in the mean sedimentation rates in Lake Veluwe, during the sampling period in 1986 (top) and 1987 (bottom), respectively. Note the differences in scales.

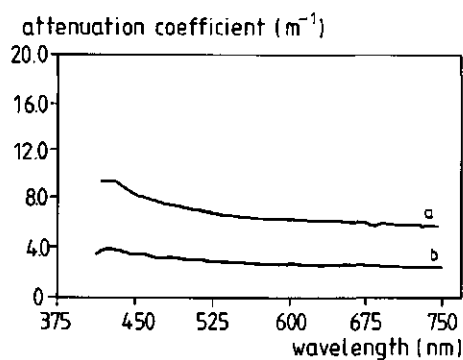


Fig. 6: Attenuation spectra of resuspended settled matter in Lake Veluwe for 4 August, 1986 (a) and 18 August, 1986 (b), respectively.

1987; Elser, 1988; Heinermann and Ali, 1988). However, the rate of increase of attenuation with increasing gilvin concentration is greatest at low gilvin concentration (Kirk, 1976; Eloranta, 1978; Canfield and Hodgson, 1983) and therefore, the impact of gilvin should not be neglected.

The relative contribution of phytoplankton to the absorption, scattering, and beam attenuation coefficient was relatively small. The relative contribution to the absorption coefficient (maximum value: 20%) was even smaller than those for water and gilvin respectively, and the relative contribution to the scattering and beam attenuation coefficient was less than about 30% on most sampling dates.

In the present Chapter, published data on chlorophyll-specific absorption coefficient and chlorophyll-specific scattering coefficient were used to estimate the relative effects of phytoplankton to the absorption, scattering, and beam attenuation coefficient. The chlorophyll-specific absorption coefficient value is dependent on size and shape of algae, chlorophyll content, and depth. Phytoplankton consisting mainly of nanoplankton increases the chlorophyll-specific absorption coefficient value considerably compared with phytoplankton dominated by larger algal cells (Kirk, 1975). However, nanoplankton was not abundant at the present study site. The influence of cell shape and differences in composition and concentration of accessory pigments on chlorophyll-specific absorption coefficient is not considered in the present Chapter. Therefore, variation in chlorophyll-specific absorption coefficient from the used value can not be ruled out completely. Probably, the chlorophyll-specific absorption coefficient was independent of depth in Lake Veluwe, since the chlorophyll-specific absorption coefficient decreases barely with increasing depth in green waters dominated by green algae and diatoms (e.g. Lake Veluwe) (Atlas and Bannister, 1980). The absorption coefficient due to phytoplankton was not underestimated because the maximum reported chlorophyll-specific absorption coefficient value was used in the present study.

Recently, several studies have been conducted to enlarge the theoretical background considering the factors controlling the value of the chlorophyll-specific scattering coefficient for marine algae (see review Bricaud *et al.*, 1983; Morel, 1987; Bricaud *et al.*, 1988) and for freshwater algae (Davies-Colley *et al.*, 1986). However, practical use of these results is still limited.

Calcium carbonate particles precipitated from the water column, a phenomenon known as 'whiting', may increase scattering in hard-water lakes markedly (Effler *et al.*, 1987; Koschel *et al.*, 1983; Weidemann *et al.*, 1985). Probably, 'whiting' played only a minor role if any at all, in Lake Veluwe because the sum of the HCO_3^- and CO_3^{2-} concentration was relatively low (ranging from about 0.9 meq l^{-1} in summer to about 2.5 meq l^{-1} in other seasons (see Chapter 1)). If 'whiting' occurred in Lake Veluwe, its effect has been attributed to tripton due to the computation method used.

The spectral distribution of Lake Veluwe showed a broad plateau from 550-700 nm. Water itself did impoverish strongly the red end of the spectrum and gilvin the blue regions of the spectrum at various depths in Lake Veluwe. Apparently, there was still sufficient gilvin present to attenuate markedly the blue regions of the spectrum although, the gilvin concentrations were relatively low. This is in accordance with the observation that gilvin plays an important role in affecting the spectral distribution in many lakes (Kirk, 1976; 1977; 1981; Watras and Baker, 1988).

Generally, phytoplankton contributes considerably to the attenuation of penetrating irradiance (Talling, 1960; Kirk, 1975) and spectral changes (Jewson, 1977; Dubinsky and Berman, 1979) in productive waters, with chlorophyll concentrations $>10 \text{ mg.m}^{-3}$. The spectral distribution curves did show an absorption trough in the vicinity of the chlorophyll-a absorption peak (675 nm) on a number of sampling dates with chlorophyll concentrations exceeding 10 mg.m^{-3} (e.g. 9 June, 1986). High tripton concentrations obscured probably the effect of absorption by chlorophyll-a on 1 September, 1986 ($55.39 \text{ mg chl-a. m}^{-3}$).

Seston attenuated strongly in the blue regions of the spectrum. This absorption was likely due to gilvin adsorbed onto suspended particles (Kirk, 1980; Davies-Colley, 1983; Hickman *et al.*, 1984) or detritus which made a large contribution to the seston. Detritus absorbs strongly in the blue regions of the spectrum due to its yellow-brown colour (Kishino *et al.*, 1984). This might explain the underwater spectra of the turbid Lake Veluwe were very similar to those for non-turbid humic lakes (Bowling *et al.*, 1986). Changes in the shape of the spectra were primarily due to changes in concentrations of particles in the water column of Lake Veluwe. There was hardly any irradiance available at wavelengths below 500 nm at depths around 0.40 m on dates with a relatively high DW concentration (9 June, 1986: 40 mg l^{-1} , 1 September, 1986: 148 mg l^{-1}).

It should be stressed again that the method used to derive the curves of gilvin+water and seston, is approximate and gives a guide only. Kirk (1979) and Bowling *et al.* (1986) discussed the shortcomings of this technique.

Lake Veluwe can be very well compared with Lake Sorell given its spectral distributions of PAR (Bowling *et al.*, 1986). Both lakes are relatively low in gilvin and moderately turbid (Lake Sorell with $g_{440} = 1.21 \text{ m}^{-1}$ and $K_d = 1.8 \text{ m}^{-1}$;). The spectral distribution of Lake Sorell showed also a broad plateau from 550-700 nm, interrupted by an absorption trough of chlorophyll. The vertical attenuation coefficient and spectral distribution of PAR in Lake Veluwe is also comparable to Lake Ginninderra (Kirk, 1979) in which turbidity was the major attenuating factor.

Wind-induced resuspension

The amount of seston in the water column was largely determined by wind-induced resuspension which is in accordance with previous results (Brinkman and Van Raaphorst, 1986). The bottom is characterized as fine sandy with an uppermost layer consisting of benthic algae and considerable amounts of detrital matter at the location of measurements. Wind-induced stirring up of the uppermost layer together with a relatively low settling rate of detritus (Brinkman and Van Raaphorst, 1986) explain the relatively high detrital content of seston. Furthermore, resuspension of sediments may be enhanced by foraging benthivorous fish (e.g. Lammens 1986).

The present observed relatively high inorganic content of settled matter in the traps is consistent with the relatively high settling rate of (re)suspended inorganic matter (Brinkman and Van Raaphorst, 1986). The highest resuspension of sediment particles occurred in May and June and in August and September in both periods measured. It is well known that the presence of macrophytes lower the resuspension by wind-induced turbulence considerably by stabilizing sediments and dissipating wave energy (Schiemer and Prosser, 1976; Schröder, 1988). The relatively low sedimentation rates in July of both years corresponded with relatively high aboveground biomass of the macrophytes (Chapter 5). On the whole, the sedimentation and consequently resuspension rates were higher in 1987 than in 1986 during the period measured. This might be explained by the lower aboveground biomass of macrophytes in 1987 than 1986 (Chapter 5).

Ecological implications

Tripton gives rise to intense scattering when present in high concentrations. However, it has little competitive effect on the collection of irradiance by phytoplankton in some waters (Kirk, 1985). Tripton also attenuated much of the blue parts of the spectrum in Lake Veluwe. The virtual abolition of most of the blue irradiance at quite moderate depths must have important ecological impacts. The chlorophyll absorption bands at the red end of the spectrum are always of limited use in aquatic systems because of rapid attenuation by water itself. Thus the ability of aquatic higher plants and many algae to photosynthesize and grow will be remarkably affected by the limited availability of blue irradiance.

Green algae and aquatic higher plants have absorption bands in the blue region of the spectrum (chlorophyll-soret band, carotenoid band) and are likely to be disadvantaged. Diatoms which have a useful absorption in the green (500-550 nm) due to the carotenoid fucoxanthin (Iverson and Curl, 1973; Kirk, 1976) will be better equipped to use the PAR available in Lake Veluwe. Cyanobacteria, with phycobiliprotein pigments absorbing strongly in the 540-660 nm region (Kirk, 1975; 1979), seems best adapted to the spectral irradiance composition in the water column.

In the present study, phytoplankton was dominated by diatoms in spring, and by green algae during the rest of the season. Apparently, green algae and diatoms were able to maintain their dominance in spite of the favourable light climate for cyanobacteria. The relative contribution of cyanobacteria to phytoplankton was higher in 1986 than in 1987. Cyanobacteria are not competitively dominant at relatively low temperatures (10°C and 17°C) though show competitive advantage at higher water temperatures (24°C) (Tilman *et al.*, 1986). The observed differences in relative contribution of cyanobacteria between the two years might be explained by the higher temperatures in 1986 than in 1987 (KNMI, climatic station). The longer lasting ice-covering of the lake during the winter of 1985/1986 than during the winter of 1986/1987 might have disadvantaged the early growth of cyanobacteria stronger in 1986 than in 1987. Further improvement of the underwater light climate requires lowering of resuspension of the sediment. Further lowering of the phytoplankton biomass will only slightly affect the underwater light climate positively on a short term, in case the tripton concentration will remain the same. However, on a long term, reduction of the phytoplankton concentration will decrease the detritus concentration, which in turn will favour visibility. Therefore, water quality management of Lake Veluwe and of comparable shallow eutrophic lakes sensitive to wind-induced resuspension, should concentrate on achieving a reduction in phytoplankton concentration and moreover, in resuspension of sediment particles in order to improve the underwater light climate for submerged macrophytes. A higher biomass of submerged macrophytes will in turn minimize the resuspension of sediments, and in this way stabilize its own light climate.

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References

- Atlas D. and T.T. Bannister, 1980. Dependence of mean spectral extinction coefficient of phytoplankton on depth, water color, and species. *Limnol. Oceanogr.* 25: 157-159.
- Blomqvist S. and C. Kofoed, 1981. Sediment trapping-A subaquatic in situ experiment. *Limnol. Oceanogr.* 23: 585-590.
- Bowling L.C., M.S. Steane and P.A. Tyler, 1986. The spectral distribution and attenuation of underwater irradiance in Tasmanian inland waters. *Freshw. Biol.* 16: 313-335.
- Bricaud A., A. Morel and L. Prieur, 1983. Optical efficiency factors for some phytoplankton. *Limnol. Oceanogr.* 28: 816-832.
- Bricaud A., A. Bedhomme and A. Morel, 1988. Optical properties of diverse phytoplanktonic species: experimental results and theoretical interpretation. *J. Plankton Res.* 10: 851-873.
- Brinkman A.G. and W. van Raaphorst, 1986. De fosfaathuishouding in het Veluwemeer. Thesis Technical University Twente, The Netherlands, 481 pp. (in Dutch with English summary).
- Canfield D.E. and L.M. Hodgson, 1983. Prediction of Secchi disc depths in Florida lakes: impact of algal biomass and organic color. *Hydrobiologia* 99: 51-60.
- Davies-Colley R.J., 1983. Optical properties and reflectance spectra of three shallow lakes obtained from a spectrophotometric study. *New Zealand J. Mar. Freshw. Res.* 17: 445-459.
- Davies-Colley R.J., R.D. Pridmore and J.E. Hewitt, 1986. Optical properties of some freshwater phytoplanktonic algae. *Hydrobiologia* 133: 165-178.
- Davies-Colley R.J. and W.N. Vant, 1987. Absorption of light by yellow substances in freshwater lakes. *Limnol. Oceanogr.* 32: 416-425.
- Dubinsky Z. and T. Berman, 1979. Seasonal changes in the spectral composition of downwelling irradiance in Lake Kinneret (Israel). *Limnol. Oceanogr.* 24: 652-663.
- Effler S.W., H. Greer, M.G. Perkins, S.D. Field, A.M. ASCE and E. Mills, 1987. Calcium carbonate precipitation and transparency in lakes: a case study. *J. Env. Eng. Div. ASCE* 113: 124-133.
- Effler S.W., R. Roop and M.G. Perkins, 1988. A simple technique for estimating absorption and scattering coefficients. *Wat. Res. Bull.* 24: 397-404.
- Eloranta P., 1978. Light penetration in different types of lakes in central Finland. *Holarctic Ecology* 1: 362-366.
- Elser J.J., 1987. Evaluation of size-related changes in chlorophyll-specific light extinction in some north temperate lakes. *Arch. Hydrobiol.* 111: 171-182.
- Heinermann P.H. and M.A. Ali, 1988. Seasonal changes in the underwater light climate of two Canadian shield lakes. *Hydrobiologia* 169: 107-121.
- Hickman N.J., P.E. McShane and D.M. Axelrad, 1984. Light climate in the Gippsland Lakes, Victoria. *Aust. J. Mar. Freshw. Res.* 35: 517-524.
- Iverson R.L. and H. Curl, 1973. Action spectrum of photosynthesis for *Skeletonema costatum* obtained with Carbon-14. *Physiol. Plant.* 28: 498-502.
- Jerlov N.G., 1976. Marine optics. Elsevier, Amsterdam, 231 pp.
- Jewson D.H., 1977. Light penetration in relation to phytoplankton content of the euphotic zone of Lough Neagh, N. Ireland. *Oikos* 28: 74-83.

- Kirk J.T.O., 1975. A theoretical analysis of the contribution of algal cells to the attenuation of light within natural waters. II Spherical cells. *New Phytol.* 75: 21-36.
- Kirk J.T.O., 1976. Yellow substances (Gelbstoff) and its contribution to the attenuation of photosynthetically active radiation in some inland and coastal South-eastern Australian waters. *Aust. J. Mar. Freshw. Res.* 27: 61-71.
- Kirk J.T.O., 1977. Use of a quanta meter to measure attenuation and underwater reflectance of photosynthetically active radiation in some inland and coastal South-eastern Australian waters. *Aust. J. Mar. Freshw. Res.* 28: 9-21.
- Kirk J.T.O., 1979. Spectral distribution of photosynthetically active radiation in some South-eastern Australian waters. *Aust. J. Mar. Freshw. Res.* 30: 81-91.
- Kirk J.T.O., 1980. Spectral absorption properties of natural waters: contributions of the soluble and particulate fractions to light absorption in some inland waters of South-eastern Australia. *Aust. J. Mar. Freshw. Res.* 31: 287-296.
- Kirk J.T.O., 1981. A Monte Carlo study of the nature of the underwater light field in, and the relationships between optical properties of, turbid yellow waters. *Aust. J. Mar. Freshw. Res.* 32: 517-532.
- Kirk J.T.O., 1983. Light and photosynthesis in aquatic ecosystems. Cambridge University Press, Cambridge, 401 pp.
- Kirk J.T.O., 1985. Effects of suspensoids (turbidity) on penetration of solar radiation in aquatic ecosystems. *Hydrobiologia* 125: 195-208.
- Kishino M., C.R. Booth and N. Okami, 1984. Underwater radiant energy absorbed by phytoplankton, detritus, dissolved organic matter, and pure water. *Limnol. Oceanogr.* 29: 340-349.
- Koschel R., J. Benndorf, G. Proff and F. Rehnagel, 1983. Calcite precipitation as a natural control mechanism of eutrophication. *Arch. Hydrobiol.* 98: 380-408.
- Lammens E.H.R.R., 1986. Interactions between fishes and the structure of fish communities in Dutch shallow eutrophic lakes. Thesis, Agricultural University Wageningen, The Netherlands, 100 pp.
- Lorenzen C.J., 1968. Carbon:chlorophyll relationships in an upwelling area. *Limnol. Oceanogr.* 13: 202-204.
- Megard R.O. and P.P. Smith, 1974. Mechanisms that regulate growth rates of phytoplankton in Shagawa lake, Minnesota. *Limnol. Oceanogr.* 19: 279-296.
- Moed J.R. and G.M. Hallegraeff, 1978. Some problems in the estimation of chlorophyll-a and phaeopigments from pre- and post acidification spectrophotometric measurements. *Int. Revue Ges. Hydrobiol.* 63: 787-800.
- Morel A., 1987. Chlorophyll-specific scattering coefficient of phytoplankton. A simplified theoretical approach. *Deep-Sea Res.* 34: 1093-1105.
- Oliver R.L. and G.G. Ganf, 1988. The optical properties of a turbid reservoir and phytoplankton in relation to photosynthesis and growth (Mount Bold Reservoir, South Australia). *J. Plankton Res.* 10: 1155-1177.
- Roijsackers R.M.M., 1985. Phytoplankton studies in a nymphaeid-dominated system: with special reference to the effects of the presence of nymphaeids on the functioning and structure of the phytoplankton communities. Thesis University of Nijmegen, The Netherlands, 172 pp.
- Sas Institute Inc., 1985. SAS/STAT™ Guide for personal computers, version 6 Edition. SAS Institute Inc. Cary NC, 378 pp.

- Schiemer F. and M. Prosser, 1976. Distribution and biomass of submerged macrophytes in Neusiedlersee. *Aquat. Bot.* 2: 289-307.
- Schröder R., 1988. Die Erosion der Uferbank des Untersees (Bodensee) Spätfolgen der Eutrophierung und hydrologischer Phaenomene. *Arch. Hydrobiol.* 112: 265-277.
- Smith R.C. and K.S. Baker, 1981. Optical properties of the clearest natural waters (200-800 nm). *Appl. Opt.* 20: 177-184.
- Smith I.R., 1979. Hydraulic conditions in isothermal lakes. *Freshw. Biol.* 9: 119-145.
- Talling J.F., 1960. Self-shading effects in natural populations of a planktonic diatom. *Wetter Leben* 12: 235-242.
- Tilman D., R. Kiesling, R. Sterner, S.S. Kilham and F.A. Johnson, 1986. Green, bluegreen and diatom algae: Taxonomic differences in competitive ability for phosphorus, silicon and nitrogen. *Arch. Hydrobiol.* 106: 473-485.
- Tyler J.E and R.W. Preisendorfer, 1962. Transmission of energy in the sea 8. Light. In M.N. Hill (ed.): *The sea Vol. I.* Wiley-Interscience, New York, p. 397-451.
- Vant W.N. and R.J. Davies-Colley, 1984. Factors affecting clarity of New Zealand lakes. *New Zealand J. Mar. Freshw. Res.* 18: 367-377.
- Vant W.N., R.J. Davies-Colley, J.S. Clayton and B.T. Coffey, 1986. Macrophyte depth limits in North Island (New Zealand) lakes of differing clarity. *Hydrobiologia* 137: 55-60.
- Vernon L.P., 1960. Spectrophotometric determinations of chlorophylls and pheophytins in plant extracts. *Anal. Chem.* 32: 1144-1150.
- Watras C.J. and A.L. Baker, 1988. The spectral distribution of downwelling light in northern Wisconsin lakes. *Arch. Hydrobiol.* 112: 481-494.
- Weidemann A.D. and T.T. Bannister, 1986. Absorption and scattering coefficients in Irondequoit Bay. *Limnol. Oceanogr.* 31: 567-583.
- Weidemann A.D., T.T. Bannister, S.W. Effler and D.L. Johnson, 1985. Particulate and optical properties during CaCO_3 precipitation in Otisco Lake. *Limnol. Oceanogr.* 30: 1078-1083.

Dynamics and attenuation characteristics of periphyton upon artificial substrate under various light conditions and some additional observations on periphyton upon *Potamogeton pectinatus* L.

Abstract

The seasonal variation in periphyton dynamics has been studied upon artificial substrate (microscopic glass slides) under various light conditions during the periods May-October 1986 and May-September 1987, in Lake Veluwe. Some additional observations on the periphyton development upon leaves of *Potamogeton pectinatus* L. have been made simultaneously. Four light conditions were created in an experimental setup by manipulating the photon flux density through artificial shading.

Periphyton upon artificial substrate exhibited a relatively high abundance with a distinct seasonal pattern. Periphyton accrual rates were highest at the beginning of June and in August and September upon slides which were incubated for two weeks. Periphyton mass increased during May and June, decreased or remained about the same during July and subsequently increased until an upper plateau was reached upon slides which were incubated from the beginning of May onwards.

Generally, periphyton mass was lower upon slides than upon *P. pectinatus*. The seasonal variation in periphyton mass was more pronounced upon *P. pectinatus* leaves than upon the slides. Apparently, macrophytes are most seriously negatively affected by periphyton at the beginning of their growing season.

Attenuation by periphyton upon slides ranged from 5 to 65% after two weeks of incubation. Periphyton upon slides which had been incubated for more than two weeks demonstrated an attenuation of more than 85%.

Water quality parameters other than photon flux density were probably more important in determining the periphyton dynamics, since only minor differences were observed in periphyton mass between the various light conditions. Chlorophyll-a content was higher with increased shading on various sampling dates.

Periphyton, especially 'older' periphyton, consisted largely of settled silt and clay particles and to a lesser extent of detrital matter on both substrate types. Living epiphytes were only a relatively small fraction.

It is concluded that a reduction of resuspension of sediment particles, giving less suspended matter in the water column, will result in lower periphytic mass.

Consequently, the photosynthetically active radiation reaching the submerged macrophytes is expected to increase considerably.

Introduction

Generally, periphyton shows luxuriant growth on macrophytes and hard substrate in eutrophic waters (Eminson and Phillips, 1978; Phillips *et al.*, 1978; Borum, 1985; Cattaneo, 1987). The term periphyton is applied for the complex community of algae, bacteria, fungi, animals, inorganic and organic detritus that is attached to substrata, according the definition of Wetzel (1983). Periphyton may lower the irradiance reaching the submerged macrophytes considerably. It may attenuate the incident irradiance by more than 80% in eutrophic waters (Sand-Jensen and Søndergaard, 1981; Bulthuis and Woelkerling, 1983).

The present Chapter focuses on the dynamics of periphyton in Lake Veluwe, with special interest in its attenuation characteristics. Lake Veluwe is a shallow eutrophic lake with relatively low macrophyte biomass at the time of the present study. The low macrophyte biomass is largely ascribed to low irradiance reaching the submerged vegetation (Chapters 4 and 5).

Several workers have shown that the growth of periphyton is affected by photon flux density (Gons, 1982; Meulemans and Heinis, 1983; Bothwell, 1988; Meulemans, 1988; Munn *et al.*, 1989; Vermaat and Hootsmans, 1991). However, the photon flux density has not been controlled in field studies as far as known.

In this study, artificial substrate (microscopic glass slides) was used to study periphyton development. Artificial substrate enables direct measurement of attenuation through an intact periphytic layer and has practical advantages in terms of manageability and replication (Meier *et al.*, 1983). Some additional observations have been made on the periphyton dynamics upon *Potamogeton pectinatus* L. plants under various light conditions to obtain insight to which extent it is permitted to extrapolate the periphyton development and attenuation characteristics upon artificial substrate to that upon macrophytes.

Main purposes of this Chapter are, firstly, to examine the periphyton dynamics and the potential impact of periphyton on light climate of submerged macrophytes during the course of the growing season (May-August; Chapters 4 and 5), and secondly, to study whether the periphyton dynamics and concurrently the attenuation characteristics of periphyton are affected by the underwater light climate in Lake Veluwe.

Materials and methods

Light climate treatments

The dynamics and attenuation characteristics of periphyton upon artificial substrate (microscopic glass slides) and leaves of *P. pectinatus* have been studied under four light conditions in Lake Veluwe during the periods May-October 1986 and May-September 1987.

Nets (Agroflor) were extended above the lake surface in 12 enclosed experimental areas of $10 \times 10 \text{ m}^2$ each (April 1986). The whole experiment involved three replicates, each composed by four treatments, notably, a control without shading (referred to as level 1) and three levels of shading reducing the incident irradiance by 26%, 45% and 73%, respectively (referred to as levels 2 to 4). The nets were removed in November 1986 and extended again above the surface of the lake in three enclosed experimental areas ($10 \times 10 \text{ m}^2$ each) in the same way and at the same location as in 1986 (representing level 2 to 4, respectively) in April 1987. Furthermore, one enclosed experimental area (also $10 \times 10 \text{ m}^2$) served as control (level 1). The experiment involved four treatments without replicates in 1987.

Periphyton upon artificial substrate

Two perspex frames with each 60 microscopic slides (Fig. 1) were positioned horizontally at fixed depths of ca. 0.15 m below the water surface, in each experimental area, at the beginning of May 1986. Six similar frames were positioned in each experimental area, at the beginning of May 1987, in the same way as in 1986. Each slide measured $38.76 \times 10^{-4} \text{ m}^2$.

The slides were sampled fortnightly in both years. A distinction was made between the so called "interval-slides" which were replaced by new slides with each sampling and thus were incubated for only two weeks and the so called "total-slides" which were incubated from the beginning of May until they were sampled (2 to 20 weeks). The interval-Series gives insight in the seasonal variation of periphyton accrual rates on a new substrate and the total-Series in the seasonal variation in accrual rate on a permanent substrate during the course of the period sampled.

The subsamples were transported separately in glass jars (150 ml) filled with tap-water. The slides were scraped visually clean with a razor blade in the laboratory and the removed periphyton was collected in tap-water for further analyses. Subsequently, this tap-water with the scraping and the tap-water in which the corresponding subsample was transported were filtered.

Periphyton mass was determined in duplicate in 1986 and in sixfold in 1987, per experimental area. Each subsample of the interval-Series consisted of two slides and each subsample of the total-Series of one slide. Particulate matter was collected on

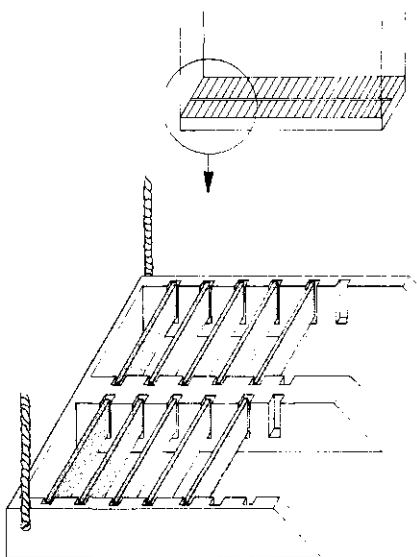


Fig. 1: Perspex frame used for incubating the slides in the water column.

precombusted and preweighed Whatman GF/C filters. The filters with collected matter were dried (24h, 105°C). Ash-free dry weight (AFDW) was calculated after combustion at 550°C (4h) as the difference between dry weight (DW) and ash weight (AW).

Periphyton chlorophyll-a content was determined in duplicate in 1986 and in sixfold in 1987, per experimental area. Each subsample of both the interval- and total-Series consisted of two slides. Particulate matter was collected on Whatman GF/C filters. Subsequently, the filters were deep frozen until they were treated according to the method of Vernon (1960) with modification to control post-acidification pH in the sample (Moed and Hallegraeff, 1978).

Duplicate subsamples of both the interval- and total-Series were taken for determination of the dominant epiphytes in 1986 and 1987. These subsamples were collected only in the control in 1986 and in the control and at the highest shading level in 1987. Each subsample consisted of two slides. The subsamples were preserved in a Lugol's solution. Dominant epiphytes were identified counting 100 to 200 individuals present in various randomly chosen slide areas, with a phase-contrast microscope.

Attenuation by periphyton was measured in duplicate in 1986 and in sixfold in 1987, per experimental area, in both the interval- and total-Series. One slide was used per measurement. Measurements were made on one sided cleaned slides as proportional

transmittance reduction relative to transmittance through a clean slide. A binocular lamp (type Olympus 6-8V 5ATB-1) was used as the only irradiance source and a Bottemanne submersible quantum flux sensor (type RA 200Q, measuring photosynthetically active radiation (PAR)) as irradiance sensor. The slides were placed above the sensor in tap-water during the measurements. In this way, an attempt was made to measure the attenuation characteristics such as are supposed to be relevant to the macrophytes.

Periphyton upon macrophytes

Eighty *P. pectinatus* plants, which had been cultured during three weeks in the laboratory (13-15°C, tap-water, no nutrients added, poor in epiphytes, 16 h light- 8 h dark), were planted in pots (filled with lake sediment, 1 plant per pot, diameter 0.18 m, depth 0.22 m), in the third week of May 1986. The pots with plants were placed on the bottom of the lake in special developed devices to prevent flushing, in four experimental areas differing in photon flux density (20 pots per experimental condition).

A distinction was made between the so called "interval-" and "total-plants" analogous to the interval- and total-slides. Eight interval-plants were sampled in each treatment with each sampling and replaced by eight periphyton-poor plants which had been cultured during three weeks in the laboratory.

Periphyton upon leaves was sampled fortnightly during the growing season of *P. pectinatus* simultaneously with sampling of periphyton upon artificial substrate.

Each subsample consisted of 10-20 leaves of *P. pectinatus*. These leaves were collected from eight interval-plants and eight total-plants randomly chosen. The leaves were collected from various plants and from various depths of the water column per subsample. It is assumed that each subsample may be considered as representative for a plant. The subsamples were transported to the laboratory in glass jars filled with tap-water. Periphyton was removed manually by stripping the leaves three times between thumb and forefinger. In this way, the leaves were visually clean and undamaged. This method is cheap and has practical advantages although some firmly attached algae may not have been removed completely. The removed matter was collected in tap-water (200 ml). This tap-water and the tap-water in which the leaves were transported, were filtered.

The surface area of the cleaned leaves was measured using a conveyor belt type Licor LI 3000 Areameter.

Periphyton mass was determined in duplicate per experimental area. Particulate matter was collected on precombusted and preweighed Whatman GF/C filters. The filters with collected matter were treated in the same way as described for periphyton upon artificial substrate.

Periphyton chlorophyll-a content was determined in duplicate per experimental area. Particulate matter was collected on Whatman GF/C filters. Subsequently, the filters with collected matter were treated in the same way as described for periphyton upon artificial substrate.

Calculations and statistical analyses

Within each experimental area, no distinction was made between the three perspex frames when sampling the slides. Therefore, the individual subsamples per experimental area were not considered as treatment replicates (Hurlbert, 1984). The mean of the subsamples for each experimental area was used for statistical analysis of time and shading effects using a Two-way ANOVA of periphyton characteristics upon artificial substrate. Generally, the standard deviation of the mean per experimental area was less than 10%. The data of periphyton upon artificial substrate in 1986 were analyzed with a Two-way ANOVA for time and shading effects. Subsequently, differences among treatments were tested by means comparisons using Tukey's HSD Test. Prior to these latter analyses the datasets were checked for homogeneity of variance by plotting the means of the experimental units against percentage of shading. A \log_{10} or power transformation was carried out in cases in which the untransformed data were suspected to be inhomogeneous. An arcsin $\sqrt{}$ -transformation was applied in cases in which ratios (e.g. periphyton AW:DW ratio) were <0.3 or >0.7 . The variances of the transformed datasets suggested to be homogeneously distributed except in three cases due to outliers. Outliers with a value of more than four times the standard deviation of the grand mean were removed from the dataset. The datasets of periphyton upon artificial substrate in 1987 were tested only for time effects by a One-way ANOVA. These datasets could not be analyzed for treatment effects because there were no independent replicates (Hurlbert, 1984). The same applied for the datasets of periphyton upon macrophytes. Generally, the datasets of periphyton upon macrophytes showed high variances among the subsamples and no attempts were made to conduct any statistical analysis.

The data were statistically analyzed with the facilities of the SAS statistical package (SAS Institute Inc., 1985). In all cases differences were judged to be statistically significant in case $p < 0.05$. Periphyton accrual rates have been calculated as linear periphyton mass increase per day of incubation.

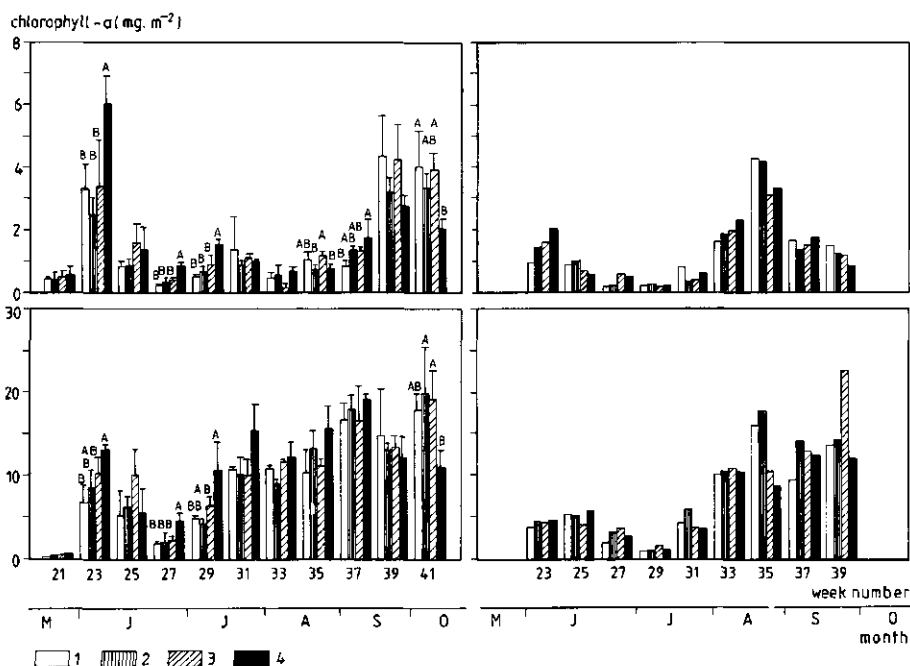


Fig. 2: Seasonal variation in mean periphyton chlorophyll-a content upon the interval-slides (top) and the total-slides (bottom) in the control (1) and at the three shading levels (2 to 4), during the periods measured in 1986 (left) and 1987 (right), respectively. The standard deviation of three replicates is given for the dataset of 1986. Means without lettering and means indicated with the same lettering are not significantly different per sampling date.

Results

Seasonal variation in periphyton dynamics

Periphyton mass upon artificial substrate, expressed in chlorophyll-a (representing the living autotrophic organic fraction), AFDW (representing the living and dead organic fraction), AW (representing the inorganic fraction) and DW (representing the organic plus inorganic fraction) were significantly affected by time in both years and in both the interval- and total-Series (Table 1). These mass characteristics showed a remarkably similar seasonal trend among the two sampling periods in all treatments, in both Series (Fig. 2 to 5, respectively). Peak values in periphyton mass were observed at the beginning and at the end of the periods measured, in the interval-Series of both 1986 and 1987. The second peak values were observed later in the season in 1986 than in 1987 (September and August, respectively). The periods between these peak values showed relatively low periphyton masses in both years.

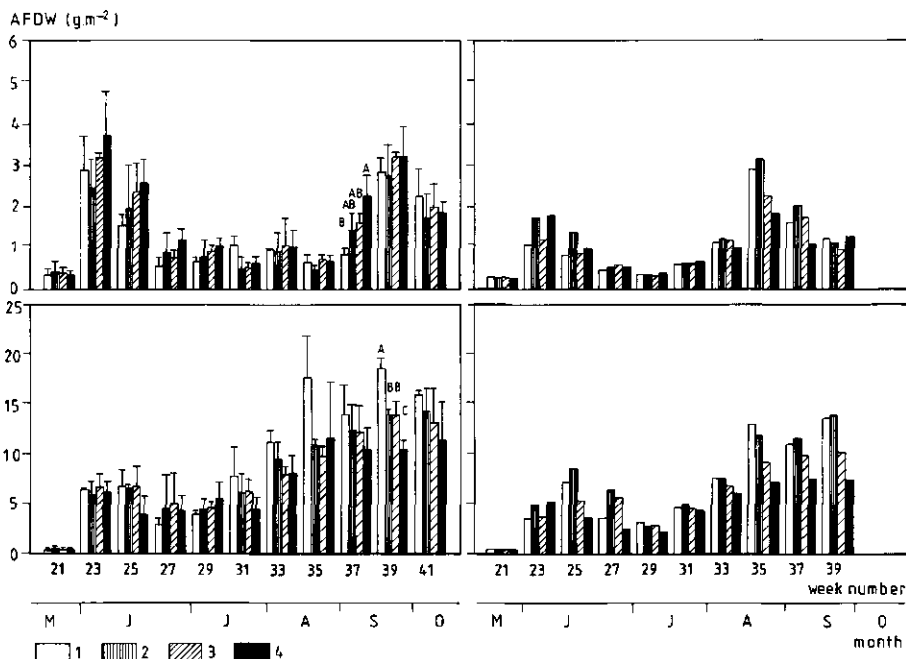


Fig. 3: Seasonal variation in mean periphyton AFDW content upon the interval-slides (top) and the total-slides (bottom) in the control (1) and at the three shading levels (2 to 4), during the periods measured in 1986 (left) and 1987 (right), respectively. The standard deviation of three replicates is given for the dataset of 1986. Means without lettering and means indicated with the same lettering are not significantly different per sampling date.

Periphyton mass increased in the total-Series of 1986 and 1987 until mid June. Subsequently, periphyton chlorophyll-a and AFDW decreased while AW and DW remained about the same. This loss of organic periphytic mass coincided with the appearance of herbivorous invertebrates (chironomids and gammarids) in the periphytic layer. Periphyton mass increased from mid July onwards until an upper plateau was reached. At the same time, only few chironomids and gammarids were observed, if any at all.

On the whole, periphyton mass expressed in chlorophyll a, AFDW, AW and DW showed relatively small differences between the two years in both the interval- and total-Series.

Ash content (AW expressed as percentage of DW) was significantly affected by time, in the interval and total-Series, in both years (Table 1). Though, it showed only minor seasonal trends (Fig. 6). Ash content remained more than 80% in the total-Series, starting at the beginning of June.

Table 1: Significance (*p*) of ANOVA for time and shading effects on chlorophyll-a content, AFDW, AW, DW, ash content and chlorophyll-a content of the organic fraction of periphyton and attenuation by periphyton in the interval- and total-Series, during the periods measured in 1986 and 1987, respectively.

	1986		1987	
	Interval	Total	Interval	Total
Chl-a ($\text{mg}\cdot\text{m}^{-1}$)				
time	0.0001	0.0001	0.0001	0.0001
shading	0.0079	0.5451	-*	-
time*shading	0.0001	0.0003	-	-
AFDW ($\text{g}\cdot\text{m}^{-2}$)				
time	0.0001	0.0001	0.0001	0.0001
shading	0.0019	0.0001	-	-
time*shading	0.3582	0.0200	-	-
AW ($\text{g}\cdot\text{m}^{-2}$)				
time	0.0001	0.0001	0.0001	0.0001
shading	0.0303	0.0001	-	-
time*shading	0.9121	0.0001	-	-
DW ($\text{g}\cdot\text{m}^{-2}$)				
time	0.0001	0.0001	0.0001	0.0001
shading	0.0053	0.0001	-	-
time*shading	0.6896	0.0001	-	-
Ash content (AW as % of DW)				
time	0.0001	0.0001 ⁺	0.0001	0.0001 ⁺
shading	0.5466	0.0260 ⁺	-	-
time*shading	0.9332	0.6474 ⁺	-	-
Chl-a ($\text{mg chl-a}\cdot\text{g}^{-1}$ AFDW)				
time	0.0001	0.0001	0.0001	0.0001
shading	0.8710	0.0001	-	-
time*shading	0.4080	0.0109	-	-
Attenuation (%)				
time	0.0001 ⁺	0.0001 ⁺	0.0001 ⁺	0.0001 ⁺
shading	0.0010 ⁺	0.0005 ⁺	-	-
time*shading	0.0001 ⁺	0.0819 ⁺	-	-

-* not determined

+ dataset arcsin $\sqrt{}$ -transformed

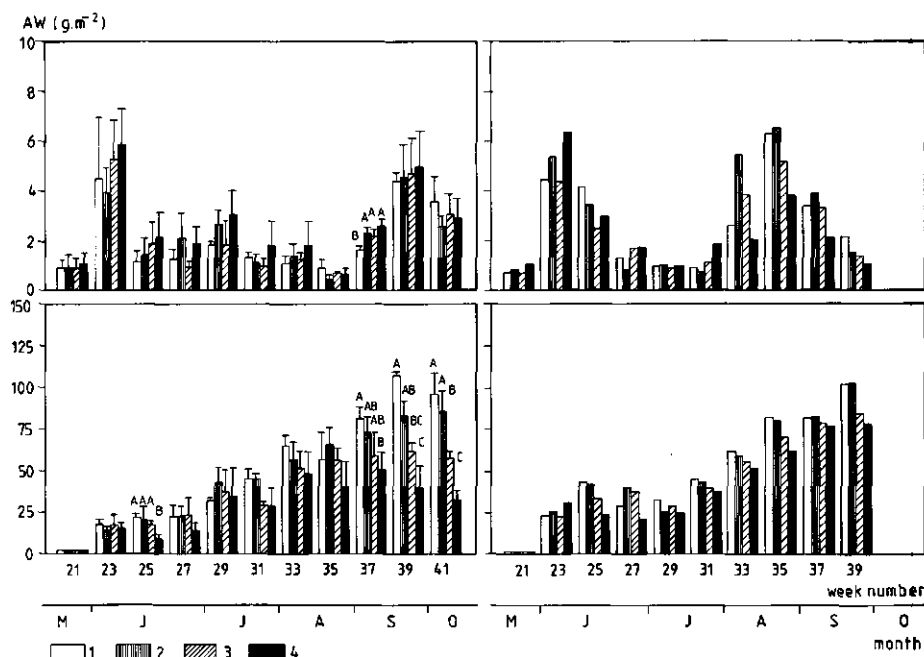


Fig. 4: Seasonal variation in mean periphyton AW content upon the interval-slides (top) and the total-slides (bottom) in the control (1) and at the three shading levels (2 to 4), during the periods measured in 1986 (left) and 1987 (right), respectively. The standard deviation of three replicates is given for the dataset of 1986. Means without lettering and means indicated with the same lettering are not significantly different per sampling date.

Chlorophyll-a expressed per unit AFDW (Fig. 7) was significantly affected by time in the interval- and total-Series, in both years (Table 1). However, it showed less distinct seasonal trends than chlorophyll-a expressed per unit area (Fig. 2). The incubated slides were covered more or less uniformly. Microscopic analysis of periphyton revealed that it consisted of inorganic (clay and/or silt particles) and detrital organic matter by far the greater part. Substantial amounts of non-living algal matter were observed especially in the total-Series.

Diatoms were the dominant group during the sampling periods in the controls of both the interval- and the total-Series (Table 2). The relative abundance of cyanobacteria was relatively low. The contribution of green algae increased with time starting at the end of May, until 40 to 50% with *Scenedesmus* and *Monoraphidium* as dominant genera in the interval- and total-Series, in both years. The contribution of green algae decreased until 10% at the end of the sampling periods except in the controls of the total-Series of 1986 in which the contribution of green algae remained 40%.

Table 2: Seasonal variation in relative abundance of green algae (GR), diatoms (DT) and cyanobacteria (CB) of periphyton in the interval- and total-Series in the control (1) and at the highest shading (4) during the periods measured in 1986 and 1987, respectively.

Date	1						4					
	Interval			Total			Interval			Total		
	GR (%)	DT (%)	CB (%)	GR (%)	DT (%)	CB (%)	GR (%)	DT (%)	CB (%)	GR (%)	DT (%)	CB (%)
20-May-86	10	80	10	10	80	10	*	-	-	-	-	-
02-Jun-86	20	70	10	20	70	10	-	-	-	-	-	-
16-Jun-86	25	70	5	25	70	5	-	-	-	-	-	-
30-Jun-86	40	60	<5	25	70	5	-	-	-	-	-	-
14-Jun-86	20	80	<5	20	80	<5	-	-	-	-	-	-
28-Jun-86	50	50	<5	70	20	10	-	-	-	-	-	-
12-Aug-86	40	60	<5	50	50	<5	-	-	-	-	-	-
25-Aug-86	40	60	<5	50	50	<5	-	-	-	-	-	-
08-Aug-86	10	90	<5	35	45	20	-	-	-	-	-	-
20-May-87	5	95	<5	5	95	<5	5	95	<5	5	95	<5
03-Jun-87	40	60	<5	40	60	<5	40	60	<5	40	60	<5
16-Jun-87	50	50	<5	50	50	<5	50	50	<5	50	50	<5
30-Jun-87	40	50	10	40	50	10	40	50	10	40	50	10
15-Jul-87	50	50	<5	40	60	<5	40	60	<5	25	75	<5
30-Jul-87	50	50	<5	15	85	<5	15	85	<5	20	80	<5
13-Aug-87	30	40	30	15	85	<5	40	60	<5	10	90	<5
25-Aug-87	5	95	<5	10	90	<5	5	95	<5	10	90	<5
09-Sep-87	10	90	<5	10	90	<5	10	90	<5	10	90	<5

* not determined

The dominant genera were much the same in the interval- and total-Series on most sampling dates, however, *Gomphonema* and *Cymbella* were observed more frequently during both seasons in the total-Series. The observed relatively high periphyton mass in June 1986 and 1987 was mainly attributed to diatoms with *Diatoma*, *Nitzschia*, and *Navicula* and in 1986 also *Synedra*, as dominant genera. *Nitzschia* and *Stephanodiscus* were dominant at the end of the growing season in 1986 and *Navicula* and *Diatoma* in 1987.

Periphyton upon *P. pectinatus* leaves showed a high variability in mass among the duplicate subsamples per treatment in 1986 (the standard deviation ranged up to 75%). Periphyton mass upon macrophytes suggested clearly a similar seasonal trend in both the interval- and total-Series as upon artificial substrate in the interval-Series at all conditions. This trend is characterized by peak values at the beginning and at the

Table 3: Seasonal variation in mean chlorophyll-a content, AFDW, AW, and DW of periphyton upon leaves of *P. pectinatus* in the interval- and total-Series in the control (1) and at the various shading levels (2 to 4) during the period measured in 1986.

Date	Chlorophyll-a (mg.m ⁻²)				AFDW (g.m ⁻²)				AW (g.m ⁻²)				DW (g.m ⁻²)			
	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4
Interval																
02-Jun-86	38	25	22	9	20.6	12.7	69.6	27.9	45.0	36.4	209	78.4	65.6	49.1	279.5	106.3
16-Jun-86	2	1	4	6	5.2	6.0	9.2	4.7	37.3	38.8	25.0	18.3	42.4	44.7	34.3	22.9
30-Jun-86	*	0	0	-	-	5.1	4.0	6.3	-	19.1	11.9	14.0	-	24.2	15.8	21.0
14-Jul-86	-	-	-	-	1.1	1.5	0.0	0.7	7.9	13.8	5.5	7.9	9.0	15.2	4.0	8.4
28-Jul-86	3	1	4	-	10.8	4.1	4.0	2.4	171.5	0.4	3.6	6.7	182.4	4.5	7.6	9.1
12-Aug-86	-	-	-	-	-	14.9	15.1	8.0	-	50.6	58.4	44.8	65.5	73.6	52.7	-
Total																
02-Jun-86	17	29	39	63	18.7	19.3	50.7	26.8	43.3	57.2	168	74.2	61.9	76.5	218.9	101.0
16-Jun-86	4	3	1	6	5.8	8.4	4.9	5.6	42.7	76.7	32.3	51.4	48.4	85.3	37.2	57.0
30-Jun-86	-	0	0	3	-	12.8	6.7	4.9	25.1	28.5	34.6	30.3	39.1	35.4	39.7	44.7
14-Jul-86	-	-	-	-	1.8	2.7	1.5	0.5	8.2	16.3	6.6	14.5	9.9	19.0	8.0	15.0
28-Jul-86	1	6	12	-	8.3	12.1	10.5	-	36.4	26.2	30.1	-	44.7	38.3	40.5	-
12-Jun-86	-	-	-	-	13.6	28.1	11.4	-	67.8	97.8	68.3	-	81.4	125.9	79.7	-

* not determined

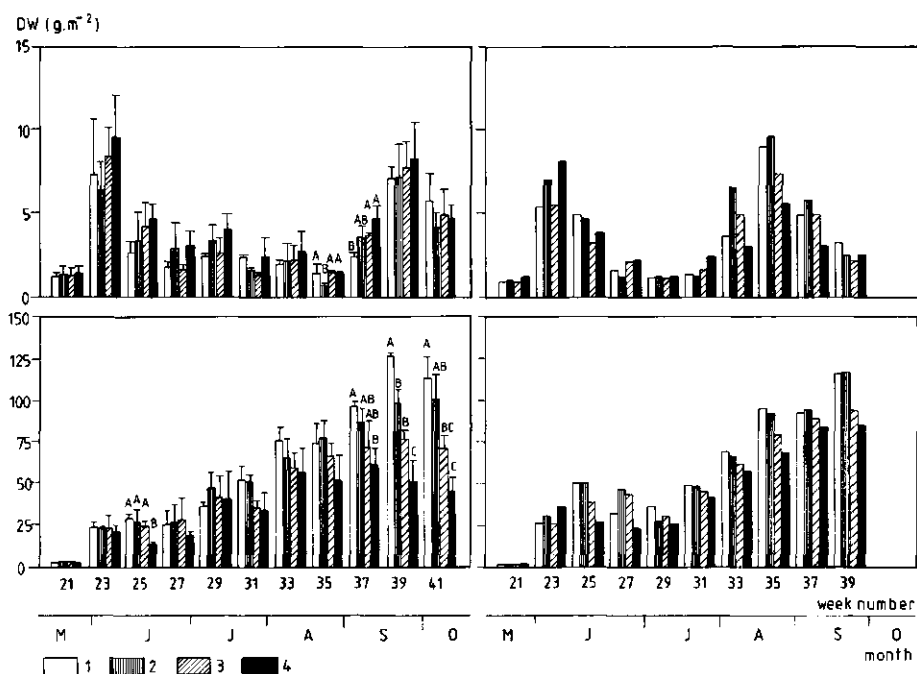


Fig. 5: Seasonal variation in mean periphyton DW content upon the interval-slides (top) and the total-slides (bottom) in the control (1) and at the three shading levels (2 to 4), during the periods measured in 1986 (left) and 1987 (right), respectively. The standard deviation of three replicates is given for the dataset of 1986. Means without lettering and means indicated with the same lettering are not significantly different per sampling date.

end of the sampling period (Table 3). The seasonal fluctuations were more pronounced upon plants than upon artificial substrate. Periphyton mass upon plants showed relatively small differences between the interval- and the total-Series per sampling date. Generally, periphyton AFDW, AW and DW was higher upon plants than upon artificial substrate in the interval-Series. Differences in periphyton mass among artificial substrate and plants were less obvious in the total-Series. Periphyton chlorophyll-a was markedly higher upon plants than upon artificial substrate only on 2 June in both Series.

Ash contents of periphyton were comparable upon plants (Table 4) and artificial substrate (Fig. 6) in both the interval- and total-Series of 1986. Data on periphyton chlorophyll-a expressed per unit AFDW (Table 4), suggested a lower chlorophyll-a content upon plants than upon artificial substrate (Fig. 7).

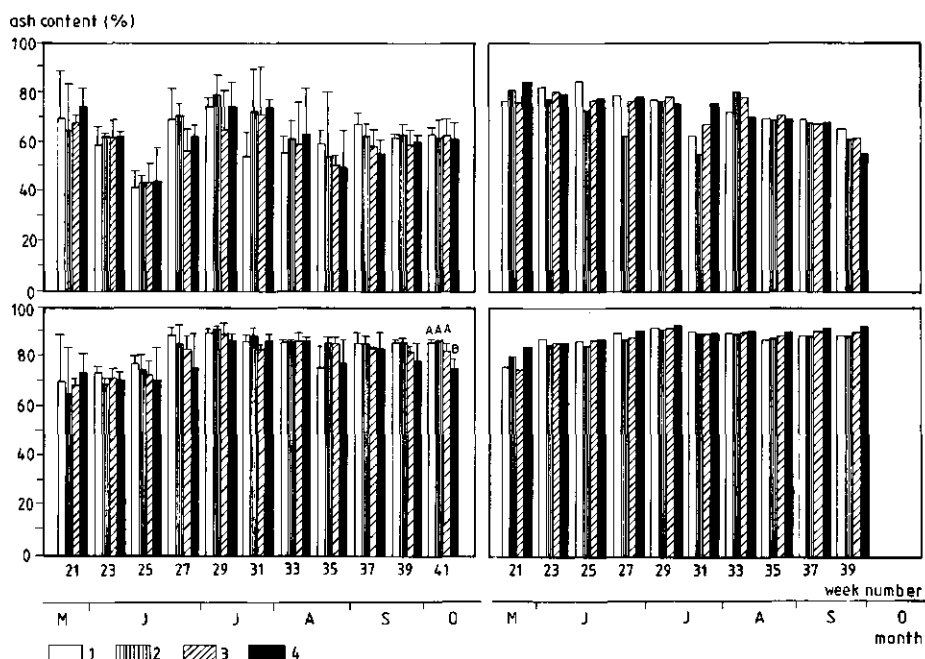


Fig. 6: Seasonal variation in mean periphyton relative ash content upon the interval-slides (top) and the total-slides (bottom) in the control (1) and at the three shading levels (2 to 4), during the periods measured in 1986 (left) and 1987 (right), respectively. The standard deviation of three replicates is given for the dataset of 1986. Means without lettering and means indicated with the same lettering are not significantly different per sampling date.

Shading effects on periphyton dynamics

Periphyton mass upon artificial substrate expressed in chlorophyll a, AFDW, AW and DW, was treatment affected in the interval- and total-Series of 1986 but, in several cases there was an interaction between time and shading (Table 1). Periphyton AFDW, AW and DW were only incidentally affected by shading in the interval-Series (Fig. 3 to 5) and periphyton chlorophyll-a was higher with increased shading on several sampling dates in both the interval- and total-Series (Fig. 2). The upper plateau of periphyton AFDW, AW and DW reached at the end of the period measured was lower with increased shading in the total-Series.

The datasets of the interval- and total-Series showed comparable shading effects on periphyton mass in 1986 and 1987.

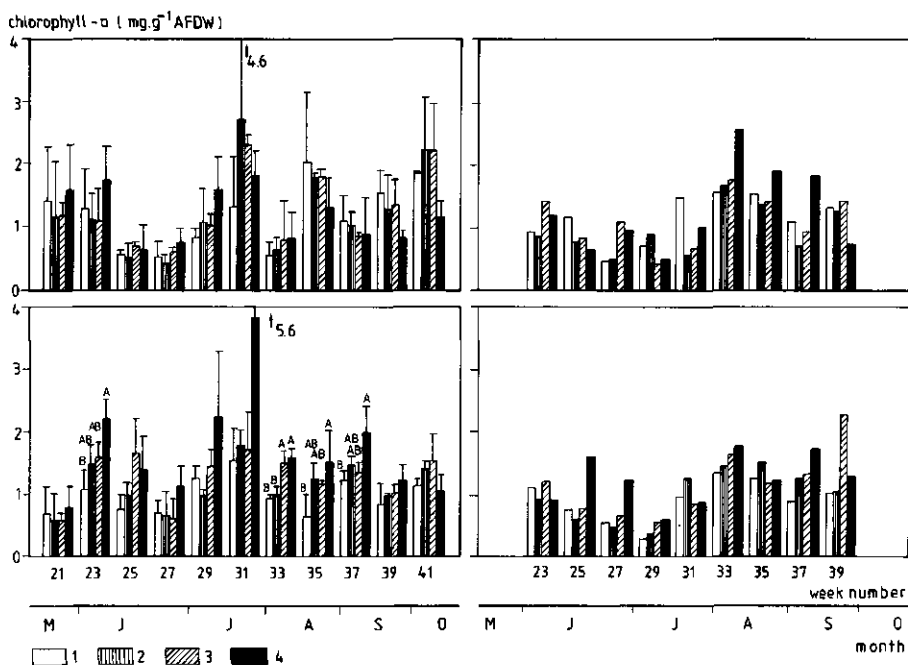


Fig. 7: Seasonal variation in mean chlorophyll-a content of periphyton upon the interval-slides (top) and the total-slides (bottom), in the control (1) and at the three shading levels (2 to 4), during the periods measured in 1986 (left) and 1987 (right), respectively. The standard deviation of three replicates is given for the dataset of 1986. Means without lettering and means indicated with the same lettering are not significantly different per sampling date.

Periphyton ash content was significantly affected by shading in the total-Series of 1986 only (Table 1). It appeared to be treatment affected on one sampling date only (Fig. 6). Periphyton chlorophyll-a content expressed per unit AFDW was not significantly affected by shading in the interval-Series (Table 1) but it demonstrated a significant impact of shading in the total-Series; chlorophyll-a content was higher with increased shading on various sampling dates (Fig. 7).

The relative abundances of algae groups were similar in the control and at the highest shading level on most sampling dates of 1987 (Table 2).

Data on periphyton mass upon macrophytes suggest variable shading effects, if any at all, in both Series of 1986 (Table 3). Though, it should be noted that the variability in replicates among the experimental conditions was high. Data on ash content and chlorophyll-a content of AFDW suggested, variable shading effects, if any at all (Table 4). A higher periphyton chlorophyll-a content with increased shading, observed upon artificial substrate, was not recognized in upon plants.

Periphyton attenuation characteristics

The attenuation characteristics of periphyton upon artificial substrate were significantly affected by time and shading in 1986 (Table 1). The seasonal variation in attenuation followed closely the observed seasonal variation in periphyton mass in the interval-Series (Fig. 8). Peak attenuations were recorded in June and at the end of the sampling periods. Periphyton in the control of the total-Series reduced the incident irradiance by more than 80% from June onwards during both sampling periods and even up until 98% in 1987. The periphyton mass-attenuation relationship can adequately be described by a Michaelis-Menten function (Vermaat and Hootsmans, 1991). This function has been applied for the present data pairs of mean periphyton mass and corresponding mean attenuation of periphyton derived from both the interval- and total-Series for the two years and the four treatments. The calculated relationship between periphyton mass (expressed in DW) and attenuation fitted very well (Fig. 9). At relatively low periphyton mass, a relatively small increase in periphyton mass results in a relatively high increase in attenuation, whereas at higher periphyton mass, a further increase hardly affects the attenuation.

Table 4: Seasonal variation in mean ash content and chlorophyll-a content of periphyton on leaves of *P. pectinatus* in the interval- and total-Series in the control (1) and at the various shading levels (2 to 4) during the period measured in 1986.

Date	Ash content (% of DW)				Chlorophyll-a (mg.g ⁻¹ AFDW)			
	1	2	3	4	1	2	3	4
Interval								
02-Jun-86	69	74	75	72	1.8	1.9	0.3	0.3
16-Jun-86	88	86	76	81	0.4	0.2	0.5	1.2
30-Jun-86	-*	79	75	67	-	0	0	-
14-Jul-86	86	92	135	95	-	-	-	-
28-Jul-86	94	9	46	74	0.2	0.3	1.0	-
12-Aug-86	-	77	80	80	-	-	-	-
Total								
02-Jun-86	70	76	77	74	0.9	1.5	0.8	2.4
16-Jun-86	88	90	87	90	0.6	0.3	0.2	1.1
30-Jun-86	60	79	87	68	0	0	0	0.6
14-Jul-86	82	86	84	97	-	-	-	-
28-Jul-86	81	57	74	-	0.1	0.5	1.1	-
12-Aug-86	83	77	86	-	-	-	-	-

-* not determined

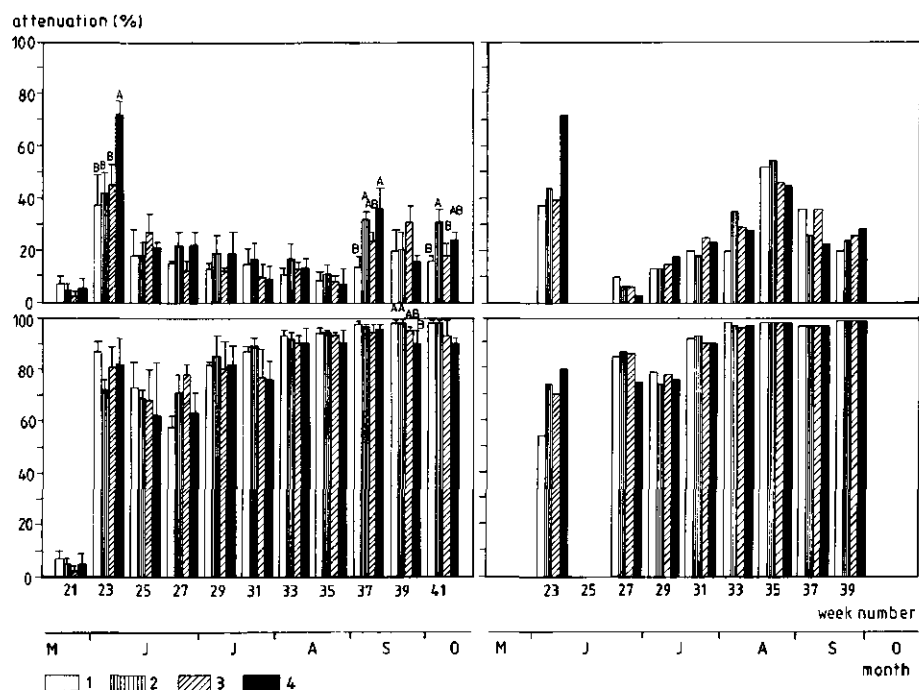


Fig. 8: Seasonal variation in mean attenuation of incident irradiance by periphyton in the interval-slides (top) and the total-slides (bottom), in the control (1) and at the three shading levels (2 to 4), during the periods measured in 1986 (left) and 1987 (right), respectively. The standard deviation of three replicates is given for the dataset of 1986. Means without lettering and means indicated with the same lettering are not significantly different per sampling date.

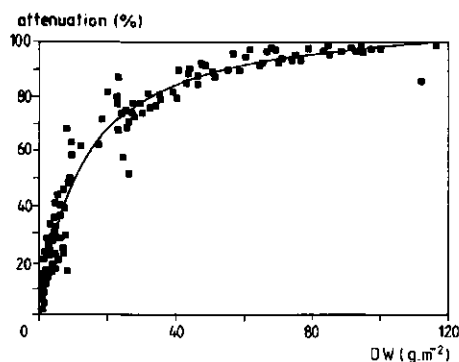


Fig. 9: Data-pairs of mean attenuation against mean periphyton mass, under various light conditions, derived from the dataset of 1986 and 1987 and the fitted Michaelis-Menten curve: $A = (110.96 \cdot DW) / (12.71 + DW)$ (C.D.=0.988) with A=attenuation (%), DW=dry weight (g.m^{-2}), and C.D.= coefficient of determination.

Discussion

Seasonal variation in periphyton dynamics

Periphyton exhibited high masses in Lake Veluwe during both sampling periods. The maximum periphyton mass measured in the total-Series (about 13.0-17.5 g AFDW.m⁻² upon artificial substrate) is within the range of values published (Vermaat and Hootsmans, 1991). The accrual rates in the interval-Series varied from 0.021 to 0.200 g AFDW.m⁻².d⁻¹. This range is comparable to the range reported for periphyton upon artificial substrate in Lake Vechten: 0.004 - 0.260 mg AFDW.m⁻².d⁻¹ (after 25 and 31 days of incubation, respectively) (Gons, 1982). Periphyton accrual rates were about a factor 10 higher in the interval-Series in Lake Veluwe than those recorded under laboratory conditions comparable in nutrient levels, light climate and water temperature: 0.0033 and 0.0118 mg AFDW.m⁻².d⁻¹ (after 10 and 20 days of incubation, respectively) (Vermaat and Hootsmans, 1991). Accumulated periphyton mass resulted mainly from growth in the latter laboratory experiment since colonization and deposition were restricted. Apparently, accumulated periphyton mass upon artificial substrate in the field largely resulted from colonization and deposition assuming comparable growth rates under laboratory and field conditions similar in nutrient levels and water temperature.

The seasonal variation in periphyton mass upon artificial substrate and plants was remarkably similar in both the interval- and total-Series of 1986 and 1987. The relatively high values of periphyton accrual rates in June corresponded with an increase in water temperature and photon flux density. A mid summer depression in periphyton growth such as observed in Lake Veluwe, has been reported for various waters (Borum and Wium-Andersen, 1980; Cattaneo and Kalff, 1978; Gons, 1982; Kairesalo, 1983, 1984; Meulemans, 1988; Takamura *et al.*, 1990). This mid summer depression has been explained by a reduction in photon flux densities as a result of shading by plant canopies (Kairesalo, 1983; Sand-Jensen, 1983) and nutrient limitation (Hooper-Reid and Robinson, 1978) due to macrophyte growth, a strongly reduced photosynthetic capacity of the periphytic algae (Meulemans, 1988) and by photoinhibition (Gons, 1982). Irradiance limited periphyton growth can be ruled out in the present study because the slides were positioned just below the water surface and no extremely high attenuation coefficients of the water column were observed at that time (Chapter 2). More likely, periphyton growth was photoinhibited in mid summer. Furthermore, competition with macrophytes for nutrients might have been involved as well in causing the mid summer depression in periphyton accrual rate, because relatively high macrophyte biomass was observed at that time (Chapters 4 and 5). The slides were not protected against grazers in the present study. Hence, the observed mid summer depression in periphyton mass might also be due to grazing

activities of the observed chironomids and gammarids. It is generally accepted that grazing may reduce the periphyton mass considerably (e.g. Mason and Bryant, 1975; Hunter, 1980; Sumner and McIntire, 1982; Brönmark, 1985; Hootsmans and Vermaat, 1985). Periphyton accrual rate was even too poor to allow for compensation of losses in organic matter in the total-Series, in July. Spontaneous detachment of the periphytic layer has been observed regularly (Gons, 1982; Vermaat and Hootsmans 1991). Such detachment has been explained by die-off of algae in the lower strata due to light limitations causing unstableness of the periphytic layer (Meulemans and Roos, 1985; Cattaneo, 1987; Meulemans, 1988). Periphyton loss was most obvious for the organic fraction in the total-Series at the present study site indicating selective grazing on the organic fraction of periphyton. Periodicity in presence of the observed chironomids and gammarids might explain the observed periodicity in periphyton losses.

The relatively high periphytic accrual rates observed in August and September in both the interval- and total-Series, corresponded with senescence of the aboveground parts of the macrophytes at the study site (Chapters 4 and 5). Decaying plant material releases nutrients and other profitable compounds, hence creating excellent circumstances for rich algal growth (e.g. Kairesalo, 1983). Furthermore, photoinhibition might have played a less important role at that time compared to the mid summer period.

Composition

Generally, relative ash content of periphyton consisting mainly of pure epiphytic algae, varies in the range of about 40-50 % dependent on the composition of algae (Castenholz, 1961; Dor, 1970; Vermaat and Hootsmans, 1991). The present study revealed that relative ash content of periphyton upon artificial substrate was little higher in the interval-Series, and much higher in the total-Series (about 80%). It follows that periphyton consisted for an important part of inorganic matter that did not originate from epiphytes only, especially in the total-Series. It is concluded that periphyton consisted largely of settled matter from the water column considering the substantial amounts of silt and clay particles observed in the periphytic layer in the total-Series and to a lesser extent in the interval-Series.

Chlorophyll-a content of the organic fraction ranged from 1 to 2 mg.g⁻¹ AFDW in the interval- and total-Series, which is much the same as the reported contents for periphyton in Lake Vechten, rich in detrital and heterotrophic organic matter (Gons, 1982). Periphyton consisting mainly of pure epiphytic algae, has a chlorophyll-a content of about 5 to 10 mg.g⁻¹ AFDW (Vermaat and Hootsmans, 1991). The relatively low chlorophyll-a content of periphyton observed in Lake Veluwe, indicates that a large fraction of the organic matter of periphyton was detrital or heterotrophic

or both.

A qualitative interrelationship between the phytoplanktonic and periphytic algae has been demonstrated in eutrophic waters (Moss, 1981; Jenkerson and Hickman, 1986). The seasonal variation in relative abundance of epiphytic algae presented in this paper coincided with that of phytoplanktonic algae (Chapter 2). Both communities performed an increase in green algae during the summer with *Scenedesmus* as the dominant genus. Furthermore, in both communities *Diatoma* and *Nitzschia* were the dominant genera in May. Generally, the fraction of diatoms was higher in periphyton than in phytoplankton.

The development of periphyton in Lake Veluwe can be characterized as follows. A new substrate is colonized mainly by epiphytes resulting in a periphytic layer with a relatively simple structure in which some silt and clay particles may settle.

Subsequently, more erect epiphytic algae such as *Cymbella* and *Gomphonema* develop, enlarging the substrate for colonization and growth (Roos, 1983). This results in a more complex structure of the layer including bacteria, fungi, heterotrophic organisms and detrital matter, facilitating further settling of suspended matter including phytoplankton. The complexity of the periphytic layer increases. Apparently, settlement of suspended matter plays an important role in determining periphyton mass. Although, it is generally recognized that periphyton may largely consist of settled matter from the water column (Schiemer and Prosser, 1976; Gons, 1982), to date little is known about the massive input of suspended matter into the periphyton. Both seasonal and shading effects on periphyton mass were much the same for the organic and inorganic fraction of periphyton and the relative contribution of inorganic matter to DW varied barely. Apparently, the inorganic input in the periphytic layer largely depends on the amount of organic matter present.

Periphyton showed comparable ash contents upon artificial substrate and macrophytes implying periphyton upon plants consisted also largely of settled matter. The relatively low chlorophyll-a content of periphyton upon plants indicated relatively high amounts of detrital matter in the periphyton.

Shading effects on periphyton dynamics

Light climate was not a dominant factor in determining periphyton mass in Lake Veluwe (expressed in AFDW, AW and DW). Shading effects, if any, were probably masked by settling of suspended matter in the periphytic layer. The observed higher chlorophyll-a content with increased shading might indicate less photoinhibition and consequently higher growth with increased shading. It should be noted that in cases chlorophyll-a content was expressed per unit AFDW, variability among light conditions may partly result from variation in contribution of the heterotrophic and detrital organic component to the organic fraction.

Possible factors which exerted the dominant control over periphyton growth might have been the periphyton growth-light response curve characteristics (Meulemans and Heinis, 1983; Meulemans, 1988), nutrient concentrations (Bothwell, 1988; Bushong and Bachmann, 1989), carbon concentrations (Munn *et al.*, 1989) and water temperature (Bothwell, 1988; Bushong and Bachmann, 1989; Vermaat and Hootsmans, 1991). In the present study, the water column was well mixed and possible differences in temperature among the treatments are ruled out.

Attenuation

A relatively high attenuation was observed for periphyton upon artificial substrate in Lake Veluwe. An attempt has been made to elucidate to which extent the input of inorganic suspended matter determined the attenuation characteristics of periphyton. In Fig. 10, the relationship of periphyton abundance (expressed in g AFDW.m⁻²) and their attenuation characteristics (as obtained in 1986 and 1987 in Lake Veluwe) is given. Furthermore, the relationship between periphyton abundance (expressed in g AFDW.m⁻²) and attenuation for mainly pure epiphytic communities is shown (after Vermaat and Hootsmans, 1991). Assuming the latter relationship is valid for the pure epiphytic community of Lake Veluwe, it is concluded that the input of inorganic matter increased the attenuation substantially (up to about 20%). Besides photon flux density, the spectral composition of PAR is of importance for growth of macrophytes (e.g. Kirk, 1983). Settled matter low in algal content shows mainly a nonselective attenuation with some additional absorption in the blue part of the spectrum in Lake Veluwe (Chapter 2). As a consequence, periphyton consisting largely of settled matter will mainly (back)scatter giving a nonselective attenuation with some additional

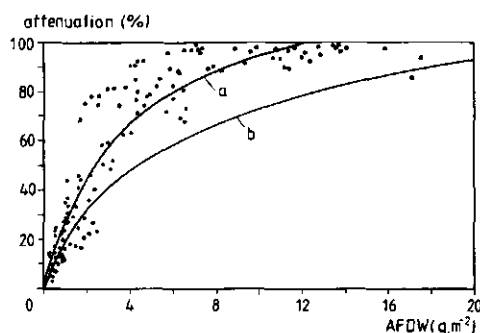


Fig. 10: Data-pairs of mean attenuation against mean periphyton mass under various light conditions, derived from the dataset of 1986 and 1987, and the fitted Michaelis-Menten curve (a). Furthermore, the relationship between attenuation and periphyton mass from laboratory cultures after Vermaat and Hootsmans (1990) is shown (b).

absorption at the blue end of the spectrum. Such a nonselective attenuation has been shown for non-pigmented algal matter, diatom frustules, calcium carbonate and bacteria in periphytic layers (Losee and Wetzel, 1983) and for an intact periphyton community in which the epiphytic algae formed also only a relatively small part of the total periphytic structure (Meulemans, 1989).

Comparison periphyton upon artificial substrate and plants

There has been controversy whether the development of periphyton on macrophytes can be represented by that on artificial substrate (Cattaneo and Kalff, 1978, 1979; Gough and Gough, 1981; Blindow, 1987). Eminson and Moss (1980) suggested that the influence of host type on periphyton community composition is greatest in infertile lakes, and that where external nutrient loading is high and the water is fertile such interactions are likely to be masked. Nevertheless, substantial differences in epiphyton density and species composition among plant species (Characeae and *P. pectinatus*) were found in a eutrophic shallow lake (Blindow, 1987).

The present results indicate that periphyton mass upon artificial substrate underestimated the mass of periphyton upon leaves of *P. pectinatus*, but represented the seasonal trend in periphyton development upon the plants appropriately. *P. pectinatus* leaves may not behave as a neutral substrate. Secretion of nutrients or organic compounds by macrophytes may stimulate periphyton growth (Howard-Williams and Davies, 1978) and physical substrate characteristics may affect the adhesion of periphyton algae (Otten and Willemse, 1988). The observed differences in periphyton dynamics between substrate may at least partly result from differences in location and position of substrate since periphyton consisted largely of settled inorganic matter, probably concealing any specific interactions between substrate and periphyton. The macrophytes formed a geometrically more diverse substrate for microfloral growth. This may have facilitated settling of suspended matter in contrast to the vertically positioned slides. Furthermore, the slides were sampled from only one depth, while the leaves were sampled over the entire depth with variable sedimentation rates and light conditions and consequently variable accrual rates.

Ecological implications

The beginning of the growing season of *P. pectinatus* is generally recognized as a critical period for growth because at that time the plants are relatively small and consequently the availability of PAR is low due to extensive attenuation by the water column (Anderson, 1978; Chapter 5). This period might even be more critical than was assumed because the beginning of the growing season of *P. pectinatus* corresponds with maximum accrual rates of periphyton and maximum attenuation. The relatively high periphyton abundance which corresponded with senescence of the aboveground

biomass at the end of the growing season, may fasten the decay of the plants and in this way shorten their growing season.

Extrapolating the results of the total-Series of artificial substrate to *P. pectinatus*, it is concluded that older leaves become soon entirely covered and that the availability of PAR is strongly reduced (up to 80%). Probably, photosynthesis may be relatively low in older leaves and consequently, older leaves may contribute little to the net growth of the entire plant. Newly formed leaves are generally covered rapidly with periphyton as well. Given the present results, a rapid turn-over of leaves may be an adequate response to grow out periphyton effects (Sand-Jensen, 1977; Losee and Wetzel, 1983). This study focused on the attenuation effects of periphyton. However, the gas and nutrient exchange between leaves of the macrophytes and the ambient water is hampered markedly with relatively high periphyton densities (Sand-Jensen, 1977; Hansson, 1989). Therefore, the growth of macrophytes is likely to be negatively affected also by the effects on these processes in the presence of such abundant layers.

It is concluded that a reduction in suspended matter in the water column will not only improve light climate in the water column (Chapter 2) but will also reduce the attenuation by periphyton considering the high amounts of settled suspended matter from the water column into the periphytic layer, and hence improve the light conditions for the submerged macrophytes considerably.

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References

- Anderson M.G., 1978. Distribution and production of sago pondweed (*Potamogeton pectinatus* L.) on a northern prairie marsh. *Ecology* 59: 154-160.
- Blindow L., 1987. The composition and density of epiphyton on several species of submerged macrophytes - the neutral substrate hypothesis tested. *Aquat. Bot.* 29: 157-168.
- Borum J., 1985. Development of epiphytic communities on eelgrass (*Zostera marina*) along a nutrient gradient in a Danish estuary. *Mar. Biol.* 87: 211-218.
- Borum, J. and S. Wium-Andersen, 1980. Biomass and production of epiphytes on eelgrass (*Zostera marina* L.) in the Oresund, Denmark. *Ophelia*, suppl. 1: 57-64.
- Bothwell M.L., 1988. Growth rate responses of lotic periphytic diatoms to experimental phosphorus enrichment: the influence of temperature and light. *Can. J. Fish. Aquat. Sci.* 45: 261-270.
- Brönmark C., 1985. Interactions between macrophytes, epiphytes and herbivores: an experimental approach. *Oikos* 45: 26-30.
- Bulthuis D.A. and W.J. Woelkerling, 1983. Biomass accumulation and shading effects of epiphytes on the leaves of *Heterozostera tasmanica*, in Victoria, Australia. *Aquat. Bot.* 16: 137-140.
- Bushong S.J. and R.W. Bachmann, 1989. In situ nutrient enrichment experiments with periphyton in agricultural streams. *Hydrobiologia* 178: 1-10.
- Castenholz R.W., 1961. An evaluation of a submerged glass method of estimating production of attached algae. *Verh. Internat. Verein. Limnol.* 14: 155-159.
- Cattaneo A. and J. Kalff, 1978. Seasonal changes in the epiphytic community of natural and artificial aquatic plants: a study of interactions between epiphytes and their substrate. *Limnol. Oceanogr.* 24: 1031-1037.
- Cattaneo A. and J. Kalff, 1979. Primary production of algae growing on natural and artificial aquatic plants: a study of interactions between epiphytes and their substrate. *Limnol. Oceanogr.* 24: 1034-1037.
- Cattaneo A., 1987. Periphyton in lakes of different trophic. *Can. J. Fish. Aquat. Sci.* 44: 296-303.
- Dor I., 1970. Production rate of the periphyton in Lake Tiberias as measured by the glass-slide method. *Israel J. Bot.* 19: 1-15.
- Eminson D. and G. Phillips, 1978. A laboratory experiment to examine the effects of nutrient enrichment on macrophyte and epiphyte growth. *Verh. Internat. Verein. Limnol.* 20: 82-87.
- Eminson D. and B. Moss, 1980. The composition and ecology of periphyton communities in freshwaters 1. The influence of host type and external environment on community composition. *Br. Phycol. J.* 15: 429-446.
- Gons H.J., 1982. Structural and functional characteristics of epiphyton and epipelon in relation to their distribution in Lake Vechten. *Hydrobiologia* 95: 79-114.

- Gough S.B. and L.P. Gough, 1981. Comment on "Primary production of algae growing on natural and artificial plants: a study of interactions between epiphytes and their substrate" (Cattaneo and Kalff). *Limnol. Oceanogr.* 26: 987-988.
- Hansson L.A., 1989. The influence of a periphytic biolayer on phosphorus exchange between substrate and water. *Arch. Hydrobiol.* 115: 21-26.
- Hooper-Reid N.M. and G.G.C. Robinson, 1978. Seasonal dynamics of epiphytic algal growth in a marsh pond: productivity, standing crop, and community composition. *Can. J. Bot.* 56: 2434-2440.
- Hootsmans M.J.M. and J.E. Vermaat, 1985. The effect of periphyton-grazing by three epifaunal species on the growth of *Zostera marina* L. under experimental conditions. *Aquat. Bot.* 22: 83-88.
- Howard-Williams C. and B.R. Davies, 1978. The influence of periphyton on the surface structure of a *Potamogeton pectinatus* L. leaf (an hypothesis). *Aquat. Bot.* 5: 87-91.
- Hunter R.D., 1980. Effects of grazing on the quantity and quality of freshwater aufwuchs. *Hydrobiologia* 69: 251-259.
- Hurlbert S.H., 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54: 187-211.
- Jenkerson C.G. and M. Hickman, 1986. Interrelationships between the epipelton, epiphyton and phytoplankton in a eutrophic lake. *Int. Revue Ges. Hydrobiol.* 71: 557-579.
- Kairesalo T., 1983. Photosynthesis and respiration within an *Equisetum fluviatile* L. stand in Lake Pääjärvi southern Finland. *Arch. Hydrobiol.* 96: 317-328.
- Kairesalo T., 1984. The seasonal succession of epiphytic communities within an *Equisetum fluviatile* L. stand in Lake Pääjärvi, Southern Finland. *Int. Revue Ges. Hydrobiol.* 69: 475-505.
- Kirk J.T.O., 1983. Light and photosynthesis in aquatic ecosystems. Cambridge University Press, Cambridge, 401 pp.
- Losee R.F. and R.G. Wetzel, 1983. Selective light attenuation by the periphyton complex. In R.G. Wetzel (ed.): *Periphyton of freshwater ecosystems*. Dr W. Junk Publishers, The Hague, p. 89-96.
- Mason C.F. and R.J. Bryant, 1975. Periphyton production and grazing by chironomids in Iderfen Broad, Norfolk. *Freshw. Biol.* 5: 271-277.
- Meier P.G., D. O'Connor and D. Dilks, 1983. Artificial substrata for reducing periphytic variability on replicated samples. In R.G. Wetzel (ed.): *Periphyton of freshwater ecosystems*. Dr W. Junk Publishers, The Hague, p. 283-286.
- Meulemans J.T. and F. Heinis, 1983. Biomass and production of periphyton attached to dead reed stems in Lake Maarsseveen. In R.G. Wetzel (ed.): *Periphyton of freshwater ecosystems*. Dr W. Junk Publishers, The Hague, p. 169-173.
- Meulemans J.T. and P.J. Roos, 1985. Structure and architecture of the periphytic community on dead reed stems in Lake Maarsseveen. *Arch. Hydrobiol.* 102: 487-502.
- Meulemans J.T., 1988. Seasonal changes in biomass and production of periphyton growing upon reed in Lake Maarsseveen I. *Arch. Hydrobiol.* 112: 21-42.

- Meulemans J.T., 1989. Reed and periphyton in Lake Maarsseveen I, structural and functional aspects. Thesis, University of Amsterdam, The Netherlands, 129 pp.
- Moed J.R. and G.M. Hallegraeff, 1978. Some problems in the estimation of chlorophyll-a and pheopigments from pre- and post-acidification spectrophotometric measurements. *Int. Revue Ges. Hydrobiol.* 63: 787-800.
- Moss B., 1981. The composition and ecology of periphyton communities in freshwaters. II. inter-relationships between water chemistry, phytoplankton populations and periphyton populations in a shallow lake and associated experimental reservoirs ('Lund tubes'). *Br. Phycol. J.* 16: 59-76.
- Munn D.J., L.L. Osborne and M.J. Wiley, 1989. Factors influencing periphyton growth in agricultural streams of central Illinois. *Hydrobiologia* 174: 89-97.
- Otten J.H. and M.T.M. Willemse, 1988. First steps to periphyton. *Arch. Hydrobiol.* 112: 127-195.
- Phillips G.L., D. Eminson and B. Moss, 1978. A mechanism to account for macrophyte decline in progressively eutrophicated freshwaters. *Aquat. Bot.* 4: 103-126.
- Roos P.J., 1983. Dynamics of periphytic communities. In R.G. Wetzel (ed.): *Periphyton of freshwater ecosystems*. Dr W. Junk Publishers, The Hague, p. 5-10.
- Sand-Jensen K., 1977. Effect of epiphytes on eelgrass photosynthesis. *Aquat. Bot.* 3: 55-63.
- Sand-Jensen K., 1983. Physical and chemical parameters regulating growth of periphytic communities. In R.G. Wetzel (ed.): *Periphyton of freshwater ecosystems*. Dr W. Junk publishers, The Hague, p. 89-96.
- Sand-Jensen K. and M. Søndergaard, 1981. Phytoplankton and epiphytic development and their shading effect on submerged macrophytes in lakes of different nutrient status. *Int. Revue Ges. Hydrobiol.* 66: 529-552.
- SAS Institute Inc., 1985. *SAS/STATtm Guide for personal computers*, version 6 Edition. SAS Institute Inc. Cary NC, 378 pp.
- Schiemer F. and M. Prosser, 1976. Distribution and biomass of submerged macrophytes in Neusiedlersee. *Aquat. Bot.* 2: 289-307.
- Sumner W.T. and C.D. McIntire, 1982. Grazer-periphyton interactions in laboratory streams. *Arch. Hydrobiol.* 93: 135-157.
- Takamura N., T. Iwakuma, M. Aizaki and M. Yasuno, 1990. Primary production of epiphytic algae and phytoplankton in the littoral zone of Lake Kasumigaura. *Marine Microbial Food Webs* 4: 239-255.
- Vermaat J.E. and M.J.M. Hootsmans, 1991. Periphyton dynamics in a temperature-light gradient. In W. van Vierssen, M.J.M. Hootsmans and J.E. Vermaat (eds.): *Dynamics of a macrophyte dominated freshwater ecosystem under eutrophication stress, an integrated approach* (in prep).
- Vernon L.P., 1960. Spectrophotometric determination of chlorophylls and pheophytins in plant extracts. *Analytic Chemistry* 32: 1144-1150.
- Wetzel R.G., 1983. Opening remarks. In R.G. Wetzel (ed.): *Periphyton of freshwater ecosystems*. Dr W. Junk Publishers, The Hague, p. 3-4.

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Survival of a *Potamogeton pectinatus* L. population under various light conditions in a shallow eutrophic lake (Lake Veluwe) in The Netherlands

with Wim van Vierssen

Abstract

In Lake Veluwe, an eutrophicated shallow lake in the Netherlands, light conditions significantly affected the total biomass production of a *Potamogeton pectinatus* L. vegetation. A negative correlation was recorded between the annual biomass production and the mean daily photon flux densities in an experimental setup, in which the photon flux densities were experimentally manipulated (four different levels of artificial shading) and the photoperiod was relatively unaffected. At the lowest mean photon flux density, the maximum total biomass was reached earlier in the growing season (end of June) than at the other photon flux densities (mid August). Tuber production started at the same time in all conditions (mid June). The number of tubers produced per gram ash-free dry weight of aboveground biomass was highest for the conditions with the lowest mean daily photon flux density. However, the total number of tubers per m² recorded at the end of the growing season was highest for the control (no artificial shading).

It is concluded that tuber initiation occurs under long-day conditions and is not controlled by mean daily photon flux densities. Tuber growth is clearly related to differences in daily photosynthetic periods. Tubers compete with aboveground biomass for photosynthate. At the highest level of shading, the photosynthetic tissue was ultimately unable to sustain tuber growth, and as a consequence, net growth of the vegetation ceased. Regarding tuber numbers of *P. pectinatus* in late summer, it is concluded that the size of the tuber bank was negatively affected by shade in the experiments.

Introduction

Over the last decades, a marked decline in the abundance of submerged aquatic macrophytes has been recorded in eutrophic aquatic ecosystems (Jupp and Spence, 1977; Phillips *et al.*, 1978). There is ample evidence that much of this decline can be attributed to cultural eutrophication (Phillips *et al.*, 1978). The gradual increase in nutrient levels has clearly promoted the growth of phytoplanktonic and epiphytic algae. It is possible that this increase in algal production eventually affects the growth of the macrophytes because light has become a growth-limiting factor (Sand-Jensen and Søndergaard, 1981; Jones *et al.*, 1983). Concurrently, the gas exchange between the leaves and the ambient water is likely to be hampered due to the presence of an abundant epiphytic community (Sand-Jensen, 1977). Allelopathic interactions between planktonic algae and macrophytes may also be involved (Van Vierssen and Prins, 1985).

Several studies have reported these mechanisms to provide a logical explanation for most of the cases in which macrophytes disappeared after eutrophication (Moss, 1976; Phillips *et al.*, 1978; Kemp *et al.*, 1983; Twilley *et al.*, 1985).

However, these mechanisms can only satisfactorily explain the complete disappearance of a vegetation in those cases where the light levels drop below the light compensation point (LCP). In general, an increase in attenuation will result in lower growth rates and, as a consequence, in a lower biomass, but as long as the amount of photosynthetically active radiation (PAR) exceeds the LCP, net growth should occur. However, the population dynamics of aquatic macrophytes do not only depend on growth rates. Many species have to survive periods unsuitable for vegetative growth each year. The life cycle of many macrophytes is characterized by the annual production of either generative (seeds) or vegetative (tubers or turions) propagules to survive such periods. In the temperate climatic zone this is usually the winter period. For that reason, the annual regeneration of the biomass also largely depends on the number and quality of the propagules being produced (Van Vierssen, 1990). Therefore, the question can be raised whether the recorded decline in the biomass of macrophytes in eutrophic and turbid ecosystems can be entirely attributed to the relatively low availability of light. Considering the life cycle and survival mechanisms of aquatic macrophytes may be equally important in evaluating the causes of their decline.

Lake Veluwe, a manmade, shallow eutrophic lake in the central part of the Netherlands (3240 ha, mean depth 1.15 m in summer) used to be a macrophyte-dominated lake. Due to strong eutrophication, the lake system gradually became dominated by cyanobacteria (*Oscillatoria agardhii* Gom.) during the 1970s (Berger and Bij de Vaate, 1983). As a consequence, macrophytes disappeared almost completely.

In recent years, the water quality has improved considerably because of a reduction in the external phosphorus load and through regular flushing of the lake (Hosper, 1984), resulting in a lower phytoplankton biomass. The macrophytic vegetation is slowly recovering, and *Potamogeton pectinatus* L. is the dominant macrophyte at present. A long-term (three years) shading experiment was conducted in Lake Veluwe during the period 1986-1988. Various levels of phytoplanktonic biomass were simulated by artificially shading the *P. pectinatus* stands. This reduced the mean daily photon flux density.

The present paper discusses some of the results of this long-term experiment, in particular the effects of low light levels on the biomass, the life cycle and the survival mechanisms of a *P. pectinatus* population based on the data collected in 1986.

Materials and methods

In Lake Veluwe (latitude 52° 20'), four different light conditions were created by artificially shading an existing, homogeneous vegetation of *P. pectinatus*. Various levels of phytoplanktonic biomass were simulated in this way and the mean daily photon flux density available for the macrophytes was reduced. In the lake 12 areas (10*10 m each) were marked out by a scaffolding framework. These 12 areas represented four different light conditions, each with three replicates. In April 1986, nets (Agroflor) were positioned above nine of these areas in such a way, that they represented three levels of shading (levels 2-4), reducing the incident light by 26%, 45% and 73%, respectively. The three remaining areas served as controls (level 1, no shading). To characterize the various light conditions for the four shading levels, these differences were quantified. Using the calculated amount of incident PAR on 21 June (Kirk, 1983), the photoperiod at various light levels was calculated for the various levels of shading.

The various areas were sampled at regular intervals (*ca.* two weeks). Four replicate samples were collected in each area.

The plants from 0.16 m² of the bottom of the lake were excavated to a depth of 0.30 m to include all the rhizomes, roots and tubers. The samples were sieved (mesh width 2 mm), and plants were collected, cleaned and separated into aboveground parts (comprising leaves, stems, flowers and fruits), belowground parts (rhizomes and roots) and tubers. The tubers were counted and a distinction was made between tubers produced in 1986 (light brown colour) and those from the perennial tuber bank (dark colour, produced before 1986). After sorting the samples, the material was dried to constant weight (24h, 105 °C). The ash-free dry weight (AFDW) was calculated after combustion at 550 °C (4 h). Samples were taken from 13 May until 3 November.

The data were analyzed using a two-way analysis of variance, followed by means comparisons using Tukey's HSD procedure (for equal cell sizes) or the Least Squares Means procedure (for unequal cell sizes; SAS Institute, 1982). Prior to this analysis, the data were tested for normality (SAS Institute, 1982) and homogeneity of variance (Bartlett). In some cases, data sets were arcsin $\sqrt{}$ -transformed (ratios). A weighted GLM was carried out in cases where the untransformed and arcsin $\sqrt{}$ -transformed data did not meet the required terms.

Results

In Fig. 1 the theoretical relationship between a photon flux density level and the daylength for that particular level is given for the various levels of shading. From this figure, it can be concluded that the daylength at low photon flux densities is hardly affected by the level of shading and is about 16.5 hours. However, an increasing level of shading considerably shortens the daylength at relatively high photon flux densities. Statistical tests revealed no significant differences among the biomass data from the replicate scaffolding frameworks. This confirmed the earlier observation that the stands of *P. pectinatus* were homogeneous. Therefore, the data from the various frameworks were lumped for each level of shading for further statistical analysis. The annual variation in mean total biomass and in the relative distribution of biomass over different plant parts of *P. pectinatus* at the various levels of shading is given in

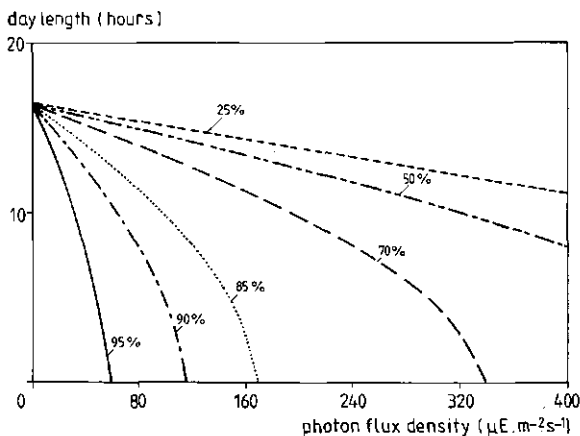


Fig. 1. Daylength at various photon flux densities ($\mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$) and different levels of shading (21 June) for Lake Veluwe.

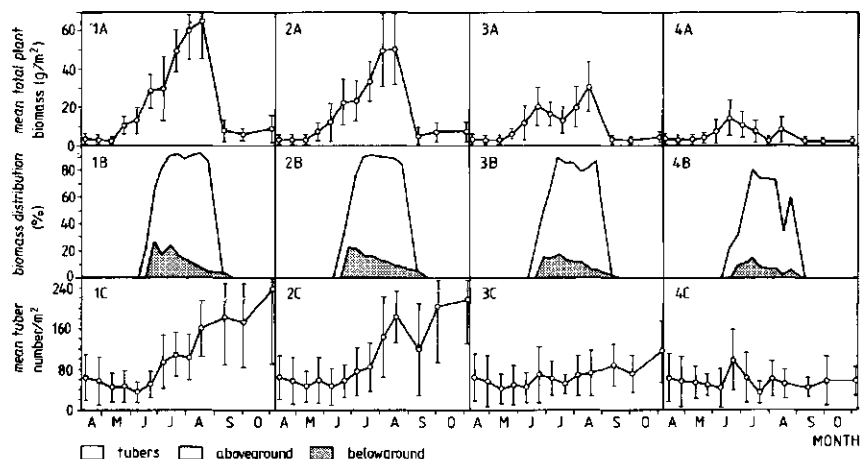


Fig. 2. Annual variation in mean total biomass (Series A), relative distribution of biomass over different plant parts (Series B), and number of tubers (Series C) of a *P. pectinatus* vegetation in Lake Veluwe under various light conditions (numbered from 1 to 4, for explanation see text). Bars indicate standard deviation of 12 replicates.

Fig. 2 (Series A and B) respectively. It is apparent that *P. pectinatus* behaves as an annual considering its aboveground biomass. Aboveground biomass was present only from April until September. From September on, only tubers were found. In the control (level 1) and at the two lowest levels of shading (levels 2 and 3), maximum total biomass was reached in mid August. At the highest level of shading (level 4), this occurred much earlier, towards the end of June. Thus, the maximum total plant biomass for the various light conditions was in general negatively correlated with the level of shading (Table 1). At the beginning of June, tuber biomass accounted for about 10% (6-24%) of the total plant biomass. This percentage was not significantly affected by the level of shading. On 23 June, when the biomass at level 4 (highest level of shading) reached its maximum, the contribution of the tuber biomass to the total plant biomass at this shading level was significantly higher than that at the other light levels (Table 1). From that date on, the aboveground biomass at the highest shading level started to decay, which is why the contribution of the tuber biomass to the total plant biomass remained highest under these conditions (Table 1). In Fig. 2 (Series C), the annual variation in the number of tubers per m² for the various levels of shading is visualized. Initially, during the first few months of the growing season, a significant decrease in numbers occurred. This decrease reflects the decay of a certain fraction of the hibernated tuber bank. On 23 June, the first newly

Table 1: Summary of some characteristics of a *P. pectinatus* vegetation in Lake Veluwe under various light conditions. Identical lettering indicates that means do not differ significantly ($p < 0.05$) between the various light conditions for every dependent variable and for 23 June and 18 August separately.

Dependent variable	Shading level	Means (\pm SE, N), 23 June		pairwise comparison of means 18 August			
Total biomass (g AFDW.m ⁻²)	1	29.0	(\pm 2.9,12)	A	65.8	(\pm 6.1,12)	A
	2	22.9	(\pm 3.5,12)	AB	50.8	(\pm 5.3,12)	AB
	3	20.4	(\pm 3.0,12)	AB	30.8	(\pm 3.9,12)	B
	4	14.3	(\pm 2.5,12)	B	7.8	(\pm 1.8,12)	C
Contribution of tubers to total biomass (%)	1	6.4	(\pm 1.5,12)	A	11.8	(\pm 1.9,12)	A
	2	7.7	(\pm 1.9,12)	A	14.1	(\pm 1.7,12)	A
	3	14.2	(\pm 3.1,12)	A	12.8	(\pm 2.5,12)	A
	4	24.2	(\pm 3.1,12)	B	38.2	(\pm 10.6,12)	B
Mean number of tubers per m ²	1	50	(\pm 8, 12)	A	161	(\pm 17, 12)	A
	2	56	(\pm 9, 12)	A	183	(\pm 16, 12)	A
	3	70	(\pm 15, 12)	A	72	(\pm 13, 12)	B
	4	98	(\pm 18, 12)	B	51	(\pm 8, 12)	B
Number of tu- ber per g AFDW aboveground biomass	1	2.9	(\pm 0.6,12)	A	3.5	(\pm 0.6,12)	A
	2	4.0	(\pm 0.8,12)	A	5.3	(\pm 0.8,12)	A
	3	6.0	(\pm 1.8,12)	AB	3.1	(\pm 0.5,12)	A
	4	11.8	(\pm 1.8,12)	B	-*	-	-
Number of tu- bers per g AFDW belowground biomass	1	32.4	(\pm 21.4,12)	A	55.4	(\pm 8.8,12)	A
	2	21.7	(\pm 5.7,12)	A	52.1	(\pm 5.5,12)	A
	3	44.6	(\pm 11.8,12)	AB	65.0	(\pm 15.5,11)	A
	4	115.0	(\pm 32.0,11)	B	-*	-	-

* Biomass was too low to calculate reliable means.

formed tubers were observed at all four light levels. Until 7 July, the number of tubers was not significantly affected by the treatments. From that date on, tuber numbers diverged significantly and a negative correlation was observed between shading level and tuber number.

On 18 August, when the mean biomass for the control (level 1) and the 2 lowest levels of shading (levels 2 and 3) reached its maximum, the number of tubers per m² was not significantly different between the control and level 2. The number of tubers in the control was significantly higher than at the two highest shading levels (levels 3 and 4). On 23 June, when the biomass at the highest shading level (level 4) reached its maximum, the number of tubers per m² was not significantly affected by the

treatments. However, the number of tubers per gram AFDW aboveground biomass showed some significant differences between the treatments (Table 1). The number at level 4 was significantly higher than those for the control and level 2, but it did not significantly differ from the number at level 3. These differences corresponded with differences in the number of tubers being produced per gram AFDW belowground biomass (Table 1). On 18 August, when the biomass at the levels 1, 2 and 3 reached its maximum, the number of tubers produced per gram AFDW aboveground biomass was not significantly affected by the level of shading, nor was the number produced per gram AFDW belowground biomass.

Discussion and conclusions

Under field conditions both an annual and a perennial life cycle has been observed in *P. pectinatus* by Van Wijk (1988). His results and the present data demonstrate that in Lake Veluwe, *P. pectinatus* shows an annual life cycle and that its annual biomass develops from hibernated tubers.

The various light regimes caused a significant difference in total biomass. It is striking that the time at which net growth ceased differed between the highest level of shading and the other experimental conditions. When biomass reached its maximum at the highest level of shading (June), this corresponded to the highest number of tubers per gram AFDW aboveground biomass found in this study. Moreover, at this shading level, maximum biomass was reached earlier in the season than at the other shading levels. This clearly suggests that the aboveground biomass is not able to sustain tuber growth and shoot growth at the same time under these conditions. The fact that aboveground plant growth stops could be interpreted as the result of too high a demand for photosynthate by the tubers.

Under all four experimental light conditions, *P. pectinatus* started to produce new tubers in mid June. This implies that the mean daily photon flux density does not influence the timing of tuberization.

In general, the production of tubers and turions is controlled by daylength (e.g. Weber and Noodén, 1976; Spencer and Anderson, 1987). The influence of the daylength is often associated with the role of the phytochrome system and photoperiodic responses in aquatic macrophytes (Chambers *et al.*, 1985). In the present study, we defined the photoperiod as the daily period with photon flux densities exceeding the lower sensitivity limit of the phytochrome system. Chatterton and Silvius (1979) used $10 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ as a limit in their definition of the photoperiod. Applying this limit to the present study, the photoperiod at all shading levels exceeded 15 hours during the

period June to mid July. This means that tuber initiation occurred under long-day conditions.

The relative tuber mass produced in *P. pectinatus* in the experiments by Spencer and Anderson (1987) at the most effective photoperiod (10 hours) was 30% of the total plant biomass. In the present study this was 25% at the highest level of shading. This shows that for the long photoperiods in Lake Veluwe, tuber production was almost as high. On 23 June, the relative contribution of tubers to the total plant biomass was highest at the highest levels of shading. This implies that the allocation of carbohydrates to the tubers is affected by the shading. As the experimental photoperiod was hardly affected by the levels of shading, we suggest that the allocation involves no phytochrome-related response, but a response related to the photon flux density at mean levels of photosynthesis. Chatterton and Silvius (1979) defined a photosynthetic period as the period during which irradiance levels were high enough to sustain net photosynthesis. *P. pectinatus* has a LCP of approximately $40 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ and a light saturation level of approximately $400 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ (G.M. van Dijk and W. van Vierssen, unpublished data). At these light levels, the photosynthetic period was considerably affected by shading. Obviously, for the same photoperiod, shortening the photosynthetic period (daily period with relatively high photon flux densities) has positive effects on tuber growth. This observation agrees with results of Gray and Holmes (1970), who recorded an increase in tuber numbers and yield of potatoes associated with short intermediate periods of shading.

The present data show that for long photoperiods tuber production in Lake Veluwe was as high as that in experiments in which short photoperiods were optimal (Spencer and Anderson, 1987). By the time the photoperiod had changed in Lake Veluwe because days became shorter (August), most of the plants were already starting to decay, which is why no data are available on tuber production in *P. pectinatus* at short photoperiods in the field.

It is concluded that *P. pectinatus* responds to shading by increasing its allocation of available carbohydrate to the tubers. Whether this mechanism is an adequate response for surviving environmental stresses, such as low light availability, largely depends on how long the aboveground biomass can sustain tuber production. From the present study, it is evident that the highest level of shading in the experiments is not optimal for the survival of the population, in view of the number of tubers per m^2 at the end of the growing season and assuming that the production of high numbers of tubers is advantageous for the survival of the population. As a consequence, it must be concluded that the simulated turbid water conditions in the experiments were sub-optimal. The stimulus for tuber production was highest at the highest level of shading, but the resulting number of tubers at the end of the growing season was lower than

for the control because tuber production already stopped in early summer. This means that the optimal response of *P. pectinatus* with respect to tuber production probably occurs under less turbid conditions, most likely even less turbid than the control conditions in the experiments discussed here.

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References

- Berger C. and A. Bij de Vaate, 1983. Limnological studies on the eutrophication of Lake Wolderwijd. A shallow hypertrophic *Oscillatoria* dominated lake in The Netherlands. Schweiz. Z. Hydrol. 45: 458-479.
- Chambers P.A., D.H.N. Spence and D.C. Weeks, 1985. Photocontrol of turion formation by *Potamogeton crispus* L. in the laboratory and natural water. New Phytol. 99: 183-194.
- Chatterton N.J. and J.E. Silvius, 1979. Photosynthate partitioning into starch in soybean leaves. I. Effects of photoperiod versus photosynthetic period duration. Plant Physiol. 64: 749-753.
- Gray D. and J.C. Holmes, 1970. The effect of short periods of shading at different stages of growth on the development of tuber number and yield. Potato Res. 13: 215-219.
- Hosper S.H., 1984. Restoration of Lake Veluwe, The Netherlands, by reduction of phosphorus loading and flushing. Wat. Sci. Tech., 17: 757-768.
- Jones R.C., K. Walti and M.S. Adams, 1983. Phytoplankton as a factor in decline of the submersed macrophyte *Myriophyllum spicatum* L. in Lake Wingra, Wisconsin. Hydrobiologia 107: 213-219.
- Jupp B.P. and D.H.N. Spence, 1977. Limitations on macrophytes in a eutrophic lake, Loch Leven. J. Ecol. 65: 175-186.
- Kirk J.T.O., 1983. Light and photosynthesis in aquatic ecosystems. Cambridge University Press, Cambridge, 401 pp.
- Kemp W.M., W.R. Boynton, R.R. Twilley, J.C. Stevenson and J. Means, 1983. The decline of submerged vascular plants in upper Chesapeake Bay: summary of results concerning possible causes. Mar. Sci. Tech. 17: 78-89.
- Moss B., 1976. The effects of fertilization and fish on community structure and biomass of aquatic macrophytes and epiphytic algal populations: an ecosystem experiment. J. Ecol. 64: 313-342.

- Phillips G.L., D. Eminson and B. Moss, 1978. A mechanism to account for macrophyte decline in progressively eutrophicated freshwaters. *Aquat. Bot.* 4: 103-126.
- Sand-Jensen K., 1977. Effect of epiphytes on eelgrass photosynthesis. *Aquat. Bot.* 3:55-63.
- Sand-Jensen K. and M. Søndergaard, 1981. Phytoplankton and epiphyte development and their shading effect on submerged macrophytes in lakes of different nutrient status. *Int. Revue Ges. Hydrobiol.* 66: 529-552.
- SAS Institute, 1982. *SAS User's Guide: Statistics*. SAS Institute, Cary NC, 923 pp.
- Spencer D.F. and L.W.J. Anderson, 1987. Influence of photoperiod on growth, pigment and vegetative propagule formation for *Potamogeton nodosus* Poir. and *Potamogeton pectinatus* L. *Aquat. Bot.* 28: 103-112.
- Twilley R.R., W.M. Kemp, K.W. Staver, J.C. Stevenson and W.R. Boynton, 1985. Nutrient enrichment of estuarine submersed vascular plant communities. 1. Algal growth and effects on production of plants and associated communities. *Mar. Ecol.* 23: 179-191.
- Van Vierssen W., 1990. Relationships between survival strategies of aquatic weeds and control measures. In A.H. Pieterse and K.J. Murphy (eds): *Aquatic Weeds*. Oxford University Press, Oxford, p. 238-253.
- Van Vierssen W. and Th.C. Prins, 1985. On the relationship between the growth of algae and aquatic macrophytes in brackish water. *Aquat. Bot.* 21: 165-179.
- Van Wijk R.J., 1988. Ecological studies on *Potamogeton pectinatus* L. I. General characteristics, biomass production and life cycles under field conditions. *Aquat. Bot.* 31: 211-258.
- Weber J.A. and L.D. Noodén, 1976. Environmental and hormonal control of turion formation in *Myriophyllum verticillatum*. *Plant Cell Physiol.* 17: 721-731.

Impact of light climate history on seasonal dynamics of a field population of *Potamogeton pectinatus* L. during a three-year period (1986-1988).

with André W. Breukelaar and Ronald Gijlstra

Abstract

The impact of light climate during the growing season and light climate history on the growth and survival of a *Potamogeton pectinatus* L. population has been studied in a eutrophic shallow lake, Lake Veluwe (The Netherlands), during the period 1986-1988. Four light conditions were created in an experimental setup by manipulating the photon flux density using artificial shading (three levels of shading and one control situation without shading), during the growing season of 1986. Part of the *P. pectinatus* vegetation in the experimental setup was shaded in the same way as in 1986 while another part was not during the growing season of 1987. No artificial shading was applied at all during the growing season of 1988.

Growth conditions for *P. pectinatus* were less favourable in 1987 than in 1986. On the whole, above- and belowground biomass were lower, the growing season was shorter, maximum aboveground biomass was lower and was reached earlier in the season, and net tuber production was lower in 1987 than in 1986 in the control situations. In both years, the above- and belowground biomass were lower, the growing season was shorter and maximum aboveground biomass was lower with higher shading. The impact of shading on relative aboveground biomass development was similar in 1986 and 1987, whereas, the impact of shading on relative tuber bank size at maximum aboveground biomass was more pronounced in 1987 than in 1986 in the experimental areas which were shaded both seasons. In both years, mean individual tuber AFDW was lowest at highest shading.

It is concluded that light climate is a dominant factor in controlling the biomass and tuber bank dynamics of a *P. pectinatus* population in Lake Veluwe. Additionally, water quality and meteorological characteristics are involved as well. At the highest shading, the photosynthetic tissue was able to sustain tuber growth and maintenance of the vegetation during a relatively short period only. As a consequence, the vegetation sloughed early in the growing season and the tuber bank size was smallest. The maximum aboveground biomass was positively correlated with the size of the hibernated tuber bank. Henceforth, the biomass development in one season is at least

partly determined by the light conditions of the previous growing season(s) through the size of the hibernated tuber bank.

The Lake Veluwe vegetation has the potential to recuperate from negative shading effects on aboveground biomass and tuber bank size under field conditions. This may require more than one growing season, which depends on actual growth conditions and size of the hibernated tuber bank.

Introduction

The area occupied by and biomass of submerged macrophytes have declined markedly during the last decades in many northern temperate aquatic ecosystems. Generally, this phenomenon is ascribed to severe eutrophication (e.g. De Nie, 1987).

Unfavourable light conditions through attenuation by phytoplankton and epiphytic algae play a key role in explaining the observed dwindling in macrophyte stands in eutrophic water (e.g. Phillips *et al.*, 1978; Kemp *et al.*, 1983; Stansfield *et al.*, 1989).

The impact of light climate on the growth and survival of a *Potamogeton pectinatus* L. population has been studied in a field experiment in Lake Veluwe (The Netherlands), during the period 1986-1988. *P. pectinatus* performs an annual life cycle surviving the winter through vegetative propagules (tubers) in Lake Veluwe (Van Wijk, 1988; Chapter 4). In the previous Chapter, it was shown that lowering the photon flux density has a negative impact on biomass production and tuber bank size of *P. pectinatus* (Chapter 4).

Early growth of *P. pectinatus* plants is mainly supported by carbohydrate from their tubers (Hodgson, 1966) and the early growth rate of the sprouting plant is positively correlated with tuber weight (Ozimek *et al.*, 1986; Spencer, 1986; Vermaat and Hootsmans, 1991). Hence, not only the size of the tuber bank but also the individual tuber weight is important for survival of the *P. pectinatus* population.

The main objectives of the present paper are, firstly, to obtain insight into the impact of photon flux density on biomass and tuber bank dynamics of a *P. pectinatus* population during a subsequent year in which the photon flux density was manipulated, secondly, to assess the importance of the hibernated tuber bank as a controlling factor for biomass dynamics and survival of a *P. pectinatus* population, and thirdly, to describe the regeneration potential of a *P. pectinatus* population which had been shaded in the previous season(s) under Lake Veluwe conditions.

Materials and methods

Light climate treatments

Four light conditions were created by artificially shading a homogeneous vegetation of *P. pectinatus* in Lake Veluwe. Nets (Agroflor) were extended above the lake surface in nine enclosed experimental areas of $10 \times 10 \text{ m}^2$ each (April 1986). The whole experiment involved three replicates (referred to as Series I to III) each composed of four treatments, notably, a control without shading (referred to as level 1) and three levels of shading reducing the incident irradiance by 26%, 45% and 73%, respectively (referred to as levels 2 to 4; Fig. 1).

The experimental setup was removed mid November 1986 after the exact locations of the various experimental areas were precisely marked. Nets were positioned again above the lake surface in six of the nine enclosed experimental areas of 1986 of $10 \times 10 \text{ m}^2$ each in April 1987. In this way, the same four light conditions were created with two replicates each (Series I and II). The nets were positioned at exactly the same locations with the same shading levels as in 1986 (Fig. 1). The light conditions were not manipulated in the remaining four experimental areas which represented a control and level 2 to 4 in 1986 (Series III; Fig. 1). To distinguish the experimental areas differing in light climate history in Series III, they are indicated by the level of shading by which they were treated in 1986 (experimental area 1 to 4).

The experimental setup was removed mid November 1987 after the exact locations of the various experimental areas were precisely marked. The various experimental areas were staked at exactly the same locations in April 1988, but the light conditions were not manipulated (Fig. 1). Thus, we can distinguish Series I and II which were shaded during the growing seasons of 1987 and 1986 and Series III which was shaded only during the growing season of 1986. The various experimental areas differing in light climate history are referred to by their Series number and by the level of shading to which they belonged in 1986 (1 to 4, respectively).

Each experimental area was divided in 100 numbered quadrates of 1 m^2 . The quadrates were randomized per sampling date and over the replicate treatments for the entire sampling period before the first sampling in 1986, so that each quadrat was sampled only once during the entire study.

Vegetation analyses

The vegetation in the experimental areas of Series I, II and III was sampled in four- or fivefold at intervals of two to three weeks in the period April-October 1986. The vegetation in the experimental areas of Series I and II was sampled in fivefold at intervals of three to five weeks, the vegetation in the experimental areas of Series III

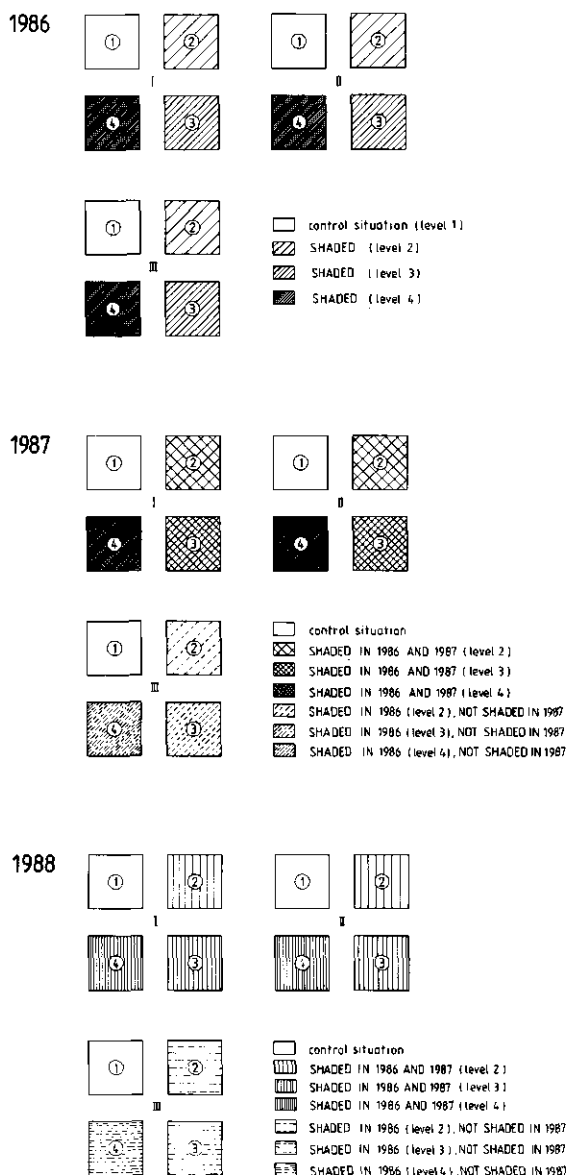


Fig. 1: Scheme of the experimental design in 1986 (top), 1987 (middle) and 1988 (bottom). The various patterns represent the various treatments and light climate histories. Number 1 to 4 represent the control (1) and the shading levels (2 to 4) in 1986. Numbers I to III represent various Series varying in light climate history: in Series I and II light climate was manipulated in 1986 and 1987, in Series III light climate was manipulated only in 1986.

in tenfold at intervals of four to eight weeks in the period April-October 1987. During the growing season of 1988, the vegetation in the experimental areas of Series I and II was sampled in fivefold in April and in July and of Series III only once in tenfold in July.

One subsample measured 0.16 m² of the bottom of the lake and was excavated to a depth of 0.30 m to include all the rhizomes, roots, and tubers. The subsamples were sieved (mesh width 2 mm), plant parts were collected, cleaned and separated into aboveground parts (including leaves, stems, flowers, and fruits), belowground parts (including rhizomes and roots) and tubers. The above- as well as the belowground plant parts and the tubers were dried to constant weight (24h, 105 °C) for ash-free dry weight (AFDW) determinations. AFDW was calculated after combustion at 550 °C (4 h) as the difference between dry weight (DW) and ash weight (AW).

The tubers were counted. A distinction was made between tubers which had recently germinated and tubers which had not. Germination was indicated by any elongation of the shoot, or appearance of a root. Germinated tubers were excluded from the tuber bank. It is assumed that the number of not germinated tubers found in the sediment equalled the tuber bank size because *P. pectinatus* tubers when visually in good shape are still viable. Individual tuber AFDW of the tubers in the tuber bank was measured in 1986 and 1987. Mean individual tuber AFDW was calculated as the grand mean of the means of all subsamples per experimental area.

No individual tuber determinations were conducted on subsamples collected in 1988. Tubers were counted and total tuber AFDW was determined per subsample in 1988.

Calculations and statistical analyses

The data of 1986 showed a marked similarity in seasonal variation in aboveground biomass and tuber bank size in Series I, II and III per treatment and no systematic pattern could be recognized in the distribution of the standard deviation over the distinct areas. The same held for Series I and II in 1987. These observations confirmed the earlier assumption that the selected *P. pectinatus* stands were more or less homogeneously distributed in the experimental setup.

The subsamples per experimental area were not independent (Hurlbert, 1984). The treatments shaded in 1987 and not shaded in 1988 (Series I and II) were only duplicated, and the treatments not shaded in 1987 and not shaded in 1988 (Series III) were not replicated. Consequently, an analysis of variance could not be applied in a proper way (Day and Quinn, 1989).

Differences between experimental areas in biomass and individual tuber characteristics were tested per Series by means comparisons using Tukey's HSD procedure (for equal cell sizes) or the Least Square Means procedure (for unequal cell sizes; SAS Institute Inc., 1985). Prior to these latter analyses the datasets were

checked for homogeneity of variance by plotting the means of the subsamples against percentage of shading. A \log_{10} transformation was carried out in cases in which the data were suspected to be inhomogeneous. The transformed datasets suggested homogeneity of variance in all datasets. Outliers with a value of more than four times the standard deviation of the mean were not observed.

Differences in variables between 1986 and 1987 per experimental area and per Series were tested by a Student's t-Test (Sokal and Rohlf, 1981).

The relative frequency distribution over distinct weight classes of tubers in the tuber bank was calculated per treatment after pooling the subsamples of the replicate experimental areas of 1986 and 1987. The Kolmogorov-Smirnov Two-Sample Test (Sokal and Rohlf, 1981) has been applied for studying differences in the frequency distributions between treatments.

Differences were judged to be significant if the probability of the appropriate statistic was <0.05 .

The hibernated tuber bank size has been estimated as the total number of tubers, including the germinated tubers, found in the sediment on the first sampling date of the growing season. The maximum aboveground biomass observed has been used to indicate aboveground biomass development.

Results

*Biomass and tuber bank dynamics of a *P. pectinatus* population in the control situations in 1986 and 1987*

Biomass and tuber bank dynamics of a *P. pectinatus* population showed marked differences between the growing seasons of 1986 and 1987 in the control situations. On the whole, above- and belowground biomass observed were lower in 1987 than in 1986 (Figs. 2 and 3). The maximum aboveground biomass of *P. pectinatus* was significantly lower and was reached much earlier in the season in 1987 than in 1986 (Table 1). Furthermore, aboveground biomass was observed from May until mid August in 1986 and only from May until July in 1987 (Fig. 2).

The yearly variation in tuber bank size showed considerable differences between the sampling periods in 1986 and 1987 (Fig. 4). The tuber bank size increased significantly during the summer 1986 and it did not change significantly during the summer 1987. It decreased substantially in the winter 1986/1987, and it remained the same in the winter 1987/1988 in the control situations (Table 2).

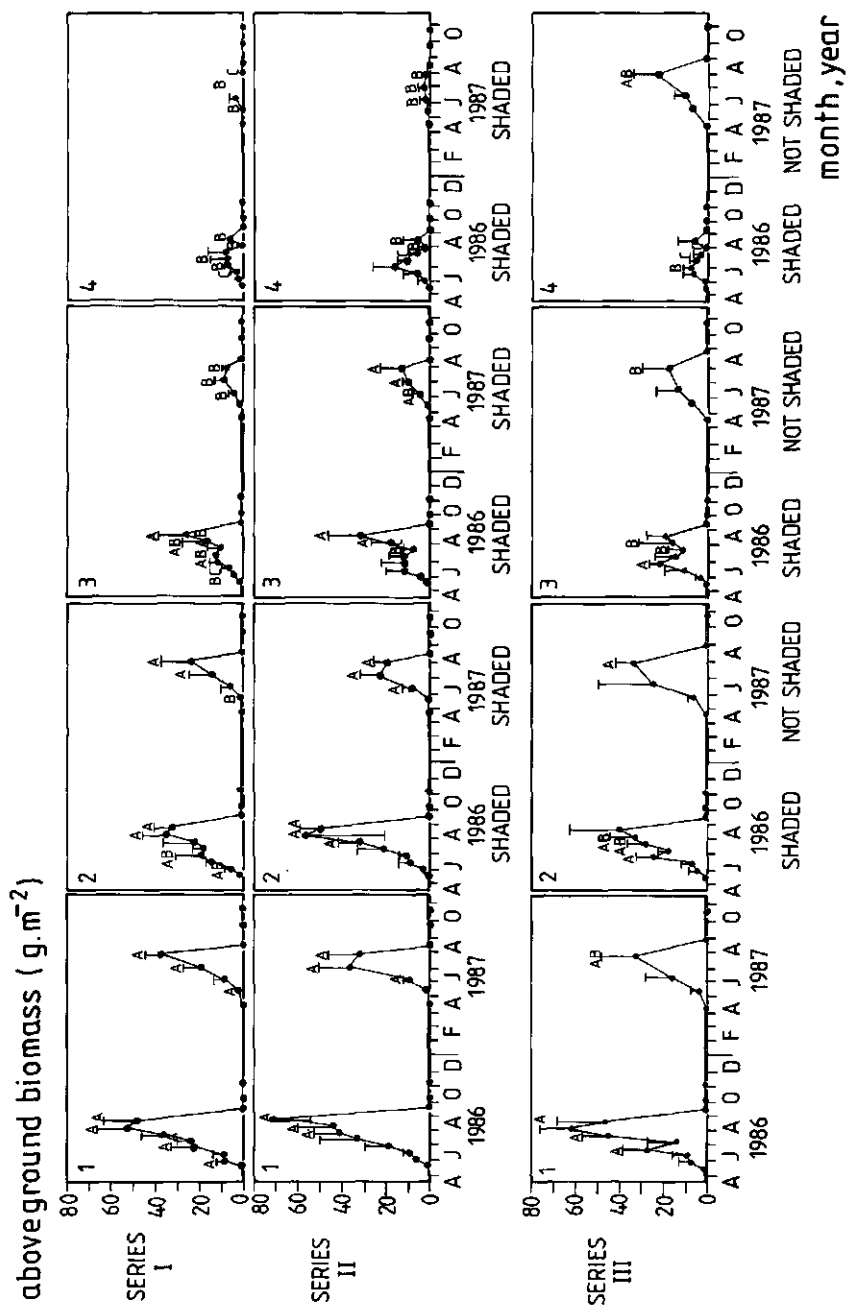


Fig. 2: Seasonal variation in mean aboveground biomass of *P. pectinatus* and standard deviation of the mean of the subsamples, in the control (I) and at treatments (2 to 4) in Series I (top), II (middle) and III (bottom) during the growing season of 1986 and 1987. Means with the same lettering are not significantly different per sampling date and per Series.

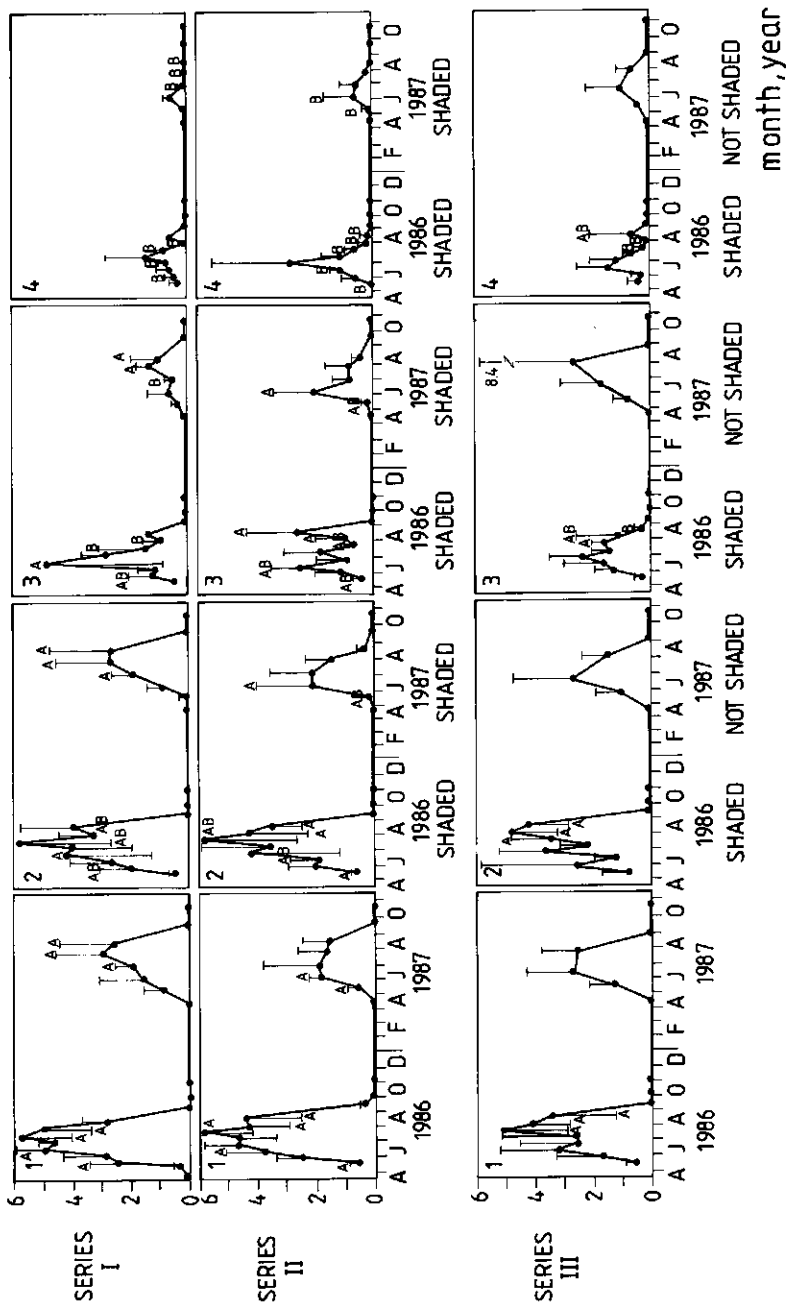
belowground biomass ($\text{g} \cdot \text{m}^{-2}$)

Fig. 3: Seasonal variation in mean belowground biomass of *P. pectinatus* and standard deviation of the mean of the subsamples, in the control (1) and at treatments (2 to 4) in Series I (top), II (middle) and III (bottom) during the growing season of 1986 and 1987. Means with the same lettering are not significantly different per sampling date and per Series.

Table 1: Mean maximum aboveground biomass and standard deviation (\pm SD) of N subsamples of a *P. pectinatus* vegetation in Lake Veluwe in the control situation (1) and experimental areas 2 to 4 differing in shading level of Series I, II and III in 1986 and of Series I and II, and the control of Series III in 1987. Means indicated with the same lettering are not significantly different per Series and per year. The sampling date on which maximum aboveground biomass was observed and the t-statistic of Student's t-Test comparing the means of 1986 and 1987 is given per experimental area. Significant t-values are indicated by an *.

Variable	Area	1986			1987					
	Mean	±SD	N	Date	Mean	±SD	N	Date	t	
Series I										
Maximum	1	52.6 ^A	±14.0	4	4-Aug	37.1 ^A	± 6.8	5	27-Jul	1.919*
abovegr.	2	34.7 ^A	±10.8	4	4-Aug	23.1 ^{AB}	±13.7	5	27-Jul	1.221
biomass	3	25.2 ^A	±12.1	4	18-Aug	8.1 ^B	± 4.2	5	30-Jun	2.598*
(g.m ⁻²)	4	7.6 ^B	± 7.7	4	21-Jul	7.6 ^C	±16.0	5	5-Jun	0.000
Series II										
Maximum	1	71.3 ^A	±15.3	4	18-Aug	36.5 ^A	±13.9	5	30-Jun	3.147*
abovegr.	2	56.3 ^{AB}	±26.0	4	4-Aug	22.7 ^A	± 8.8	5	30-Jun	2.384*
biomass	3	31.2 ^{BC}	±14.7	4	18-Aug	12.7 ^A	±10.0	5	30-Jun	1.975*
(g.m ⁻²)	4	15.1 ^C	±10.6	4	23-Jun	2.3 ^B	± 2.5	5	30-Jun	2.303*
Series III										
Maximum	1	61.6 ^A	±14.4	4	4-Aug	31.9 ^{AB}	±16.0	10	27-Jul	2.987*
abovegr.	2	39.4 ^A	±22.6	4	18-Aug	33.3 ^A	± 7.9	10	27-Jul	-
biomass	3	21.4 ^A	± 4.4	4	23-Jun	17.6 ^B	±11.8	10	27-Jul	-
(g.m ⁻²)	4	7.1 ^B	± 3.0	4	23-Jun	21.9 ^{AB}	±11.6	10	27-Jul	-

About 45% of the tubers found in the sediment had germinated in the control situations on the first sampling date in 1986 (29 April) and 1987 (15 April). Germination was restricted to the beginning of the growing season (Table 3). About 50 and 100 tubers.m⁻² remained dormant during the growing seasons of 1986 and 1987, respectively (Fig. 4).

Mean individual tuber AFDW was higher in 1986 than in 1987 in the control situations at maximum aboveground biomass (shown significantly only in Series II) (Table 4).

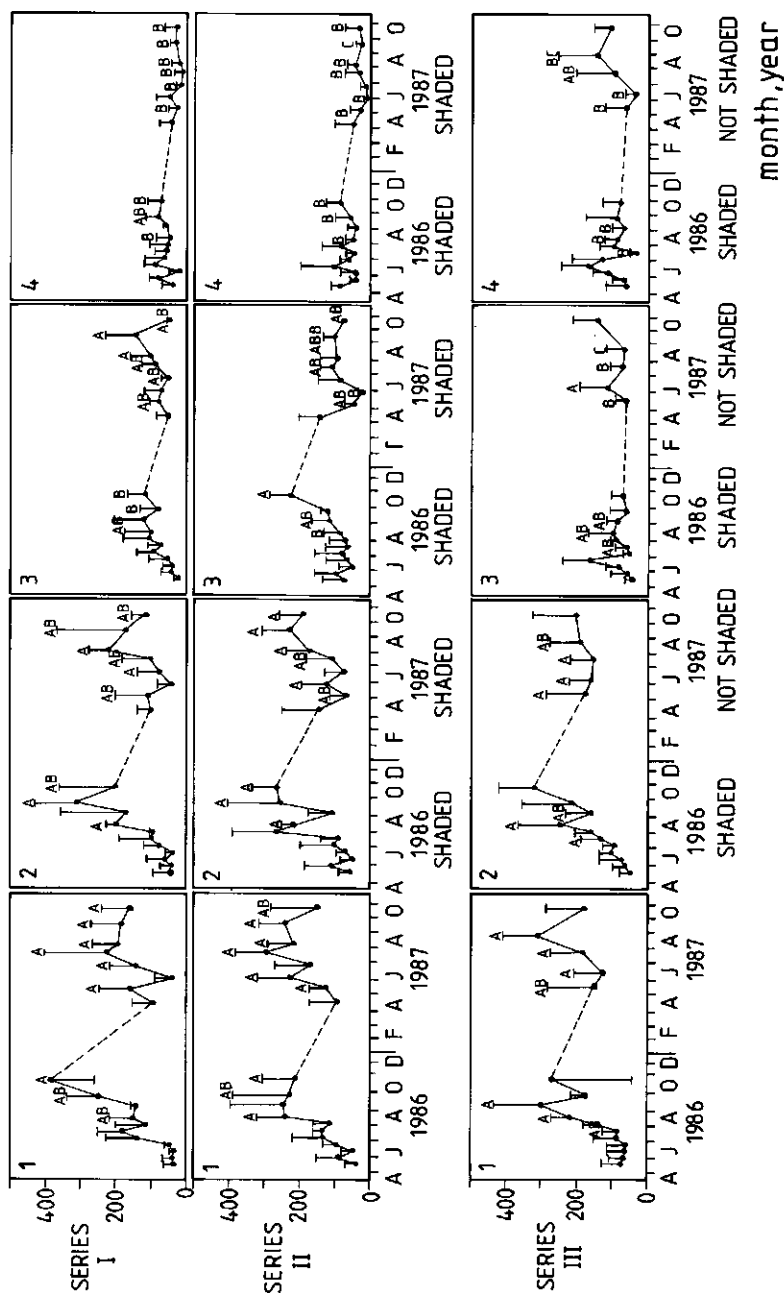
tuber bank size (number $\cdot m^{-2}$)

Fig. 4: Seasonal variation in mean tuber bank size of *P. pectinatus* and standard deviation of the mean of the subsamples, in the control (1) and at various treatments (2 to 4) in Series I (top), II (middle) and III (bottom) during the growing season of 1986 and 1987. Means with the same lettering are not significantly different per sampling date and per Series.

Table 2: Mean size of tuber bank estimated as the total number of tubers found in the sediment and standard deviation (\pm SD) of N subsamples, in autumn 1986 (3 November), and autumn 1987 (29 October) and size of the hibernated tuber bank in spring 1986 (end of April), 1987 (mid May) and 1988 (mid April), respectively in Series I to III in the experimental areas 1 to 4. Means indicated with the same lettering are not significantly different per Series and per sampling. The t-statistic of Student's t-Test comparing the means of spring and autumn 1986 (t_{1986}), autumn 1986 and spring 1987 ($t_{86/87}$), spring and autumn 1987 (t_{1987}) and autumn 1987 and spring 1988 ($t_{87/88}$), respectively, is given per experimental area. Significant t-values are indicated by an *.

1986		1987			1988			t_{1986}		$t_{86/87}$		t_{1987}		$t_{87/88}$	
Spring*		Autumn		Spring		Autumn		Spring		Autumn		Spring		Autumn	
Mean \pm SD	N	Mean \pm SD	N	Mean \pm SD	N	Mean \pm SD	N	Mean \pm SD	N	Mean \pm SD	N	Mean \pm SD	N	Mean \pm SD	N
Series I															
1 79 \pm 45	7	385 ^A \pm 129	4	191 ^A \pm 103	5	161 ^A \pm 79	5	170 ^A \pm 81	5	5.154*	5	2.212*	5	0.462	0.159
2 79 \pm 45	7	203 ^{AB} \pm 155	4	120 ^{AB} \pm 112	5	119 ^{AB} \pm 36	5	121 ^A \pm 45	5	1.787	5	0.821	5	0.017	0.069
3 79 \pm 45	7	120 ^B \pm 45	4	99 ^{AB} \pm 26	5	50 ^{AB} \pm 37	5	45 ^B \pm 30	5	1.315	5	0.773	5	2.167*	0.210
4 79 \pm 45	7	75 ^B \pm 37	4	35 ^B \pm 27	5	34 ^B \pm 32	5	13 ^B \pm 8	5	0.316	5	1.652	5	0.048	1.273
Series II															
1 79 \pm 45	7	211 ^A \pm 94	4	141 ^A \pm 50	5	144 ^{AB} \pm 133	5	165 ^A \pm 70	5	2.951*	5	1.262	5	0.042	0.279
2 79 \pm 45	7	264 ^A \pm 67	4	71 ^{AB} \pm 59	5	186 ^A \pm 67	5	136 ^A \pm 28	5	5.221*	5	4.048*	5	2.576*	0.377
3 79 \pm 45	7	222 ^A \pm 60	4	58 ^{AB} \pm 36	5	73 ^{AB} \pm 38	5	34 ^B \pm 22	5	4.305*	5	4.476*	5	0.573	1.776
4 79 \pm 45	7	84 ^B \pm 40	4	43 ^B \pm 30	5	31 ^B \pm 4	5	16 ^B \pm 16	5	0.181	5	1.549	5	0.793	1.819
Series III															
1 79 \pm 45	7	270 ^A \pm 241	4	146 ^A \pm 133	10	176 ^A \pm 108	10	+	-	1.841*	-	0.864	-	0.525	-
2 79 \pm 45	7	319 ^A \pm 102	4	174 ^A \pm 112	10	201 ^A \pm 121	10	-	-	4.863*	-	1.770	-	0.491	-
3 79 \pm 45	7	70 ^A \pm 34	4	58 ^A \pm 63	10	141 ^A \pm 72	10	-	-	0.314	-	0.303	-	2.603*	-
4 79 \pm 45	7	75 ^A \pm 52	4	61 ^A \pm 32	10	103 ^A \pm 48	10	-	-	0.121	-	0.437	-	2.184*	-

* Estimated as the mean observed in the control situation at the location of the experimental setup

+ Not determined

Table 3: Seasonal variation in mean fraction of recently germinated tubers of *P. pectinatus* (% of the total number of tubers in the sediment) and standard deviation (\pm SD) of N subsamples, in Series I and II in the control situation (1) and in experimental areas 2 to 4 differing in shading level during the growing season of 1986 and 1987, respectively. Means indicated with the same lettering are not significantly different per Series and per sampling date. The fraction was zero from the end of June onwards in both years in all experimental areas (data not shown).

Date	1			2			3			4			N
	Mean	\pm SD		NMean	\pm SD		NMean	\pm SD		NMean	\pm SD		
	(%)			(%)			(%)			(%)			
Series I													
29-Apr-86	44*	± 32	7	44*	± 32	7	44*	± 32	7	44*	± 32	7	
13-May-86	17 ^A	± 22	5	50 ^A	± 39	5	42 ^A	± 23	5	31 ^A	± 8	5	
26-May-86	15 ^A	± 18	5	15 ^A	± 17	5	13 ^A	± 22	5	7 ^A	± 9	5	
09-Jun-86	0 ^A	± 0	4	25 ^A	± 50	4	0 ^A	± 0	4	0 ^A	± 0	4	
23-Jun-86	2 ^A	± 5	4	0 ^A	± 0	4	5 ^A	± 8	4	0 ^A	± 0	4	
07-Jul-86	0 ^A	± 0	4	0 ^A	± 0	4	4 ^A	± 7	4	2 ^A	± 3	4	
14-Apr-87	40 ^A	± 16	5	38 ^A	± 11	5	33 ^A	± 23	5	25 ^A	± 21	4	
13-May-87	17 ^A	± 4	5	5 ^A	± 7	5	19 ^A	± 5	5	9 ^A	± 10	5	
05-Jun-87	17 ^A	± 19	5	16 ^A	± 14	4	18 ^A	± 20	5	9 ^A	± 14	5	
30-Jun-87	0 ^A	± 0	4	0 ^A	± 0	4	0 ^A	± 0	4	0 ^A	± 0	4	
Series II													
29-Apr-86	44*	± 32	7	44*	± 32	7	44*	± 32	7	44*	± 32	7	
13-May-86	25 ^A	± 17	5	26 ^A	± 27	5	23 ^A	± 21	5	11 ^A	± 16	5	
26-May-86	2 ^A	± 4	5	5 ^A	± 8	5	1 ^A	± 3	5	2 ^A	± 4	5	
09-Jun-86	0 ^A	± 0	4	0 ^A	± 0	4	0 ^A	± 0	4	0 ^A	± 0	4	
23-Jun-86	1 ^A	± 2	4	3 ^A	± 5	4	0 ^A	± 0	4	1 ^A	± 1	4	
07-Jul-86	0 ^A	± 0	4	1 ^A	± 1	4	3 ^A	± 6	4	2 ^A	± 5	4	
14-Apr-87	49 ^A	± 32	5	19 ^A	± 2	5	24 ^A	± 9	5	47 ^A	± 10	5	
13-May-87	15 ^A	± 11	5	9 ^A	± 13	5	27 ^A	± 22	5	48 ^A	± 31	5	
05-Jun-87	7 ^A	± 5	5	15 ^A	± 11	4	16 ^A	± 29	5	17 ^A	± 33	4	
30-Jun-87	0 ^A	± 0	4	0 ^A	± 0	4	0 ^A	± 0	4	0 ^A	± 0	4	

* Estimated as the mean observed in the control situation at the location of the experimental setup.

Table 4: Mean individual tuber AFDW and standard deviation (\pm SD) of N subsamples at maximum aboveground biomass in the experimental areas 1 to 4 and relative mean individual tuber AFDW (%) of *P. pectinatus* in experimental areas 2 to 4 expressed as a fraction of the value in the corresponding controls of Series I, II and III in 1986 and 1987, respectively. Means indicated with the same lettering are not significantly different per Series and per year. The t-statistic of Student's t-Test comparing the means of experimental areas 2 to 4 with the control is given per year and per Series. The t-statistic of Student's t-test comparing the means of 1986 and 1987 ($t_{86/87}$) in the control situation per area is shown also. Significant t-values are indicated by an *.

1986						1987						$t_{86/87}$
Mean	\pm SD	N			t	Mean	\pm SD	N			t	
(mg.tuber ⁻¹)			(%)			(mg.tuber ⁻¹)			(%)			
Series I												
1	38 ^A	± 15	4	-	-	27 ^A	± 10	5	-	-	-	1.057
2	23 ^A	± 6	4	61	1.608	29 ^A	± 18	5	107	1.419	-	-
3	39 ^A	± 10	4	103	0.096	19 ^A	± 3	5	70	0.612	-	-
4	22 ^A	± 10	4	58	1.537	13 ^A	± 7	4	48	0.965	-	-
Series II												
1	34 ^A	± 8	5	-	-	20 ^A	± 6	5	-	-	-	2.644*
2	27 ^A	± 3	5	80	1.419	21 ^A	± 11	5	105	0.160	-	-
3	38 ^A	± 8	5	112	0.612	19 ^A	± 4	5	95	0.277	-	-
4	22 ^A	± 20	3	65	0.965	12 ^A	± 13	3	60	1.117	-	-
Series III												
1	31 ^A	± 8	4	-	-	24 ^A	± 8	9	-	-	-	1.339
2	32 ^A	± 8	4	103	0.153	23 ^A	± 7	10	96	0.275	-	-
3	33 ^A	± 15	4	106	0.204	26 ^A	± 11	10	108	0.425	-	-
4	21 ^A	± 4	4	68	1.963*	33 ^A	± 13	10	138	1.697	-	-

The seasonal trends in the relative frequency distribution over the distinguished tuber weight classes in the control situations was similar in 1986 and 1987. It remained the same from the beginning of the sampling period until the end of June. Relatively many tubers were observed in the three lightest weight classes and relatively few in the heaviest weight classes during this period (Fig. 5; 26 May, 1986 and 5 June, 1987) which indicates that heavy tubers germinated more frequently than lighter tubers. The relative contribution of tubers in the heavier weight classes increased from the end of June onwards. Concurrently, the contribution of the lightest weight classes remained considerable. This observation implies that new tubers continued to be formed and that the already formed tubers kept growing at the same time considering tuber production starts around mid June in Lake Veluwe (Chapter 4). The tubers were distributed more equally over the various weight classes in the controls at the time the

above- and belowground biomass had sloughed completely and tuber formation and growth had ceased (Fig. 5; sampling date 12 September, 1986 and 25 September, 1987).

The overwintering of tubers was not weight-selective during the winter 1986/1987 in the controls. The relative frequency distribution was the same on the last sampling date in 1986, 3 November and on the first sampling date in 1987, 14 April (Fig. 6).

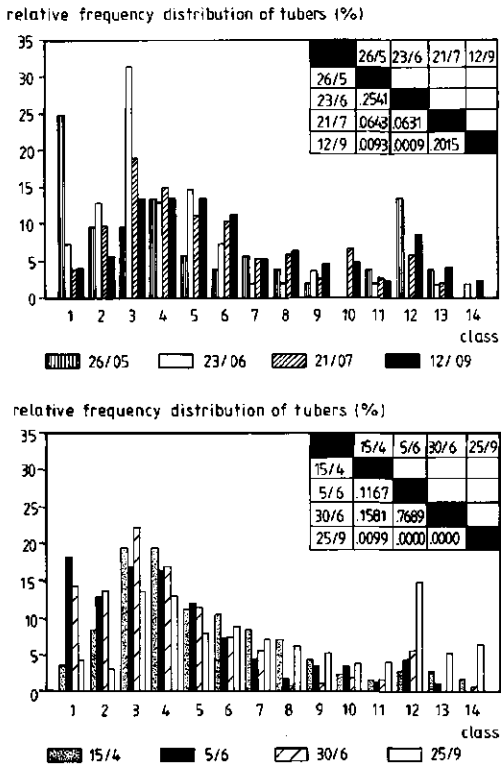


Fig. 5: Relative frequency distribution of tubers in the tuber bank of *P. pectinatus* in the controls of Series I and II in the distinguished weight classes, on some selected sampling dates in 1986 (top) and 1987 (bottom). Significances (*p*) of Kolmogorov-Smirnov Two-Sample Test for differences in relative frequency distribution between these sampling dates are given in a cross-table. Class 1=AFDW<0.0025, 2=0.0025≤AFDW<0.0050, 3=0.0050≤AFDW<0.0100, 4=0.0100≤AFDW<0.0150, 5=0.0150≤AFDW<0.0200, 6=0.0200≤AFDW<0.0250, 7=0.0250≤AFDW<0.0300, 8=0.0300≤AFDW<0.0350, 9=0.0350≤AFDW<0.0400, 10=0.0400≤AFDW<0.0450, 11=0.0450≤AFDW<0.0500, 12=0.0500≤AFDW<0.0750, 13=0.0750≤AFDW<0.1000, 14=AFDW≥0.1000 (with AFDW in g).

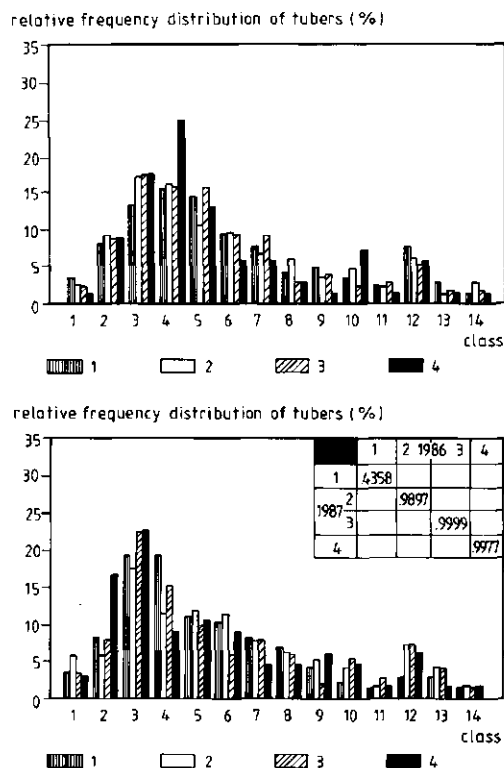


Fig. 6: Relative frequency distribution of tubers in the tuber bank of *P. pectinatus* in distinguished weight classes in the controls (1) and at various shading levels (2 to 4) in Series I to III on 3 November 1986 (top) and in Series I and II on 14 April 1987 (bottom). Classes are the same as in Fig. 5. Significances (p) of Kolmogorov-Smirnov Two-Sample Test for differences in relative frequency distribution between autumn 1986 (3 November) and spring 1987 (14 April) are given in a cross-table per treatment (bottom).

Biomass and tuber bank dynamics of a *P. pectinatus* population under manipulated light conditions during two subsequent seasons (1986-1987): Series I and II

The above- and belowground biomass were significantly lower in the shaded areas than in the control situations on various sampling dates in both Series and years. Generally, above- and belowground biomass were lower with increased shading. The vegetation had almost completely disappeared in the areas with the highest shading in 1987; mean maximum aboveground biomass was only about 5 g AFDW.m⁻², mean maximum belowground biomass only about 0.5 g AFDW.m⁻² (Figs. 2 and 3). The maximum aboveground biomass observed was lower with increased shading and it was found much earlier in the season in the experimental areas with the highest shading

than in the control situations (Table 1). The aboveground biomass sloughed earlier in the season with increased shading (Fig. 2). The impact of shading on the relative maximum aboveground biomass in experimental areas 2 to 4 (expressed as a percentage of the biomass in the control situation) was not significantly different in 1986 and 1987 in both Series I and II (Fig. 7).

The tuber bank size did not differ among the experimental areas at the beginning of the sampling period in 1986. However, it was smaller with increased shading from July onwards during both 1986 and 1987 (Fig. 4). The size of the hibernated tuber bank in the experimental areas with highest shading was about half the size of that in the control situations on the first sampling date in 1987 (Table 2). The relative tuber bank size in experimental areas 2 to 4 (expressed as a percentage of the tuber bank size in the control situation) at the time aboveground biomass was maximum, was smaller in 1987 than in 1986, although not significantly in all cases (Fig. 7). On the whole, the tuber bank size increased significantly at the lowest and remained the same at the two highest shading levels during the summer 1986. It did not change significantly in most experimental areas during the summer 1987; it increased significantly only at the lowest shading in Series II, and it even decreased significantly at the highest but one shading in Series I (Table 2). Apparently, net tuber production was relatively low in all experimental areas in 1987; hardly high enough to compensate germination and natural depletion in the experimental areas with highest shading. Generally, net tuber production rate was lower with increased shading in both years.

The tuber bank size decreased substantially in the winter 1986/1987, and it remained the same in the winter 1987/1988 (Table 2).

Germination did not differ among the experimental areas differing in light climate in both Series I and II and both years. It was restricted to the first part of the growing season at all experimental conditions (Table 3).

Mean individual tuber AFDW at maximum aboveground biomass was usually lower in the experimental areas with highest shading than in the control situations in both Series I and II and both years, although not shown significantly. Shading effects on relative mean individual tuber AFDW at maximum aboveground biomass did not differ between the two years (Table 4). No differences were observed in the relative frequency distributions over the tuber weight classes between the control and the three shading levels on all sampling dates in 1986 and between the control and the two lowest shading levels on all sampling dates in 1987. However, it did significantly differ between the control and the highest shading level at the time just before tuber production started (13 May and 5 June) and at the end of the growing season (13 August and 25 September). At that time, relatively few tubers were observed in the heaviest weight classes at the highest shading level, compared with the control at these sampling dates (Fig. 8; 25 September, 1987). The overwintering of tubers was

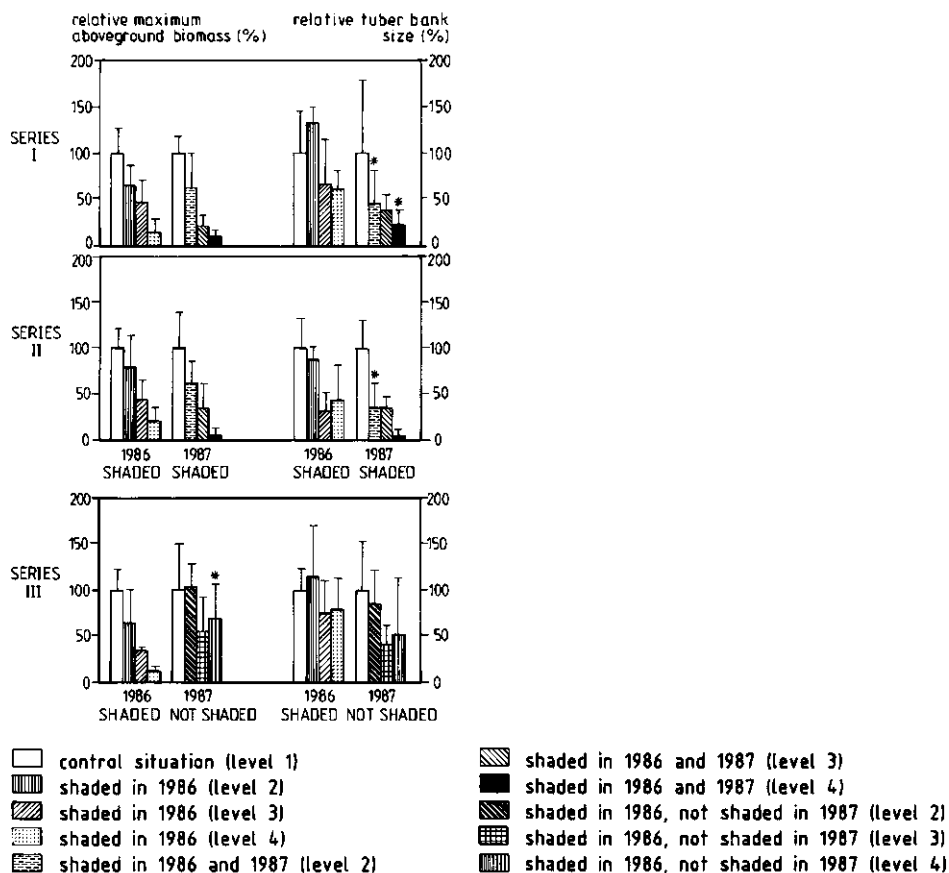


Fig. 7: Mean relative maximum aboveground biomass (expressed as percentage of the value reached in the corresponding control; left) and tuber bank size (expressed as percentage of the value reached in the corresponding control; right) of *P. pectinatus* at maximum aboveground biomass at the various treatments in Series I and II (top and middle) and Series III (bottom) during the growing season of 1986 and 1987. Given are relative means and standard deviation of the mean of the subsamples. Means of 1987 indicated with an * are significantly different (Student's t-Test) from their corresponding means in 1986.

not weight-selective during the winter 1986/1987 for all experimental conditions. The relative frequency distribution over tuber weight classes on the first sampling date in 1987 (15 April) did not differ significantly from that on the last sampling date in 1986 (3 November) at all experimental conditions (Fig. 6).

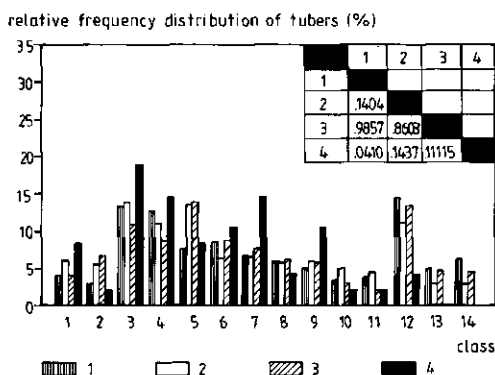


Fig. 8: Relative frequency distribution of tubers in the tuber bank of *P. pectinatus* in distinguished weight classes in the control (1) and at various shading levels (2 to 4) in the shaded Series (Series I and II) on 25 September, 1987. Classes are the same as in Fig. 5. Significances (p) of Kolmogorov-Smirnov Two-Sample Test for differences in relative frequency distribution between the treatments are given in a cross-table.

Biomass and tuber bank dynamics under manipulated light conditions in one season and under not manipulated light conditions in the subsequent season (1986-1987): Series III

Biomass and tuber bank dynamics in the experimental areas differing in light climate in Series III in 1986 showed the same trends as described for Series I and II. The biomass and tuber bank dynamics in 1987 appeared to be affected by shading during the growing season of 1986. The above- and belowground biomass in experimental areas 3 and 4 were lower than in the control situation on some sampling dates in 1987 (Figs. 2 and 3). Maximum aboveground biomass was observed at the same time (27 July) at all four experimental areas differing in light climate history though similar in present seasonal light climate (Fig. 2). It was lower in experimental area 3 than in the control situation, but it showed no significant differences between area 4 (highest shading level in 1986), and the control (Table 1). The tuber bank size was smaller with increased shading during the previous season, on most sampling dates in 1987 (Fig. 4).

In 1987, the relative maximum aboveground biomass in area 4 had recuperated considerably from the shading effects in 1986. It was significantly higher in 1987 than in 1986 (Fig. 7). In contrast, the relative tuber bank size showed hardly any recovery of the shading effects of 1986 at maximum aboveground biomass in 1987 (Fig. 7). The relative tuber bank size was the same in 1986 and 1987 in each experimental area. However, the tuber bank size showed no significant differences among the four areas at the end of the growing season of 1987. The tuber bank size increased significantly in experimental area 3 and 4 during the growing season of 1987 (Table 2).

Mean individual tuber AFDW at maximum aboveground biomass seemed highest in area 4, compared to the other areas, although, this could not be shown significantly (Table 4).

Relatively few tubers were observed in the heaviest weight classes before tuber production had started (14 June, 1987) in experimental area 4 as was the case in Series I and II at that time. The relative frequency distribution was more equally divided over the various weight classes at the end of the growing season (Fig. 9). The relatively high mean individual tuber weight and the relative frequency distribution with many tubers in the heavier weight classes in area 4 indicate the recently formed tubers were relatively heavy.

Additional observations during the growing season of 1988: Series I, II and III

In 1988, no shading was applied at all. The data of Series I and II show that the shading effects during two previous growing seasons were still obvious in the biomass and tuber bank dynamics in the season of 1988. The data show a tendency of lower biomass and smaller tuber bank size with increased shading during the two previous growing seasons at the end of July (not shown significantly in all cases) (Table 5). Although, the mean tuber bank size hibernated was only 15 tubers.m⁻² in the experimental areas which were treated with the highest shading (Table 2), the tuber bank size had already recovered up to 60 tubers.m⁻². Thus, even at small hibernated

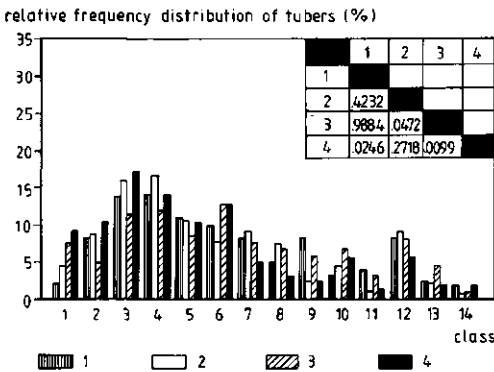


Fig. 9: Relative frequency distribution of tubers in the tuber bank of *P. pectinatus* in distinguished weight classes at experimental conditions 1 to 4 in the not shaded Series III) on 29 October 1987. Classes are the same as in Fig. 5. Significances (*p*) of Kolmogorov-Smirnov Two-Sample Test for differences in relative frequency distribution between the treatments are given in a cross-table.

tuber bank size, the vegetation showed a potential to recuperate. These observations are consistent with those after one year of shading (Series III in 1987). The data of Series III of 1988 show that the *P. pectinatus* vegetation had recovered almost completely from the shading treatments for one growing season in the second year after treatment (Table 5). The belowground biomass and tuber bank size did not differ significantly among the experimental areas. Only the aboveground biomass showed significant differences among the experimental areas at the end of July, although not for the level with the highest shading.

Discussion

Biomass and tuber bank dynamics of a P. pectinatus population in the control situations in 1986 and 1987

The present study revealed considerable differences in biomass and tuber bank dynamics of *P. pectinatus* between 1987 and 1986 in the control situations. The above- and belowground biomass were higher, the growing season was longer, the maximum aboveground biomass was observed much later in the season and was about twice as high in 1986 than in 1987. Further, tuber production was much lower in 1987 than in 1986. These differences in biomass and tuber bank dynamics are ascribed to less favourable growth conditions in 1987 than in 1986. Mean weekly incident photon flux density and water temperature were lower and the mean daily attenuation coefficient of the water column was higher in 1987 than in 1986 (Chapter 2). The importance of light conditions and temperature for the growth of submerged macrophytes is shown by various experimental studies (Barko and Smart, 1981; Barko *et al.*, 1982; Spencer, 1986). Furthermore, Scheffer *et al.* (1991) showed, by using multiple logistic regression, the biomass development of *P. pectinatus* is positively related with water temperature and light climate in a chain of six dutch lakes with Lake Veluwe one of them.

Accordingly, biomass and tuber bank dynamics of a *P. pectinatus* population in Lake Veluwe during a growing season are at least partly dependent on actual water quality and meteorological conditions.

Table 5: Mean above- and belowground biomass and tuber bank size of *P. pectinatus* and standard deviation (\pm SD) of N subsamples in the control (1) and in experimental areas 2 to 4, in Series I to III on sampling date 20 July 1988. Means indicated with the same lettering are not significantly different per Series.

Variable	1			2			3			4		
	Mean	\pm SD	N	Mean	\pm SD	N	Mean	\pm SD	N	Mean	\pm SD	N
Series I												
AFDW above (g.m^{-2})	39.6 ^A	± 18.1	5	24.8 ^{AB}	± 8.9	5	26.8 ^{AB}	± 21.1	5	6.8 ^B	± 6.8	5
AFDW below (g.m^{-2})	6.0 ^A	± 3.3	5	4.0 ^A	± 2.0	5	4.3 ^A	± 21.1	5	1.4 ^A	± 0.9	5
Tuber bank (m^{-2})	270 ^A	± 83	5	188 ^{AB}	± 51	5	128 ^{AB}	± 38	5	45 ^B	± 23	5
Series II												
AFDW above (g.m^{-2})	32.7 ^{AB}	± 10.9	5	52.4 ^A	± 24.5	5	12.1 ^B	± 13.4	5	17.7 ^B	± 7.1	5
AFDW below (g.m^{-2})	3.6 ^{AB}	± 1.6	5	6.9 ^A	± 2.6	5	2.8 ^B	± 2.5	5	2.8 ^B	± 1.5	5
Tuber bank (m^{-2})	249 ^A	± 89	5	213 ^A	± 180	5	65 ^A	± 36	5	71 ^A	± 21	5
Series III												
AFDW above (g.m^{-2})	37.6 ^A	± 17.0	10	17.0 ^B	± 11.4	10	21.1 ^{AB}	± 8.3	10	30.8 ^A	± 17.0	10
AFDW below (g.m^{-2})	7.3 ^A	± 4.9	10	3.5 ^A	± 6.2	10	5.2 ^A	± 2.1	10	4.5 ^A	± 2.8	10
Tuber bank (m^{-2})	271 ^A	± 147	10	343 ^A	± 241	10	182 ^A	± 79	10	226 ^A	± 164	10

Biomass and tuber bank dynamics of a *P. pectinatus* population under manipulated light conditions during two subsequent seasons (1986-1987)

In Chapter 4, it was derived that the photosynthetic tissue is unable to sustain tuber growth and maintenance of the vegetation at the highest shading. As a consequence, the vegetation sloughs soon after tuber production starts, the growing season is shortened and relatively few tubers are produced resulting in a relatively small tuber bank at these conditions. The present observations support these conclusions. The above- and belowground biomass were lower, the growing season was shorter and the tuber bank smaller with increased shading in both Series I and II and both 1986 and 1987.

In the present Chapter, maximum aboveground biomass and tuber bank size at maximum aboveground biomass were used to indicate biomass development and tuber bank size during a growing season. The aboveground biomass decreases rapidly and completely as soon as it has reached its maximum. From that time onwards tuber production and growth ceases. Therefore, it is assumed the vegetation has reached a certain critical physiological age at maximum aboveground biomass which is not necessary directly related to the number of days after germination of the tuber. The shading effects on relative maximum aboveground biomass were the same in 1986 and 1987. The impact of shading on tuber bank size at maximum aboveground biomass, however, was more pronounced in 1987 than in 1986. These distinct shading effects in the second year of treatment might result, firstly, from a smaller hibernated tuber bank at the beginning of the growing season with increased shading, and secondly, from a too low tuber production in 1987 as a result of too low photosynthesis due to unfavourable growth conditions.

Individual tuber weight at maximum aboveground biomass and the relative frequency distribution over the tuber weight classes did not significantly differ among the treatments in 1986. These data could be interpreted as that competition for carbohydrate between tubers controls the tuber weight distribution which is a generally recognized phenomenon in terrestrial plants (Wurr, 1977; see review Watson and Casper, 1984).

Individual tuber weight at maximum aboveground biomass, however, was lower and fewer tubers were observed in the heavier weight classes at the highest shading level in 1987. Obviously, the tuber bank consisted of more relatively light tubers at the highest shading compared with the control and the other shading levels in 1987. This phenomenon might be explained as follows. The relatively heavy tubers germinated more frequently than the lighter ones at all conditions and tuber production was negligible at the highest shading level. As a result, relatively many tubers contributed to the lighter weight classes and almost no tubers to the heavier classes at the highest shading compared to the control at the end of the growing season. Whether shading

has a direct impact on individual tuber weight remains unclear from the present results.

It is concluded that light climate is a predominant factor in determining the biomass and tuber bank dynamics of a *P. pectinatus* population in Lake Veluwe. Although, net growth of established vegetation occurs even under the highest shading, the photosynthetic tissue is not able to sustain tuber production. The tuber bank contained about 80 tubers.m⁻² at the beginning of the experiment (April 1986) and merely about 30 tubers.m⁻² after two growing seasons of shading at the highest shading level. These data suggest the vegetation may disappear completely at these conditions on a longer term. In addition to artificial shading this disappearance might be enhanced by unfavourable water quality and meteorological conditions.

Hibernated tuber bank size as a regulating factor for dynamics of a *P. pectinatus* population

The reestablishment of the vegetation at the beginning of the growing season is almost completely dependent on the hibernated tuber bank. The contribution of generative reproduction is negligible due to the poor germination of seeds (Van Wijk, 1988; Kautsky, 1990). The aboveground biomass development in experimental areas differing in hibernated tuber bank size but similar in their light climate (the controls of Series I and II and the four areas of Series III in 1987), has been correlated with their hibernated tuber bank size. The relationship between maximum aboveground biomass and hibernated tuber bank size appeared to be adequately described by a Michaelis-Menten function (Fig. 10). It should be stressed, however, that this derived correlation is only valid for the growth conditions of 1987. The observed maximum aboveground biomass in experimental areas with shading (levels 3 to 4 of Series I and II in 1987) was much lower than their predicted values according the derived Michaelis-Menten function (Fig. 11). This is due to the shading. It is concluded that biomass development in one season is determined by both the actual light climate conditions during the growing season and the light conditions of the previous growing season(s) through the hibernating tuber bank.

The present results revealed that about 50% of the hibernated tuber bank remained dormant assuming the decay rate of hibernated dormant tubers was low at all experimental conditions during the growing season. This is a higher fraction than found by other investigators, who indicated that only about 20% of preconditioned tubers from Lake Veluwe (Van Wijk, 1989; Vermaat and Hootsmans, 1991) and an eutrophic stream (Madsen and Adams, 1988) remained dormant under laboratory conditions. Generally, an increase in water temperature is considered as the dominant factor to release tubers from dormancy (Madsen and Adams, 1988; Van Wijk, 1989). Apparently, individual tubers from the same population may vary in physiological

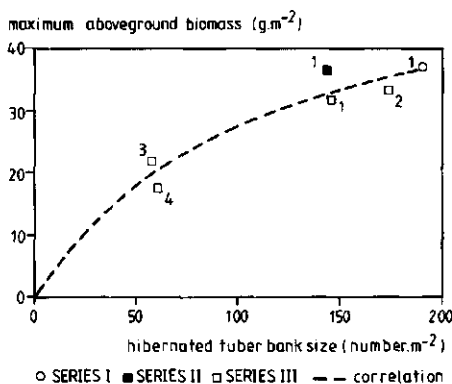


Fig. 10: Data-pairs of mean maximum aboveground biomass reached and mean size of the hibernated tuber bank of *P. pectinatus*, in experimental area 1 to 4 of Series III and the controls (1) of Series I and II in 1987, and the fitted Michaelis-Menten function ($B = 58.9 \cdot T / (114.6 + T)$ C.D. = 0.99 $p = 0.0375$ with B = maximum aboveground biomass (g.m⁻²), T = hibernated tuber bank size (numbers of tubers.m⁻²), C.D. = coefficient of determination and p = significance).

activity due to differences in environmental conditions on site regulating their release from dormancy considering the observed difference in dormancy between laboratory and field conditions (20% and 50%, respectively). Most dormant tubers had an healthy appearance which may indicate the tuber bank of *P. pectinatus* is potentially perennial in Lake Veluwe. A perennial tuber bank gives competitive advantage in terms of long term survival of a population under environmental stress conditions, like perennial seed banks (Grime, 1979). A perennial tuber bank may be another factor explaining the worldwide distribution of *P. pectinatus*. However, the question arises to which extent these dormant tubers will contribute to the reestablishment of the vegetation in a subsequent season. Germination was selective for heavy tubers and mainly light tubers remained dormant. Light tubers are less advantageous because they contain less carbohydrate to sustain early growth of the sprout (Hodgson, 1966; Ozimek *et al.*, 1986).

The biomass and tuber bank of *P. pectinatus* can be diminished to great extent by grazing of waterfowl. Waterfowl often consume more than 40% of the aboveground biomass of *P. pectinatus* (e.g. Martin and Uhler, 1939; Anderson and Low, 1976; Kiørboe, 1980; Van Wijk, 1988). In the present study, waterfowl grazing on the aboveground biomass was prevented by nets and strings extended above the water surface in the experimental areas with and without artificial shading, respectively, during the growing season. However, grazing by Bewick's swans on tubers may have occurred at the study site in the net-free periods (from mid November 1986 until April 1987 and from mid November 1987 until April 1988). Lake Veluwe is an

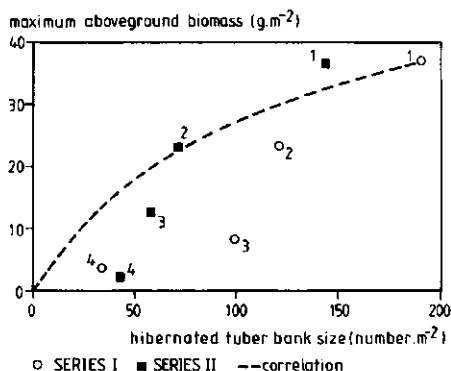


Fig. 11: Data-pairs of mean maximum aboveground biomass reached and mean size of the hibernated tuber bank of *P. pectinatus*, in experimental area 2 to 4 in Series I and II respectively, in 1987. Furthermore, the relation between maximum aboveground biomass and hibernated tuber bank size derived from Fig. 10 is shown.

important resting and foraging site of Bewick's swans (*Cygnus bewickii*) in winter (October-March). Over 1000 individuals were regularly observed during the winters of 1986/1987 and 1987/1988 in Lake Veluwe (Hoejenbos and Oonk, 1988). The tubers of *P. pectinatus* are an important food source for Bewick's swans (Bick and Van Schaik, 1980; Dirksen, 1982). Field observations have shown that *P. pectinatus* tubers are grazed until tuber density becomes too low with a minimum density of 6.5 g AFDW.m⁻² (Beekman *et al.*, 1981). Then, it is more profitable in terms of energy to forage on a more abundant food source than on tubers. This minimum density corresponds with a tuber density of about 220 tubers.m⁻² assuming a mean tuber AFDW of about 30 mg.tuber⁻¹. Grazing may explain the marked decline in tuber bank size in winter in experimental areas with autumn tuber densities exceeding 220 tubers.m⁻² (control areas and experimental areas 2, winter 1986/1987). Concurrently, the tuber bank size hardly varied in winter at autumn tuber densities of less than 220 tubers.m⁻² (experimental areas 3 and 4, winter 1986/1987; all experimental areas, winter 1987/1988). Grazing on tubers was not weight-selective, considering the relative frequency distribution of tubers over distinguished weight classes was similar in autumn 1986 and spring 1987.

Regeneration of a P. pectinatus population under Lake Veluwe conditions

The negative impact of shading during one season was notable in above- and belowground biomass and tuber bank size during the first subsequent growing season under natural light Lake Veluwe conditions. No apparent impact was recorded in the next growing season; the vegetation had completely recuperated. Even after two years

with artificial shading, the vegetation showed a potential to recuperate. After two years of shading, the hibernated tuber bank was only 15 tubers.m⁻² at the beginning of the season and it had already regained a density of 60 tubers.m⁻² at the end of July. It is concluded that the Lake Veluwe *P. pectinatus* vegetation has the potential to regain their control density as long as tubers are present in the sediment. This may require more than one growth season depending on actual growing conditions and size of the hibernated tuber bank.

Ecological implications

In the present Chapter, an attempt has been made to elucidate the importance of light climate history on biomass dynamics of *P. pectinatus*. Although, the statistical significance of the results was sometimes limited, the ecological implications of the present results were sufficient to obtain insight in the complex pattern of relationships between light climate, tuber bank and biomass development in the *P. pectinatus* population dynamics. The following conceptual model has been derived (Fig. 12). Light climate affects the biomass development through photosynthesis (relationship 1). Further, light climate is also involved in the tuber production (relationship 2). Firstly, the induction of tuber production is controlled by photoperiodic daylength. Secondly, tuber production and reallocation of photosynthate are enhanced by short photosynthetic daylength (Chapter 4). Recently produced tubers are filled with photosynthate which is produced by the photosynthetic tissue. The aboveground biomass affects the tuber production and concurrently the bank size (relationship 3). Reestablishment of the vegetation at the beginning of the growing season is at least partly controlled by the hibernated tuber bank. The maximum aboveground biomass is positively correlated with hibernated tuber bank size (relationship 4).

So far, very few field studies have been conducted to study the dynamics and life cycles of plant populations under various environmental conditions, although their importance is recognized (Farmer and Adams, 1989). More studies on the impact of environmental factors on the life cycle of submerged macrophytes are required to get insight in the macrophyte biomass dynamics. Hereby, growth strategy analysis (Murphy *et al.*, 1990) and modelling growth by computer simulation (e.g. Best, 1990; Hootsmans and Van Vierssen, 1991) might be useful tools. Studies on the life cycles and on factors affecting these are of particular importance in a management context e.g. by revealing parts of a life cycle vulnerable to management impact or critical in species establishment and -distribution.

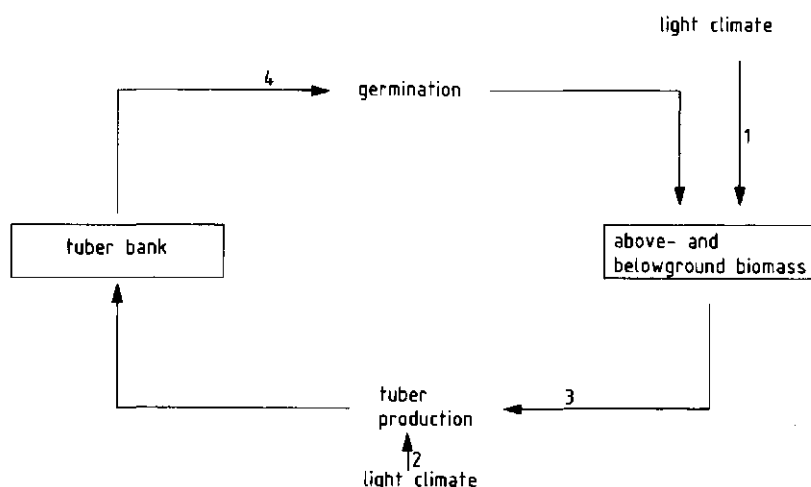


Fig. 12: Diagram of the relationships between tuber bank and biomass of *P. pectinatus* and the impact of shading.

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References

- Anderson M.G. and J.P. Low, 1976. Use of sago pondweed by waterfowl on the Delta Marsh, Manitoba. *J. Wildl. Manage.* 40: 233-242.
- Beekman J., K. van Dijk and S. Dirksen, 1981. De begrazing van fonteinkruidvelden in de Lauwersmeer door de Kleine Zwaan (*Cygnus bewickii*). Studentenverslag, Zoölogisch Laboratorium, Rijksuniversiteit Groningen, 30 pp. (in Dutch).
- Barko J.W. and M. Smart, 1981. Comparative influences of light and temperature on the growth and metabolism of selected freshwater macrophytes. *Ecological Monographs* 51: 219-235.

- Barko J.W., D.G. Hardin and M.S. Matthews, 1982. Growth and morphology of submerged freshwater macrophytes in relation to light and temperature. *Can. J. Bot.* 60: 877-887.
- Best E.P.H., 1987. Seasonal growth of the submerged macrophyte *Ceratophyllum demersum* L. in mesotrophic Lake Vechten in relation to insolation, temperature and reserve carbohydrates. *Hydrobiologia* 149: 231-243.
- Best E.P.H., 1990. Models on metabolism of aquatic weeds and their application potential. In: A.H. Pieterse and K.J. Murphy (eds). *Aquatic Weeds*. Oxford University Press, Oxford, p. 255-273.
- Bick H. and A.W.J. van Schaik, 1980. Oecologische visie randmeren. Advies van de Natuurwetenschappelijke Commissie van de Natuurbeschermingsraad, 291 pp. (in Dutch).
- Brinkman A.G. and W. van Raaphorst, 1986. De fosfaathuishouding in het Veluwemeer. Thesis, Technical University Twente, The Netherlands, 481 pp. (in Dutch with English summary).
- Day R.W. and G.P. Quinn, 1989. Comparisons of treatments after an analysis of variance in ecology. *Ecological Monographs* 59: 433-463.
- Dirksen S., 1982. The importance of pondweed for Bewicks swans in the Lauwersmeer. *Limosa* 55: 30-31 (in Dutch with English summary).
- De Nie H.W., 1987. The decrease in aquatic vegetation in Europe and its consequences for fish population. EIFAC, Occasional Paper no. 19, FAO, Rome, 52 pp.
- Farmer A.M. and M.S. Adams, 1989. A consideration of the problems of scale in the study of the ecology of aquatic macrophytes. *Aquat. Bot.* 33: 177-189.
- Grime J.P., 1979. *Plant strategies and vegetation processes*. Wiley, Chichester, 222 pp.
- Hodgson R.H., 1966. Growth and carbohydrate status of sago pondweed. *Weeds* 14: 263-268.
- Hoejenbos M. and C. Oonk, 1988. Kleine zwanen (*Cygnus bewickii*) en tafeleenden (*Aythya ferina*) op de randmeren. *Het Vogelaar* 36: 244-250 (in Dutch).
- Hootsmans M.J.M. and W. van Vierssen, 1991. Computer simulations of macrophyte dynamics during lake recovery after eutrophication. *Verh. Internat. Ver. Limnol.* (in press).
- Hosper S.H., 1984. Restoration of Lake Veluwe, The Netherlands, by reduction of phosphorus loading and flushing. *Wat. Sci. Tech.* 17: 757-768.
- Hurlbert S.H., 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* 54: 187-211.
- Kautsky L., 1990. Seed and tubers banks of aquatic macrophytes in the Askö area, northern Baltic proper. *Holarctic Ecology* 13: 143-148.
- Kemp W.M., W.R. Boynton, R.R. Twilley, J.C. Stevenson and J. Means, 1983. The decline of submersed vascular plants in Upper Chesapeake Bay: Summary of results concerning possible causes. *Mar. Sci. Tech.* 17: 78-89.
- Kjørboe T., 1980. Distribution and production of submerged macrophytes in Tipper Grund (Ringkøbing Fjord, Denmark), and the impact of waterfowl grazing. *J. Appl. Ecol.* 17: 675-687.
- Leentvaar P., 1961. Hydrobiologische waarnemingen in het Veluwemeer. *De Levende Natuur* 64: 273-279 (in Dutch).
- Madsen J.D. and M.S. Adams, 1988. The germination of *Potamogeton pectinatus* L. tubers: environmental control by temperature and light. *Can. J. Bot.* 66: 2523-2526.

- Martin A.C. and F.M. Uhler, 1939. Food of game ducks in the United States and Canada. Tech. Bull. U.S. Dep. Fenn. 123: 1-23.
- Murphy K.J., B. Rørslett and I. Springuel, 1990. Strategy analysis of submerged lake macrophyte communities: an international example. *Aquat. Bot.* 36: 303-323.
- Ozimek T., K. Prejs and A. Prejs, 1986. Biomass and growth rate of *Potamogeton pectinatus* L. in lakes of different trophic state. *Ekol. Polska* 34: 125-131.
- Phillips G.L., D. Eminson and B. Moss, 1978. A mechanism to account for macrophyte decline in progressively eutrophicated freshwaters. *Aquat. Bot.* 4: 103-126.
- Sas Institute Inc., 1985. SAS/STAT[™] Guide for personal computers, version 6 Edition. Sas Institute Inc. Cary NC, 378 pp.
- Scheffer M., M.R. de Redeljkheid and F. Noppert, 1991. Predictability of distribution and dynamics of submerged vegetation in a chain of shallow lakes. (submitted).
- Sokal R.R. and F.J. Rohlf, 1981. Biometry. W.H. Freeman and Company, San Francisco, 859 pp.
- Spencer D.F., 1986. Early growth of *Potamogeton pectinatus* L. in response to temperature and irradiance: morphology and pigment composition. *Aquat. Bot.* 26: 1-8.
- Stansfield J., B. Moss and K. Irvine, 1989. The loss of submerged plants with eutrophication III. Potential role of organochlorine pesticides: a palaeoecological study. *Freshw. Biol.* 22: 109-132.
- Van Wijk R.J., 1988. Ecological studies on *Potamogeton pectinatus* L. I. General characteristics, biomass production and life cycles under field conditions. *Aquat. Bot.* 31: 211-258.
- Van Wijk R.J., 1989. Ecological studies on *Potamogeton pectinatus* L. III. in reproductive strategies and germination ecology. *Aquat. Bot.* 33: 271-300.
- Vermaat J.E. and M.J.M. Hootsmans, 1991. Intraspecific variation in *Potamogeton pectinatus* L., a controlled laboratory experiment. (in prep).
- Watson M.A. and B.B. Casper, 1984. Morphogenetic constraints on patterns of carbon distribution in plants. *Ann. Rev. Ecol. Syst.* 15: 233-258.
- Wurr D.C.E., 1977. Some observations of patterns of tuber formation and growth in the potato. *Potato Res.* 20: 63-75.

Perspectives for submerged macrophytes in shallow lake restoration projects in The Netherlands

with Ellen van Donk

Abstract

Some well-documented studies on restoring eutrophic lake systems in The Netherlands by fish stock management have been evaluated with the emphasis on the role of macrophytes. Furthermore, the factors determining the light climate for submerged macrophytes in a large shallow eutrophic lake (Lake Veluwe) have been assessed and the potential success of biomanipulation in large scale projects is discussed.

Today relatively little attention has been paid to macrophyte management although the importance of macrophytes in lake restoration has been recognized regularly. The biomanipulation strategy was successful in small scale projects. In a large scale project however, wind-induced resuspension may largely determine the underwater light climate through attenuation by the water column and periphytic layer. Therefore, restoration of relatively large waterbodies by fish stock management only is expected not to lead to any noteworthy improvement of the light climate for submerged macrophytes. Additional measures aimed at reducing wind-induced resuspension of sediment particles and reestablishing of the macrophyte stands are required for successful biomanipulation strategy.

Water quality management should pay more attention to management of macrophyte stands in biomanipulation projects because macrophytes enhance a more stable and diverse ecosystem. Restoration objectives and the methods of their achievement must be carefully planned since an abundant submerged macrophyte vegetation may have undesirable effects as well.

Introduction

It is widely recognized that eutrophication threatens many macrophyte-dominated aquatic ecosystems over the whole world. An increase in algal biomass, concurrent water turbidity and a marked decline in the abundance of submerged vegetation has been recorded in many northern temperate aquatic systems over the last decades as a result of severe eutrophication (e.g. De Nie, 1987). Generally, there are two main strategies to control eutrophication in freshwaters. Firstly, a reduction of the external and internal load of nutrients (Björk, 1985), and, secondly, control of the internal ecological processes by e.g. fish stock management (McQueen *et al.*, 1986; Benndorf, 1988). Reducing the nutrient loading may provide acceptable long-term solutions but it can take a long time before a eutrophic ecosystem is completely recovered (Gons *et al.*, 1986; Hosper and Meijer, 1986). This delay in recovery has been explained by disturbance of the food chain due to eutrophication.

The decline in submerged vegetation is accompanied by an alteration of the habitats and food conditions for fish. The food chain of severely eutrophicated waters is generally characterized by a lack of predatory fish (e.g. Northern pike, *Esox lucius* L.), large biomass of planktivorous and benthivorous fish (mainly bream *Abramis brama* L.) (Lammens, 1986; Grimm, 1989), low abundance of herbivores (e.g. *Daphnia*), and relatively high phytoplankton densities causing low transparency of the water column (Hosper, 1989). Furthermore, bream, in search of benthic food, enhance resuspension of sediments and concurrently promote nutrient recycling (Ten Winkel and Meulemans, 1984; Lammens, 1986). Because of these negative effects of bream on water quality, it has been attempted to restore the food chain by reducing the bream stock and enlarging the predatory fish stock. An abundant predatory fish stock controls the cyprinids and hence enhances the grazing pressure on phytoplankton. This 'biomanipulation' has shown promising results in various studies with respect to improved water quality in terms of reduction in algal biomass and turbidity (e.g. Shapiro and Wright, 1984; Carpenter *et al.*, 1985; Benndorf *et al.*, 1988; Meijer *et al.*, 1989; Van Donk *et al.*, 1990*).

The importance of macrophytes as stabilizing structures in these restored aquatic ecosystems has been recognized in some of these studies (Ozimek *et al.*, 1990). However, restoration programmes by biomanipulation are mainly concentrating on fish stock management and relatively little attention has been paid to macrophyte management until now.

The present paper gives an overview of the role of macrophytes in some well-documented restoration projects in The Netherlands and expectations for large scale restoration projects. The potential role of submerged macrophytes in restoration programmes before and after biomanipulation is discussed and evaluated.

Case studies

Lake Zwemlust

The hypertrophic Lake Zwemlust (area 1.5 ha, Z_m 1.5 m) was characterized by algae blooms in summer, reducing the Secchi disk transparency to less than 0.3 m. The lake has been object of an extensive limnological study since the removal of planktivorous fish (bream) and the replacement of the water in March 1987 (Van Donk *et al.*, 1990*). The Secchi depth increased to the lake bottom (2.5 m) in the subsequent summer of 1987, and concurrently, submerged macrophytes responded rapidly to the improved light conditions. Six species of submerged macrophytes were present besides the introduced *Chara globularis*. The macrophytes colonized 10% of the lake area. Other species did not appear in 1988 and 1989, but the area covered by macrophytes increased by seven and ten times, respectively. *Elodea nuttallii* was the dominant species. It contributed about 70% and 82% to the total macrophyte biomass in 1988 and 1989, respectively. *E. nuttallii* accumulated substantial amounts of nitrogen, causing N-limitation of phytoplankton growth resulting in a persistent clear water phase (Ozimek *et al.*, 1990). Undesirable features of the increase in macrophytes were firstly, direct nuisance to swimmers and, secondly, large scale development of snails, especially *Lymnaea peregra*, which may harbour the parasite *Trichobilharzia ocellata*; the cercariae of this trematode cause schistosome dermatitis (swimmer's itch) (Van Donk *et al.*, 1989; 1990*).

Lake Bleiswijk

The hypertrophic Lake Bleiswijk, a narrow shallow lake (length 2 km, 14.4 ha, Z_m 1.1 m) was characterized by high algae concentrations, a Secchi disk transparency of about 0.2 m, and absence of submerged macrophytes during the summers of 1980-1986. The lake was divided in two compartments and in one compartment most of the planktivorous and benthivorous fish was removed and predatory fish was introduced in April 1987. This biomanipulation resulted in an increase in Secchi disk transparency to 1.1 m within two months. Concurrently, Characeae (*Chara vulgaris* var. *longibracteata*) became abundant and other macrophytes (*Potamogeton pectinatus*, *P. crispus*, and *Ceratophyllum demersum*) developed during the subsequent summer. High zooplankton densities caused low algal concentrations until July. Then, the

zooplankton densities decreased, but the algal concentration remained low. This phenomenon was explained by nutrient limitation as a result of high abundance of submerged vegetation or by inhibition of algal growth through allelopathic substances secreted by the macrophytes or by both mechanisms (Meijer *et al.*, 1989). The non-treated compartment of the lake remained turbid and no submerged vegetation was present (Meijer *et al.*, 1989).

Lake Breukeleveen

Lake Breukeleveen (180 ha, Z_m 1.45 m) is a compartment of the eutrophic Lake Loosdrecht. Earlier investigations (Leentvaar and Mörzer Bruijns, 1962) indicated that the macrophytic vegetation changed markedly since 1942, when almost the entire bottom of the lake was covered with Characeans. By 1961 the Characeans had disappeared and only a few submerged macrophyte species, mostly possessing floating leaves (*Nuphar lutea*, *Nuphar alba*) were recorded. Lake Breukeleveen was selected to study the effects of whole-lake food-web manipulation on a large scale. The external P-load has been reduced from 1.2 to 0.5 g P.m⁻².y⁻¹ by measures taken from 1970-1984 (sewage systems, dephosphorization). The water transparency (Secchi depth *ca.* 0.3 m), however, did not improve. Also the reduction of the planktivorous population from 150 to 57 kg.ha⁻¹ in March, 1989 did not result in an increase in water transparency. The dominance of cyanobacteria, rotifers and planktivorous fish had not changed in favour of submerged macrophytes and piscivorous fish. Apparently, the underwater light climate was still unfavourable for macrophyte growth due to resuspension of bottom material and relatively high concentrations of cyanobacteria filaments inhibiting the filtering mechanisms of largebodied zooplankton (Van Donk *et al.* 1990^b).

Lake Veluwe

Lake Veluwe (area 3240 ha, Z_m 1.20 m) is since 1957 one of the shore lakes, situated between the dikes of the reclaimed Flevoland polders and the former coastline of the 'old land'. Another shore lake (Lake Wolderwijd) will be subject to biomanipulation within due time. Lake Veluwe was characterized by a high transparency of the water column and a dense submerged vegetation in its early years (Leentvaar, 1961). It gradually changed into a turbid, eutrophic lake with relatively low macrophyte biomass in the 1980s (Hosper and Meijer, 1986) due to cultural eutrophication starting in the early sixties.

Investigations of the light climate for submerged macrophytes in Lake Veluwe during May-September in 1986 and 1987 revealed that the availability of Photosynthetically Active Radiation (PAR) for submerged macrophytes was largely determined by wind-

induced resuspension of sediment particles.

The vertical attenuation coefficient of the water column varied between 1.56 en 6.76 m^{-1} . Depletion of irradiance was largely attributed to tripton (detrital and inorganic matter) whereas phytoplankton had only additional effects. The contribution of water and gilvin (dissolved yellow substances) to the beam attenuation coefficient was even negligible (Table 1). The tripton concentration was positively correlated with wind velocity (Brinkman and Van Raaphorst, 1986; Chapter 2).

Attenuation by periphyton upon artificial substrate ranged up to more than 90% of the incident PAR. This diminution of PAR was largely ascribed to the backscatter properties of resuspended clay and silt particles settled from the water column into the periphytic layer (Chapter 3).

Resuspended sediment particles not only affected the quantity but, to a large extent, also the spectral distribution of PAR available for the submerged macrophytes. Resuspended detritus in the water column was a strong absorber of the blue regions of the spectrum and also the settled clay and silt particles in the periphytic layer performed a selective attenuation for the blue regions. Consequently, the spectral distribution of PAR was progressively compressed with depth into region between 550 and 700 nm (Chapters 2 and 3) which may be unfavourable for optimal plant growth (e.g. Kirk, 1983).

Table 1: Mean, minimum and maximum relative contribution of water, gilvin, phytoplankton and tripton to the absorption coefficient (*a*), scattering coefficient (*b*), and beam attenuation coefficient (*c*) during the end of June until the end of September, 1986 (N=8) and end of April until the beginning of September, 1987 (N=9) in Lake Veluwe, measured fortnightly (Chapter 2).

Component	<i>a</i> (m^{-1})			<i>b</i> (m^{-1})			<i>c</i> (m^{-1})		
	Mean	Min	Max	Mean	Min	Max	Mean	Min	Max
1986									
Water	18	6	24	ca.0	ca.0	ca.0	3	1	5
Gilvin	29	11	40	ca.0	ca.0	ca.0	4	1	8
Phytoplankton	11	6	19	8-16	3-7	16-33	8-15	4-6	17-31
Tripton	42	27	68	84-92	67-84	93-97	79-85	61-75	89-91
1987									
Water	10	5	16	ca.0	ca.0	ca.0	2	1	2
Gilvin	16	9	26	ca.0	ca.0	ca.0	3	2	4
Phytoplankton	13	6	20	15-30	6-12	31-62	14-27	6-11	28-52
Tripton	62	38	72	70-85	38-69	88-94	69-81	45-69	84-89

Discussion

The main objective of biomanipulation in restoring lake systems is to improve the underwater light climate with zooplankton reducing the phytoplankton while nutrient levels stay high. Biomanipulation should create conditions to enhance growth of submerged macrophytes since light climate is generally recognized as a key factor regulating growth and distribution of submerged macrophytes in eutrophic waters. The biomanipulation strategy was successful in relatively small scale projects (Lake Zwemlust and Lake Bleiswijk). The water transparency was high and an abundant macrophyte stand had developed within two years after the biomanipulation in these lakes. The restored vegetation increased the stability of the macrophyte dominance situation by preventing phytoplankton blooms through nitrogen limitation in Lake Zwemlust and likely through allelopathic substances secreted by *Chara* sp. in Lake Bleiswijk (Meijer *et al.*, 1989).

Biomanipulation, however, did not improve the underwater light climate in a relatively large scale project (Lake Breukeleveen) and the submerged vegetation did not develop. The current light climate for submerged macrophytes in Lake Breukeleveen was probably largely determined by resuspended sediment particles as has been demonstrated for Lake Veluwe. Here wind-induced resuspension of sediment particles had a major negative impact on the quantity and spectral distribution of PAR available for the submerged vegetation through attenuation by resuspended particles in the water column and settled resuspended particles in the periphytic layer in Lake Veluwe. Lake Breukeleveen and Lake Veluwe are similar with regard to factors favouring wind-induced resuspension through the position of the SW-diagonal (the square Lake Breukeleveen) or the length axis (the rectangular Lake Veluwe), in the prevailing SW wind, the absence of islands giving maximal fetch, their shallowness and easily resuspending uppermost layer of the bottom consisting of fine matter (Brinkman and Van Raaphorst, 1986; Gons, 1987).

Lake Zwemlust and Lake Bleiswijk are less sensitive to wind-induced resuspension in spite of their shallowness and easily resuspending uppermost layer of the bottom (Lake Zwemlust: mainly silt; data not presented; Lake Bleiswijk: mainly clay (Meijer *et al.*, 1989)), because these small lakes have a relatively short fetch and are sheltered from the wind by trees along the shore or in the surroundings.

Dense submerged macrophyte stands occurred in Lake Veluwe and Lake Breukeleveen in the 1940s and 1950s. Apparently, at that time, these stands flourished in a favourable light climate by which wind-induced resuspension was limited. Rooted submerged macrophytes reduce stirring up of sediments by stabilizing the sediment and dissipating wave energy (Carpenter and Lodge, 1986; Schröder, 1988).

From these observations we hypothesize that shallow macrophyte-dominated lakes sensitive to wind-induced resuspension of sediment particles, may switch irreversibly into a turbid state with low macrophyte density if any at all, when the macrophytes decline considerably due to a temporarily active factor (*e.g.* eutrophication, disease, storm). Afterwards, regeneration of the macrophyte stands may be prevented by unfavourable light conditions through wind-induced resuspension of sediment particles (Fig. 1). Such a phenomenon was observed in Australia, where reestablishment of the submerged vegetation was prevented by wind-induced resuspension after a tropical storm had swept away the entire submerged vegetation (Gerbeaux and Ward, 1988). Wind-induced resuspension of sediment particles may explain the limited improvements of water quality, water transparency, after biomanipulation in Lake Breukeleveen although fish control was successful in terms of standing crops of planktivorous and benthivorous fish populations.

The effectiveness of biomanipulation in large shallow eutrophic lakes which are more frequently subject to wind-induced resuspension of sediment particles than small lakes may be limited when only fish stock management is applied. Fig. 2 (left part) illustrates that biomanipulation through fish stock management leads to a restored food chain (more zooplankton, less algae, higher irradiance penetration, more macrophytes, more predatory fish, less planktivorous fish, more zooplankton, etc.) in lakes in which wind-induced turbulence plays no dominant role. However, biomanipulation leading to successful control of algae by zooplankton will hardly improve the underwater light climate and concurrent growth of macrophytes when

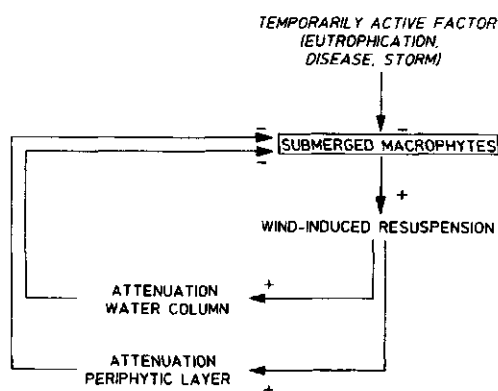


Fig. 1: Scheme of the hypothetical interactions among macrophytes and their light climate in a shallow lake sensitive to wind-induced resuspension of sediment particles. A temporarily active factor reducing the submerged macrophyte biomass leads to increased wind-induced resuspension, increased attenuation by both the water layer and the periphytic layer, lower macrophyte biomass, more wind-induced resuspension, etc.

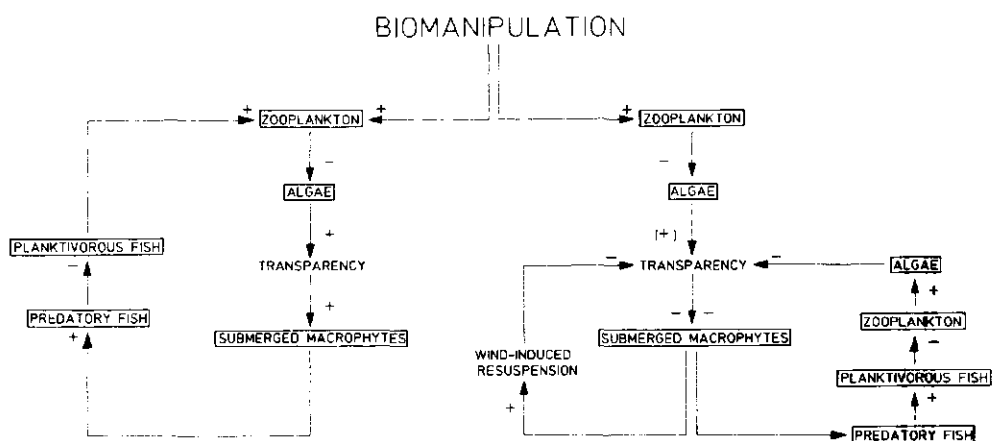


Fig. 2: Scheme of hypothetical interactions among the biota and their environment in shallow, eutrophic Dutch lakes in which wind-induced resuspension of sediment particles plays no role (left, after Hosper, 1989) or in which it does play a role (right) after biomanipulation (removal of planktivorous fish and introducing predatory fish). Arrows indicated with a + sign represent an increase; with a - sign a decrease in rate or quantity, respectively.

wind-induced resuspension predominates; a positive impact of biomanipulation on transparency will be prevented by high attenuation of resuspended sediment particles (Fig. 2, right part). Consequently, the macrophyte biomass will remain low and the food chain is likely to change again to low predatory fish, high planktivorous fish, low zooplankton, high algae *etc.* short after the biomanipulation. Additional measures besides fish stock management are required to get a clear water phase and an abundant submerged vegetation in lakes sensitive to wind-induced resuspension of sediment particles. Firstly, the underwater light climate must be improved before plants can colonize and morphometric measures are required to reduce the wind-induced resuspension (*e.g.* creation of sheltered areas by temporarily windshields; shortening of the fetch by islands or dikes; dredging). The importance of morphometric characteristics on wind-induced resuspension has been recognized by others as well (Duarte and Kalff, 1988), although it received little attention up to now. Secondly, there must be plants to take advantage of the improved light conditions (Moss, 1990). Active management in order to stimulate a submerged vegetation may be necessary to accelerate the process (*e.g.* introduction of vegetative or generative organs, planting nymphaeids, inoculation of *Chara*). Nymphaeids may strongly reduce wave-action by a well-developed canopy of floating leaves and thus increase sedimentation and trap drifting material (*e.g.* dead leaves) because of the reduced

water movements in and around their stands (Brock, 1985). Inoculation of *Chara vulgaris* stands showed to be effective in stabilizing the sediments against wind-induced resuspension because of its rhizoidal growth within the substrate leading to clear water conditions (Crawford, 1979).

The buffering mechanisms (stabilization of sediment, dissipating of wave energy, nutrient uptake, secretion of allelopathic substances) which stabilize the plant community are reinstated by restoring the submerged vegetation. Furthermore, submerged macrophytes may indirectly improve their own light climate by creating refuges for zooplankton and for the spawning of pike (Grimm, 1981, 1983; Hakkari and Bagge, 1985; Raat, 1988). Macrophytes not only stabilize the underwater light climate, but also enhance the diversity of species by offering substratum to periphytic organisms and food to herbivores, periphyton grazers (like Molluscs and Chironomids), organisms associated with the detritus food chain and water fowl (e.g. Bewick's swan foraging on *P. pectinatus* tubers).

Macrophytes may also have undesirable effects on water quality. Nutrients may increase in systems with a high internal nutrient load as a result of macrophyte presence (Malthus *et al.*, 1990). Consequently, the increased transparency may be of short duration. Furthermore, luxurious plant growth may be accompanied by an abundance of snails. In particular *Lymnaea peregra* was infected with larvae causing swimmers itch (schistosome dermatitis); an additional undesirable additional effect, in waters intensively used for recreational purposes (Van Donk, 1990^a).

In conclusion, more research on the impact of macrophytes on the functioning of shallow aquatic ecosystems is required. Water quality managers should pay more attention to management of a submerged vegetation considering its buffering mechanisms in stabilizing the dominance of macrophytes and its positive impact on species diversity. But the restoration objectives and the methods of their achievement must also be carefully planned because an abundant submerged vegetation may have undesirable effects as well.

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References

- Benndorf J., 1988. Objectives and unsolved problems in ecotechnology and biomanipulation: A preface. *Limnologica* (Berlin) 19: 5-8.
- Benndorf J., H. Schulz, A. Benndorf, R. Unger, E. Penz, H. Kneschke, K. Kossatz, R. Dumke, U. Hornig, R. Kruspe and S. Reichel, 1988. Food web manipulation by enhancement of piscivorous fish stocks: long-term effects in the hypertrophic Bautzen reservoir. *Limnologica* (Berlin) 19: 97-110.
- Björk S., 1985. Lake restoration techniques. In: Proceedings International congress 'Lakes Pollution and Recovery', Rome, p. 281-292.
- Brinkman A.G. and W. van Raaphorst, 1986. De fosfaathuishouding in het Veluwemeer. Thesis, Technical University Twente, The Netherlands, 481 pp. (in Dutch with English summary).
- Brock T.C.M., 1985. Ecological studies on nymphaeid water plants with emphasis on production and decomposition. Thesis, Catholic University Nijmegen, The Netherlands, 204 pp.
- Carpenter S., J.F. Kitchell and F.R. Hodgson, 1985. Cascading trophic interactions and lake productivity. *Bioscience* 35: 634-639.
- Carpenter S.R. and D.M. Lodge, 1986. Effects of submerged macrophytes on ecosystem processes. *Aquat. Bot.* 26: 341-370.
- Crawford S.A., 1979. Farm pond restoration using *Chara vulgaris* vegetation. *Hydrobiologia* 62: 17-31.
- De Nie H.W., 1987. The decrease in aquatic vegetation in Europe and its consequences for fish population. EIFAC, Occasional Paper no. 19, FAO, Rome, 52 pp.
- Duarte C.M. and J. Kalff, 1988. Influence of lake morphometry on the response of submerged macrophytes to sediment fertilization. *Can. J. Fish. Aquat. Sci.* 45: 216-221.
- Gerbeaux P. and J.C. Ward, 1988. The light climate of Lake Ellesmere and its effect on the growth of aquatic plants. *Verh. Internat. Verein. Limnol.* 23: 1979-1984.
- Gons H.J., R.D. Gulati and L. van Liere, 1986. The eutrophic Loosdrecht lakes: current ecological research and restoration perspectives. *Hydrobiol. Bull.* 20: 61-75.
- Gons H.J., 1987. The relationship between water transparency and suspended particles in the Loosdrecht lakes, with regard to swimming water standards. Internal Report 1987-12; WQL Report, 61 pp. (in Dutch).
- Grimm, M.P. 1981. The composition of northern pike (*Esox lucius* L.) populations in four shallow waters in The Netherlands, with special reference to factors influencing O⁺ pike biomass. *Fish. Management* 12: 61-79.
- Grimm M.P., 1989. Northern pike (*Esox lucius* L.) and aquatic vegetation, tools in the management of fisheries and water quality in shallow waters. *Hydrobiol. Bull.* 23: 59-65.
- Hakkari L. and P. Bagge, 1985. On fry densities of pike (*Esox lucius* L.) in Lake Sainaa Finland. *Verh. Internat. Verein. Limnol.* 22: 2560-2565.
- Hosper S.H. and M.L. Meijer, 1986. Control of phosphorus loading and flushing as restoration methods for Lake Veluwe, The Netherlands. *Hydrobiol. Bull.* 20: 183-194.
- Hosper S.H., 1989. Biomanipulation, new perspectives for restoration of shallow, eutrophic lakes in The Netherlands. *Hydrobiol. Bull.* 23: 5-10.

- Kirk J.T.O., 1983. Light and photosynthesis in aquatic ecosystems. Cambridge University Press, Cambridge, 401 pp.
- Lammens E.H.R.R., 1986. Interactions between fishes and the structure of fish communities in Dutch shallow eutrophic lakes. Thesis, Agricultural University Wageningen, The Netherlands, 100 pp.
- Leentvaar P., 1961. Hydrobiologische waarnemingen in het Veluwemeer. De Levende Natuur 64: 273-279 (in Dutch).
- Leentvaar P. and M.F. Mörzer Bruijns, 1962. The pollution of the Loosdrecht lakes and its consequences. De Levende Natuur 65: 42-48 (in Dutch).
- Malthus T.J., E.P.H. Best and A.G. Dekker, 1990. An assessment of the importance of emergent and floating-leaved macrophytes to trophic status in the Loosdrecht lakes (The Netherlands). Hydrobiologia 191: 257-263.
- McQueen D., J.R. Post, E.L. Mills, 1986. Trophic relationships in pelagic ecosystems. Can. J. Fish. Aquat. Sci. 43: 1571-1581.
- Meijer M.L., A.J.P. Raat and R.W. Doef, 1989. Restoration by biomanipulation of the Dutch shallow, eutrophic Lake Bleiswijkse Zoom: first results. Hydrobiol. Bull. 23: 49-57.
- Moss B., 1990. Engineering and biological approaches to the restoration from eutrophication of shallow lakes in which aquatic plant communities are important components. Hydrobiologia 200/201: 367-377.
- Ozimek T, R.D. Gulati and E. van Donk, 1990. Can macrophytes be useful in biomanipulation of lakes? The Lake Zwemlust example. Hydrobiologia 200/201: 399-408.
- Schröder R., 1988. Die Erosion der Uferbank des Untersees (Bodensee). Spätfolgen der Eutrophierung und hydrologischer Phänomene. Arch. Hydrobiol. 112: 265-277.
- Raat A.J.P., 1988. Synopsis of biological data on the northern pike, *Esox lucius* L. Synopsis No. 30 Rev. 2, FAO, Rome, pp. 178.
- Shapiro J. and D.I. Wright, 1984. Lake restoration by biomanipulation: Round Lake Minnesota, the first two years. Freshw. Biol. 14: 371-388.
- Ten Winkel E.H. and J.T. Meulemans, 1987. Effects of fish upon submerged vegetation. Hydrobiol. Bull. 18: 157-158.
- Van Donk E., R.D. Gulati and M.P. Grimm, 1989. Food-web manipulation in Lake Zwemlust: positive and negative effects during the first two years. Hydrobiol. Bull. 23: 19-34.
- Van Donk E., M.P. Grimm, R.D. Gulati and J.P.G. Klein Breteler, 1990^a. Whole-lake food-web manipulation as a means to study community interactions in a small ecosystem. Hydrobiologia 200/201: 275-290.
- Van Donk E., M.P. Grimm, R.D. Gulati, P.G.M. Heuts, W.A. de Kloet and L. van Liere, 1990^b. First attempt to apply whole-lake food-web manipulation on a large scale in The Netherlands. Hydrobiologia 200/201: 291-302.
- Van Donk E., 1990. Necessity of aquatic plant management after lake restoration by biomanipulation. In Proceedings EWRS/AAB 8th Symposium on Aquatic Weeds, p. 91-96.

Samenvatting en conclusies

Eutrofiëring, dat wil zeggen een toename in aanbod van nutriënten, vormt de laatste decennia een van de belangrijkste bedreigingen voor aquatische ecosystemen in zoete, brakke en mariene wateren. Bij eutrofiëring profiteren de waterplanten, de planktonische en de epifytische algen van het toegenomen voedselaanbod. Als gevolg van deze grotere algendichtheden verslechtert het lichtklimaat voor de ondergedoken waterplanten doorgaans aanzienlijk. De groei van de waterplanten neemt af en op den duur kan de ondergedoken vegetatie zelfs volledig verdwijnen. Met de waterplanten verdwijnen ook vele organismen die voor hun voedsel, voortplanting en/of habitat daarvan afhankelijk zijn. Dit geldt voor organismen zowel in het water (b.v. snoek en verschillende macrofaunasoorten) als daarbuiten (b.v. foeragerende vogels). Waterplanten spelen een essentiële rol in het functioneren van aquatische ecosystemen. Voor waterkwaliteitsbeheer van geëutrofieerde systemen is het dan ook van belang de invloed van het lichtklimaat op de groei en overleving van waterplanten nader te kennen.

In 1985 is bij de vakgroep Natuurbeheer van de Landbouwuniversiteit te Wageningen, onder begeleiding van Prof. Dr W. van Vierssen, een onderzoek begonnen naar de effecten van eutrofiëring op de dynamiek van door waterplanten gedomineerde zoetwater-ecosystemen. In dit project waarbij verschillende medewerkers van deze vakgroep actief waren, is uitgegaan van een modelmatige benadering waarbij resultaten van laboratorium en veldexperimenten geïntegreerd zijn in een simulatie-model. Een deel van de resultaten van dit onderzoek is recentelijk gepubliceerd in een wetenschappelijk proefschrift (M.J.M. Hootsmans en J.E. Vermaat).

In het voor u liggende proefschrift zijn de resultaten gepresenteerd van een driejarig veldonderzoek (1986-1988), uitgevoerd in opdracht van DBW/RIZA, dat deel uitmaakte van dit eutrofiëringsproject. De volgende vragen staan hierbij centraal:

- hoe wordt het lichtklimaat in het Veluwemeer voor de ondergedoken waterplanten gekarakteriseerd en door welke componenten in het water wordt het bepaald?
- wat is de invloed van het lichtklimaat op de groei en overleving van Schedefonteinkruid (*Potamogeton pectinatus*) in het Veluwemeer?

Het Veluwemeer (3240 ha, gemiddeld 1.15 m diep in de zomer) is eind jaren vijftig ontstaan bij de aanleg van de polder Oostelijk Flevoland. Het ligt tussen het 'nieuwe' en 'oude' land. In de eerste jaren na aanleg werd het Veluwemeer gekenmerkt door helder water en een dichte vegetatie bestaande uit o.a. verschillende soorten

kranswieren (*Chara* sp.), fonteinkruiden (*Potamogeton* sp.), Aarvederkruid (*Myriophyllum spicatum*), Waterpest (*Elodea canadensis*), Stijve waterranonkel (*Ranunculus circinatus*) en Smalbladige waterweegbree (*Alisma gramineum*). In de jaren zestig raakte het Veluwemeer langzaam maar zeker steeds eutrofer. Dit leidde regelmatig tot blauwalgenbloei en de waterplanten verdwenen vrijwel volledig in de jaren zeventig. Toen eind jaren zeventig een defosfateringstrap bij de rioolwaterzuiveringsinstallaties van Elburg en Harderwijk in gebruik was genomen en het meer werd doorgespoeld met fytoplankton- en fosfaatarm water, bleek dat dit effectieve beheersmaatregelen zijn. Het patroon van de jaarlijks weerkerende blauwalgenbloei werd doorbroken, de helderheid van het water verbeterde sterk en de waterplanten keerden terug. Halverwege de jaren tachtig was Schedefonteinkruid de meest voorkomende waterplant. Verder kwamen plaatselijk Doorgroeid fonteinkruid (*Potamogeton perfoliatus*) en kranswieren voor. Een volledig herstel in dichtheid en diversiteit van de ondergedoken vegetatie bleef echter uit. Vermoed werd dat het lichtklimaat nog steeds een beperkende factor vormde voor een optimale ontwikkeling van waterplanten en dat aanvullende beheersmaatregelen noodzakelijk waren. In dit proefschrift is de hypothese getoetst dat de groei van waterplanten in het Veluwemeer gelimiteerd zijn door het lichtklimaat als gevolg van een hoge planktonische en epifytische biomassa.

Hoofdstuk 2 behandelt het lichtklimaat onder water gedurende het groeiseizoen van Schedefonteinkruid. De helderheid van het water was in 1986 en 1987 gering: de verticale extinctiecoëfficiënt varieerde tussen 1.56 tot 6.76 m^{-1} en bedroeg in 1986 gemiddeld 2.2 m^{-1} , in 1987 3.4 m^{-1} . In het water wordt licht weggenomen: door het water zelf, in het water opgeloste humusachtige organische stoffen (aangeduid als gilvin), fytoplankton, zwevende dode organische stof (dode algen, plantdelen, dieren) en zwevende anorganische deeltjes (klei- en slibdeeltjes). De twee laatste componenten vormen samen het tripton. Het gehalte aan chlorofyl-a varieerde van 2 tot 85 mg.m^{-3} , de sestonconcentratie (som van het fytoplankton en het tripton) van 8 tot $148 \text{ mg.drooggewicht.l}^{-1}$ en de gilvinconcentratie van 0.79 tot 1.11 m^{-1} (uitgedrukt als absorptiecoëfficiënt bij 440 nm).

Het licht in het water blijkt sterk verstrooid te worden, met name door het tripton. De relatieve bijdrage van het water zelf en het gilvin aan de bundelextinctiecoëfficiënt was gering (minder dan 5%). Het fytoplankton draagt voor 6 tot 20% bij aan de grootte van de absorptiecoëfficiënt, voor 3 tot 33% aan de verstrooiingscoëfficiënt en voor minder dan 30% aan de bundelextinctiecoëfficiënt. Tripton is er dus voor het grootste deel verantwoordelijk voor dat de lichtintensiteit in het water sterk afneemt met de diepte. Het spectrum van het licht verandert aanzienlijk van samenstelling naar gelang de diepte van het water; dit is een gevolg van een selectieve absorptie

door de componenten in de waterlaag. Opgelost gilvin en gilvin geadsorbeerd aan tripton absorberen sterk het blauwe deel van het spectrum. De hoeveelheid tripton in het water is positief gerelateerd aan windsnelheid. Geconcludeerd is dat het lichtklimaat onder water in sterke mate wordt bepaald door bodemmateriaal dat door wind is opgewerveld. Het fytoplankton is slechts van ondergeschikt belang voor het lichtklimaat.

In hoofdstuk 3 zijn de resultaten beschreven van de ontwikkeling, samenstelling en lichtdoorlatendheid van het perifyton op kunstmatig substraat (objectglasjes). Daarnaast zijn er enkele aanvullende observaties verricht aan perifyton op bladeren van Schedefonteinkruid. Deze perifytonkarakteristieken zijn bestudeerd bij vier experimentele lichtcondities.

De perifytonontwikkeling werd enerzijds gevolgd op substraat dat telkens gedurende twee weken geïncubeerd was en anderzijds op substraat dat vanaf half mei tot het moment van bemonstering in het Veluwemeer was geïncubeerd (respectievelijk aangeduid als interval- en totaalserie).

De perifytonontwikkeling op kunstmatig substraat vertoonde een duidelijke periodiciteit in beide series. Aanwassnelheid en perifytondichtheid waren maximaal aan het begin en aan het einde van het groeiseizoen van Schedefonteinkruid en relatief daartussenin, waarschijnlijk als gevolg van begrazing door gammariden en/of chironomiden. Foto-inhibitie en een door nutriënten beperkte groei kunnen echter ook een rol hebben gespeeld.

De perifytonontwikkeling vertoonde nauwelijks verschillen bij de experimentele lichtcondities in beide series.

Kiezelalgen vormden de dominante groep aan het begin en aan het einde van het groeiseizoen; groen- en kiezelalgen waren dominant daar tussenin. Gedurende het gehele seizoen was de relatieve bijdrage van blauwalgen aan de totale epifytische gemeenschap slechts gering. Het perifyton bestond voor een groot deel uit gesedimenteerde anorganisch deeltjes (klei- en slibdeeltjes) en dood organisch materiaal (detritus).

Het perifyton dat zich gedurende twee weken in het Veluwemeer had kunnen ontwikkelen, nam 10 tot 50% van het invallende licht weg. Perifyton dat zich langer dan twee weken had kunnen ontwikkelen, nam uiteindelijk meer dan 90% van het invallende licht weg.

Het perifyton vertoonde een zelfde periodiciteit in dichtheid op de bladeren van Schedefonteinkruid als op kunstmatig substraat, zij het dat de dichtheid hoger was op de bladeren dan op kunstmatig substraat. Het perifyton op bladeren en op kunstmatig substraat bestond voor een belangrijk deel uit klei-, slib- en detritusdeeltjes.

Opwerveling van bodemmateriaal beïnvloedt het lichtklimaat van de ondergedoken waterplanten dus sterk negatief: enerzijds leidt het tot zeer troebel water en anderzijds tot een dichte perifytonlaag die weinig licht doorlaat.

Hoofdstuk 4 en 5 behandelen de groei en overleving van Schedefonteinkruid bij experimentele lichtcondities.

Schedefonteinkruid vertoont een eenjarige levenscyclus in het Veluwemeer. Aan het einde van de zomer (augustus-september) sterven stengels, bladeren, wortels en wortelstokken volledig af. Schedefonteinkruid overwintert door middel van tubers (vegetatieve overlevingsorganen). In het voorjaar, als de watertemperatuur stijgt, lopen de tubers massaal uit. Schedefonteinkruid produceert ook zaden maar deze kiemen in het veld slecht. Voor de overleving van de vegetatie in de winter zijn de tubers daarom van cruciaal belang.

Hoofdstuk 4 behandelt de invloed van het lichtklimaat op de vegetatieontwikkeling van Schedefonteinkruid. Daartoe zijn boven een homogene Schedefonteinkruidvegetatie drie typen netten gespannen (1.5 m boven het wateroppervlak) die respectievelijk 26%, 45% en 73% van de invallende lichtinstraling wegnamen. In de vegetatie ontstonden op deze wijze vier lichtcondities nl. een blanco (d.w.z. geen beschaduwing) en drie met beschaduwing. De fotoperiode was bij alle lichtcondities vrijwel hetzelfde terwijl de fotosynthetische periode korter was met toenemende beschaduwing. De fotoperiode is gedefinieerd als de tijdsduur per dag waarin de lichtintensiteit meer dan $10 \mu\text{E}\cdot\text{s}^{-1}\cdot\text{m}^2$ bedraagt, de fotosynthetische periode als de tijdsduur per dag waarin de lichtintensiteit hoog genoeg is voor een netto fotosynthese.

Elke lichtconditie werd gerealiseerd in een gebied van totaal 300 m², verdeeld over drie proefgebieden. Van april tot november 1986 is de vegetatie elke twee weken bemonsterd.

De boven- en ondergrondse biomassa waren gedurende het grootste deel van het groeiseizoen lager met toenemende beschaduwing. Bij alle lichtcondities begon de tuberproductie in de tweede helft van juni, rond de langste dag. In die periode waren de relatieve bijdrage van tubers aan de totale biomassa en het aantal tubers per hoeveelheid boven- en ondergrondse biomassa het hoogst bij de hoogste beschaduwing. Hierbij viel het tijdstip van maximale bovengrondse biomassa vroeger in het seizoen en was het vegetatie seizoen korter dan bij de overige lichtcondities. Aan het einde van het groeiseizoen werd de tuberbank kleiner bij toenemende beschaduwing. Afgeleid is dat tubervorming begint bij een fotoperiode van ca. 16 uur (lange-dagcondities) onafhankelijk van de fotosynthetische periode. Tuberproductie en reallocatie van carbohydraten zijn daarentegen hoger bij een kortere fotosynthetische periode.

In hoeverre een verhoogde tuberproductie en reallocatie van carbohydraten naar de tubers een adequate respons is op een verkorte fotosynthetische periode, is sterk afhankelijk van de hoeveelheid beschikbaar fotosynthaat waarmee de tubers gevuld moeten worden. De hoeveelheid fotosynthaat is afhankelijk van de hoeveelheid fotosynthetisch actieve delen (bovengrondse biomassa) en van de fotosynthese bij gegeven lichtcondities. Bij de hoogste beschaduwingsgraad kan de bovengrondse biomassa niet voldoende fotosynthetiseren om de groei van zowel tubers als van bovengrondse delen te onderhouden.

Geconcludeerd is dat beschaduwingsgraad een negatief effect had op de ontwikkeling van biomassa en op de omvang van de tuberbank. Optimale tuberproductie van Schedefonteinkruid vindt waarschijnlijk plaats in helderder water dan in de blanco situatie van dit experiment.

In hoofdstuk 5 wordt de invloed van het lichtklimaat op de groei en overleving van Schedefonteinkruid besproken. Daartoe is de vegetatieontwikkeling van Schedefonteinkruid bij verschillende lichtcondities gedurende drie seizoenen gevolgd (1986-1988). In 1986 zijn met kunstmatige beschaduwingsgraad vier lichtcondities gecreëerd in een homogene Schedefonteinkruidvegetatie. In 1987 is slechts een gedeelte van deze vegetatie op identieke wijze en een ander gedeelte niet meer beschaduwde. In 1988 is er geen kunstmatige beschaduwingsgraad meer toegepast.

In 1987 waren de groeiomstandigheden slechter dan in 1986. In de blanco situatie waren de boven- en ondergrondse biomassa, de maximale bovengrondse biomassa en de netto tuberproductie in 1987 lager dan in 1986. Verder was het vegetatie seizoen korter en was de maximale bovengrondse biomassa in 1987 vroeger in het seizoen bereikt dan in 1986.

In het tweede jaar (1987) had de beschaduwingsgraad dezelfde effecten op de biomassa en tuberbankontwikkeling als in 1986. In beide jaren namen de boven- en ondergrondse biomassa en de maximale bovengrondse biomassa af bij toenemende beschaduwingsgraad en werd het groeiseizoen korter.

Geconcludeerd is dat bij de huidige waterkwaliteit in het Veluwemeer het lichtklimaat onder water een dominante factor is voor de vegetatieontwikkeling van Schedefonteinkruid. Daarnaast kunnen verschillen in waterkwaliteit en/of weersomstandigheden tot aanzienlijke verschillen in vegetatieontwikkeling leiden. De vegetatieontwikkeling tijdens het groeiseizoen uitgedrukt in maximale bovengrondse biomassa was positief gecorreleerd met de omvang van de tuberbank aan het begin van het seizoen. De overlevingskansen van een vegetatie op langere termijn zijn mede bepaald door de omvang van de tuberbank. De vegetatieontwikkeling hangt dus niet alleen van de waterkwaliteit in het desbetreffende seizoen af maar ook via de tuberbank van de waterkwaliteit in de voorafgaande periode(n). Bij een verbetering

van het lichtklimaat onder water kan Schedefonteinkruid zich herstellen. Dit herstel is afhankelijk van het lichtklimaat en het weer; de snelheid van herstel is mede afhankelijk van de omvang van de tuberbank aan het begin van het seizoen.

In hoofdstuk 6 wordt de betekenis van de ondergedoken waterplanten geëvalueerd bij restauratie van sterk eutrofe systemen door middel van actief biologisch beheer. Onder actief biologisch beheer, ook wel biomanipulatie genoemd, wordt verstaan het (direct) beïnvloeden van de biotische component(en) in het water, zodanig dat het biologische systeem zelf wordt ingeschakeld bij de bestrijding van algenproblemen. Praktische mogelijkheden liggen vooral op het gebied van visstandsbeheer. Actief biologisch beheer blijkt een effectieve strategie te zijn in de bestrijding van ongewenste effecten van eutrofiëring in relatief kleine wateren. Het succes van actief biologisch beheer in grootschalige projecten is echter mede afhankelijk van de gevoeligheid van het systeem voor opwerveling van bodemmateriaal door wind. Indien als gevolg van eutrofiëring of een andere tijdelijk actieve factor de ondergedoken vegetatie verdwijnt, zal in systemen gevoelig voor opwerveling van bodemmateriaal door wind, de hoeveelheid opgewerveld bodemmateriaal een sturende factor zijn voor het lichtklimaat onder water. In dergelijke systemen zijn aanvullende maatregelen nodig voor verbetering van het lichtklimaat onder water voordat de ondergedoken vegetatie zich kan herstellen. Daarbij valt te denken aan morfologische ingrepen zoals het creëren van luwteplekken door aanleg van eilanden, dijken en windsingels. Naar verwachting zal dan tenminste op deze luwteplekken het lichtklimaat onder water verbeteren zodat zich lokaal vegetatiekernen kunnen ontwikkelen. Tevens zouden waterkwaliteitsbeheerders de groei en verspreiding van waterplanten kunnen stimuleren, bijvoorbeeld door herintroductie van soorten zoals nymfeïden die een sterk dempende werking hebben op de waterbeweging.

Curriculum vitae

Gerda van Dijk is op 19 april 1960 geboren te Bunnik. Zij behaalde in 1978 het Atheneum-B diploma aan het Christelijk Lyceum te Zeist. In hetzelfde jaar begon zij met haar studie biologie aan de Landbouwniversiteit te Wageningen. In 1985 behaalde zij haar doctoraalexamen. De doctoraalstudie bestond uit de vakken Natuurbeheer en Natuurbehoud, Hydrobiologie en Aquatische Oecologie (Vakgroep Aquatische Oecologie te Nijmegen). Verder bracht zij in het kader van haar doctoraalstudie drie maanden door aan het 'Center for Aquatic Weeds' te Gainesville, Florida, en drie maanden aan de Universiteit 'Tras os Montes' te Vila Real, Portugal. Van 1985 t/m 1989 was zij in dienst van de Landbouwniversiteit als tijdelijk wetenschappelijk medewerkster bij de vakgroep Natuurbeheer in het kader van de projecten "Relatie tussen dagelijkse zuurstof fluctuaties en biologische waterkwaliteits-criteria in een laagland beek" in opdracht van de STORA, en "Licht en waterplanten in het Veluwemeer" in opdracht van DBW/RIZA. In het laatste project werd de basis gelegd voor dit proefschrift. Gedurende de laatste zes maanden van haar contract werd zij door de vakgroep Natuurbeheer in de gelegenheid gesteld verder aan haar proefschrift te werken.

Vanaf 1990 was zij in dienst van het Rijksinstituut voor Natuurbeheer, afdeling Ecotoxicologie, als projectmedewerkster van het project "Ecosysteemherstel van chemisch belaste gebieden" in kader van het Project Ecologische Inpasbaarheid van menselijk handelen met Stoffen (PEIS) in opdracht van het Ministerie van VROM-DGM.

Sinds september 1991 is zij aangesteld als aquatisch ecologe bij het Rijksinstituut voor Volksgezondheid en Milieuhygiëne, Laboratorium voor Water- en Drinkwateronderzoek.