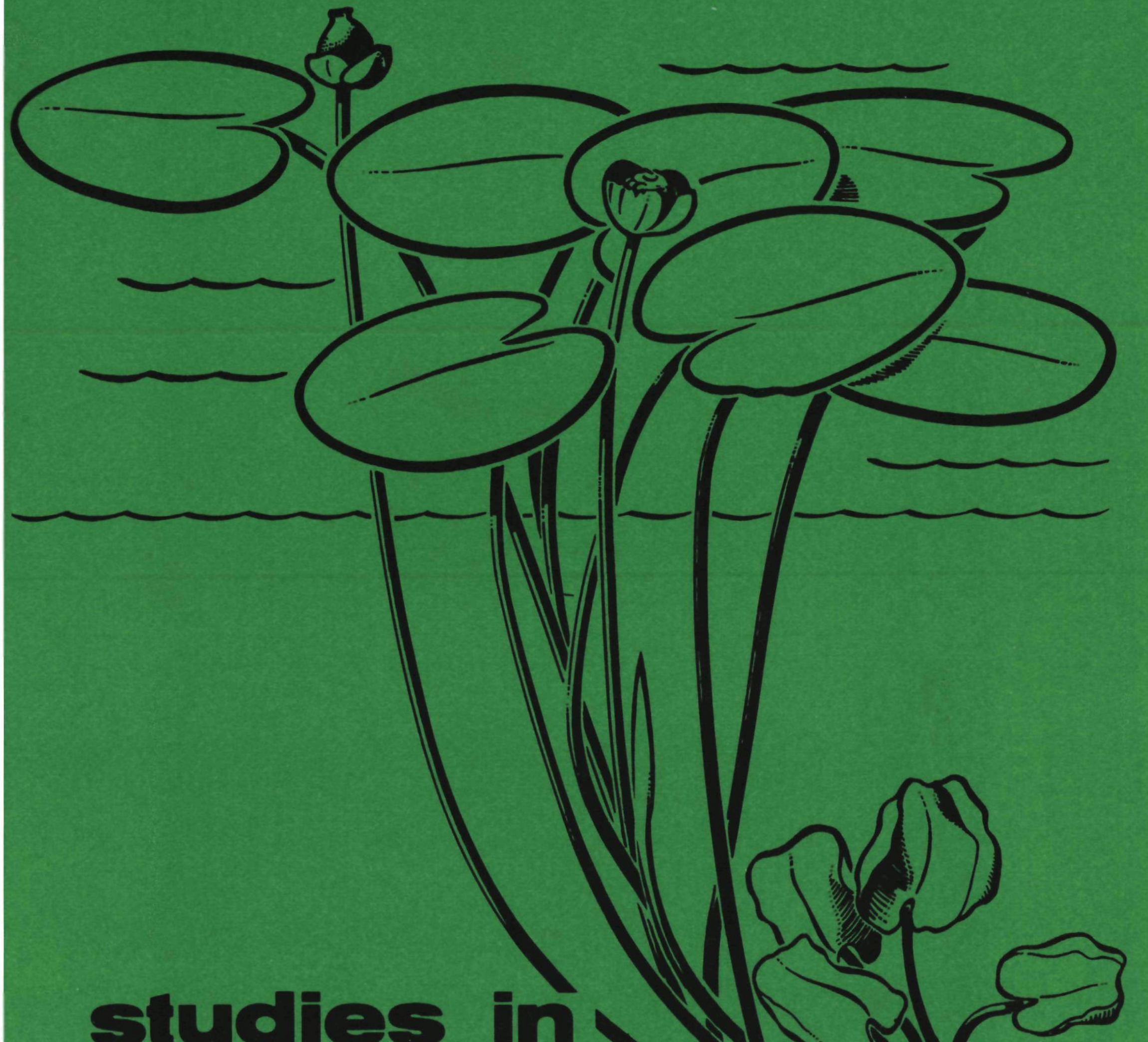
G. van der Velde



studies in nymphaeid-dominated systems

STUDIES IN NYMPHAEID—DOMINATED SYSTEMS
with special emphasis on those dominated by *Nymphoides peltata* (Gmel.) O. Kuntze (Menyanthaceae)

Promotor: Prof.Dr. C. den Hartog

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AAN DE KATHOLIEKE UNIVERSITEIT TE NIJMEGEN,
OP GEZAG VAN DE RECTOR MAGNIFICUS, PROF.DR. P.G.A.B. WIJDEVELD,
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Aan mijn ouders

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Studies on nymphaeid-dominated systems, with special emphasis on those dominated by *Nymphoides peltata* (Gmel.) O. Kuntze (Menyanthaceae).

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REMARKS ON STRUCTURAL, FUNCTIONAL AND SEASONAL ASPECTS OF NYMPHAEID—DOMINATED SYSTEMS

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INTRODUCTION

Macrophytes have an important function in shallow water communities. The concept function can be regarded as a comprehension of all activities and performances of the organisms of a community, such as primary production, respiration, decomposition and nutritional relations and more specific non-energetic properties (Den Hartog, 1978).

Macrophytes influence the physico-chemical properties of littoral and shallow waters (Sculthorpe, 1967, Hutchinson, 1975, Wetzel, 1975; Marshall and Westlake, 1978). They cause differences in oxygen content in the water between day and night due to photosynthesis and respiratory activity, they play a role in cycling of mineral and organic compounds in water bodies, they secrete organic compounds, which are important for the carbon budget in lakes and they absorb and store nutrients from water and sediments (Pieczynska and Ozimek, 1976) In waters with high macrophyte biomass the amount of elements accumulated in macrophytes can be higher than the amount in water (Bernatowicz, 1969). Lime incrustations are formed on macrophyte surfaces (Wetzel, 1975). Wave action is often reduced by the presence of macrophytes. Further they change light conditions where they grow and can intercept light to a considerable extent (Pieczynska and Ozimek, 1976).

As more specific non-energetic properties their function as a substrate for other littoral and shallow water organisms such as algae, bacteria, fungi and various groups of animals, and as shelter, nursery and spawning site must be mentioned. The living plant tissue can be consumed by various animals (Gaevskaya, 1969), while decaying macrophyte material plays an important role in the detritus food chain. In this way macrophytes contribute to the formation of a sapropelium layer on the bottom; due to this process the water can become shallower so that succession towards a marsh can take place. The macrophytes stabilize bottom sediments and protect banks (Marshall and Westlake, 1978). They form structured communities.

The concept community structure can be defined in various ways; according to Den Hartog (1978, 1979) at least three major components can be distinguished:

A the floristic and faunistic composition of the community

B. the arrangement of the organisms in space and time
C. the relations between the organisms within the community, as well as their relations with the surrounding environment.

There are several reasons why macrophytes in shallow waters can be considered to be the basic frame of an ecosystem, viz. they form an bulk of biomass and by their morphological differentiation (structure) they offer many possibilities for the settlement of other organisms. Important factors with respect to this settlement are the patterns of leaf production and leaf-shedding, the decomposition and the turn-over of the various plant parts. The morphological differentiation of the aquatic macrophytes differs considerably so that a great number of growth forms based on the habit of the plants can be recognized; these seem to be linked with a certain habitat type and determine the physiography of the community to a high degree (Den Hartog, 1978). The growth forms of aquatic plants have been amply described by Den Hartog and Segal (1964), Segal (1968), Den Hartog (1967, 1977), Hogeweg and Brenkert-van Riet (1969a), Hutchinson (1975) and Mäkirinta (1978).

In 1973 the Laboratory of Aquatic Ecology (Catholic University of Nijmegen) started with a research project on structure, dynamics and function of macrophyte-dominated aquatic communities; a begin was made with broad ecological research projects on various structurally different and ecologically linked aquatic macrophyte systems, such as the nymphaeid, the seagrass, the *Ruppia* and *Zannichellia-Potamogeton pectinatus* systems (Den Hartog, 1978) in anology with the international seagrass project.

Nymphaeids, which are distinguished as a growth form by all authors, which have described growth forms, are very common in all freshwater areas of The Netherlands. In shallow water they can dominate the community. Nymphaeid communities have been studied by the author since June 1974. Various aspects of the nymphaeid system have been studied separately, but also in relation to each other. Investigations were started on communities dominated by the nymphaeid species *Nymphoides peltata* (Gmel.) O. Kuntze (mainly results of investigations on the community dominated by this species are presented in this thesis), *Nuphar lutea* (L.) Sm., *Nymphaea alba* L. and *Nymphaea candida* Presl. The latter species was discovered for the first time in The Netherlands during these investigations and the species is now known from several localities (Roelofs and Van der Velde, 1977; Giesen and Van der Velde, 1978; Mennema and Van Ooststroom, 1979).

Till now only case studies on the nymphaeid systems were presented. In the present paper general remarks are made on the structural, functional and seasonal aspects of nymphaeid-dominated systems, to explain the general line of the research project.

THE STUDY AREAS

Most investigations have been carried out in the Oude Waal, an old river bed of the river Waal near Nijmegen (see for a description Van der Velde and Brock, 1980). Here extensive stands of *Nymphoides peltata*, *Nuphar lutea* and *Nymphaea alba* occur. Many observations were further made in the Haarsteegse Wiel near Vlijmen (see Van der Velde and Brock, 1980) on *Nuphar lutea* and *Nymphaea candida.*

In some other waters only certain ecological aspects have been studied. In the Bemmelse strang near Bemmel, an old river bed of the river Waal, the biomass of *Nymphoides peltata* was studied (Van der Velde, Giesen and Van der Heijden, 1979); in the Singel in Leiden only the aquatic macrofauna of floating leaves of *Nymphaea alba* and *Nuphar lutea* was investigated.

The development and decomposition of floating leaves and flowers of *Nymphoides peltata* was followed in two concrete tanks situated on the area of the Catholic University of Nijmegen (Van der Velde and Van der Heijden, 1980).

STRUCTURAL ELEMENTS OF A NYMPHAEID—DOMINATED SYSTEM

The vertical differentiation of the nymphaeid vegetation offers niches to many other organisms, and so several compartments within the nymphaeid system can be distinguished each with its characteristic species combination (Fig. 1).

Certainly, there is an exchange in species between the various compart-

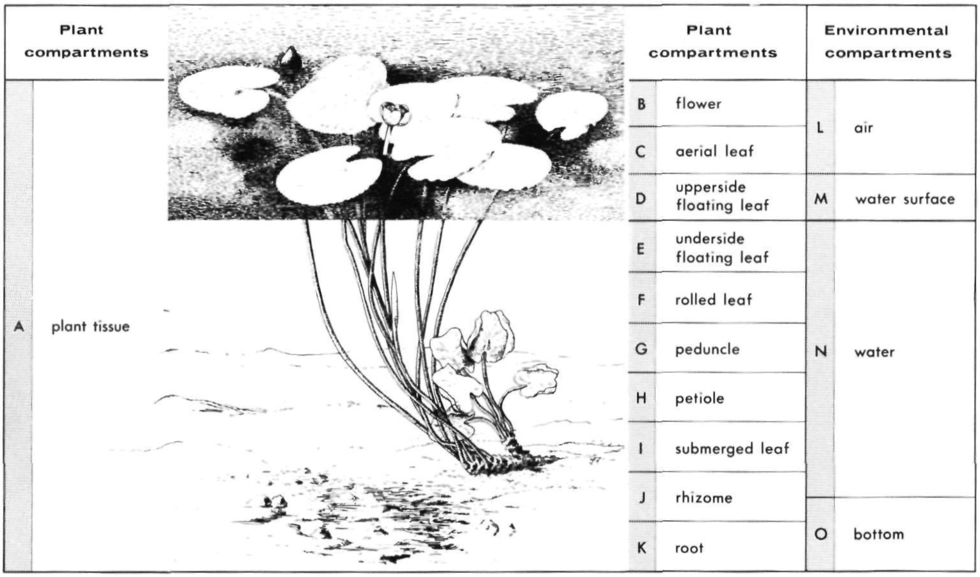

Fig. 1 *Nuphar lutea* (L.) Sm. showing the general structure of a nymphaeid, and the various compartments which can be distinguished in a nymphaeid-dominated system.

ments; the possibility to occur in different compartments varies for each species and depend on its adaptations, e.g. whether it is adapted to one or two different media. Water forms a barrier for most terrestrial insects, so only some specialized groups can occur in nymphaeid-dominated systems. When more parts of aquatic plants are situated above the water surface more insect species are able to utilize the plant tissue as food, as illustrated by Gaevskaya (1969), who summarized the animal species which consume freshwater plants all over the world. According to her 78 species of Coleoptera have been found to feed on semi-submerged plants (helophytes), 21 species on floating-leaved plants, and 7 on completely submerged plants, and only 11 species were recorded as feeding on plants of these three categories. For Diptera these figures are 78, 21, 18 and 31, for Lepidoptera 63, 4, 0 and 8.

The complex life cycles of certain fauna elements, for instance that of the Ephydrid fly *Notiphila brunnipes* R.-D. (see Van der Velde and Brock, 1980) make it possible that one species can occur in several different nymphaeid compartments during the various stages of its development. The beetle *Donacia crassipes* (F.) (Chrysomelidae) occurs as an imago in compartment D, the eggs are deposited in compartment E, while larvae and pupae occur in compartment K; another Chrysomelid beetle, *Pyrrhalta (Galerucella) nymphaeae* (L.) f. *typica* occurs during all its life stages (imago, egg, larva, pupa) in compartment D. These two beetles complete their whole life cycle on *Nymphaea* and *Nuphar.*

It is also possible that only one stage in the life cycle of a species occurs in a nymphaeid compartment, while it is further completely independent of the system, for example imagos of Apidae which are flower visitors (Van der Velde and Van der Heijden, 1980). So there are also important biological relations with the surrounding environment of the nymphaeid community.

It is clear that for each species the relation with the nymphaeid system has to be investigated and that ecological studies on important species are urgently needed to understand the complex processes in the compartment and at least the nymphaeid system as a whole.

According to the mode of space utilization, the following structural elements can be distinguished within the nymphaeid system. The compartments, where these structural elements occur, are given within parentheses (see Fig. 1):

1. The nymphaeid itself, which is differentiated into parts above and on the water surface, parts in the water column and underground parts. The space utilization of nymphaeids is very extensive. From the rhizome in the substratum groups of long-stalked floating leaves and peduncles develop; sometimes there are also some submerged ground leaves. Although the floating leaves may cover the surface for nearly 100%, the water column itself contains only the petioles and peduncles, and possibly some accompanying macrophytes. The nymphaeid is the frame of the community on which most of the other elements depend.
2. Associated macrophytes (compartment L—O).

3. Phytoplankton (compartment N).
4. Epiphyton (compartment E—J).
5. Endophytes (compartment A).
6. Microbial organisms (compartment A—O).
7. Mining fauna (compartment A).
8. Sessile aquatic epifauna (compartment E—K).
9. Vagile aquatic epifauna (compartment E—K).
10. Terrestrial fauna (compartment D, B).
11. Neustonic fauna (compartment M).
12. Aerial fauna (compartment L).
13. Zooplankton (compartment N).
14. Nekton (compartment N).
15. Benthic infauna (compartment O).
16. Vagile bottom fauna (compartment O).

Our knowledge of the various elements is till now insufficient to conceive a model of the whole ecosystem based on species composition, species characteristics, dynamics, seasonal aspects, energy flows and so on, as of several structural elements only preliminary data are available and some have not yet been studied at all. Each structural element should be studied in each compartment for at least a year by using transects so that the temporal and spatial patterns and the changes of these patterns become known. Connections between processes in different compartments can only be elucidated by an integrated study of these compartments during at least a whole year.

THE STRUCTURE OF NYMPHAEIDS

Nymphaeids are aquatic plants which possess mainly floating leaves, have their flowers above or floating on the water surface and are rooted in the bottom (Fig. 1).

Nymphaeids occur in very different families such as the Menyanthaceae, Nymphaeaceae, Potamogetonaceae, etc. Certainly most differences in structure between the nymphaeid species have a taxonomical base (Fig. 2).

The structure of the nymphaeid species further depends on several environmental factors such as the water-level, the age of the plant and the time of the year. Submerged leaves are always present in just germinated or young plants; in this stage floating leaves are not yet developed. In some nymphaeid species such as *Nuphar lutea* submerged leaves are present on new branches of the rhizome during the whole year; in *Nymphoides peltata*, when fullgrown small submerged leaves only occur in autumn and winter. The floating leaves often replace submerged leaves when the plant is fullgrown *(Nymphoides peltata)* or on older parts of the rhizome *(Nuphar, Nymphaea).*

The length of the petioles usually varies with the water-level. When the water-level drops stiffer aerial leaves with relatively short petioles often develop (Fig. 3 and 4). Such aerial leaves develop in the case of *Nuphar lutea* already when the water-level drops to less than 20 cm. Structurally such a

Fig. 2 Above: *Nymphaea alba* L. and *Nuphar lutea* (L.) Sm. in the Oude Waal near Nijmegen (summer of 1975). Note that in contrast to *Nymphaea alba* all *Nuphar* leaves are situated flat on the water surface.
Below: *Nymphoides peltata* (Gmel.) O. Kuntze with some *Hippuris vulgaris* L. in the Oude Waal near Nijmegen (summer of 1975). Note the slowing down of waves by the floating leaves.

Fig. 3 Emerged stand of *Nuphar lutea* (L.) Sm. in the Oude Waal near Nijmegen (summer of 1976). Some leaves are still floating but most leaves are stiff, short-petioled aerial leaves.

Fig. 4 Emerged stand of *Nymphoides peltata* (Gmel.) O. Kuntze, with stiff, short-petioled aerial leaves in the Oude Waal near Nijmegen (summer of 1976).

Nuphar-plant can be considered to be a helophyte or when it is totally emerged as one of the terrestrial growth forms.

The nymphaeids appear to be adapted to water-level fluctuations of several metres, due to growth by cell enlargement of the petioles of floating leaves (Funke, 1951). Further they can survive emergence. In the summer of 1976 the Oude Waal, where most of the fieldwork of this study has been carried out, dried up; in the following years when water had returned (autumn 1976) no distinct changes in the area of the nymphaeid stands have been observed as could be proved by comparing aerial photographs taken before and after the drawdown. This has been found also in *Nuphar* species in the United States. Hestand and Carter (1974, 1975) found in Lake Tohopekaliga in central Florida that the area of stands of *Nuphar macrophyllum* (Small) E.O. Beal occupied the same area before and after a spring-summer drawdown; in Lake Ocklawama (Florida) they found a slight reduction of *Nuphar* in the transects and plots after emergence in wintertime, but the area even increased compared with that before the emergence after the winter drawdown. Beard (1973) found, however, a strong reduction of *Nuphar* stands in Wisconsin after emergence in wintertime, caused by frost and floating away of rhizomes when water returned.

In streams nymphaeid species often cannot develop floating leaves and they also do not flower there *(Nuphar lutea)*; in these habitats they possess only submerged leaves and structurally they can be considered as magnopotamids.

The differences in structure between flowers of the various nymphaeid species are highly dependent on the taxonomical relationships of the species and not influenced by environmental factors.

With respect to the rooting systems of Dutch nymphaeids two types can be distinguished, viz. a stoloniferous type with short and long shoots such as in *Nymphoides peltata* and a type with coarse rhizomes such as in *Nuphar lutea* and *Nymphaea alba.* One specimen of the stoloniferous type can cover a large area in a water by means of runners within a year; a specimen of the type with rhizomes must extend its area mainly by seed dispersal, because the growth of a rhizome is relatively slow.

PHENOLOGY, PRODUCTION AND DECOMPOSITION OF FLOATING LEAVES

The seasonal development of the nymphaeids themselves is an important study object, as they form the frame of the system on which other elements can interact. The study has been directed particularly on the floating leaves, as these are the most characteristic feature of the nymphaeids.

Marking of floating leaves and flowers makes it possible to study development, growth and production, decomposition, turn-over of individual leaves and flowers and to follow the succession of periphyton, micro- and macrofauna in relation to the age and condition of each individual leaf. Further the development and phenology of these organs can be followed in this way.

Fig. 5 Floating leaf of *Nuphar lutea* (L.) Sm. marked with Rotex-tape on which a number is printed. The covering paper is removed and the tape is fixed around the petiole by means of a staple, without damaging the petiole, the other end of the tape is drawn through the leaf-sinus and bent above the leaf surface like a flag, so that it can easily be read. Only completely unrolled leaves have been marked in this way.

Leaves and flowers have been marked with Rotex-tape on which a number was printed (Fig. 5). As one plant forms too many leaves to follow the fate of each of them plots were made of P.V.C.-tubes of one square metre in the case of *Nuphar* and *Nymphaea* and of 0.25 m^2 in the case of *Nymphoides* (Fig. 6). Observations and marking of newly unrolled leaves took place every week during the growth season (in the case of *Nymphoides* in the concrete tanks every two or three days), while at each date air and / or water temperature were measured. Different damage patterns of floating leaves were distinguished in the field (see for *Nymphoides peltata* Lammens and Van der Velde (1978), Heine and Van der Velde (1978) and Van der Velde (1979)) and each type of damage was estimated as a percentage of the leaf area per leaf. Production and decomposition of floating leaves within the plots could so be followed during the season. Of each leaf at each date length and width were measured; in this way growth of each leaf can be measured. Further samples were made monthly which were used for biomass measurements in

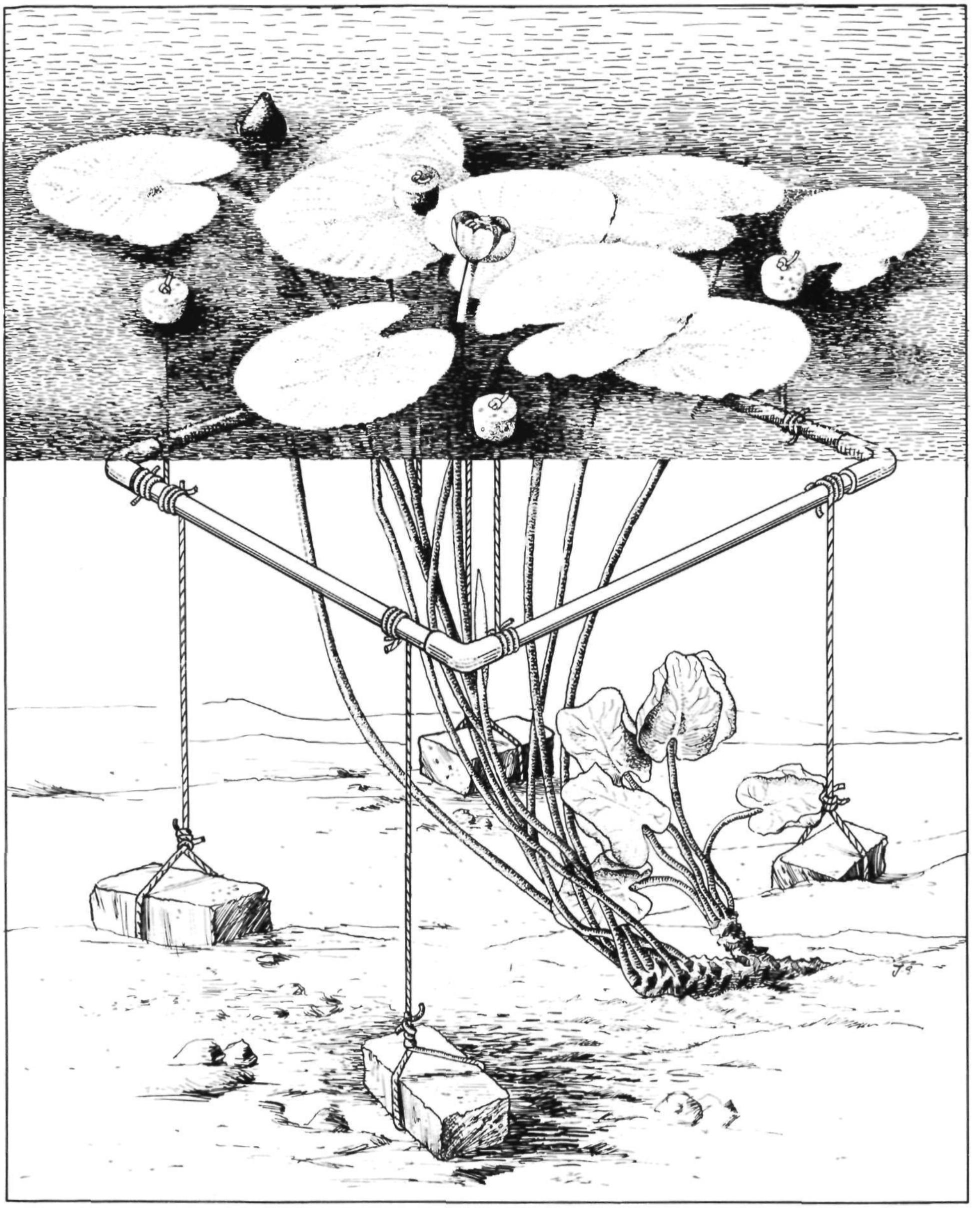

Fig. 6 Plot of *Nuphar lutea* (L.) Sm. with a perforated P.V.C.-tubing frame of 1 m^2, held at ca. 15 cm under the water surface by cork floaters so that the unrolling of floating leaves is not hindered, and anchored at each edge by stones.

relation to the leaf surface, while also the relation between leaf length and width and leaf surface was determined. In this way the biomass of each leaf can be calculated, while also the damage of each leaf can be expressed in terms of biomass. So the processes in a plot can be followed quantitatively in various ways.

As so many data were gathered a computer program appeared to be necessary for elaboration. A program is now in development by the Mathematical-Statistical Advice division of the Catholic University of Nijmegen, so that here only some preliminary results can be dealt with.

The results for 1976 from the Oude Waal have been obtained from different plots, as new plots had to be laid out because the plots emerged during the season, while the plot of *Nymphoides* could not be observed further because all stands of this species emerged. During 1977 one plot of *Nymphaea alba* and one of *Nuphar lutea* were followed in the Oude Waal near Nijmegen and one plot of *Nymphaea candida* and one of *Nuphar lutea* in the Haarsteegse Wiel near Vlijmen without problems, while in 1978 two plots of 0.25 m^2 of *Nymphoides peltata* were followed in two concrete tanks situated on the area of the Catholic University of Nijmegen. The development of floating leaves and flowers as found in 1977 for *Nuphar lutea*, *Nymphaea alba* and *Nymphaea candida* can be read from Fig. 7 and from Fig. 3 in Van der Velde and Brock (1980). These figures show clearly that the development of all these species follows the rise and decrease of temperature during the season while the peaks of the number of floating leaves and flowers coincide with the highest temperatures measured during the season. In all cases the development of floating leaves and flowers is fairly regular, so that one can be concluded that all these nymphaeid species have their largest photosynthetic area when insolation is at its maximum, as the temperature course is highly correlated to insolation, and that the increase and decrease of insolation is followed by increase and decrease of the number of floating leaves.

The vegetation period of floating leaves, the number of floating leaves and the turn-over differed however per species and to a certain extent per locality. *Nymphaea candida* had the shortest vegetation period, *Nuphar lutea* and *Nymphaea alba* had an intermediate period, while *Nymphoides peltata* had the longest period with floating leaves (Table 2). The total number of floating leaves which developed per plot of 1 m^2 differed very much. *Nymphoides* in the two concrete tanks developed most leaves per square metre viz. 2552 and 2492 respectively, *Nymphaea alba* in the Oude Waal 108, *Nuphar lutea* in Haarsteeg 77, *Nuphar lutea* in the Oude Waal 59 and *Nymphaea candida* in the Haarsteegse Wiel the lowest number viz. 43.
The ratio maximum number of floating leaves present in a plot / total number of leaves developed during the season in a plot was highest in the case of *Nymphoides* viz. 4.73 and 3.99 respectively, in *Nymphaea alba* 2.53, in *Nuphar lutea* from Haarsteeg 2.48, in *Nuphar lutea* from the Oude Waal 2.46 and in the case of *Nymphaea candida* only 1.59. With respect to mean and maximum leaf persistence after unrolling at the water surface the leaves of

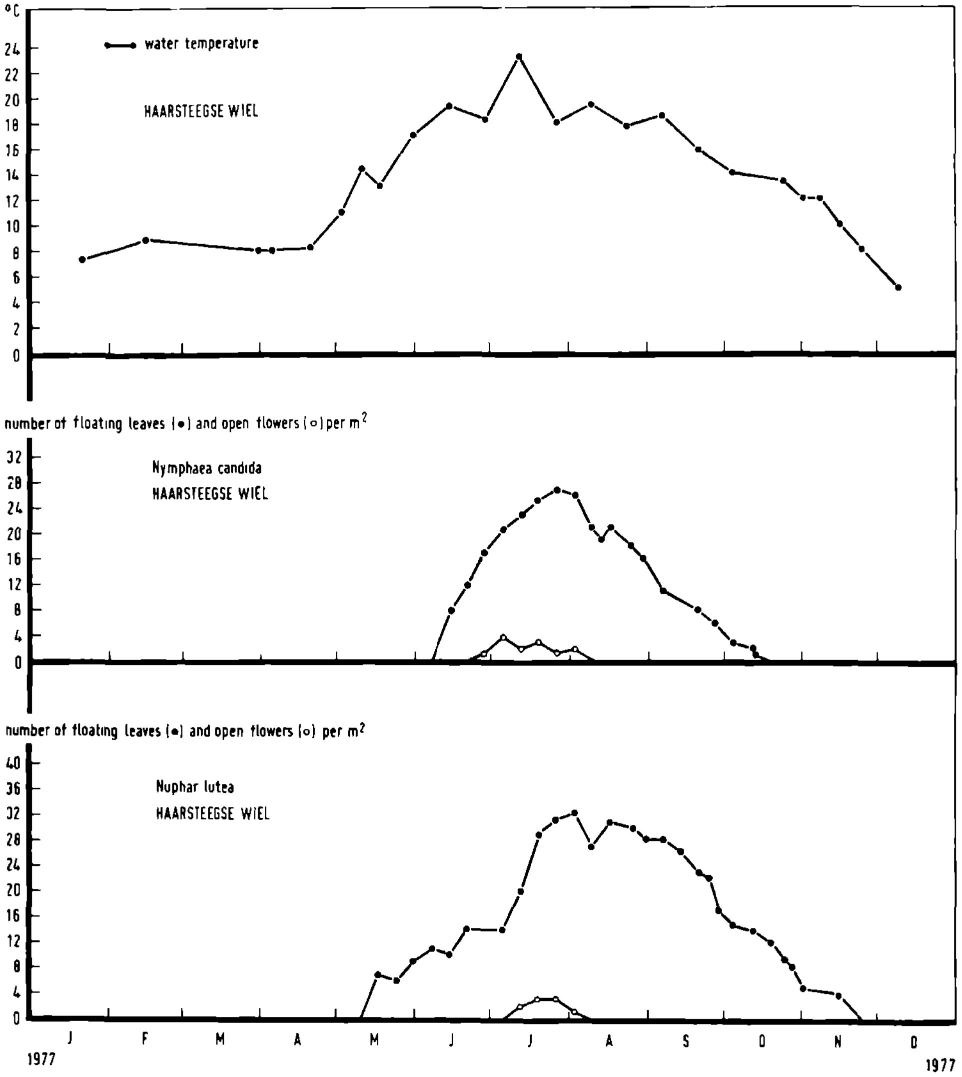

Fig. 7 The course of water temperature, the development of floating leaves and flowers of *Nymphaea candida* Presl and *Nuphar lutea* (L.) Sm. in two plots of 1 m² in the Haarsteegse Wiel in 1977.

Nymphaea candida persisted longest, while those of *Nuphar lutea* and *Nymphaea alba* differed in this respect not very much (Table 1 and 2). The leaves of *Nymphoides peltata* persisted shortest, the smaller leaves of the flowering stems of this species persisted shorter than those springing from the short shoots.

The ratio vegetation period / mean leaf persistence gives an impression of

Table 1

Leaf persistance in days	0-10	11-20	21-30	31-40	41-50	51-60	61-70	71-80	81-90	91-100	Total number of leaves
Species, locality and year: %											
Nuphar lutea Oude Waal 1976	3.4	5.6	15.7	33.8	24.7	14.6	1.1	1.1	-	-	89
Nuphar lutea Oude Waal 1977	-	6.8	16.9	35.6	28.8	3.4	5.1	3.4	-	-	59
Nuphar lutea Haarsteegse Wiel 1977	6.5	9.1	11.7	15.6	19.4	15.6	14.3	6.5	1.3	-	77
Nymphaea alba Oude Waal 1976	5.6	16.7	28.4	13.5	20.4	9.8	4.2	1.4	-	-	215
Nymphaea alba Oude Waal 1977	5.6	12.0	10.2	16.7	29.6	8.3	13.9	3.7	-	-	108
Nymphaea candida Haarsteegse Wiel 1977	2.3	13.9	4.7	13.9	32.6	11.6	4.7	14.0	-	2.3	43
Nymphoides peltata Oude Waal 1976	20.5	42.5	32.8	4.2	-	-	-	-	-	-	73
Nymphoides peltata concrete tank 1 1978	9.6	32.4	43.3	13.8	0.9	-	-	-	-	-	638
Nymphoides peltata concrete tank 2 1978	18.1	41.4	35.3	5.0	0.2	-	-	-	-	-	623
Nymphoides peltata concrete tank 1 1978											
short shoot leaves	7.1	29.1	46.7	16.0	1.1	-	-	-	-	-	537
flowering stem leaves	22.8	50.5	24.8	1.9	-	-	-	-	-	-	101
Nymphoides peltata concrete tank 2 1978											
short shoot leaves	11.4	39.9	42.1	6.3	0.3	-	-	-	-	-	411
flowering stem leaves	31.1	44.3	22.2	2.4	-	-	-	-	-	-	212

Table 1 Distribution of floating leaves per species, locality and year expressed as percentages of the total number of leaves followed, per leaf persistence class of 10 days. A leaf is considered to be lost when it has decayed for 95—100% or has disappeared. In 1976 the stands of *Nymphoides peltata* (Gmel.) O. Kuntze emerged so that only 73 leaves could be followed before emergence. In the case of *Nymphoides peltata* from the concrete tanks the data are given separately for the leaves developed from short shoots and those developed from flowering stems.

Table 2

Species, locality and year:		Total number of leaves:	mean leaf persistence days	S.D. days	maximum leaf persistence days	vegetation period days	turn-over rate
Nuphar lutea	Oude Waal 1976	83	39.17	11.21	71	149	3.80
Nuphar lutea	Oude Waal 1977	57	38.39	13.08	74	169	4.40
Nuphar lutea	Haarsteegse Wiel 1977	65	49.89	15.20	87	191	3.83
Nymphaea alba	Oude Waal 1976	111	39.25	13.27	73	191	4.87
Nymphaea alba	Oude Waal 1977	93	46.16	14.77	78	173	3.75
Nymphaea candida	Haarsteegse Wiel 1977	36	52.14	14.80	94	127	2.44
Nymphoides peltata	Oude Waal 1976	73	18.22	7.39	36	-	-
Nymphoides peltata	concrete tank 1 1978	638	22.14	8.53	46	203	9.17
Nymphoides peltata	concrete tank 2 1978	623	16.38	9.98	50	193	11.78
Nymphoides peltata	concrete tank 1 1978						
short shoot leaves		537	23.31	8.24	46	203	8.71
flowering stem leaves		101	16.66	11.65	32	109	6.54
Nymphoides peltata	concrete tank 2 1978						
short shoot leaves		411	20.43	9.71	50	193	9.45
flowering stem leaves		212	14.62	7.49	39	120	8.21

Table 2 The mean leaf persistence of floating leaves in days with standard deviation, the maximum leaf persistence (a leaf is considered to be lost when it has decayed for 95—100% or has disappeared), vegetation period with floating leaves and 'turnover rate' (expressed as the ratio vegetation period / mean leaf persistence) per species, per locality and per year. In 1976 the stands of *Nymphoides peltata* (Gmel.) O. Kuntze emerged so that only 73 leaves could be followed before emergency. Leaves broken of within 10 days in the field have not been taken into consideration in the case of *Nymphaea alba* L., *Nymphaea candida* Presl and *Nuphar lutea* (L.) Sm. In the case of *Nymphoides peltata* from the concrete tanks the data are given separately for the leaves developed from short shoots and those developed from flowering stems.

the 'turn-over rate'; so it is clear that the turn-over of floating leaves is highest in *Nymphoides peltata*, and lowest in *Nymphaea candida* while *Nuphar lutea* and *Nymphaea alba* do not differ very much and take an intermediate position.

THE STRUCTURE OF NYMPHAEID VEGETATION AND ASSOCIATED MACROPHYTES

The spatial arrangement of nymphaeids shows a number of characteristic patterns which can be divided into vertical, horizontal and three-dimensional ones. Stratification may be mentioned as an example of a vertical pattern, zonation as a horizontal one. Three-dimensional patterns are caused by the branching pattern of the underground parts of the nymphaeids.

Structurally nymphaeids can be considered as intermediate between helophytes and submerged aquatic plants. This is also reflected in the zonation patterns; in wind exposed lakes often a littoral border zonation can be found where with increasing depth a helophyte zone is bordered by a nymphaeid zone, and this in its turn is replaced by a zone with only submerged aquatic plants (Hogeweg and Brenkert, 1969a). The nymphaeid species studied grow in general not deeper than 3 metres (Van der Voo and Westhoff, 1961), but depending on the clarity and depth of the water they can settle some metres deeper, but then are usually not able to form floating leaves (Glück, 1924). In small and shallow habitats such a distinct zonation pattern as described above often can not be observed as here many growth forms can occur together.

The nymphaeids fill up the available space in a characteristic way, so that there is space for associated macrophyte species; this has lead to the description of associations based on combinations of nymphaeids with aquatic plants of different growth forms in vegetational studies according to the Braun-Blanquet school. The *Myriophylleto-Nupharetum* Koch 1926 for instance is such an association. According to Den Hartog and Segal (1964) the association is composed of some large nymphaeids, while elodeids and myriophyllids cover the bottom to a very small degree. At the water surface the percentage of covering is very high, owing to the large floating leaves of the nymphaeids which intercept a great deal of the light. As a result of the reduced light and bareness of the bottom the Characeae, which generally form closed communities in deeper water (Charetea), are able to extend under the *Myriophylleto-Nupharetum* and can cover the bottom with a dense mat. Both communities occur also completely separately, according to these authors, and certainly the bond between such vegetation layers in aquatic vegetation is facultative and not obligate. This is also examplified by other studies.

Hogeweg and Brenkert-van Riet (1969b) studied the affinities between growth forms in aquatic vegetations in India and Czechoslovakia. In India they found nymphaeids often in association with potamids, positive affinities were found here towards utricularids, myriophyllids and hydrocharids. Negative affinities were found with respect of charids, parvopotamids, lemnids and *Potamogeton nodosus* Poir., either on account of a different milieu preference or owing to the attainment of optimum development in the alternating season In the case of vallisneriids and ottelids no positive affinity could be detected, although the combination with nymphaeids is common. In the case of Czechoslovakia positive affinities between nymphaeids and magnopotamids, myriophyllids and ceratophyllids were found, while negative affinities were found with parvopotamids (as in India), isoetids, marsiliids, emergent pseudohydrophytes and algae.

There is a difference in the coverage of the floating leaves of the different nymphaeid species, dependent of the kind of species, the way of development of leaves during the season and the time of the year. For example, in the Oude Waal at Nijmegen, the coverage of *Nymphaea alba* was much higher than that of *Nuphar lutea* in the same locality. *Nymphaea alba* produces a large number of leaves per square metre which overlap each other very much, while *Nuphar lutea* produces a lesser amount of leaves which are spread on the water surface so that the leaves have less overlap resulting in more light for submerged leaves and associated macrophytes. The interception of daylight by nymphaeids by which other aquatic vegetation is suppressed, is in study as a biological control-method of aquatic weeds at Wageningen (Pitlo, 1978).

In old river beds in The Netherlands often pure stands of nymphaeids (*Nymphoides peltata, Nymphaea alba* and *Nuphar lutea*) can be found almost without companion species This may be caused by high turbidity of the water by fine mud when it is flooded by the river and by plankton blooms.

Eutrophication which leads to plankton blooms and heavy increase of epiphyton and filamentous algae and so to a strong reduction of light in the water (Phillips et al , 1978) can be the cause of the disappearance of many submerged macrophytes associated with nymphaeids in many waters in The Netherlands. Submerged stages of the nymphaeid species themselves can in this way also be hampered in their development, but when the rhizomes are large enough and floating leaves are formed, they become immune from shading of this kind and the nymphaeid stands can so persist under heavily eutrophicated conditions.

PHYTOPLANKTON

Phytoplankton forms the second source of primary production in the nymphaeid system. Phytoplankton may exercise some influence on the development of the nymphaeids in spring by light interception. This may account for the fact that in pools situated closely together the spring development of the nymphaeids is not always simultaneous, but may be retarded by several weeks. When the nymphaeid develops its floating leaves it can be expected that biomass and species composition of the phytoplankton are influenced by shading. Further, nymphaeids can influence phytoplankton by allelopathy or by competition for nutrients. When the nymphaeids are in dormancy there is no influence on the development of phytoplankton and during this period phytoplankton is the principal primary producer in the nymphaeid system. On an annual basis during this period phytoplankton is the principal structural element, that contributes to the primary production of the nymphaeid system. Therefore, on an annual basis its contribution to the primary production of the system may not be underestimated.

There is an exchange between the epiphyton on the nymphaeid and the phytoplankton, which can influence the species composition of the phytoplankton under the floating leaves and vice versa. Competition between epiphyton and phytoplankton for nutrients and light can be expected.

Investigations on the relations between nymphaeids and phytoplankton have been carried out in the Oude Waal near Nijmegen by Mr. R.M.M. Roijackers; his results will be published in a separate publication.

EPIPHYTON

All submerged above-ground parts of nymphaeids are suitable for the settlement of epiphyton. The epiphytic ‘fitotecton’, in the terminology of Lakatos (1976), is very important with respect to primary production. The presence of macrophytes means an enormous extension of available substrate for the epiphyton, which is totally dependent on the presence of durable substrates such as stones and shells when macrophytes are absent. That the amount of plant substrate is the limiting factor for the development of the epiphyton can be clearly shown by placing large surfaces of artificial substrate in waters by which the biomass of epiphyton increased (Pieczynska and Ozimek, 1976).

The nymphaeid plant can be considered as a substrate for the settlement of epiphyton but perhaps also as a source of nutrients. There is evidence from other macrophyte hosts that the epiphyton can influence the cells of the macrophyte so that nutrients leach from the macrophyte tissue (Howard-Williams and Davies, 1978). Evidence of the utilization by the epiphyton of dissolved organic products released by various macrophyte hosts has been provided by Linskens (1963). Fitzgerald (1969), Allen (1971), Harlin (1973, 1975). McRoy and Goering (1974) and Langlois (1975). Further there can be influence of algicidal substances on the epiphyton (Fitzgerald, 1969). Therefore, differences between the epiphyton of macrophyte hosts and artificial substrates may be expected. The influence of excretions on the epiphytic community is, however, not known, so that epiphytic populations are considered to be largely determined by the physicochemical conditions of the water and not by the substrate to which they are attached (Eminson, 1978). Pieczynska and Spodniewska (1963), Hutchinson (1975) and Moss (1976) found that the kind of substrate is not very important for the community structure, but Prowse (1959) cultured epiphyte-free macrophyte species, which he transferred to a pond and afterwards found that each of them obtained a distinctly different diatom population. Other factors may have caused such differences, Pieczynska and Ozimek (1976) remarked that the various littoral sites differ in conditions for the epiphyton growth and that epiphyton communities in particular zones of the littoral have a distinct character.

Siver (1977) found in one pond differences in diatom populations on glass slides, leaves of *Potamogeton robbinsii* Oakes and on *Nymphaea odorata* Ait. On glass slides *Achnanthes minutissima* Kutz. was most dominant (ca. 40% of the epiphytic community). *Eunotia incisa* W. Sm. ex Greg. and *Cocconeis placentula* var. *euglypta* (Ehrenberg) Cleve were less common, comprising less than 10% of the glass communities and never being dominant. On *Potamogeton robbinsii Achnanthes minutissima*, *Cocconeis placentula* var. *euglypta* and *Eunotia incisa* composed on average 26, 24 and 22% of the total population, while *Anomoeneis vitrea* (Grun.) Ross composed averagely 10%. The most common species on *Nymphaea odorata* were *Anomoeneis vitrea* (58%), *Achnanthes minutissima* (13%), *Eunotia incisa* (10%) and *Cocconeis placentula* var. *euglypta* (7%). Although the most important species did occur on the various substrates the relative dominance showed distinct differences.

This is also the conclusion of Ho (1979) who compared artificial substrates (cellulose acetate foil) and macrophytes on different places within the Schohsee (Western Germany) and found also in the case of *Nymphaea alba* and *Nuphar lutea* no difference in species composition of epiphyton between these species, the foil and neighbouring macrophytes. It can be concluded that there are distinct quantitative differences in the epiphytes of various substrates but no distinct qualitative differences.

The relations between macrophytes and epiphyton are antagonistic. The macrophytes provide the substrate for epiphyton which results into a larger number of organisms within the system, but they also limit the light conditions and reduce to some extent algal growth. The light conditions change with the season and the development of a macrophyte stand. In the case of nymphaeid-dominated stands there is much transmission at the beginning and the end of the growth season, but when floating leaves develop self-shading sets in. Further in summer large green cottonwool-like masses of filamentous algae *(Mougeotia, Oedogonium, Spirogyra)* can develop between the nymphaeids, which algae are reservoirs of epiphytic propagules, especially diatoms, but which algae also diminish light in the water column (Ho, 1979).

Not only the development but also the growth form of the macrophyte is important for the manner of influencing the light conditions. *Potamogeton robbinsii* for instance grows parallel to the bottom sediment on a locality studied by Siver (1978), this author remarked that in this case a vertical differentiation of epiphyton related to different light conditions, temperature or oxygen could not be found. In nymphaeids a vertical differentiation, caused by light, temperature and oxygen conditions together, certainly exist. Other chemical factors were also measured such as pH etc. but these appeared not to differ significantly from the surface layer to the bottom in nymphaeid

Table 3

	Taxa: Depth	20 cm %	50 cm %	100 cm %
I	Achnanthes lanceolata (de Brébisson) Grunow	11	12	5
	Synedra tabulata (Agardh) Kützing	12	3	3
	Fragilaria capucina Desmazières (Kützing)	9	2	-
	Nitzschia linearis W. Smith	6	2	1
	Nitzschia palea (Kützing) W. Smith	5	2	0.4
	Melosira varians Agardh	5	2	2
	Nitzschia kützingiana Hilse	5	4	3
	Fragilaria capucina var. mesolepta (Rabenhorst) Grunow	2	5	-
	Epithemia sorex Kützing	1	1	-
	Cymbella affinis Kützing	1	1	-
	Fragilaria construens (Ehrenberg) Grunow	0.3	0.4	-
	Achnanthes lanceolata f. ventricosa Hustedt	3	-	-
	Cocconeis placentula Ehrenberg	2	-	-
	Diatoma vulgare Bory	2	-	-
	Fragilaria intermedia Grunow	1	-	-
	Cocconeis scutellum Ehrenberg	0.3	-	-
	Cymatopleura solea (de Brébisson) W. Smith	0.3	-	-
	Caloneis amphisbaena (Bory) Cleve	0.3	-	-
II	Rhopalodia gibba (Ehrenberg) O. Müller	11	37	14
	Gomphoneis olivaceum (Lyngbye) Cleve	-	6	4
	Achnanthes microcephala (Kützing) Grunow	-	3	-
	Synedra acus var. radians (Kützing) Hustedt	-	1	-
III	Gomphonema angustatum (Kützing) Rabenhorst	3	-	5
	Rhoicosphenia curvata (Kützing) Grunow	2	0.4	2
	Amphora ovalis Kützing	2	-	5
IV	Eunotia lunaris (Ehrenberg) Grunow	6	7	35
	Synedra acus Kützing	-	2	2
	Gomphonema acuminatum Ehrenberg	-	1	3
	Fragilaria virescens Ralfs	-	-	3
	Fragilaria brevistriata Grunow	-	-	2
	Eunotia pectinalis (Dillwyn) Rabenhorst	-	-	1
	Fragilaria pinnata Ehrenberg	-	-	0.4
	Cyclotella comta (Ehrenberg) Kützing	-	-	0.4
V	Cocconeis pediculus Ehrenberg	6	6	5
	Navicula exigua (Gregory) Grunow	3	3	4
	Gyrosigma acuminatum (Kützing) Rabenhorst	0.3	0.4	0.4
	Total number of taxa	26	22	22

Table 3 Relative abundance of diatom species on petioles of *Nuphar lutea* (L.) Sm. from 20 cm under the water surface to the bottom (100 cm). The results presented here are from one sample taken from the Oude Waal (Date: 22 July 1975).
Five categories are distinguished: I. species having their greatest abundance on 20 cm below the water surface, II. idem on 50 cm depth below the water surface, III. idem on 20 and 100 cm depth, IV. idem on 100 cm depth, V. species with an abundance not related to depth.

Table 4

Depth:	1 Open water	2 Open vegetation	3 Dense vegetation
Above the water surface	100 %	100 %	100 %
5 cm under water	71	65	65
10 cm under water	63	45	38
20 cm under water	42	30	25
40 cm under water	29	18	15
70 cm under water	17	12	7

Table 4 Light intensity at various depths, expressed as percentage of surface light, 1: in open water, 2: *in an open stand of Nuphar lutea* (L.) *Sm.* and 3: *in a dense stand* of *Nuphar lutea.*

stands. The vertical differentiation of the diatom community on petioles of *Nuphar lutea* is shown in Table 3. In Table 4 the light conditions related to depth for a *Nuphar lutea* vegetation are given. As could be expected the decrease of light is higher in a *N. lutea* stand than in open water; the difference is largest 10—20 cm below the surface. The temperature of the surface water layer can be several degrees higher than below in the daylight, but temperatures under floating leaves remain lower than in unshaded water of the same depth. The surface layer is rich in oxygen, while near the muddy bottom under the nymphaeids the oxygen content is always much lower (only 9—44% of that of the water surface).

It appeared from investigations carried out in the Oude Waal near Nijmegen during 1976 that the epiphyton of floating leaves consists mainly of diatoms. Further a number of Chlorophyceae such as *Coleochaete scutata* Bréb., *Coleochaete soluta* Pringsh. and *Ulothrix* spec. and some Cyanophyceae such as *Gloeotrichia pisum* (Ag.) Thur. and *Gloeotrichia natans* Rabenh. occur as epiphytes.

Den Hartog (1959) mentioned that *Coleochaete scutata* is much more abundant on the under surface of leaves of *Nymphaea alba, Nuphar lutea* and *Stratiotes aloides* L. than on *Typha-* and *Phragmites* stalks. Ho (1979) found that the mean cell volume of this species expressed as a percentage of total cell volume per sample was highest on emergents.

Hutchinson (1975) stated with respect to *Gloeotrichia pisum* that horizontally orientated glass slides were colonized on their undersides by this species but not at their upper surface. Ho (1979) found that this species grows abundantly on all kinds of aquatic macrophytes and non-living objects in the Schöhsee, but particularly on floating leaves; this can be caused by the horizontal orientation of the flat leaves of the nymphaeids together with the light conditions present there. The only other species Ho (1979) found more on nymphaeids than on other growth forms are the diatom *Cyclotella comta*

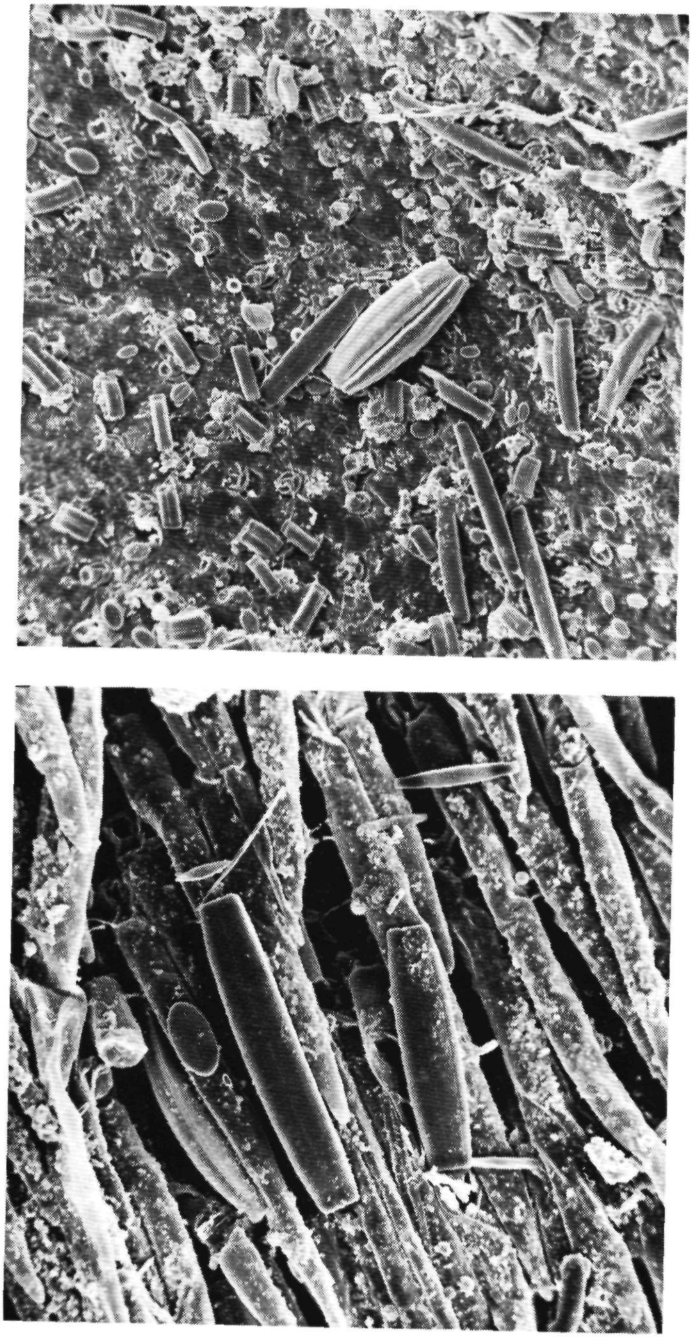

Fig. 8 Scanning photographs of epiphyton of a floating leaf of *Nuphar lutea* (L.) Sm. A: large numbers of diatoms at the underside of a floating leaf, B: epidermal hair-cells of the petiole which form a good lodging place for diatoms and other small algae.

and the green alga *Oedogonium boscii* Wittrock sec. Hirn.

According to De Graaf (1955) the epiphyton of floating leaves of *Nymphaea alba* and *Nuphar lutea* is poor with respect to Chlorophyceae. He considered the low light intensity at the underside of the leaves as a primary cause; another cause suggested by him could be a short leaf persistence. According to De Graaf (1955) *Coleochaeta scutata* is a characteristic species; he observed *Bulbochaete* spec. and *Oedogonium* spec. sporadically, while diatoms were dominant.

Ho (1979) found also a dominance of diatoms on nymphaeids *(Nuphar lutea, Nymphaea alba).* In contrast with helophytes and *Polygonum amphibium* L., on which more green algae occurred, more bluegreen algae were found on *Nymphaea* and *Nuphar*, even more than on submerged macrophytes. The fact that the epiphyton of *Nymphaea alba* and *Nuphar lutea* has a greater mutual similarity than with that of *Polygonum amphibium*, also a nymphaeid, can be caused by the different depths at which they grow; and subsequently by other light and temperature conditions at the different sites. It is remarkable that *Potamogeton lucens* L. which is often associated with *Nuphar* and *Nymphaea* shows the largest similarity with these in general epiphyte composition of all submerged plants as found by Ho (1979).

The dominance of diatoms on nymphaeids *(Nuphar, Brasenia)* has also been found by Woelkerling (1976) and Gough and Woelkerling (1976) in Wisconsin waters with very different physico-chemical properties.

The manner of development of plant parts plays also a role with respect to the epiphyton settlement; this is an aspect often totally neglected in epiphyton studies. In the floating leaves a zone bordered by two lines from the leaf tip to the tips of the basal lobes is already colonized before the leaf unrolls itself at the water surface (Fig. 9). This area is in *Nuphar lutea* 18—25% of the whole leaf area, in *Nymphaea alba* 18-·28%, and in *Nymphoides peltata* 27—43%. The development of periphyton at both sides of this area starts when the leaf has unrolled itself and has become subjected to other light, oxygen and temperature conditions. At the leaf margin there is full sunlight, so that the floating leaves are often fringed by filamentous Chlorophyceae such as *Oedogonium pringsheimii* Cramer, 1859, which are very scarce at the leaf underside. The transmission of light through the lamina of a floating leaf without epiphyton is for the investigated nymphaeids at average 1.00—1.37%. Ho (1979) mentions 2%, for two overlapping laminae 0.2%. Under the leaves a light decrease to 54% could be measured with a Griffin Environmental Comparator. Near the midrib the light appeared to be diminished with 20—27% (average 24%) in an open stand of *Nuphar lutea* and with 37—46% (average 39%) in a dense vegetation. Between the midrib and the leaf margin these values were 13—18% (average 15%) in the open stand and 21—30% (average 25%) in the dense stand.

The differences in the diatom composition of both areas of *Nuphar lutea* leaves are shown in Table 5.

Considering only species with a relative abundance of more than 5%, two

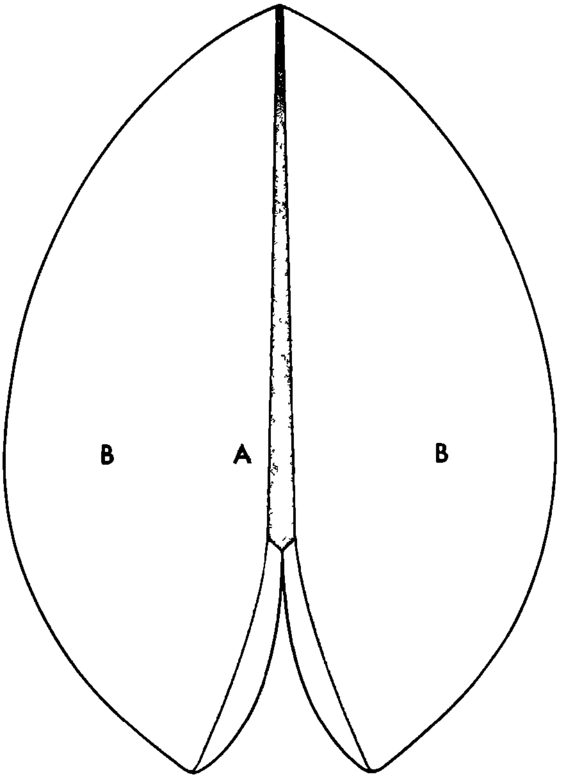

Fig. 9 Underside of a floating leaf of *Nuphar lutea* (L.) Sm. showing two areas, viz. area A which is already colonized by the epiphyton before the leaf has unrolled itself, and area B which is colonized later when the leaf has unrolled itself at the water surface.

species have a clear optimum near the midrib viz. *Fragilaria virescens* and *Gomphonema angustatum.* Along the leaf margin eight species have their optimum viz. *Nitzschia linearis, Navicula gracilis* var. *schizonemoides, Melosira italica, Fragilaria capucina* var. *mesolepta, Fragilaria pinnata, Synedra tabulata, Achnanthes microcephala* and *Diatoma vulgare.* The species of the other groups distinguished in Table 5 had no relative abundance above 5%.

Apart from the difference in initial epiphytic settlement between the two areas the differentiation can also be caused by the phototactic character of diatoms. Diatoms are mainly positively phototactic. Van der Werff and Huls (1957—1974) remark, however, that in strong light diatoms, as far as they are capable, react negative and move to sites where the light intensity is lower. Further Jørgensen (1955) and Cholnoky (1968) found that the influence of light on the occurrence of diatoms is often connected to temperature. It is interesting to compare the diatoms of the floating leaves and of the petioles (Tables 3 and 5). It is remarkable that *Gomphonema angustatum* occurs mostly near the midrib of the floating leaves of *Nuphar*

Table 5

	Taxa:	A	B
		%	%
I	Fragilaria virescens Ralfs	8.5	0.8
	Gomphonema angustatum (Kützing) Rabenhorst	5.5	1.7
	Cocconeis pediculus Ehrenberg	4.1	3.6
	Cocconeis placentula Ehrenberg	3.2	0.8
	Gomphonema acuminatum Ehrenberg	2.4	1.7
	Lycmophora gracilis (Ehrenberg) Grunow	2.3	0.8
	Cyclotella comta (Ehrenberg) Kützing	2.2	1.7
	Navicula rhynchocephala Kützing	2.1	0.8
	Gyrosigma acuminatum (Kützing) Rabenhorst	2.1	0.8
II	Fragilaria intermedia Grunow	3.8	-
	Achnanthes lanceolata (de Brébisson) Grunow	3.2	-
	Synedra ulna (Nitzsch) Ehrenberg	2.6	-
	Rhoicosphenia curvata (Kützing) Grunow	2.6	-
	Fragilaria brevistriata Grunow	2.7	-
	Fragilaria capucina Desmazières	2.4	-
	Fragilaria vaucheriae (Kützing) Petersen	0.8	-
	Rhopalodia gibba (Ehrenberg) O. Müller	0.5	-
	Cocconeis scutellum Ehrenberg	0.5	-
	Melosira varians Agardh	0.2	-
	Cymbella aspera (Ehrenberg) Cleve	0.2	-
	Eunotia lunaris (Ehrenberg) Grunow	0.2	-
	Eunotia pectinalis (Dillwyn) Rabenhorst	0.2	-
	Cymbella cymbiformis (Agardh? Kützing) van Heurck	0.2	-
	Synedra acus var. radians (Kützing) Hustedt	0.1	-
III	Pinnularia gibba Ehrenberg	-	0.8
	Plagiogramma staurophorum (Gregory) Heiberg	-	0.8
	Cymbella affinis Kützing	0.2	0.8
	Amphora ovalis var. pediculus Kützing	0.2	0.8
	Gomphoneis olivaceum (Lyngbye) Cleve	0.5	2.6
	Fragilaria construens (Ehrenberg) Grunow	0.2	2.6
	Diatoma elongatum (Lyngbye) Agardh	3.0	3.5
	Achnanthes lanceolata f. ventricosa (Hustedt)	0.2	4.4
	Nitzschia linearis W. Smith	3.0	5.3
	Navicula gracilis var. schizonemoides Van Heurck	0.2	5.3
	Melosira italica (Ehrenberg) Kützing	3.3	6.1
	Fragilaria capucina var. mesolepta (Rabenhorst) Grunow	0.2	6.1
	Diatoma vulgare Bory	5.8	7.0
	Achnanthes microcephala (Kützing) Grunow	4.6	7.9
	Fragilaria pinnata Ehrenberg	5.8	10.6
	Synedra tabulata (Agardh) Kützing	9.9	13.2
IV	Nitzschia kützingiana Hilse	3.5	3.6
	Nitzschia palea (Kützing) W. Smith	3.5	3.5
	Navicula exigua (Gregory) O. Müller	2.4	2.6
	Total number of taxa	41	28

where the light is diminished strongly and also on dark places on the petiole 100 cm under the water surface). It is possible that specimens of this species have settled near the midrib when the leaf occurred near the bottom. Species as *Nitzschia linearis* and *Fragilaria capucina* var. *mesolepta*, which are on the leaf more abundant near the margin, occur on the petioles also on places with more light (50 and 20 cm under the water surface).

With respect to oxygen demand of the diatom species some data are known. According to Scheele (1952) and Cholnoky (1968) *Cocconeis pediculus* is rather indifferent with respect to oxygen and it is found over the whole petiole in equal amounts. *Rhopalodia gibba* can tolerate lack of oxygen fairly well according to Cholnoky (1968) and it occurs in large numbers at a depth of 100 cm, i.e. near the bottom on the petioles. *Fragilaria capucina* var. *mesolepta* and *Gomphoneis olivaceum*, which are abundant at 50 cm depth, are species which need much oxygen according to this author. The species occurring on the petioles at 20 cm depth demand, according to Cholnoky (1968), a high oxygen level, e.g. *Achnanthes lanceolata, Synedra affinis, Fragilaria capucina, Nitzschia linearis, Nitzschia palea, Nitzschia kützingiana* and *Melosira varians.*

An other factor which must be taken into consideration is the deposition of $CaCO_3$ on the plant parts (see also Allanson, 1973). On scanning photographs it was visible that *Nymphaea alba* had much lime incrustation, *Nymphoides peltata* less and *Nuphar lutea* little. Cattaneo and Kalff (1978) found on other macrophytes that the amount of $CaCO_3$ is the main cause of differences in diversity of epiphytic communities on macrophytes. On *Nuphar lutea* leaves in the Oude Waal near Nijmegen most diatom species were found viz. 41, on *Nymphoides peltata* leaves 40, and on *Nymphaea alba* leaves only 23.

In 1976 the succession of diatoms on *Nuphar* leaves was investigated and compared with that on a P.V.C. tube frame placed at a depth of 10 cm. The initial diatom communities appeared to differ considerably but the differences between the P.V.C. tube and matured floating leaves with respect to their diatom community became smaller when succession proceeded so that it can be concluded that particularly the first settlement of diatoms is strongly dependent on the kind of substrate.

The turn-over of plant parts is another important factor (see Table 2). There is a continuous production of leaves during the season so that the succession of epiphyton on leaves starts at different dates under different light and temperature conditions, while by continuous decomposition of

Table 5 Relative abundance of diatom species of floating leaves of *Nuphar lutea* (L.) Sm.: area A near the midrib of the leaf, area B one centimetre from the leaf margin (see Fig. 9). The results presented here are from one sample taken from the Oude Waal (Date: 26 May 1975). Four categories have been distinguished: I. species having their greatest abundance along the midrib, II. species, only occurring along the midrib, III. species having their greatest abundance near the leaf margin and IV. species indifferently occurring in both areas.

the leaves the succession again and again is broken off during the season. With the ageing of the leaves the consistency changes also, and this too can cause differences in epiphyton settlement.

On matured fresh leaves of *Nuphar lutea* collected from different sites in the Oude Waal near Nijmegen at 15 and 29 June 1975 *Synedra tabulata* (11.6% of the total diatom population), *Fragilaria pinnata* (8.2%) and *Diatoma vulgare* (6.4%) were most numerous, on those of *Nymphaea alba* *Achnanthes lanceolata* f. *ventricosa* (36.4%), *Amphora ovalis* var. *pediculus* (20.2%), *Achnanthes lanceolata* (8.7%) and *Achnanthes microcephala* (6.9%) were dominant, while on *Nymphoides peltata* leaves *Cocconeis pediculus* (23.3%), *Cocconeis placentula* (8.1%) and *Rhopalodia gibba* (5.6%) were most numerous. The leaves of *Nuphar* and *Nymphaea* become in general older than those of *Nymphoides* (Table 1 and 2). For this reason it is interesting that *Cocconeis* species, which are known as pioneers under the epiphytes, are very dominant on *Nymphoides* leaves. *Cocconeis placentula* is often the first diatom which settles on plants (Sieburth and Thomas, 1973) forming a flat mucilage layer, although it may be also epilithic (Jones, 1978). The species is typical for living plant tissue, as Willer (1923) found that *Cocconeis placentula* could move away from dying portions of an *Elodea* leaf and became concentrated on the still living parts. Geitler (1977) found typical defense reactions of cells of *Fontinalis antipyretica* Hedw. as reaction on the occurrence of *Cocconeis placentula* and concluded that this diatom is not totally harmless to its host.

Further, the epiphytic community is influenced by grazing of animals such as snails, chironomid larvae (Mason and Bryant, 1975a) and Oligochaetes (Learner et al., 1978). Due to the grazing activity of snails tracks on the leaves become free of epiphyton and succession has to start again. So a mosaic is formed of small parts with different succession stages of epiphyton on one plant part.

The epiphyton can have a negative influence on the plant parts where they settle. According to Ho (1979) first settlement on macrophytes is by bacteria within 1—2 days, followed by diatoms, and in two to three weeks by green and bluegreen algae. The primary colonizing bacteria can cause cuticular erosion and epidermal pitting (Howard-Williams and Davies, 1978), and so the decomposition can be accelerated by the epiphytic settlement.

High fertility of the water leads to an increase of epiphytes on macrophytes (Eminson, 1978); these influence in a negatively way the photosynthetis of the macrophyte in all submerged parts. Sand-Jensen (1977) showed a reduction in eelgrass photosynthesis due to the presence of epiphytic diatoms. In the nymphaeids photosynthesis takes place mainly in the floating leaves so that the epiphyton can only influence photosynthesis of submerged parts.

From the above the general conclusion can be drawn that the situation of epiphyton on nymphaeids is very complex because of the many interrelations between the epiphytic community, the host macrophyte and its environment, and therefore much research is still needed. A further study has to performed on structure and species composition in relation to the age and condition of the various plant parts during a whole year using transects so that the influence of depth and wave-action can also be studied. Wave-action seems to be unfavourable for the settlement of epiphyton, but may assist in the dispersal of diaspores (Ho, 1979). Physico-chemical data have to be studied on different depths and during a whole year in relation to the development of the nymphaeids, so that a model can be made of the epiphytic community in space and time. Production and biomass of epiphyton have to be the subject of an other study for which the work of Ho (1979) offers a good starting point.

ENDOPHYTES

The endophytes of the nymphaeids consist mainly of fungi which inhabit the floating leaf tissue (Van der Aa, 1978; Lammens and Van der Velde, 1978). Material collected from nymphaeids in the Oude Waal and the Haarsteegse Wiel is now in study by the Centraal Bureau voor Schimmelcultures at Baarn.

MICROBIAL ORGANISMS

Till now no study is made of the microbial organisms occurring on the nymphaeid plant material but certainly they are very important with respect to decomposition, so that it is an important desideratum for further research.

ACCOMPANYING FAUNA

The nymphaeid structure offers many possibilities for a rich fauna; ten structural fauna elements can be distinguished, which are treated here per compartment (see Fig. 1). The bond with nymphaeids varies per species and can be very loose to obligate. In the latter case the species use the nymphaids as food. Most investigations have been carried out on the macrofauna of floating leaves (compartment A, D and E) in eutrophic waters. Therefore, the results of these investigations are treated here in more detail, while only short remarks are made on the fauna of the other compartments. The main differentiation of the fauna shows a vertical arrangement. Therefore the fauna of the different compartments is treated here more or less in sequence from above to below.

Compartment L. (Air)

The aerial space above the water surface and the nymphaeid stands is used by birds and adult, winged insects. As most conspicuous birds swifts (*Apus apus* (L.)), swallows (*Hirundo rustica* L. and *Delichon urbica* (L.)) and terns (*Sterna hirundo* L. and *Chlidonias niger* (L.)) can be mentioned, as most conspicuous insects the large Odonata (Anisoptera).

Swifts, swallows and dragonflies all prey on the very numerous insects such as Ephemeroptera, Nematocera and Trichoptera coming from the floating leaves and the water surface. The terns mainly prey on small fish which are very abundant under and between the nymphaeids, but occasionally they feed on insects too.

Compartment B. (Flower)

The flowers of the nymphaeids are situated above or on the water surface. They attract by special features, peculiar to each species, all kinds of insects, even visitors of terrestrial flowering plants, which are not specific for a nymphaeid system, but also those insects normally occurring in the compartments C and D such as Ephydrid flies. Also some spiders, normally occurring in the compartment C and D, e.g. *Pirata piraticus* (Clerck) (Lycosidae) and *Erigone atra* (Blackwall) (Micryphantidae) can be found in the flowers where they prey on insects.

The function of the flowers for the fauna (especially insects) and vice versa of the fauna for pollination is illustrated here by studies on the autecology of the Ephydrid fly *Notiphila brunnipes* (Van der Velde and Brock, 1980) and on the floral biology of *Nymphoides peltata* (Van der Velde and Van der Heijden, 1980).

The fact that peduncles of nymphaeid flowers are often partially above the water surface is important for the emergence of some insects with aquatic larvae such as Trichoptera and Odonata, and also for egg deposition under water e.g. by certain species of Odonata.

Compartment C. (aerial leaf)

The aerial leaves have many insect species in common with the upperside of floating leaves (compartment D). In contrast to these the aerial leaves function as watching post (Odonata) and also as shelter side. With the exception of the petioles they are not used as egg deposition site, they are also not used as a sunning and sitting site of frogs, and they can not be walked over by Rallidae. Further no damage of aquatic animals occurs.

Compartment D. (upperside floating leaf)

The upperside of floating leaves is used by many species occurring also in the compartments B, C, D, L and M (see for a comparison of the fauna of compartment B with that of D Van der Velde and Van der Heijden (1980)).

The fauna on the upperside of floating leaves consists of vertebrates such as Rallidae (*Fulica atra* L., *Gallinula chloropus* (L.)) which run over the leaf blades in their search for food (mainly insects and in the case of *Fulica atra* also fresh leaves and parts of flowers of nymphaeids), the green frog (*Rana esculenta* (L.)) which can sit on the leaves for preying on insects and for sunning, and further of many insects and some species of spiders. To study the qualitative and quantitative composition of the last mentioned taxa on the floating leaves an insect-lime method gives the best results (Deonier, 1972). A description of the method used in the Oude Waal near Nijmegen can be found in Van der Velde (1978) and in Van der Velde and Brock (1980).

Some preliminary results can be given here. In total approximately 23,000

specimens representing more than 200 taxa were caught belonging to two classes viz. Hexapoda (99.4%) and Arachnida (0.6%). The following taxa in sequence of decreasing numbers were present.
Hexapoda: Diptera 60.91% (Nematocera 26.55%, Brachycera 7.51% and Cyclorrapha 26.85%), Trichoptera 35.09%, Hemiptera 1.93% (Homoptera 0.85% and Heteroptera 1.08%), Hymenoptera 1.02%, Coleoptera 0.23%, Collembola 0.13%, Lepidoptera 0.04%, Thysanoptera 0.04% and Odonata 0.01%.
Arachnida: Lycosidae 0.50% and Micryphantidae 0.10%.

The most important insect species with respect to the numbers caught are:
Trichoptera: *Cyrnus crenaticornis* (Kolenati), *Cyrnus flavidus* MacLachlan, *Agraylea sexmaculata* Curtis, *Oecetis lacustris* (Pictet).
Diptera Nematocera: *Cricotopus* spec., *Corynoneura edwardsi* (Brundin), *Parachironomus biannulatus* (Staeger), *Procladius* spec., *Pentapedilum sordens* (Van der Wulp), *Parachironomus frequens* (Malloch), *Parachironomus vitiosus* (Goethghebuer) (Chironomidae), Sciaridae (=Lycoriidae), Culicidae, Ceratopogonidae, Psychodidae, Bibionidae and Tipulidae.
Diptera Brachycera: *Spatiophora hydromyzina* Fall.*, *Hydromyza livens* (F.)* (Scatomyzidae=Scatophagidae=Cordyluridae), *Hydrellia* spp., *Notiphila dorsata* Stenh.* and *Notiphila brunnipes* R.-D.* (Ephydridae).
Diptera Cyclorrapha: *Hydrophorus praecox* (Lehm.), *Dolichopus latelimbatus* (Macq.)*, *Campsicnemus picticornis* (Zett.)*, *Raphium antennatum* (Carl.)* (Dolichopodidae).
Hemiptera Homoptera: *Rhopalosiphum nymphaeae* (L.)* (Aphididae).
Hemiptera Heteroptera: *Gerris lacustris* L., *Gerris argentatus* (Zetterstedt) (Gerridae), *Mesovelia furcata* Mulsant et Rey* (Mesoveliidae).
Hymenoptera: *Praon adjectum* Haliday, *Ademon decrescens* (Nees), *Trioxys auctus* (Haliday) (Braconidae), Ichneumonidae.
Coleoptera: *Donacia crassipes* F. * (Chrysomelidae).
Collembola: *Isotoma viridis* Bourlet (Isotomidae).
Odonata: *Ischnura elegans* van der Linden (Agrionidae).

Some characteristic species lack in this list such as the beetle *Pyrrhalta nymphaeae* (L.) f. *typica* which replaces *Donacia crassipes* in sheltered habitats, but does not occur in the Oude Waal and the characteristic dragonfly *Erythromma najas* (Hansemann) which occur in the Oude Waal but is not caught with the insect-lime method used. Species marked with an asterisk in the list above are more or less typical for a nymphaeid system.

The fauna of compartment D is semi-aquatic, neustonic or terrestrial. The floating leaves form a flat extension of the littoral border, consisting of many small islands, which can be reached by swimming, flying or walking over the water surface with the risk of drowning or being eaten. The temperature of a floating leaf surface can be some degrees higher than the surroundings due to solar radiation on bright days (Dale and Gillespie, 1976; Van der Velde and Brock, 1980), which makes them attractive as sunning site.

With respect to occurrence in time the moments of emergence and the number of generations of each species within a growth season are important. The spatial distribution is caused by the kind of activities carried out by the animals within the nymphaeid zone, e.g. egg deposition (in sheltered sites or in exposed sites), or predation in relation to the spatial distribution of the prey. To understand the differences in occurrence of the various species their autecology has to be studied. An example of such a study is given by Van der Velde and Brock (1980).

The specimens of Chironomidae caught with the insect-lime method appeared to be females for 77%. It is known that males of the Chironomidae form clouds near the littoral border; females fly in such clouds for copulation. After copulation they fly to the open water for egg deposition (Beattie, 1978). Most specimens of Chironomids were caught with the insect-lime method on the floating leaves bordering the open water. This is perhaps also the reason for a similar occurrence of the predatory fly *Hydromyza livens*, which has a preference to prey on Chironomids (Brock and Van der Velde, in prep.).

With respect to food relations four categories within the fauna of the upperside of floating leaves can be distinguished:

A. species eating from the nymphaeids, e.g. the beetle *Donacia crassipes*, which consumes the upper epidermis and palissade parenchyma, the aphid *Rhopalosiphum nymphaeae* which sucks tissue fluids, and flies of the family Ephydridae which consume fluids from decaying parts.

B. species which have no distinct food relations with the nymphaeids e.g. Nematocera and Trichoptera. They occur on the floating leaves because they can rest there after emergence or they use them for egg deposition.

C. Predators living from other insects present (Scatomyzidae, Dolichopodidae, Muscidae, Empididae, Heteroptera semi-aquatica, Odonata, Aranea).

D. Parasites parasitizing on aphids and Diptera (Braconidae) and on Trichoptera, aquatic Lepidoptera and aquatic Coleoptera (Ichneumonidae).

Compartment M. (water surface)

In this compartment water birds and neustonic fauna occur. Some species of water birds, which swim between the floating leaves must be mentioned e.g. ducks, the great crested grebe (*Podiceps cristatus* (L.), the coot (*Fulica atra*) and the moorhen (*Gallinula chloropus*). The great crested grebe eats fish and can build its nests with leaves of *Nymphaea* and *Nuphar*, the coot eats floral leaves of *Nuphar* and parts from the floating leaves of the nymphaeid species and builds often its nest from floating leaves and petioles, ducks eat submerged leaves and sometimes the anthers of *Nymphaea alba*. The moorhen eats mainly insects from the floating leaves; this species can also run over the leaves of *Nymphaea alba*, without causing these to become submerged. In contrast coots cause submersion of the leaves, when they try to walk over them.

The neustonic fauna consists of some species of spiders and insects already mentioned for compartment D, such as *Pirata piraticus*, *Erigone atra*, Gerridae, Mesoveliidae, *Hydrophorus* spp., *Hydrellia* spp., Nematocera (occurring for egg deposition or after emergence) and Trichoptera (often crawling on the water surface). Neustonic insects and spiders often flee to floating leaves when they are disturbed on the water surface; they can also use the floating leaves as sunning site or for other activities (nymphs of Gerridae often hatch here).

Compartment A. (plant tissue)

The plant tissue can be inhabited by real miners e.g. the larvae of *Hydromyza livens* mine in the leaf blades and petioles of *Nuphar lutea* where they consume the plant tissue and also obtain oxygen by means of their pointed stigmata.

Compartment E. (underside floating leaf)

The floating leaves form also a habitat for aquatic animals. In the upper water layer the oxygen content is higher than below; the soft bottom is mostly poor in oxygen. By means of crawling over the petioles or by swimming the animals who need a substrate in an oxygen-rich environment reach the floating leaves and avoid the unfavourable circumstances of the sapropelium layer. Many animal species lay their eggs under the leaves or on peduncles or petioles. Among them are species which occur as imago on the leaf upperside (compartment D) e.g. the beetle *Donacia crassipes*, the fly *Hydromyza livens*, Odonata, Trichoptera, Chironomidae and aquatic Lepidoptera. Other groups such as snails, leeches, water mites, water bugs etc. also lay often their eggs at the leaf underside. A special study on the occurrence of eggs on nymphaeids will be very fruitful.

The light under nymphaeid floating leaves is diminished which is favourable for negatively phototactic animals such as flatworms and leeches.

Except for some insects and pulmonate snails (Lymnaeidae) primarily aquatic invertebrates usually are not able to consume the fresh leaf tissue, but consume decaying parts. The epiphyton in which diatoms usually are dominating forms the main source of food under the floating leaves. The epiphyton layer catches also some detritus, which is a food resource for some detritivores. The animals found under the leaves are consumers of epiphyton, detritivores, sessile filter-feeders or predators.

The following macroinvertebrate groups were found at the underside of floating leaves: Nematocera (Chironomidae, Ceratopogonidae), Trichoptera, Ephemeroptera, Coleoptera, Odonata, Heteroptera, Lepidoptera, Hirudinea, Gastropoda, Bivalvia, Oligochaeta, Hydrozoa, Turbellaria, Ectoprocta, Acari, Porifera (small colonies), Isopoda, Amphipoda, Ciliata (colonies), Rotatoria (colonies).

The following taxa were the most abundant:

Nematocera: *Cricotopus sylvestris* gp., *Parachironomus* sp., *Endochironomus* sp., *Corynoneura* sp., cf *Bezzia* sp.

Trichoptera: *Orthotrichia costalis* (Curtis), *Agraylea multipunctata* Curtis, *Cyrnus flavidus* MacLachlan, *Cyrnus crenaticornis* (Kolenati)

Ephemeroptera: *Cloeon dipterum* (L.), *Caenis horaria* (L.)

Coleoptera: *Donacia crassipes* F. (young larvae)

Odonata: *Ischnura elegans* van der Linden

Heteroptera: *Sigara striata* (L.)
Lepidoptera: *Nymphula nymphaeata* (L.)
Hirudinea: *Erpobdella octoculata* (L.), *Glossiphonia heteroclita* (L.), *Helobdella stagnalis* (L.).
Gastropoda: *Acroloxus lacustris* (L.), *Gyraulus albus* (Müller)
Oligochaeta: *Stylaria lacustris* (L.)
Hydrozoa: *Pelmatohydra oligactis* (Pallas)
Turbellaria: *Bothromesostoma essenii* M. Braun
Ectoprocta: *Plumatella repens* (L.)
Acari: *Limnesia undulata* (Müller)
Isopoda: *Asellus aquaticus* (L.)
Amphipoda: *Gammarus pulex* (L.)
Ciliata: *Vorticella* sp.
Rotatoria: *Sinantherina socialis* (L.).

Nearly none of these species are characteristic in the sense that they only occur on nymphaeids and all have also been recorded from other substrates or macrophyte growth forms with the exception of *Donacia crassipes* (Macan and Kitching (1976); Mason and Bryant (1974, 1975b); Soszka (1975a and b); Higler (1977)).

Six macroinvertebrate groups were most numerous (together always more than 90% of the total numbers of individuals collected from the floating leaves), viz. Nematocera, Trichoptera, Hirudinea, Oligochaeta, Gastropoda and Turbellaria (Fig. 10), but with respect to the share of each group there are large differences between the waters studied. On the nymphaeids of Lake Druzno in Poland Karassowska and Mikulski (1960) found in general a dominance of Hirudinea, in the Oude Waal there was a dominance of Nematocera (mainly Chironomidae), in the Singel at Leiden Gastropods were relatively important, while in the Haarsteegse Wiel Trichoptera were dominant. Karassowska and Mikulski (1960) do not give physico-chemical data.

The Singel in Leiden is highly eutrophicated by organic pollution (plankton blooms), while the chlorinity is here highest, the Oude Waal is flooded by the river Waal and has a relative high chlorinity and some pollution while the Haarsteegse Wiel is unpolluted and very clear, with a very low chlorinity.

The results presented in Fig. 10 are also influenced by the horizontal distribution of the taxa within the nymphaeid zone, and the depths and sites where each nymphaeid species grows. There are large differences in the nymphaeid zones studied qua species and depths. In the Singel there is a broad zone of *Nymphaea alba*, bordered by a small zone of *Nuphar lutea*, which grows deepest here, in the Oude Waal there are broad zones of *Nymphoides peltata*, growing mostly in shallower water than the other nymphaeids, very broad zones of *Nuphar lutea*, while *Nymphaea alba* grows here mostly shallower in sheltered sites within the *Nuphar* zone, in the Haarsteegse Wiel there is a broad *Nuphar lutea* zone with *Nymphaea candida* growing from 1 to 3 metres deep mostly at the outer margins of the *Nuphar* zone (Roelofs and Van der Velde (1977)).

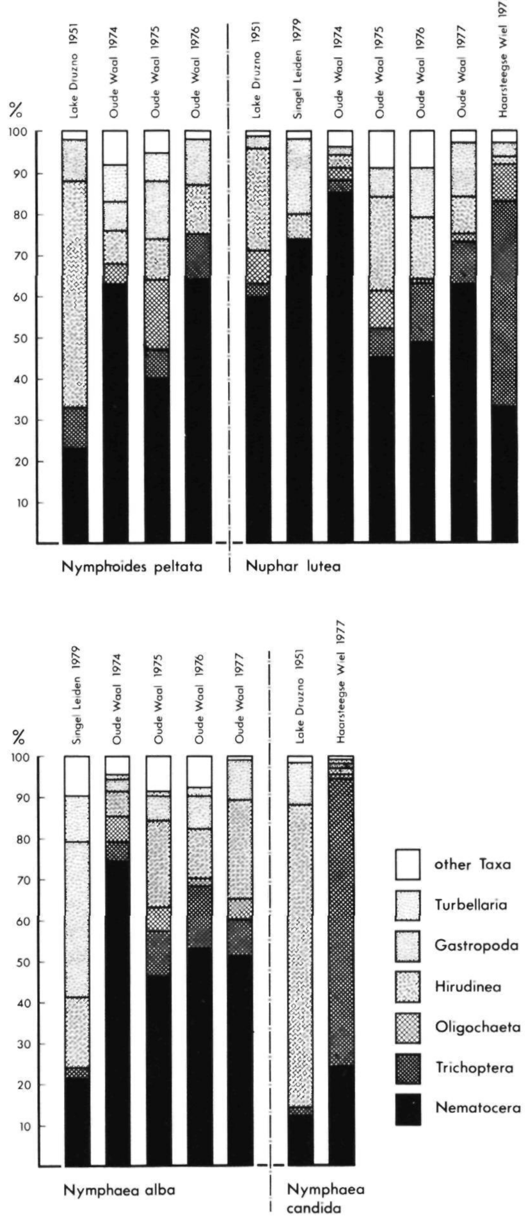

Fig. 10 General relative composition of the macroinvertebrate fauna found on the underside of floating leaves of the different nymphaeid species studied in various localities and in different years. Of each group the average percentage of the total number of macroinvertebrates caught during a growth season is given. The results for each nymphaeid species and each year are based on samples which were taken at regular intervals during a growth season.

In the nymphaeid zones in the Haarsteegse Wiel and in the Oude Waal the horizontal distribution of the macrofauna was studied by means of samples (15 undamaged leaves per sample) taken in transects during the season from the littoral border to the open water. Results on the aquatic macrofauna of floating leaves of *Nuphar lutea* in the Haarsteegse Wiel and the Oude Waal in 1977 are summarized in Table 6. There were distinct differences in distribution of a number of macroinvertebrate groups within the nymphaeid zone in the Haarsteegse Wiel. Here Rotatoria, Oligochaeta, Hirudinea, Gastropoda, Ephemeroptera, Odonata and Trichoptera were most numerous near the littoral border, Ectoprocta in the centre of the nymphaeid stand while Nematocera and Turbellaria were most numerous on floating leaves bordering the open water. In the Oude Waal Turbellaria and Gastropoda were most numerous near the littoral border, Oligochaeta, Hirudinea and Trichoptera in the centre of the nymphaeid stand, while Nematocera had the largest numbers on the floating leaves bordering the open water. It is possible that the thick sapropelium layer near the littoral border in the Oude Waal causing unfavourable oxygen conditions is the cause of the somewhat other distribution pattern in certain macroinvertebrate groups than in the Haarsteegse Wiel, where the sapropelium layer on sand is relatively thin and oxygen conditions are more favourable. In both waters however Gastropods were most numerous near the littoral border and Nematocera near the open

Table 6

Nuphar lutea

	Haarsteegse Wiel 1977				Oude Waal 1977			
Taxa:	**number of specimens**	**A %**	**B %**	**C %**	**number of specimens**	**A %**	**B %**	**C %**
Rotatoria	10	80	20	-				
Turbellaria	9	-	33	67	7	57	14	29
Ectoprocta	112	16	61	23				
Oligochaeta	346	56	42	2	52	35	48	37
Hirudinea	100	69	27	4	222	31	56	13
Gastropoda	114	57	33	10	278	47	38	15
Ephemeroptera	25	76	24	-				
Odonata	10	90	10	-				
Nematocera	1244	29	30	41	1465	20	24	56
Trichoptera	2081	41	37	22	196	19	50	31
minimum depth in cm		50	120	150		110	130	180
maximum depth in cm		130	170	250		150	175	200

Table 6 Relative horizontal distribution of aquatic macroinvertebrate taxa in *Nuphar lutea* (L.) Sm. stands in the Haarsteegse Wiel and the Oude Waal in 1977 based on samples of 15 undamaged floating leaves taken in transects (A, B and C) at regular intervals during the season. Taxa represented by less than 5 individuals have not been taken into consideration. A: floating leaves bordering the littoral border vegetation, B: floating leaves in the centre of the *Nuphar* zone, C: floating leaves bordering the open water (see also Fig. 11, 12 and 13).

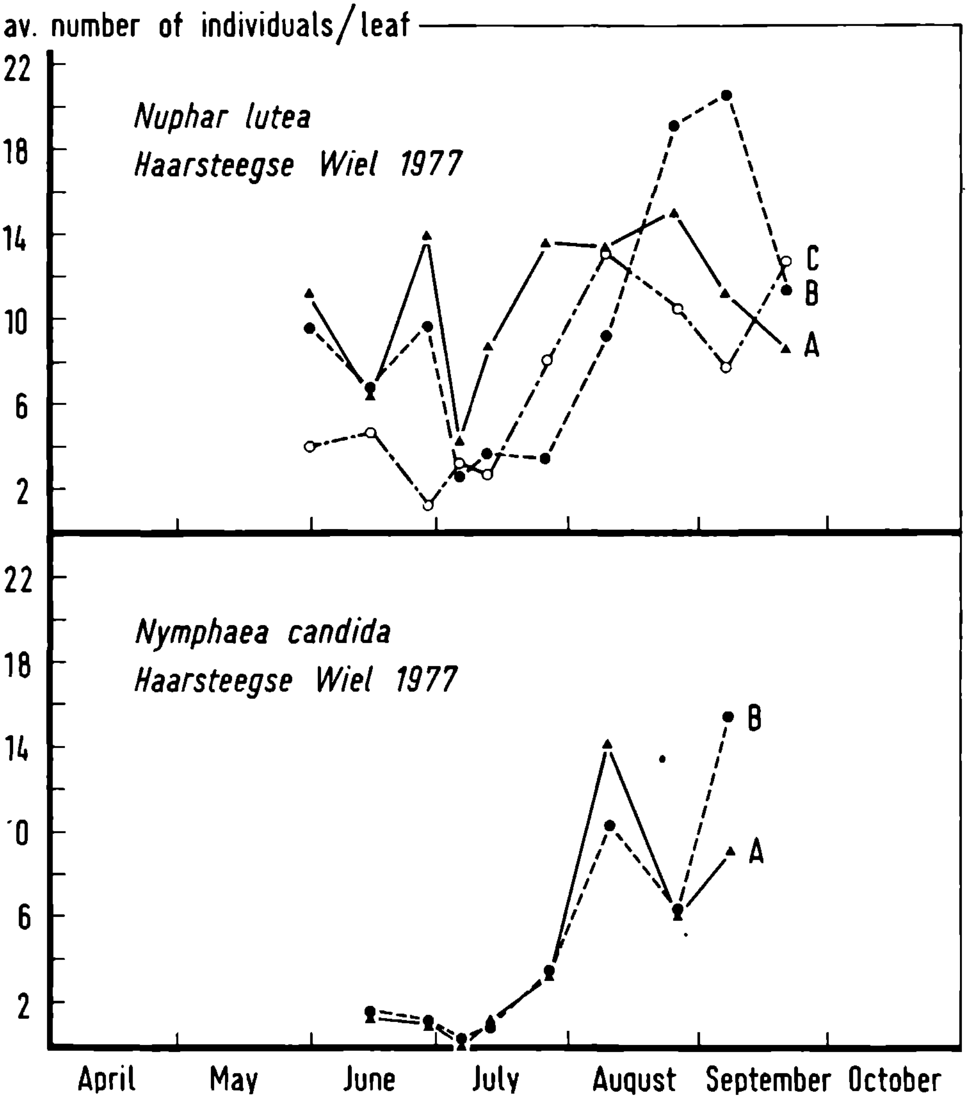

Fig. 11 Average numbers of macroinvertebrates per floating leaf underside of *Nuphar lutea* (L.) Sm. and *Nymphaea candida* Presl during 1977 in the Haarsteegse Wiel. Samples of 15 undamaged floating leaves were taken at each date in transects from shallow to deep. The depths for *Nuphar lutea* are: A 0.50 — 1.30 m, B 1.20 — 1.70 m, C 1.50 — 2.50 m. The depths for *Nymphaea candida* are: A 1.25 — 2.10 m, B 1.80 — 3.00 m (see also Table 6).

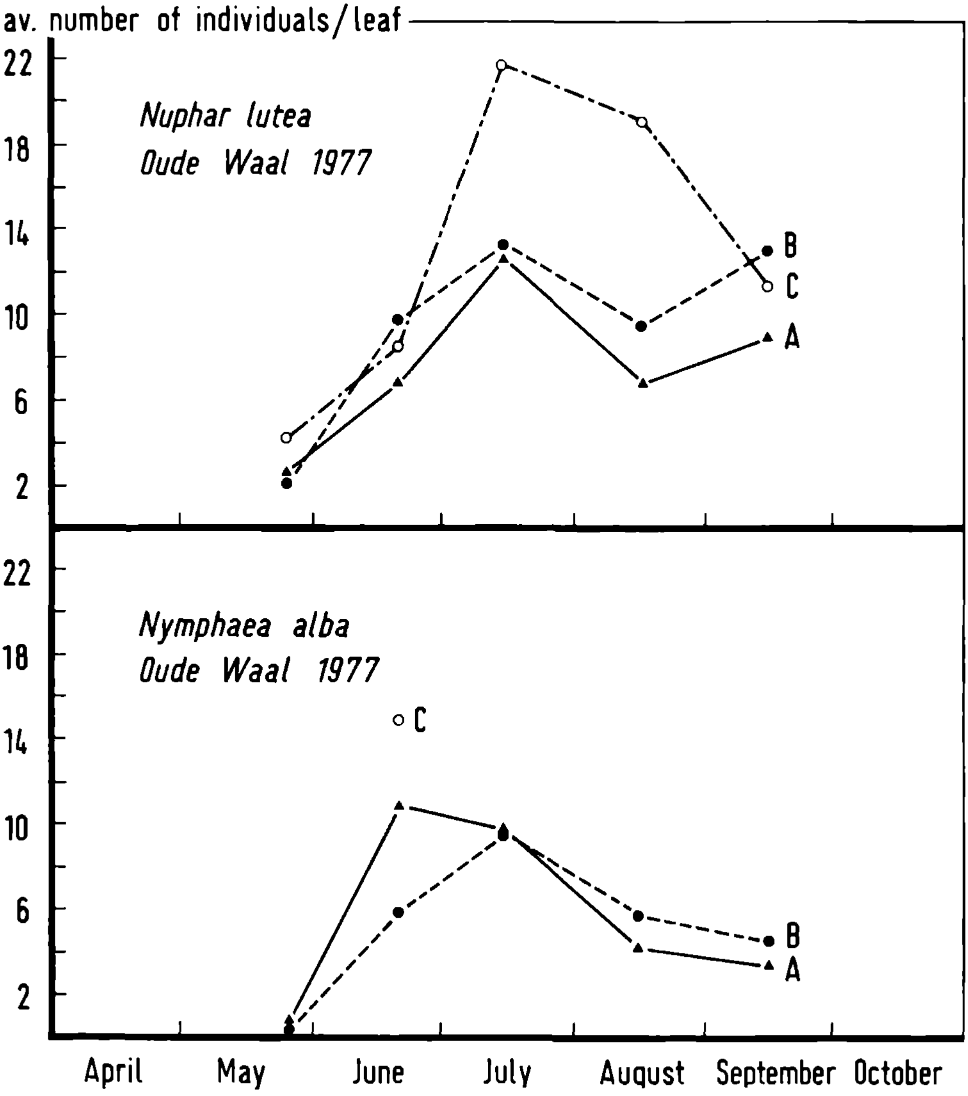

Fig. 12 Average numbers of macroinvertebrates per floating leaf underside of *Nuphar lutea* (L.) Sm. and *Nymphaea alba* L. during 1977 in the Oude Waal. Samples of 15 undamaged leaves were taken at each date in transects from shallow to deep. The depths for *Nuphar lutea* are: A 1.10 — 1.50 m, B 1.30 — 1.75 m, C 1.80 — 2.00 m. The depths for *Nymphaea alba* are: A 1.10 — 1.25 m, B 1.70 — 2.00 m, C 2.00 m (see also Table 6).

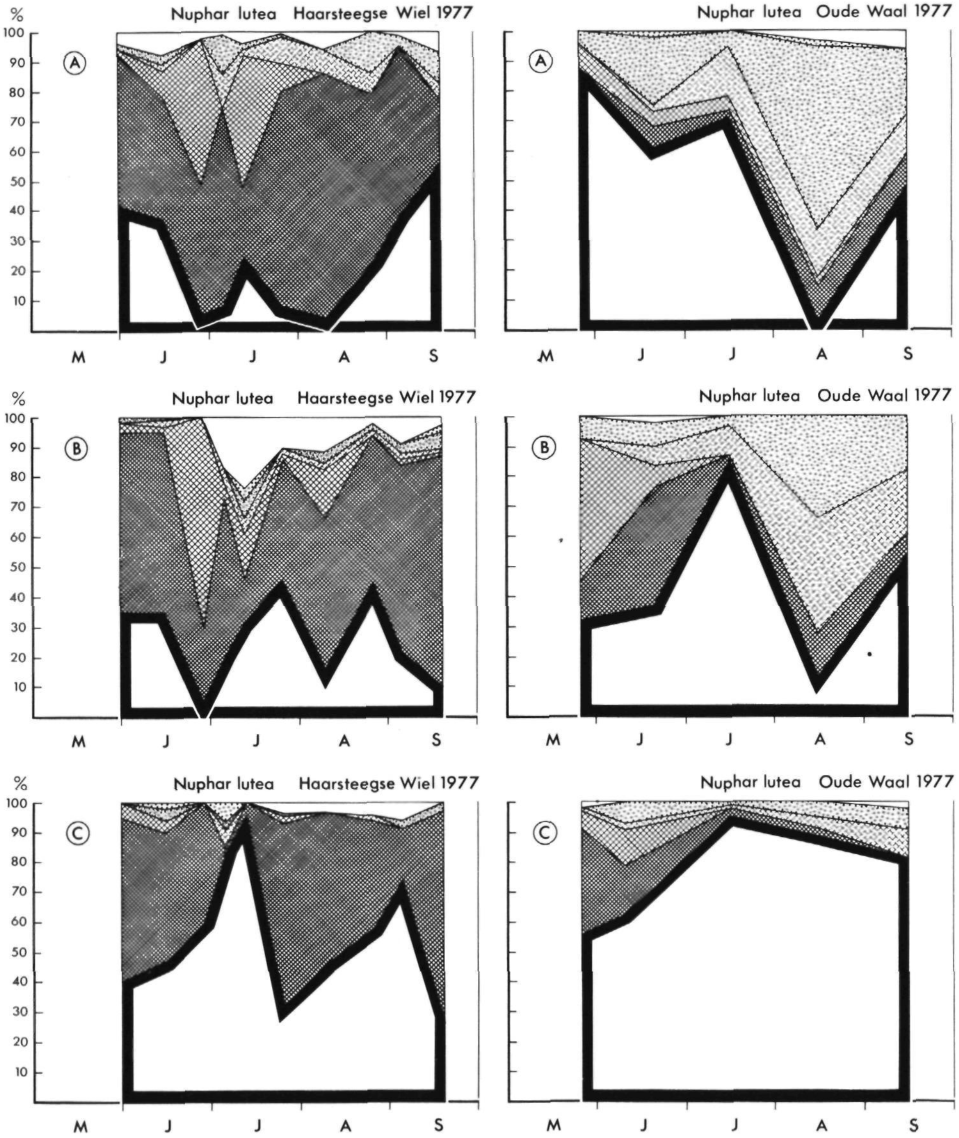

Fig. 13 Changes in the relative share of each macroinvertebrate group on floating leaf undersides of *Nuphar lutea* (L.) Sm. during the growth season of 1977 in the Haarsteegse Wiel and the Oude Waal. Samples of 15 undamaged floating leaves were taken at each date in transects from shallow to deep. *Nuphar lutea* Haarsteegse Wiel depths: A 0.50 — 1.30 m, B 1.20 — 1.70 m, C 1.50 — 2.50 m; Oude Waal depths: A 1.10 — 1.50 m, B 1.30 — 1.75 m, C 1.80 — 2.00 m.

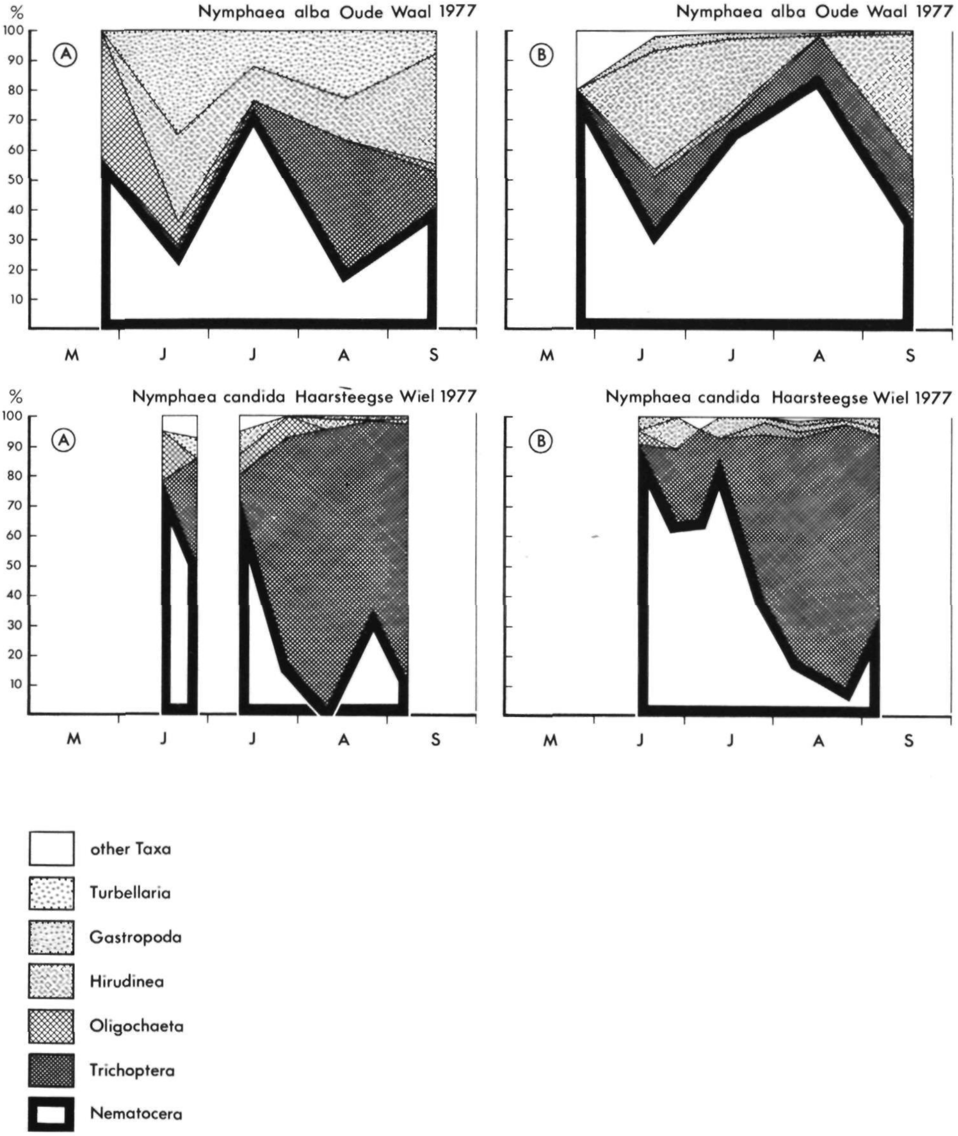

Fig. 14 Changes in the relative share of each macroinvertebrate group on floating leaf undersides of *Nymphaea candida* Presl in the Haarsteegse Wiel and of *Nymphaea alba* L. in the Oude Waal during the growth season of 1977. Samples of 15 undamaged floating leaves were taken at each date in transects from shallow to deep. *Nymphaea candida* depths: A 1.25 — 2.10 m, B 1.80 — 3.00 m. *Nymphaea alba* depths: A 1.10 — 1.25 m, B 1.70 — 1.90 m.

water. For the first-mentioned group this is due to the very favourable food conditions in the littoral border.

The distribution of adult Chironomidae caught with insect-lime on the floating leaves showed the same pattern as that of the larvae so that the distribution of the larvae seems to be determined by the preference of females to lay their eggs near the open water (see further under Compartment D).

There are large changes in the numbers of macroinvertebrates during the season on the floating leaves and also in the share of each group (Fig. 11, 12, 13, 14). This is mainly caused by three factors:

1. the reproduction pattern of the different species during the season. The large peaks in the fluctuations follow always large peaks in the numbers of eggs (Gerrish and Bristow, 1979).
2. the emergence of diverse generations of insects by which the numbers can be very low at certain moments during the growth season.
3. the condition of the leaves. Fresh leaves are consumed only by a small number of macroinvertebrates such as some species of Chironomids, Lepidoptera and Gastropods, but most species of Gastropods, Oligochaeta and Chironomids are able to consume the decaying parts of floating leaves so that there is an increase in numbers of these groups related with an increase of the decay of floating leaves during the season (Table 7). There are further large differences in the process of decomposition of the floating leaves of the different nymphaeid species. *Nuphar lutea* leaves were infected by fungi during the whole season in contrast to the other nymphaeid species studied on which fungi became abundant after the beginning of August. Many more macroinvertebrates occur on *Nuphar* leaves than on other floating leaves because the epiphyton, an other food source for these invertebrates, is here also well developed. During the decay the leaves of *Nuphar* do fragment very easily in contrast to the leaves of other nymphaeids so that there is a remarkable decrease of leaf surface which can explain the lower numbers of macroinvertebrates in stage 4 in Table 7 compared with stage 3. On decaying *Nymphoides* and *Nymphaea* leaves (stage 4) the highest numbers of macroinvertebrates were found.

As hatching of their eggs takes time and the epiphyton development and colonization of the leaf surface takes several days the leaf persistence plays also an important part with respect to the numbers of macroinvertebrates. On artificial substrata (macrophyte models) Mason (1978) found that equilibrium of the macroinvertebrate coenosis occurred at about 35 days; Meier et al. (1979) found the maximum number of macroinvertebrates on artificial substrates after 39 days; afterwards the numbers decreased, due to the emergence of insects. It can be read from Table 1 that an equilibrium of the macroinvertebrate fauna on most leaves of *Nymphoides peltata* will never be reached while many leaves of *Nuphar* and *Nymphaea* persist longer than 39 days so that here such an equilibrium as mentioned above is possible. The short leaf persistence of leaves of *Nymphoides peltata* can also be the

Table 7

		Nymphoides peltata				Nymphaea alba				Nuphar lutea			
Taxa	individuals/100 leaves stage	1	2	3	4	1	2	3	4	1	2	3	4
Ciliata		-	-	-	-	8	36	10	-	-	-	-	-
Porifera		-	-	-	-	-	6	2	2	5	14	3	-
Hydrozoa		33	-	-	-	3	2	2	6	167	-	5	-
Turbellaria		9	15	9	18	5	14	5	10	7	4	40	-
Ectoprocta		-	-	-	-	10	8	60	14	22	36	23	2
Oligochaeta		16	21	82	49	15	72	38	84	165	20	140	268
Hirudinea		10	27	33	33	112	202	215	190	164	426	562	316
Gastropoda		16	13	26	65	27	22	95	128	80	52	190	340
Acari		1	1	6	1	-	6	8	-	2	10	18	30
Isopoda		-	1	-	1	-	2	2	2	5	2	20	32
Ephemeroptera		1	1	1	1	2	-	5	10	2	4	3	12
Odonata		-	-	-	1	-	-	-	2	-	2	3	10
Heteroptera		1	-	2	2	2	-	-	-	3	-	3	2
Nematocera		23	31	143	169	187	148	363	808	538	342	1158	736
Trichoptera		1	5	15	15	45	72	113	152	80	114	120	102
Lepidoptera		4	2	1	2	-	2	-	-	2	2	-	2
Total number of individuals/100 leaves		115	117	318	357	419	592	818	1408	1242	1028	2288	1852

Table 7 Numbers of aquatic macroinvertebrates per 100 floating leaves of different age and in different stages of decemposition of *Nymphoides peltata* (Gmel.) O. Kuntze, *Nymphaea alba* L. and *Nuphar lutea* (L.) Sm. (Oude Waal, 1975). Stage 1: fresh leaves with little periphyton, stage 2: matured leaves with much periphyton, stage 3: leaves with yellow areas some decayed parts, stage 4: leaves decayed for more than 50% (the total area of these leaves is in general smaller than that in the case of other stages due to decomposition).

cause that colonies of Ciliata, Porifera and Ectoprocta were not found on the floating leaves of this species during my investigations while they were found on *Nymphaea* and *Nuphar* leaves.

The average numbers of individuals per floating leaf per season varied in *Nymphoides peltata* (Oude Waal) from 0.93—1.79, in *Nymphaea alba* (Oude Waal) from 6.38—19.43, *Nymphaea alba* (Singel) 2.19, *Nuphar lutea* (Oude Waal) 8.77—15.47, *Nuphar lutea* (Singel) 3.33, *Nuphar lutea* (Haarsteegse Wiel) 9.28 and *Nymphaea candida* (Haarsteegse Wiel) 4.80. The fluctuations during a particular season were very large.

Karrassowska and Mikulski (1960) found an average number of macroinvertebrates per leaf in Lake Druzno (Poland) of 0.15 in the case of *Nymphoides peltata*, 1.08 in the case of *Nuphar lutea* and 0.24 in the case of *Nymphaea candida* and they concluded that nymphaeids are not very suitable as feeding ground for fish. My investigations show however a much more abundant macrofauna, while the macrofauna of other nymphaeid parts also must be taken into consideration. So it can be supposed that the unsheltered fauna can be consumed easily by fish under the floating leaves.

The microfauna of the floating leaf underside is another topic for further investigations. Two Cladoceran species can be very common, viz. *Sida crystallina* (O.F. Müller) which is attached to the leaves with the aid of a sucker on its neck and *Peracantha truncata* (O.F. Müller). Both species were found in all the localities investigated. The occurrence of these species on nymphaeids is also recorded by Berg and Nygaard (1929) and Creutzberg and Leentvaar (1969).

Compartment I. (submerged leaf)

The Chironomid fauna of submerged leaves of *Nuphar lutea* has been studied by Mackey (1977a) in the rivers Thames and Kennet (Great Britain). In both rivers he found the same 11 species on the leaves. Maximum abundance and biomass occurred in July, and was caused by large populations of *Cricotopus bicinctus* gp. and *Cricotopus sylvestris* gp., which made up by weight 88% of the total chironomid population while the total populations of the other species remained fairly constant during summer. The submerged leaves of *Nuphar* catch much fine detritus from the seston, and this forms together with the epiphyton the basis for the occurrence of most Chironomidae (Mackey, 1979). Currents can remove the detritus. Mackey (1977a) found no chironomids on the petioles.

There was a high production of the chironomids in the *Nuphar* zone. *Cricotopus sylvestris* gp. was more productive than *Cricotopus bicinctus* gp. Both species accounted for 75% of the production (Mackey, 1977b). Mackey (1977c) mentioned fish as main predators of the chironomids on the submerged leaves of *Nuphar.*

Some preliminary investigations on the submerged leaves of *Nuphar lutea* in the Oude Waal showed that the fauna of these has many species in common with the floating leaf undersides, but there can be quantitative differences. Mackey (1977a) found no Ectoprocta or Porifera on the leaves, however large colonies of the sponge *Ephydatia fluviatilis* were found on submerged leaves in the Oude Waal, suggesting a longer leaf persistence of submerged leaves than of the floating ones.

Compartment F, G and H. (rolled leaf, peduncle, and petiole)

So far these compartments have hardly been investigated. Some chironomid larvae were found mining in petioles, other species of chironomids in rolled leaves. On the petioles of the nymphaeids studied often the creeping colonies of *Cristatella mucedo* Cuv. (Ectoprocta) were found. Floating petioles of waterlilies can play a role in the dispersal of the hydrozoan *Cordylophora caspia* (Pallas) in some areas (Roos, 1979).

Compartment J. (rhizome)

Almost nothing is known of the fauna of rhizomes, short-shoots and long-shoots. Sometimes the bivalve *Dreissena polymorpha* (Pallas), a filter feeder was found attached to short and long shoots of *Nymphoides peltata.* Rhizomes, long- and short-shoots are eaten by the muskrat (*Ondatra zibethicus* (L.)) (Heine and Van der Velde, 1978).

Compartment K. (root)

Some insect larvae pierce their stigmata in the roots in order to obtain oxygen from them, while they also pupate there, e.g. *Donacia crassipes* on *Nymphaea* and *Nuphar* roots and *Notiphila brunnipes* on roots of *Nymphoides peltata.* Roots are also eaten by muskrats (Heine and Van der Velde, 1978).

Compartment N. (water)

In the water under the nymphaeids nektonic and zooplanktonic species can be found. Zooplankton is very numerous; particularly Cladocera, Copepoda and Ostracoda occur in large numbers under the nymphaeids in the Oude Waal.

Of the nektonic fauna fish are most conspicuous such as pike (*Esox lucius* L.), often hidden under floating leaves at the margin with the open water, perch (*Perca fluviatilis* L.) and white fish such as *Rutilus rutilus* (L.). During my investigations young fish in particular were found swimming in schools under the nymphaeids. The function of nymphaeids for fish is till now badly known. For quantitative studying of young *Rutilus rutilus* in waterlily beds Bagenal (1974) constructed a buoyant net, which was tested by Hewitt (1979).

Mackey (1979) found that 74% of the chironomids eaten by fish in the river Thames could come from the *Nuphar* zone, 85% of these or 63% of all chironomids were *Cricotopus* larvae. Fish can play a role in the dispersal of seeds of nymphaeids. Luther (1901) (see Von Kirchner et al., 1917) recorded that fruit flesh and seeds were eaten by *Scardinius erythrophthalmus* (L.). Of 39 seeds of *Nuphar lutea* found in the intestines four germinated within 6 weeks in a germination experiment. Seeds collected in the field did not germinate after 5 months, so that passage through the intestine has accelerated the germination capacity of the seeds. Lammens (1976) records seeds and fruitparts of *Nymphaea alba* in the stomachs of *Blicca björka* (L.). Seeds of *Nuphar lutea* were also found in the excreta of the fish-eating heron (*Ardea cinerea* L.) and in the stomachs of the great crested grebe (*Podiceps cristatus*) (Heslop-Harrison, 1955) so they can be dispersed to other waters.

Compartment O. (bottom)

The bottom fauna under nymphaeids in the Oude Waal consists mainly of Oligochaeta, Chironomidae and Molluscs of which large mussels such as *Anodonta anatina* (L.), *Anodonta cygnea zellensis* (Gmel.) and *Unio pictorum* (L.) are very important with respect to biomass. The bottom fauna of the nymphaeid system is now in study by Mr. Th.C.M. Brock.

PERSPECTIVES FOR FURTHER RESEARCH

As many desiderata for further research as well as gaps in our knowledge have been mentioned in the chapters before, it can be concluded that the picture of the Dutch nymphaeid systems dominated by *Nuphar lutea, Nymphaea alba, Nymphaea candida* and *Nymphoides peltata* is far from complete and needs more elaboration. It will further be necessary to study at least some aspects of these nymphaeid communities in other areas as the frame components, the nymphaeid species mentioned before are widely distributed in Europe and Asia. The next step must be to study other nymphaeid communities in the temperature zone of North America and in the tropical zones of the world, so that a classification of nymphaeid communities of the whole world can be made, which can lead to a much better understanding of their historical background and evolutionary origin and life form spectra.

Examples of parallelism and vicariant species can be expected, e.g. the fly *Hydromyza livens* is replaced by *Hydromyza confluens* Loew on *Nuphar advena* Ait. in North America (Welch, 1914, 1917), Ephydrid flies also play an important role in the nymphaeid systems of North America (Deonier, in lit.), while *Donacia* species occur on North American nymphaeids (Schneider and Moore, 1977), just as in Europe.

In general it can be expected that how larger the various plant organs are and how longer they persist, the more possibilities there are for other organisms to settle and to use the structure in various ways; the richest nymphaeid communities can be expected in the tropical zones of the world, because here the richest fauna can be found and because here the largest nymphaeids occur (*Victoria*, etc.), but also because they can persist here throughout the year.

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STRUCTURE, BIOMASS AND SEASONAL CHANGES IN BIOMASS OF *NYMPHOIDES PELTATA* (GMEL.) O. KUNTZE (MENYANTHACEAE), A PRELIMINARY STUDY

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ABSTRACT

Van der Velde, G , Giesen, Th G and van der Heijden, L , 1979 Structure, biomass and seasonal changes in biomass of *Nymphoides peltata* (Gmel) O Kuntze (Menyanthaceae), a preliminary study *Aquat Bot* , 7 279—300

A study has been made on structure and biomass of *Nymphoides peltata* (Gmel) O Kuntze in an old river branch of the river Waal (The Netherlands) Some notes have been made on the ecology and distribution of the species The external morphology of the species has been described

Correlations have been calculated between parameters such as leaf surface and length of the different plant parts with their ash-free dry weight The mean ash free dry weight of the flowers including the pedicels for each developmental stage has been determined

Biomass samples have been taken during a whole year in the centre of a dense *Nymphoides* bed, so that the seasonal changes in biomass per m² could be followed

In contrast with the other plant parts, the roots showed a very high percentage of ash in June when root biomass is lowest, in winter the roots show absolutely and relatively the highest biomass The mean ratio aboveground biomass—underground biomass was highest at the end of June (3 20) and lowest in January (0 27)

The correlation between leaf surface (per m²) and total biomass (per m²) can be described by a quadratic regression equation

As variation in time of nearly all measurements was large, more information is needed to describe the changes in biomass on the sampling site more exactly The general reliability of the results of the study must also be tested in other localities

INTRODUCTION

In 1974 an investigation was initiated on the structure and dynamics of nymphaeid communities in the surroundings of Nijmegen, The Netherlands.

Nymphoides peltata (Gmel.) O. Kuntze is the dominant species of one of the vegetation types under investigation. An earlier paper dealt with some aspects of decomposition of *N peltata* (Lammens and van der Velde, 1978). This paper deals with observations and measurements on structure and biomass of the species in a former river bed of the river Waal between Bemmel and Lent, north of Nijmegen during 1976 and 1977.

The purpose of this investigation was two-fold, viz. (1) to measure the biomass and changes in biomass per m^2 in a pure stand of *N. peltata*, and (2) to find correlations between biometrical data and biomass. With the aid of these correlations an estimation of plant mass and loss of material by decomposition can be made in terms of biomass by simple measurements in the field.

As correct descriptions and figures of the total morphological structure of the plant are mostly completely lacking in literature, an account of the external morphology of *N. peltata* is also given.

NOTES ON DISTRIBUTION AND ECOLOGY

N. peltata occurs in central, west and southern Europe, north and west Asia, Kashmir, the Himalaya and Japan (Glück, 1924). Further, the species has been introduced in North America (Glück, 1924; Stuckey, 1974). In Europe the species extends north to the 60th degree of latitude (Hegi, 1927; Hultén, 1950); the northern limit of distribution coincides more or less with the 16°C July isotherm.

N. peltata is the only species belonging to the genus occurring in moderately cold temperate areas. Nearly all other species occur in the tropics and sub-tropics of both hemispheres (Meusel et al., 1978). After Müller-Stoll and Krausch (1959), *N. peltata* is not so much thermophilous in the sense of needing warm summers, but in not tolerating cold winters.

In Europe there are perhaps two races, a west European sub-oceanic and a Siberian continental race (Meusel et al., 1978). The cytogeography of the genus *Nymphoïdes* is described by Ornduff (1970). *N. peltata* is hexaploid ($x = 9$) having $2n \doteq 54$, as recorded from Germany and Kashmir.

In The Netherlands *N. peltata* occurs commonly in polder and fluviatile areas. Here it is a true freshwater species which does not occur in areas where the average chlorinity rises above about 300 mg/l. It occurs in eutrophic, alkaline waters at a water depth of 0.3—3.0 m.

The plant occurs on clay or sapropelium; it grows best on mineral bottoms such as clay. The presence of *N. peltata* is an indication of a dynamic environment with water movements caused by wind, currents or/and tidal oscillations. The plant occurs in ditches, canals, waterways and "break-through" pools of dikes ("wielen"), but is most frequent in backwaters, especially those which are strongly influenced by high water of the river and are flooded in winter (van der Voo and Westhoff, 1961). It has been found most frequently at water depths from 1 to 1.5 m and the average degree of coverage increases with depth.

DESCRIPTION OF THE AREA STUDIED

Samples for biomass measurements were taken from an old river branch, situated in the northern river forelands of the river Waal between Lent and

Bemmel, north of Nijmegen (Fig. 1). The eutrophic, alkaline water, which is strongly influenced by the river, has a depth of 2—3 m. In this locality beds of *N. peltata* occur on a bottom consisting of a sapropelium layer, 20—50 cm thick, deposited on heavy river clay.

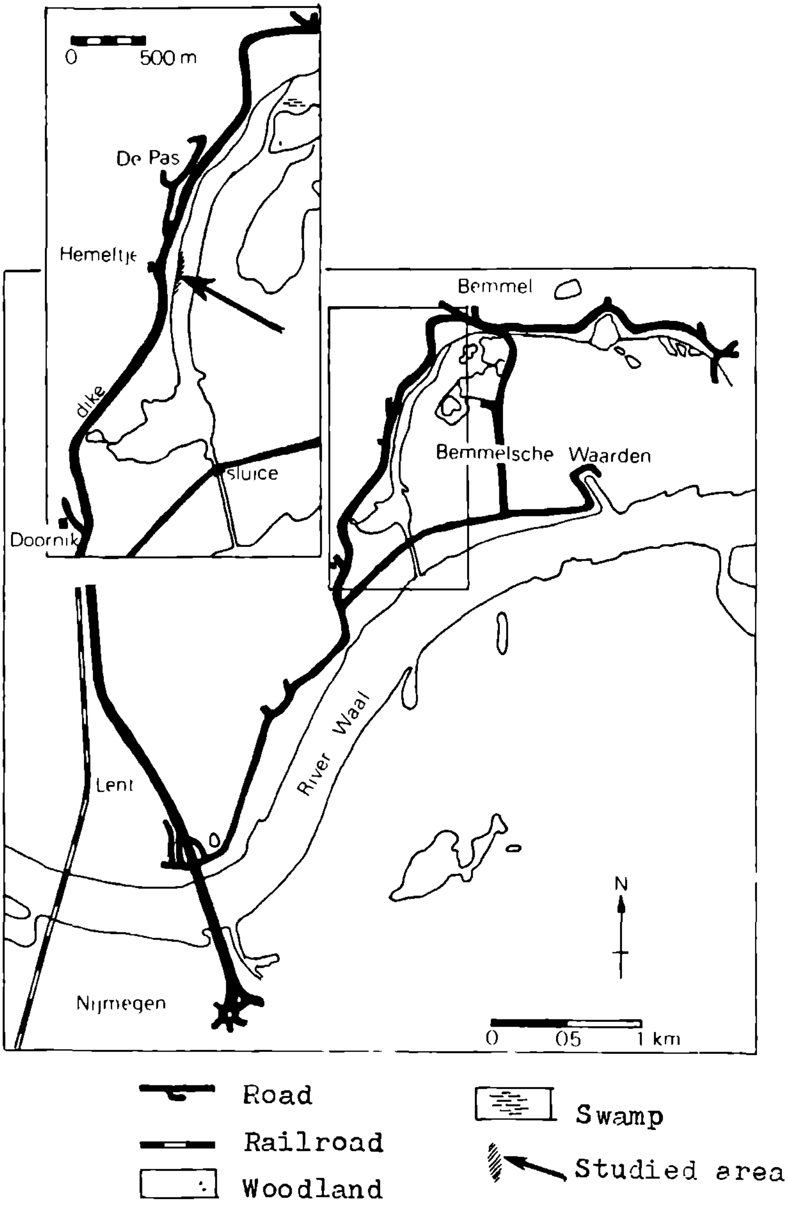


Fig 1. Map of the study area The sampling site is marked by an arrow.

MATERIAL AND METHODS

Samples of *N. peltata* were taken at a water depth of 10—50 cm at a distance of 1—3 m from the banks by means of a 50 × 50 cm frame made of PVC tubes. A surface of 0.25 m^2 per sample was dug out. Eighteen samples were taken on five dates. The samples were taken to the laboratory in plastic bags where the length, and in the case of leaf blades also width, of the various plant parts were measured and the number of roots on short and long shoots, leaves, short and long shoots, and flowers and fruits were counted. As not all roots could be dug out undamaged, the number of roots could be determined by counting the fresh root marks.

The surface of each leaf blade was calculated by the formula

$$\left(\frac{l + w}{4}\right)^2 \pi$$

in which l is the leaf length measured from the leaf tip to the tip of the basal lobe, and w is the maximum width of the leaf. The reliability of this formula has been tested by measuring 20 leaf blades with a leaf area meter LI-3000 connected with a LI-3050 A recorder (relative error 1%). The average relative difference between both methods was 2.8%, the latter method producing slightly higher values. This was caused by slight overlap of the basal lobes in some leaves, as the larger leaves had to be split into two halves when measuring with the leaf area meter. The above mentioned formula was chosen because its application is simple; further, no leaves had to be sectioned and the measurements could even be made in situ, without damaging the vegetation.

The plant material was cleaned as well as possible by washing with tap water and by polishing with a cloth to remove mud, attached fauna and periphyton. The various plant parts (flowers, fruits, leaves, petioles, short shoots, long shoots (flowering stems included) and roots) were then packed separately in aluminium foil and dried at 105°C for approximately 12 h and weighed. The material was ashed at a temperature of 550°C for 12 h and weighed (Vollenweider, 1969). All biomass data have been expressed in mg or g ash-free dry weight/m^2. In the case of the roots it appeared necessary to calculate a mean biomass per whole root for each date separately.

Samples of all different plant parts have also been collected to find a correlation between parameters such as surface and length of these plant parts and their ash-free dry weight. Linear, quadratic and cubic regression equations have been calculated with a regression analysis program with the aid of an IBM computer. For each plant part the most reliable regression equation was chosen from the three calculated ones, on the grounds of the lowest standard error (S.E.) and the highest correlation (R^2). Further, the reliability of the line or curve chosen was tested with Student's *t*-test.

THE STRUCTURE OF *NYMPHOIDES PELTATA*

N. peltata is a glabrous aquatic plant with floating leaves, emerged flowers and stolons creeping in and on the bottom layer (Fig. 2). The system of stolons can be divided into long and short shoots, which are anatomically identical (Wagner, 1895). The difference between long and short shoots is only in the length of the internodes.

According to Glück (1924), the long shoots can reach a length of 16.5—122 cm. They creep over the bottom and are green in colour. The internodes are after our measurements (5—) 10—40 (—75) cm long and 0.3—1.0 cm thick; according to Glück (1924) they are 8.5—22.3 (—47.5) cm long and (0.2—) 0.3—0.7 cm thick. The nodes of the long shoots possess (2—) 5 (—7) adventitious roots and one leaf per node. In the axil of such a leaf a flowering stem or a short shoot can develop.

The total length of a short shoot varies, according to Glück (1924), from 1.8—21.3 cm with 5—24 short internodes which can be 0.2—0.6 (—2.0) cm long and 0.48—0.70 cm thick; according to our measurements the total length of a short shoot varies from (0.5—) 2—10 (—15) cm, with internodes at most 0.6 cm long. The short shoots are whitish in colour and are anchored in the bottom by roots. The short shoots are situated laterally and alternating

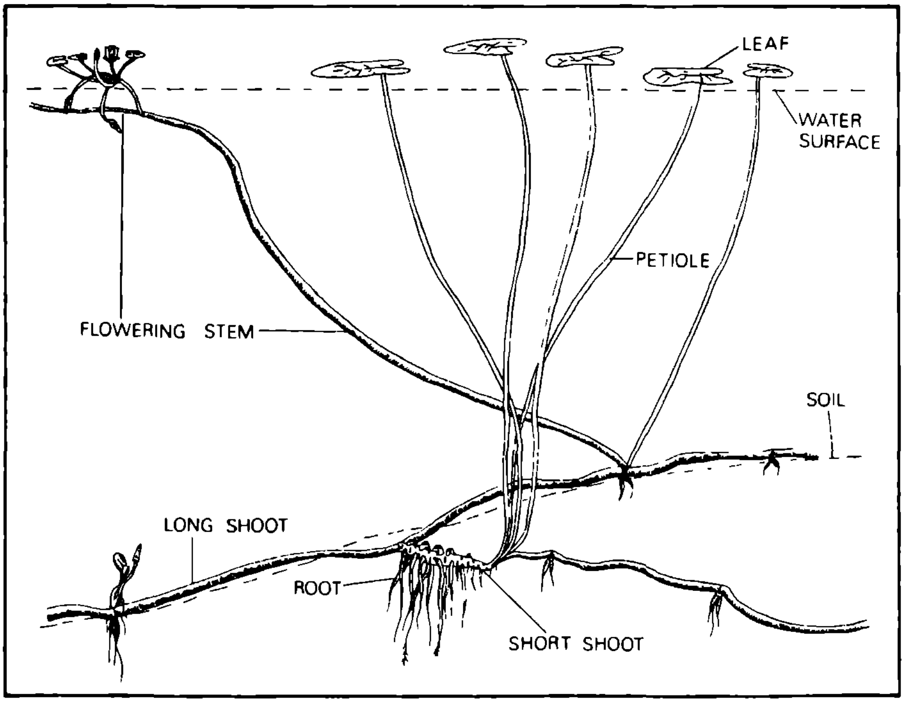


Fig. 2. General structure of *Nymphoides peltata.*

along the long shoots. They give rise to leaves which grow in a 2/5 spiral (Wagner, 1895). A short shoot has, after our observations, (0.5—) 2 (—8) leaves and (1—) 4—6 (—18) roots/cm. From the base of each leaf mark 2—3 adventitious roots descend; their length reaches to about 40 cm (Fig. 2). The roots grow laterally and from the underside of the short shoot, sparsely from the upperside (Glück, 1924). These roots are only sporadically branched or provided with much smaller rootlets. From the axil of a leaf of a short shoot a long shoot can develop (Fig. 3). This long shoot can be considered to be one of the second order (de Wit, 1966); it can produce short shoots of the second order. The branching pattern can repeat itself in this way several times, so that one plant can cover a considerable area.

Short shoots with thickened roots hibernate and form new leaves and long shoots in spring (Fig. 3). Short shoots should, according to Glück (1924), increase in numbers under the influence of decreasing temperature and daylength, so that the most short shoots should occur in winter. Our observations showed that the longest short shoots were found in spring and early summer (Fig.4).

The length of the petioles of normal vegetative leaves varies with the water depth from 30—300 cm. The length of the leaf-blades, (0.8—) 5—9 (—15) cm,

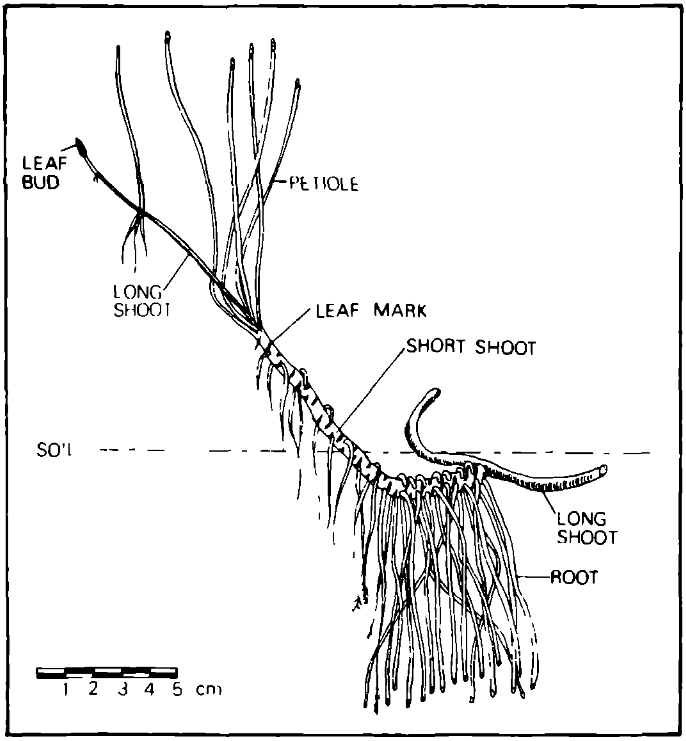


Fig. 3. Structure of a hibernating short shoot of *N. peltata*.

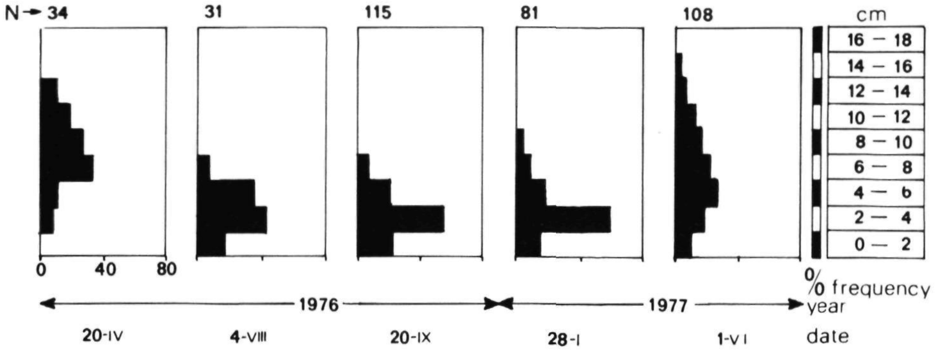


Fig. 4. Frequency of short shoots of *N. peltata* in length classes. *N* = number of short shoots measured.

varies with the bottom composition, water depth and the time of the year in which they are produced. The leaves are nearly always floating on the water surface. The petioles are very flexible but at the end of the growing season there are some leaves which grow some cm above the water surface and at the end of autumn there are only very small winter leaves, often with a leaf area of only 1 cm^2, below the water surface, as also recorded by Glück (1924).

The changes in leaf size and their frequency during the season can be read from Fig. 5, where leaves are classified into size classes. In winter (28 January) only very small leaves, which do not develop into floating ones, are present. In spring and early summer (June) small folded leaves appear, which soon become unfolded under the influence of increasing light and temperature. These leaves belong to size class 2; they grow fast and will soon reach size class 3. During the season these leaves are replaced by larger ones, as can be seen by comparing the results of the 26 June and 26 July sampling (Fig. 5). In summer new leaves can grow faster under water, so that small leaves have a lower frequency. In August smaller leaves become more frequent and replace the larger ones. This is also due to the appearance of more generative shoots, which bear smaller leaves. Later in September the new leaves remain smaller and later on only submerged winter leaves are present.

The dependency of the leaf size on the water depth can be demonstrated by means of the results obtained from a *N. peltata* bed in a pond connected with the Bisonbaai along the river Waal. Samples of 0.25 m^2 were taken in a transect from the banks to open water and the water depths were measured. All leaves of the samples were measured, the mean leaf surface per leaf was calculated for each sample. A cubic regression equation appeared to be the most reliable for the correlation between leaf surface and water depth (Fig. 6). The regression equation is significant as P is between 0.01 and 0.02. Thus smaller leaves occur mainly near the banks in shallow water, then follows a zone with more medium-sized leaves, and near the margin of the vegetation with the open water large leaves are the most numerous.

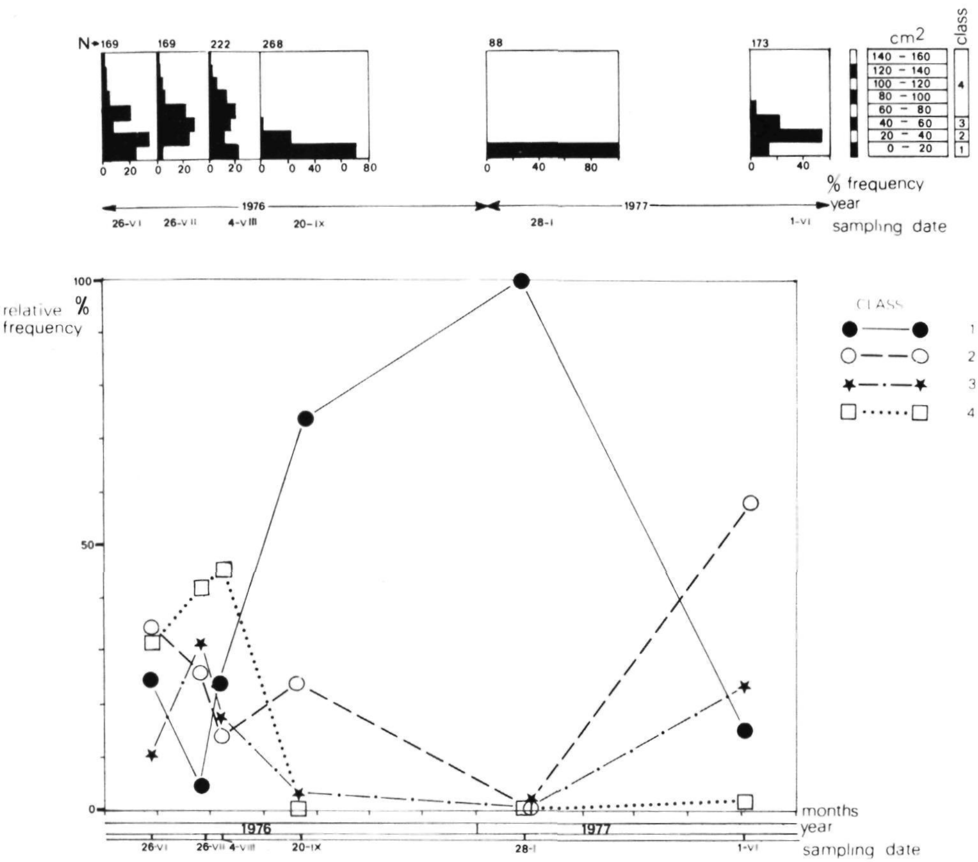


Fig. 5. Frequency of leaves of *N. peltata* in size classes (surface in cm²) during the season. *N* = number of leaves measured.

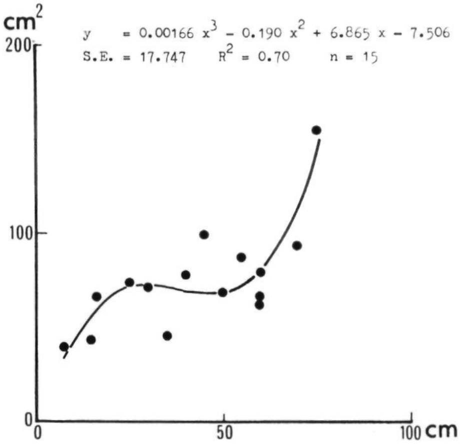


Fig. 6. Correlation between water depth and mean leaf surface per leaf of *N. peltata* in a transect in a pond connected with the Bisonbaai, July 1976.

The flowering stem (Fig. 7) develops just as a short shoot in the leaf axil from the node of a long shoot. It consists of a stolon comparable to a long shoot growing to the water surface. The first internode can become very long. Its growth stops when the water surface has been reached so that it is about as long as the petioles of the vegetative leaves. The nodes of the flowering stem usually bear no roots.

The leaves of the flowering stem differ from the vegetative leaves by being stiffer and smaller in size (2—5 cm long) and having relatively short petioles; they often rise above the water surface. The leaves stabilize the terminal, cymose flower clusters and hold them near the water surface. The pedicels, which are up to 10 cm long, curve during their growth to above the water surface where anthesis takes place. The corolla withers after only 1 day. The pedicels of withered flowers curve down again into the water, where the fruits mature. A description of the flowers, the floral biology and seed production will be given in a separate paper (see also Ornduff, 1966). Optimal flowering occurs in July and August, while the vegetative growth continues from April to November.

Regularly, plants can be found which differ from the description given above by the fact that the apex of a long shoot grows to the water surface so that the petioles of the vegetative leaves are shorter than normal with respect

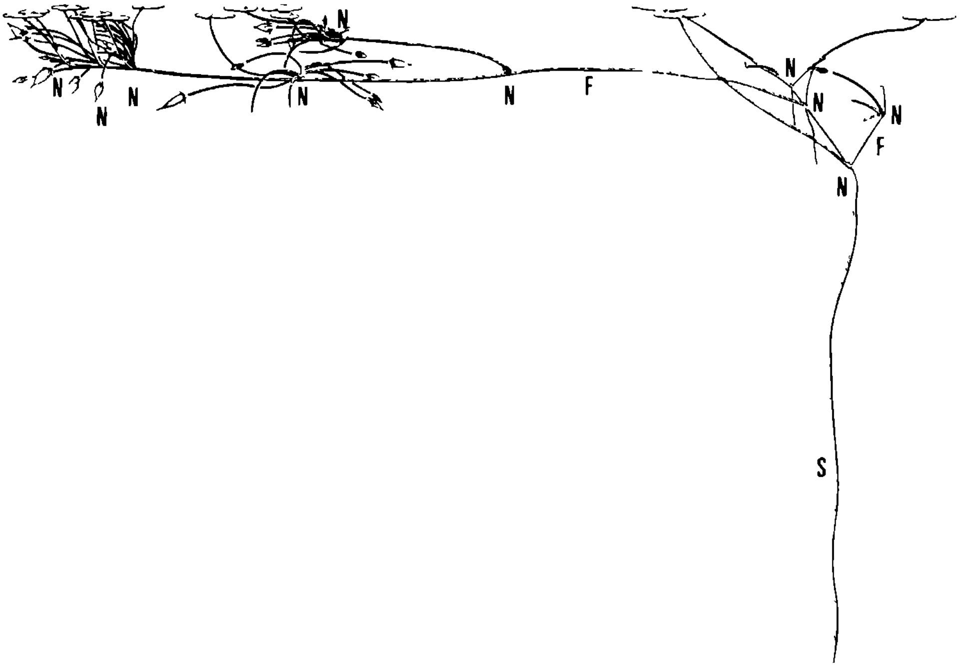


Fig. 7. Structure of a flowering stem of *N. peltata.* N = node, F = flowering stem, S = long shoot.

to water depth, as can be seen in Fig. 7; this has also been noticed by Funke and Bartels (1937) and Funke (1951) during their growth experiments with *N. peltata*. All branchings in *N. peltata* appear to be sympodial.

Very good figures which show complete plants belonging to the genus *Nymphoides* are given by Aston (1973) for the Australian species. One of these species *N. geminata* (R.Br.) O. Kuntze shows, with the exception of the upper part of the flowering stem, a general structure identical to that of *N. peltata*.

MEASUREMENTS OF BIOMASS

Biomass of various plant parts related to biometrical values

Samples of all different plant parts have been collected in the field for each plant part on only one date.

The flowers with pedicels were divided into eight developmental stages, each of which was treated separately. The numbers of each stage collected were 18, 15, 11, 11, 6, 14, 9 and 8, respectively. The mean measures of the various developmental stages are given in Table I. By dividing the total biomass (ash-free dry weight) by the number of flowers of each stage, mean biomass values were calculated.

During the development of the flower, the pedicel included, the mean ash-free dry weight appears to increase from 1.8 to 68.8 mg. The relative increase in ash-free dry weight of the pedicel is greater than that of the flower during the development to the moment of anthesis (Fig. 8, stages 1—6). After flowering, the corolla withers (Fig. 8, Stage 7) and its ash-free dry weight decreases.

The percentage of ash during the development can be read from Fig. 9. The pedicel shows two increases in the percentages of ash, viz. during early growth and after flowering when the pedicel curves down into the water. The gynoecium shows a distinct increase in the ash percentage after anthesis associated with fruit setting.

Of other plant parts, length, and in the case of leaves also surface area, have been measured or calculated in cm or cm^2, and the ash-free dry weight was determined in g. For the correlation between the biometrical data of each individual plant part and the ash-free dry weight, regression equations were calculated.

Linear regression equations were found for short shoots and roots, quadratic regression equations for leaf length and leaf surface, fruits and petioles, and a cubic regression equation for the long shoots (Fig. 10). All equations appeared to be highly significant as P was between 0.002 and 0.01 in the case of fruits and smaller than 0.001 in all other cases.

For the petioles it was necessary to calculate two quadratic regression equations, one for petioles shorter than about 35 cm and one for petioles larger than that length. The path of the curve can mean that the petiole grows to a length of about 35 cm mainly by cell-division by which biomass can increase,

TABLE I

Mean biometrical values of flowers and pedicels of *N. peltata* during their development (stages 1—8, see Fig. 8)

Developmental stage	Pedicel		Bud		Bud		Style + ovary		Ovary		Ovary	
	Length (mm)	S.D. (mm)	Length (mm)	S.D. (mm)	Diam. (mm)	S.D. (mm)	Length (mm)	S.D. (mm)	Length (mm)	S.D. (mm)	Max. width (mm)	S.D. (mm)
1	3.1	0.9	3.6	0.9	2.3	0.5						
2	10.9	2.6	7.1	0.9	3.7	0.5						
3	23.4	7.7	10.5	0.7	5.1	0.2						
4	43.1	8.3	12.9	0.6	6.1	0.0						
5	59.3	28.8	20.1	1.1	8.8	0.9						
6	89.5	14.9					12.3	2.4	5.4	0.4	3.1	0.3
7	87.8	15.6					12.9	2.1	6.4	1.7	3.8	1.1
8	99.6	23.1					12.7	1.6	8.2	1.3	5.0	0.6

but when the petiole further grows out its biomass decreases probably due to cell enlargement, as this process needs energy from respiration (Black and Edelman, 1970). By means of cell enlargement the petioles can quickly reach a great length adapted to high water-levels. Funke (1951) has set young plants of *N. peltata* under water and found that the young leaves (the old ones generally do not react any more) can grow about 1 cm/h during 1 or 2 days (23 cm/day), but a more rapid growth of 35 cm/day could also be recorded. At

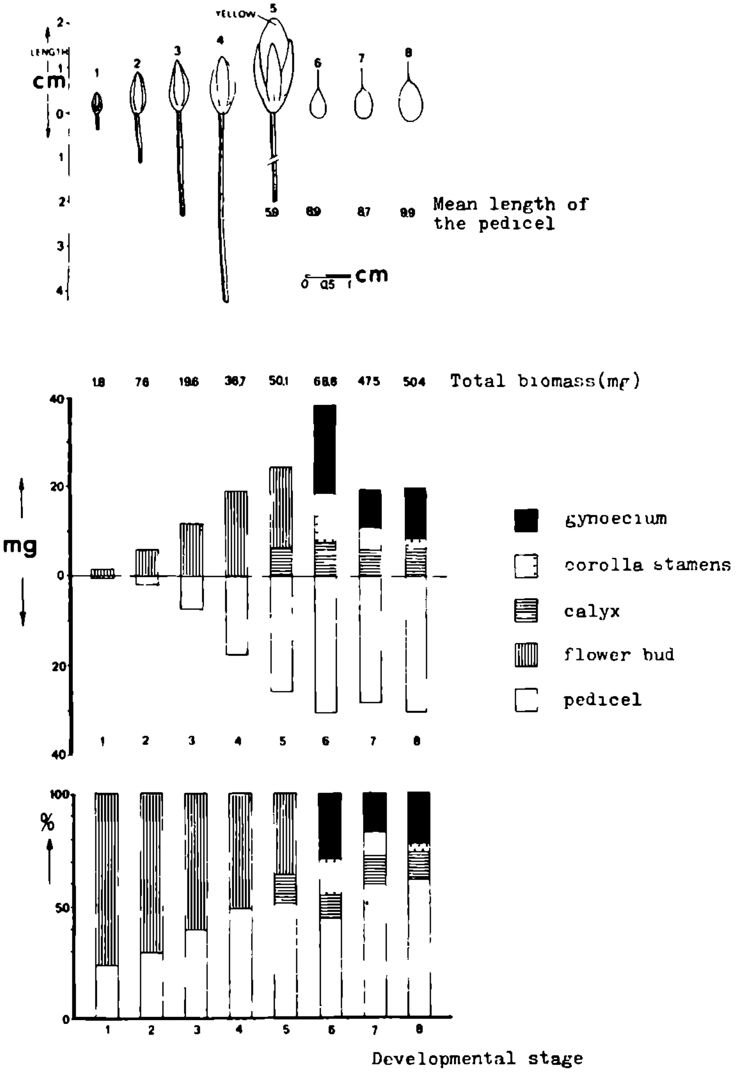


Fig. 8. Developmental stages of the flower of *N. peltata*, the pedicel included (above) (fruit body in stages 6—8 schematically drawn), the ash-free dry weight (middle) and the relative share of different flower parts in the ash-free dry weight (below).

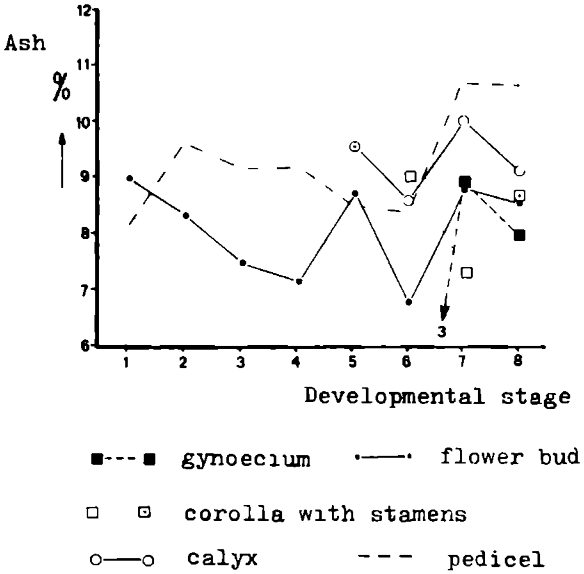


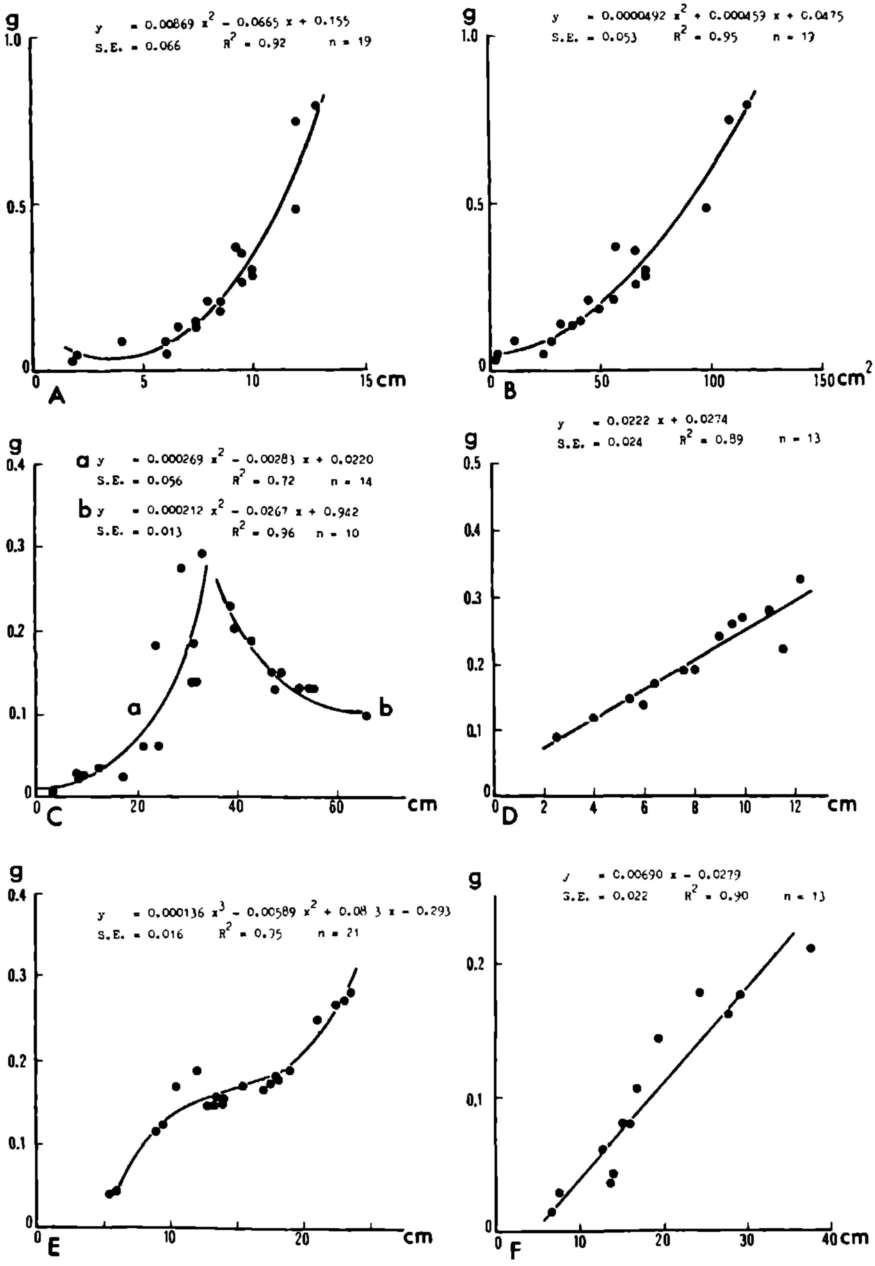
Fig. 9. The percentage of ash of the various flower parts and the pedicel of *N. peltata* related to dry weight during the development of the flower (stages 1—8 corresponding with those in Fig. 8). Flower bud means all flower parts together.

high water-levels or in turbid water, especially in spring, they must grow out by using their own energy resources.

Seasonal changes in biomass

Samples have been taken during a whole year to study seasonal changes in biomass and to determine the share of the various plant parts with respect to the total biomass/m^2 during the season (Tables II and III).

The percentage of ash related to the dry weight is calculated for each plant part at each sampling date (Fig. 11). The ash content of flowers (pedicels included) ranged from 10.7—14.4% (the mean values per date from 11.1—14.4%), of leaf blades from 9.1—17.4% (the mean values per date from 10.7—14.8%), of petioles from 7.9—21.2% (the mean values per date from 10.7—16.6%), of long shoots from 3.9—16.0% (the mean values per date from 6.3—14.1%), of short shoots from 4.9—15.5% (the mean values per date from 6.0—15.3%) and of roots 5.6—50.7% (the mean values per date from 7.5—47.5%). It appeared that in some plant parts there is an obvious change in the percentage of ash during the season. Leaves and petioles do not change very much, while short and long shoots show a somewhat higher percentage of ash in early summer during the period of strong growth and later in June, when flowering starts. The roots show relatively a very high ash content in the early summer. All other differences fall within the standard deviations (Fig. 11).


g
1.0
0.5
0
y = 0.00869 x² − 0.0665 x + 0.155
S.E. = 0.066 R² = 0.92 n = 19
0
5
10
15 cm
A
g
1.0
0.5
0
y = 0.0000492 x² + 0.000459 x + 0.0475
S.E. = 0.053 R² = 0.95 n = 13
0
50
100
150 cm²
B
g
0.4
0.3
0.2
0.1
0
a y = 0.000269 x² − 0.00283 x + 0.0220
S.E. = 0.056 R² = 0.72 n = 14
b y = 0.000212 x² − 0.0267 x + 0.942
S.E. = 0.013 R² = 0.96 n = 10
a
b
0
20
40
60
cm
C
g
0.5
0.4
0.3
0.2
0.1
0
y = 0.0222 x + 0.0274
S.E. = 0.024 R² = 0.89 n = 13
0
2
4
6
8
10
12
cm
D
g
0.4
0.3
0.2
0.1
0
y = 0.000136 x³ − 0.00589 x² + 0.08 3 x − 0.293
S.E. = 0.016 R² = 0.75 n = 21
0
10
20
cm
E
g
0.2
0.1
0
y = 0.00690 x − 0.0279
S.E. = 0.022 R² = 0.90 n = 13
0
10
20
30
40 cm
F

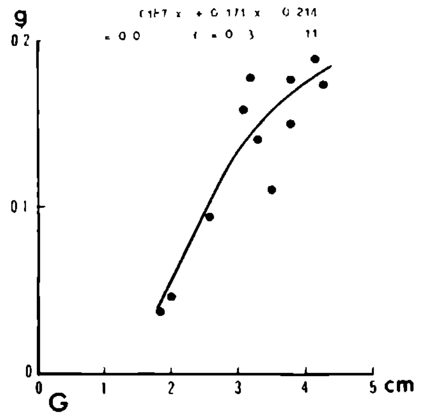


Fig 10 A, Correlation between the length of a leaf of *N peltata* and its ash free dry weight, 20 April 1976 B, Correlation between the surface area of a leaf and its ash free dry weight, 20 April 1976 C, Correlation between the length of the petiole and its ash-free dry weight, 4 Aug 1976 D, Correlation between the length of a short shoot and its ash free dry weight, 20 April 1976 E, Correlation between the length of a long shoot measured from node to node and its ash free dry weight, 20 April 1976 F, Correlation between the length of a root and its ash-free dry weight, 28 Jan 1977 G, Correlation between the length of a fruit of *N peltata* including the calyx and its ash-free dry weight, 4 Aug 1976

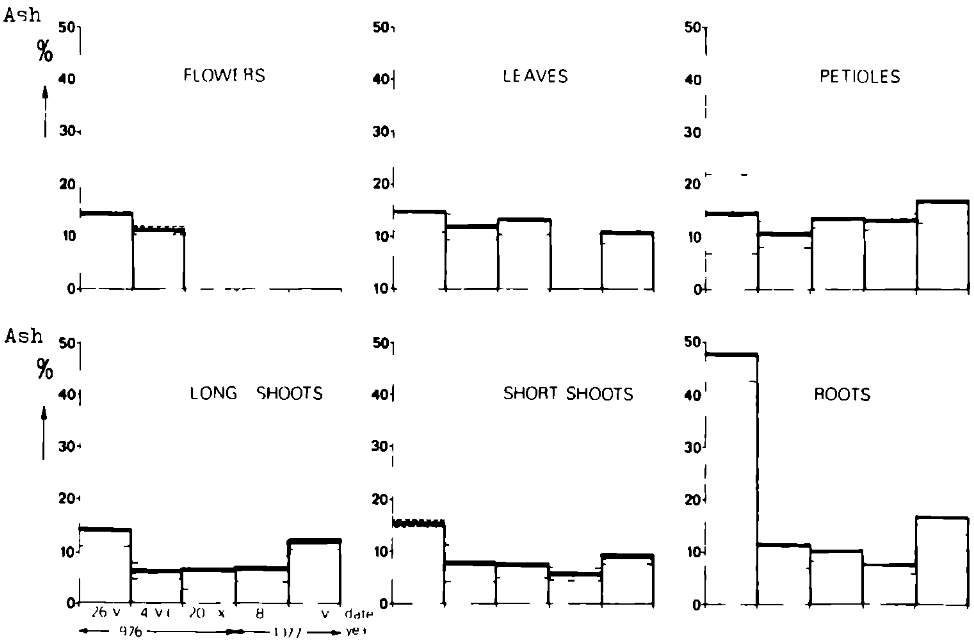


Fig. 11 The percentage of ash of various plant parts of *N peltata* related to dry weight during the season Broken lines mean standard deviations

TABLE II

Numbers and biometrical data of various plant parts of *N. peltata*/m^2 at various dates (Flowering stems have been included under long shoots; the number of long shoots could not be counted as the samples contained many fragments)

Date	Sample	Flowers (number m^{-2})	Leaves (number m^{-2})	Short shoots (number m^{-2})	Roots (number m^{-2})
26 June 1976	1	252	532	56	512
	2		148	28	640
4 Aug. 1976	3		156	31	569
	4	275	244	38	869
	5	81	344	63	1738
	6		131	44	588
	7	144	369	81	2681
20 Sept. 1976	8		388	144	3252
	9		380	144	2812
	10		208	48	1136
	11		204	44	612
	12		192	84	1252
28 Jan. 1977	13		164	132	2468
	14		104	96	1732
	15		84	96	1372
1 June 1977	16		292	116	1536
	17		228	116	2224
	18		168	200	3620

Date	Sample	Leaves (cm^{2}m^{-2})	Short shoots (cm m^{-2})	Long shoots (cm m^{-2})
26 June 1976	1	19036	124	3930
	2	8380	104	1148
4 Aug. 1976	3	9994	155	508
	4	11700	86	1647
	5	19525	234	3606
	6	10650	177	453
	7	20675	283	6303
20 Sept. 1976	8	4632	574	3386
	9	7352	422	4598
	10	3414	102	724
	11	4235	100	606
	12	1982	197	944
28 Jan. 1977	13		340	2208
	14		322	680
	15		280	388
1 June 1977	16	9424	532	832
	17	7380	808	2704
	18	5804	1262	1936

Further, the relative changes in biomass can be read from Table IV, where per date the mean ash-free dry weight per cm^2 of leaves, per cm of long and short shoots and per root is given. The biomass/cm^2 leaf surface was rather constant. For the long shoots the biomass/cm appeared to be highest in early June and lowest in August. The biomass/root was highest in early June and lowest at the end of June.

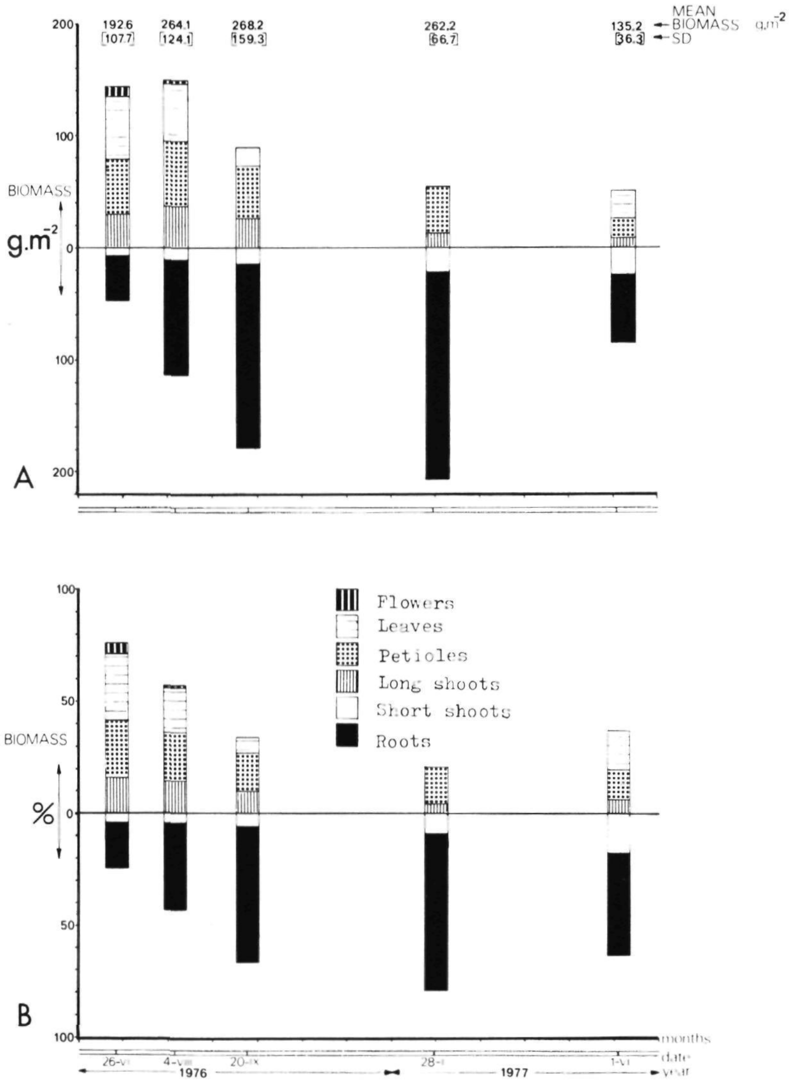


Fig. 12. The share (ash-free dry weight) of the different plant parts in total biomass of *N. peltata* at each sampling date and its occurrence above and under the sediment. A = absolute mean values; B = relative mean shares of each plant part to the whole plant biomass/m^2 at each date. Long shoots and flowering stems have been given together as long shoots. The data on flowers include the pedicels.

TABLE III

Ash-free dry weight and dry weight of various plant parts of *N. peltata*/m^2 at various dates (Data on flowers and pedicels are given together as flowers, winter leaves and petioles are given under petioles, long shoots and flowering stems have been combined and are given as long shoots)

Date	Sample	Flowers (g m^{-2})	Leaves (g m^{-2})	Petioles (g m^{-2})	Long shoots (g m^{-2})	Short shoots (g m^{-2})	Roots (g m^{-2})	Total (g m^{-2})
		Ash-free dry weight						
26 June 1976	1	16.46	82.54	78.32	47.01	8.43	35.84	268.80
	2		31.80	20.34	14.02	5.49	44.80	116.45
4 Aug. 1976	3		50.63	50.49	10.64	11.23	45.50	168.49
	4	10.88	42.32	28.81	29.06	3.32	69.50	183.89
	5	3.41	60.96	77.74	74.01	15.63	139.00	370.75
	6		38.76	58.00	13.78	13.94	47.00	171.48
	7	2.16	62.34	73.66	65.06	7.94	214.50	425.66
20 Sept. 1976	8		16.38	51.76	43.14	23.08	292.80	427.16
	9		33.60	85.32	56.23	25.43	253.20	453.78
	10		15.69	32.43	9.66	6.13	102.40	166.31
	11		14.74	27.80	11.52	6.62	55.20	115.88
	12		6.88	35.68	11.72	10.82	112.80	177.90
28 Jan. 1977	13			45.83)	21.48	21.12	246.80	335.23
	14			47.07)	6.83	19.78	173.20	246.88
	15			35.01)	9.41	22.94	137.20	204.56

1 June 1977	16		29.32	19.24	3.72	12.88	39.72	104.88
	17		21.90	15.36	11.52	21.68	54.88	125.34
	18		18.36	18.36	12.64	35.12	90.88	175.36
		Dry weight						
26 June 1976	1	19.23	94.22	86.68	53.51	9.98	72.70	336.32
	2		38.42	25.32	16.69	6.47	80.29	167.19
4 Aug. 1976	3		56.97	54.81	11.25	11.89	48.20	183.12
	4	12.26	46.77	32.53	31.36	3.66	79.79	206.37
	5	3.85	68.92	88.44	77.93	16.49	158.49	414.12
	6		43.65	63.68	14.53	14.90	51.76	136.76
	7	2.42	73.85	84.57	70.96	9.13	254.45	495.38
20 Sept. 1976	8		19.83	59.34	45.87	24.51	327.52	477.07
	9		38.78	97.70	64.30	27.05	273.43	501.26
	10		17.62	38.41	10.12	6.52	116.63	189.30
	11		16.70	32.02	12.05	7.20	61.40	129.37
	12		7.92	40.64	12.20	12.18	125.33	198.27
28 Jan. 1977	13			52.71*	23.50	22.42	269.73	368.36
	14			54.87*	7.37	21.33	188.47	272.04
	15			39.87*	9.85	24.12	145.96	219.80
1 June 1977	16		33.44	22.48	4.24	14.08	46.45	120.69
	17		24.54	19.48	13.24	24.16	68.60	150.02
	18		20.20	21.44	14.16	38.32	106.75	200.87

* Winter leaves included.

TABLE IV

Mean ash-free dry weights of various plant parts of *N. peltata* in the course of a season

Date	Mean	Leaves ($g\ cm^{-2}$)	Long shoots ($g\ cm^{-1}$)	Short shoots ($g\ cm^{-1}$)	Roots (g/root)
26 June 1976		0.0041	0.0139	0.0599	0.0700
	S.D.	0.0004	0.0016	0.0115	—
4 Aug. 1976		0.0037	0.0200	0.0620	0.0800
	S.D.	0.0008	0.0073	0.0286	—
20 Sept. 1976		0.0039	0.0139	0.0563	0.0901
	S.D.	0.0006	0.0028	0.0099	—
28 Jan. 1977		—	0.0146	0.0673	0.1000
	S.D.	—	0.0084	0.0096	—
1 June 1977		0.0031	0.0051	0.0263	0.2520
	S.D.	0.0001	0.0012	0.0019	—

Long shoots grow especially in spring and early summer, together with the short shoots (Fig. 12). In winter there are mainly roots with short shoots, a few long shoots and some small leaves, which have been weighed together with the petioles. It is very striking that the mean total biomass/m^2 does not differ significantly in the months August, September and January, as the differences all fall within the standard deviations, while biomass is low in June. The high values of root biomass in winter and low values in June can mean that the roots are the organs in which nutrients are stored in winter, these are used especially during the period of strong growth in spring and early summer.

The ratio between aboveground and underground biomass is highest in June and lowest in January (Table V). We could calculate a correlation between leaf area/m^2 and total biomass/m^2 using all data collected (Fig. 13). As the sampling area has an almost constant depth and a homogeneous bottom composition, it has been supposed that its influence on leaf surface is constant. Therefore, the total biomass can be calculated as ash-free dry weight/m^2 with the following quadratic equation

$$y = 172.6\,x^2 - 284.2\,x + 250.4$$

$$\text{S.E.} = 41.0,\ R^2 = 0.84,\ n = 16,\ P < 0.001$$

y = ash-free dry weight in $g\ m^{-2}$, and x = leaf area in $m^2\ m^{-2}$.

The dry weight/m^2 can be calculated with the formula

$$y = 199.2\,x^2 - 321.7\,x + 278.2$$

$$\text{S.E.} = 42.4,\ R^2 = 0.87,\ n = 16,\ P < 0.001$$

y = dry weight in $g\ m^{-2}$, and x = leaf area in $m^2\ m^{-2}$. This formula also gives a description of the development of total biomass/m^2 related to the leaf area/m^2 during the season.

TABLE V

Ratio between aboveground (A) and underground (U) parts of *N. peltata* (Short shoots and roots are considered as underground parts, the other plant parts as aboveground parts)

Date	Sample	*A* (g m^{-2})	*U* (g m^{-2})	*A/U*	Aver. *A/U* per date	S.D.
26 June 1976	1	224.33	44.27	5.07	3.20	2.65
	2	66.16	50.29	1.32		
4 Aug. 1976	3	111.76	56.73	1.97	1.52	0.41
	4	111.07	72.82	1.53		
	5	216.12	154.63	1.40		
	6	110.54	60.94	1.81		
	7	203.22	222.44	0.91		
20 Sept. 1976	8	111.28	315.88	0.35	0.56	0.20
	9	175.15	278.63	0.63		
	10	57.78	108.53	0.53		
	11	54.06	61.82	0.87		
	12	54.28	123.62	0.44		
28 Jan. 1977	13	67.31	267.92	0.25	0.27	0.02
	14	53.90	192.98	0.28		
	15	44.42	160.14	0.28		
1 June 1977	16	52.28	52.60	0.99	0.67	0.30
	17	48.78	76.56	0.64		
	18	49.36	126.00	0.39		

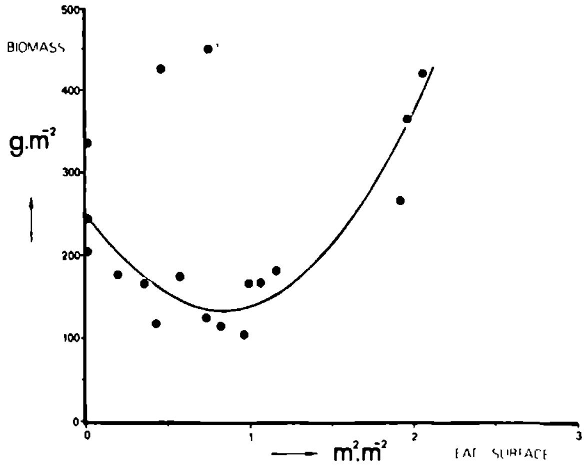


Fig. 13. Correlation between total leaf area/m^2 and the total biomass (ash-free dry weight)/m^2 of *N. peltata*. Two values have not been used for the calculation as they clearly fall outside the general picture.

DISCUSSION AND CONCLUSION

The results presented here must be considered to be preliminary although the various formulas calculated during this investigation produced very reliable results, they have only been used in the direct surroundings of Nijmegen, and have not yet been tested in other field situations and on other dates. Their general applicability has still to be proved. If they also appear to be valid in other situations they may be a useful and non-destructive tool for biomass determination.

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OBSERVATIONS ON THE DECOMPOSITION OF *NYMPHOIDES PELTATA* (GMEL.) O. KUNTZE (MENYANTHACEAE) WITH SPECIAL REGARD TO THE LEAVES

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ABSTRACT

Lammens, E.H.R.R. and G. van der Velde, 1978. Observations on the decomposition of *Nymphoides peltata* (Gmel.) O. Kuntze (Menyanthaceae) with special regard to the leaves. *Aquat. Bot.*, 4: 331—346.

In spring, summer and autumn, there is a continuous decomposition of *Nymphoides* leaves by means of physiological and consumptive or damaging processes.

The first process can take place in two ways: viz. by gradually dying off of the oldest leaves and by mass decomposition after the flowering period. In autumn, when the growth stops, this process of physiological decomposition is continued by the fungus *Septoria villarsiae* Desm. (Fungi imperfecti). The rust *Puccinia scirpi* DC, of which the aecidia have been found on the leaves in June, does not seem to play a role of any significance. Detritivorous benthos organisms, particularly *Asellus aquaticus* L. (Crustacea, Isopoda), take care of the fragmentation and partial digestion of dead, rotten plant material.

Independent of these processes, decomposition is also caused by animals which eat and damage the living leaves. This decomposition is caused by pulmonate snails, especially *Lymnaea stagnalis* (L.) (Gastropoda, Lymnaeidae), the larvae of *Nausinoe nymphaeata* L. (Lepidoptera, Pyralidae) and *Cricotopus trifasciatus* (Meig.) (Diptera, Chironomidae), the Coot (*Fulica atra* L.) (Aves, Rallidae) and the Muskrat (*Ondatra zibethicus* (L.)) (Mammalia, Rodentia).

Leaves of seedlings on temporarily dry mud bottoms are eaten by terrestrial slugs, viz. *Deroceras laeve* (Müller) (Gastropoda, Limacidae), during moist weather conditions.

INTRODUCTION

In 1974 an investigation was started on the structure and dynamics of nymphaeid communities in the surroundings of Nijmegen, The Netherlands.

Nymphoides peltata (Gmel.) O. Kuntze is the dominant species of one of the vegetation types under investigation. The general structure of this community will be reported in another paper. This paper will deal with our observations on the decomposition of leaves of *Nymphoides peltata* in the "Oude Waal" near Nijmegen and some neighbouring ponds during the summer and autumn of 1974 and 1975. The quantitative aspects of decomposition will be reported later.

According to Odum (1971) the process of decomposition consists of three steps.

(1) Dying off, fragmentation and consumption.

(2) Liberation of organic matter by the activities of micro-organisms (Dickinson and Pugh, 1974).

(3) Formation of detritus. The more resistant materials such as cellulose, hemicellulose, lignin and some other compounds of the cell wall remain. Their decomposition takes more than a year.

The different factors which play a role in the decomposition of the leaves of *Nymphoides* can be divided into internal physiological factors and external factors such as consumption and damage by animals and infection by fungi and bacteria.

DESCRIPTION OF THE AREA STUDIED

The area in which the investigations were carried out, the "Oude Waal" and some neighbouring ponds, is situated to the east of Nijmegen in the Ooypolder near the river Waal (Fig. 1). The "Oude Waal" has a length of about 1 km and a breadth of about 250 m. Three quarters of the "Oude Waal" is a great shallow eutrophic water (Fig. 1,C), a former river bed with a depth, varying in summer from year to year, between 0.5 and 1.5 m. It has a clay and sand bottom; in some parts it is a mixture of both. In most localities the

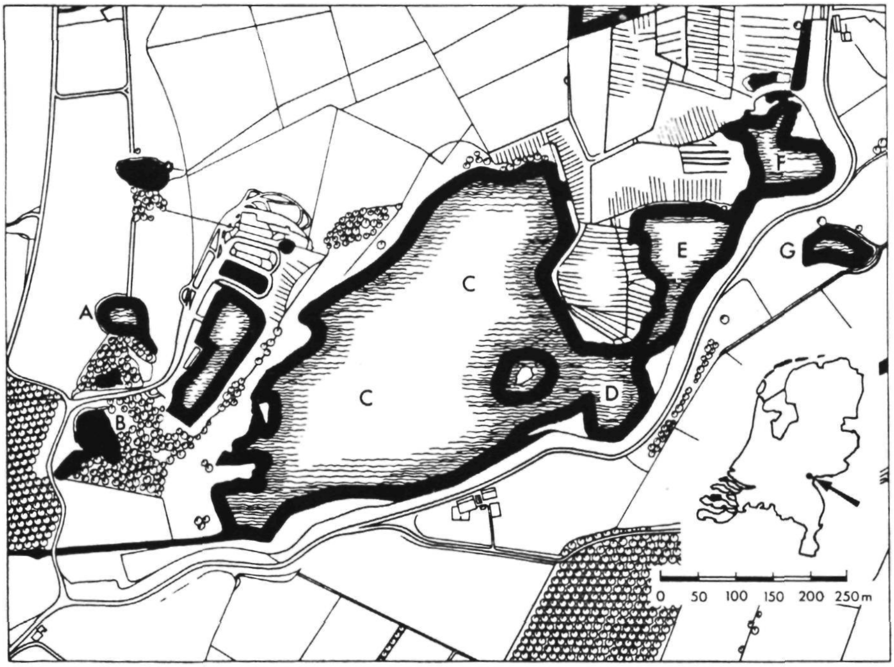


Fig. 1. Map of the area studied.

bottom is covered by a thick layer of sapropelium. Connected to this broad are three ponds (Fig. 1, D,E,F), which are also interconnected. The depth of these ponds increases towards their centre to a depth of 2.5 m (pond D), 5.5 m (pond E) and 5.5 m (pond F), respectively. They have a bottom consisting of a sand—clay mixture, which is more or less covered by a layer of sapropelium, the thickness of which increases towards the centre. The vegetation in the large broad consists of a wide zone of *Nymphoides* and this zone is often surrounded on one side by beds of *Nuphar lutea* (L.) Sm. and *Nymphaea alba* L. and by littoral border plants on the other: in the ponds, *Nymphoides* is dominant to a depth of 2 m. The vegetation of the connections between the ponds is also dominated by *Nuphar* and *Nymphaea*.

MANNER OF INITIAL DECOMPOSITION

Physiological factors

a. Dying of the old leaves (Fig. 2)

During the growth season young leaves develop steadily and the old ones deteriorate. The leaves at first become yellow, and than brown and weak, before they begin to decay. During the deterioration the leaf loses its hydrophobous character and sinks somewhat under the water. The aerial cavities become filled with water and the leaf begins to fragment, the fragments sinking to the bottom.

The physiological decomposition of the older leaves is a common phenomenon in herbs and is probably regulated by hormones just as the abscission in shrubs and trees (Osborne, 1963).

b. Mass decomposition after the flowering period

At a certain time, at the end of August or the beginning of September, when the plant has formed many fruits, up to 1000 per m^2, the flowering stems begin to decay at their bases and break off from the stolon. Together with these flowering stems, the vegetative parts also deteriorate in those localities where flowering was very profuse. By this process vegetation belts 15 m wide can be reduced to zones less than 2 m wide (Figs. 3 and 4). Where flowering has been less profuse, deterioration of vegetative stems usually takes place several weeks later. In localities where flowering has been poor, only the flowering stems die and deterioration of vegetative parts takes place much later.

External factors

a. Damage by wind and wave action

In contrast to the damage by wave and wind action to leaves of *Nymphaea alba* and *Nuphar lutea*, it plays a subordinate role in *Nymphoides* vegetation since the *Nymphoides* belt is usually sheltered by littoral border plants; its

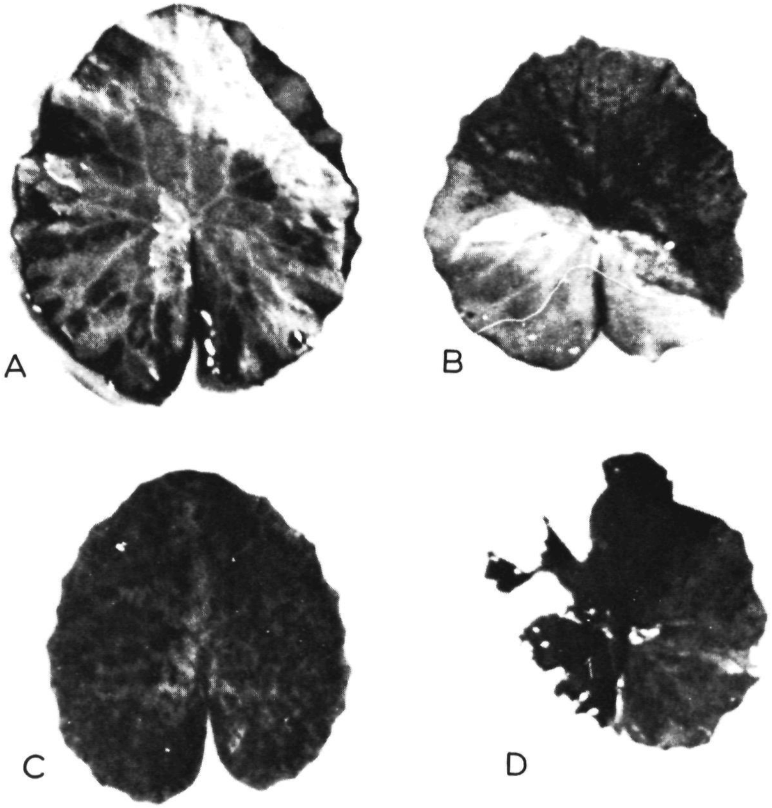


Fig. 2. Dying of the old leaves. A. Green leaf; B. yellow-brown leaf; C. brown leaf; D. fragmenting leaf.

leaves and petioles are very flexible. When exposed, the high leaf density slows the waves down and causes the water within the vegetation to become rather stagnant.

b. Consumption and damage of the living plant by animals

According to Gaevskaya (1969), the following animal species eat parts of the living plant: *Cricotopus trifasciatus* (Meig.) (Diptera, Chironomidae) which eats from the floating leaves, *Cambaroides schrenkii* (Kessler) (Decapoda, Astacidae) which eats leaves and stalks, and *Anas penelope* L. (Aves, Anatidae), which eats shoots. Gaevskaya (1969) also mentions *Chironomus nymphaeae* Willem, based on the paper by Willem (1908). Willem (1908), however, mentioned as food "Nénuphar", which is the French name for *Nymphaea*, while the French name for *Nymphoides* is "Faux-Nénuphar" (Willem, 1910). Ching and Chih-Tang (1965) record the Muskrat, *Ondatra zibethicus* (L.) as a consumer of *Nymphoides peltata.*

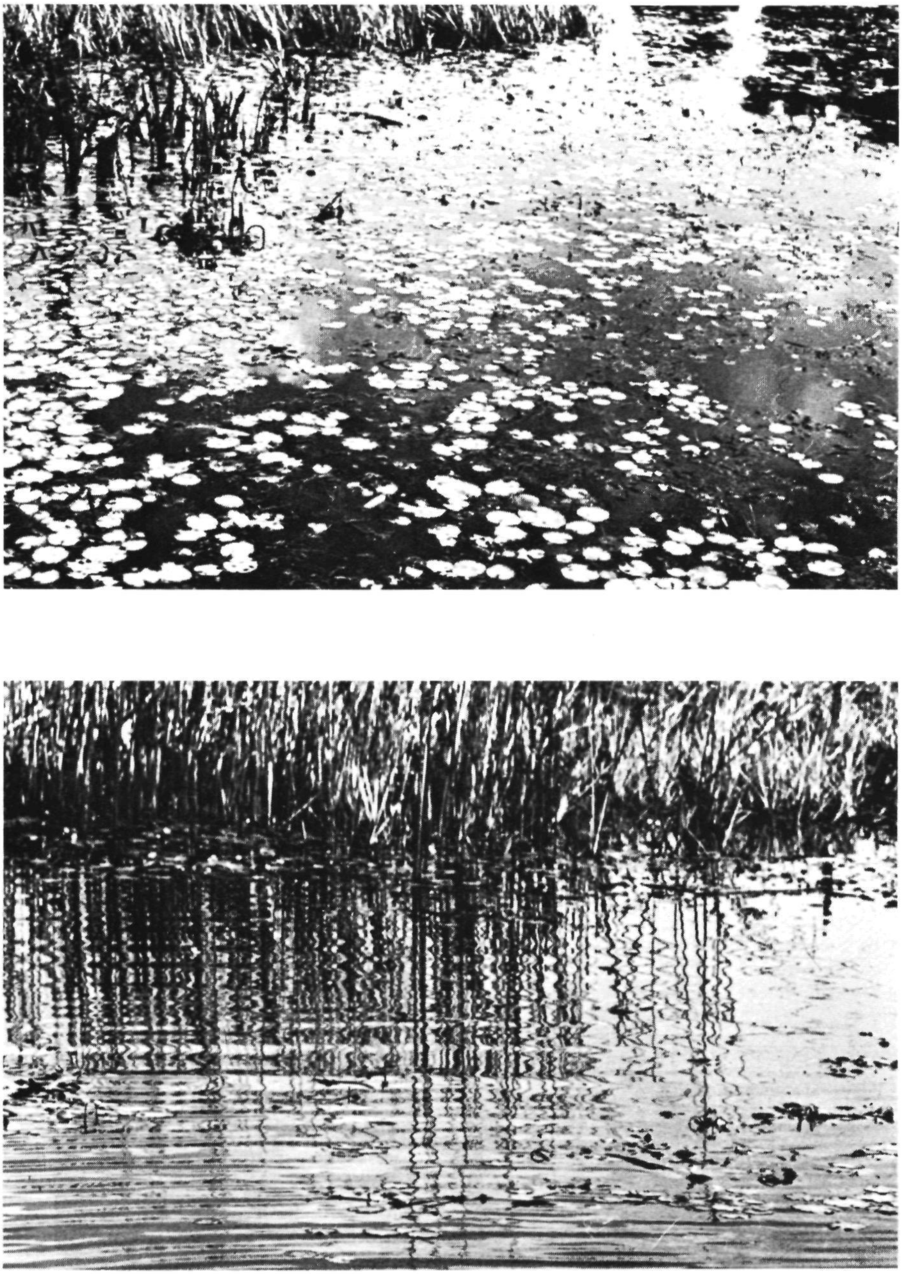


Fig. 3. Mass decomposition after the flowering period. Above, after medium flowering; below, after intensive flowering, the vegetation belt disappeared almost completely. Both photographs were made on 2 October 1975.

Fig. 4. Detail of mass decomposition. Decaying flowering stems with ripe fruits can be seen in the water together with leaves (which are heavily damaged by *Cricotopus trifasciatus*).

The most important consumers of *Nymphoides* in the "Oude Waal" are *Lymnaea stagnalis* (L.) (Gastropoda, Lymnaeidae), *Nausinoe nymphaeata* L. (Lepidoptera, Pyralidae), *Cricotopus trifasciatus* and the Coot, *Fulica atra* L. (Aves Rallidae). In addition the Muskrat must be mentioned. Damage caused by the larvae of *Holocentropus picicornis* (Stephens), *Cyrnus flavidus* McLachlan and *C. crenaticornis* (Kolenati) (Trichoptera, Polycentropodidae), which damage the leaves by cutting off small pieces from the edge in order to support their webs on the underside of the leaves, appears to be of minor importance.

Snails. Gaevskaya (1969) gives a list of 38 plant species which have been eaten by *Lymnaea stagnalis*, but does not mention *Nymphoides*. According to Frömming (1956) *Lymnaea stagnalis* is an omnivore, which eats algae, fresh and rotten phanerogams and dead animals. It also feeds on microorganisms, pollen etc., which occur on the surface film. The young animals eat first from rotting parts of the phanerogams. When they are half grown they begin to eat fresh parts. *Lymnaea stagnalis* consumes more old than young leaves; the stronger nerves are also eaten together with the petioles. On fresh leaves of various plant species they become larger and grow faster than on a diet of meat or dead leaves.

Lymnaea stagnalis rasps small to large rounded pieces from the margin or roughly rounded gaps in the leaves of *Nymphoides* (Fig. 5). Sometimes these gaps are very irregular. It is not always possible to distinguish the damage caused by *Lymnaea* from that of the *Nausinoe* larvae, but the latter can be found under the leaves and eat often relatively large surfaces, leaving one of the epidermis intact, while this is eaten completely by *Lymnaea*. *Lymnaea stagnalis* uses the under surface of the leaves of *Nymphoides* to deposit its egg masses.

Other Lymnaeidae, e.g. *Galba palustris* (Müller) and *Radix peregra* (Drap.) can also eat the leaves of *Nymphoides*, as appears from aquarium experiments and observations in such small habitats as ditches. Their damage is considerably less than that caused by *Lymnaea stagnalis*. The snails often creep and feed on the upper side of the leaves; the young snails only rasp this side superficially. In the "Oude Waal" these species have not been observed as consumers of *Nymphoides peltata*.

Wagner (1895) wrote that most of the seedlings of *Nymphoides* are eaten by snails, so that very few seedlings grow. In localities where *Nymphoides* emerged during a period of low water level in summer, we found many seedlings, possibly because the snails could not reach them during the dry weather. On moist days the leaves were eaten by the slug *Deroceras laeve* (Müller) (Fig. 6).

Nausinoe nymphaeata. Nausinoe nymphaeata has been recorded by Gaevskaya (1969) from 19 species of food plants, most of them aquatics with floating leaves. *Nymphoides peltata*, however, was not mentioned as a food plant for this species. In the "Oude Waal" many leaves of this plant were damaged and the observed damage was greater than that to leaves of *Nuphar* and *Nymphaea.*

Its life history and habits have been described by Müller (1892), by Wesenberg-Lund (1943) and extensively by Reichholf (1970). A short description of the activities especially of the caterpillars of the second generation is given based on the literature mentioned. The development of the first generation proceeds similarly but without hibernation. The hydrophilous

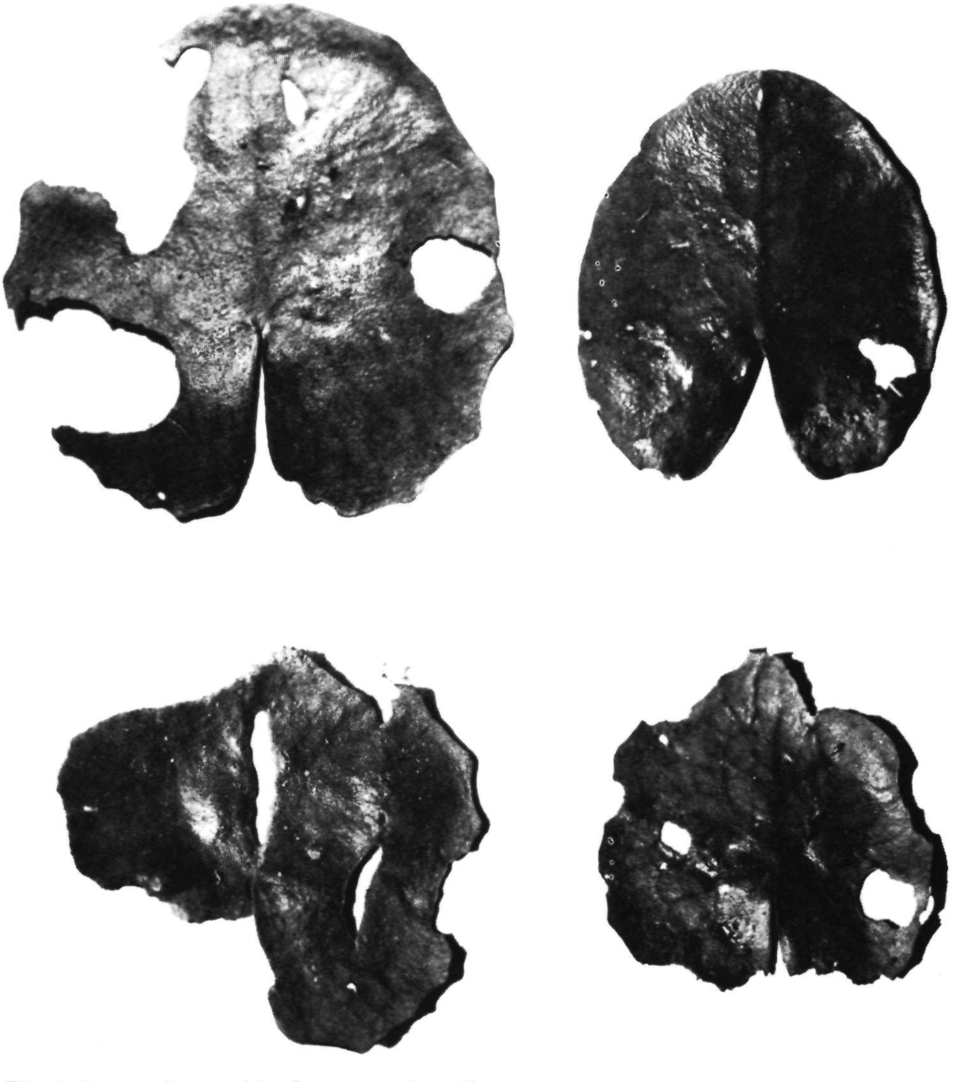


Fig. 5. Leaves damaged by *Lymnaea stagnalis.*

larvae of the second generation hibernate in the water. The first generation completes its life-cycle in June—September, the second one in the period from the end of August to June (Reichholf, 1970). The eggs are laid in rows on the underside near the edge of a floating leaf; the newly hatched hydrophilous larva is surrounded by water and the spiracles are closed, so that it must respire via the cuticula. Subsequent to hatching, the larvae disperse over the leaves. They mine for a few days in the leaf or cut out a small piece from the edge of the leaf with which they cover themselves on the underside of the leaf. They then cut an oval piece out of the leaf and commence first with "window-feeding" and later with leaf perforation (Fig. 7, A and B). In its case, consisting of two elliptical leaf fragments spun together, it is still surrounded by water. The case is replaced several times by cutting out new leaf fragments without any important alteration in its habits. It then sinks to the bottom with the rotten leaves, to which the case has been attached, where it overwinters (Müller, 1892) or it hibernates in a hole which is bored in a stem of the food plant (Reichholf, 1970). With the arrival of spring it crawls up to the young shoots of the food plant and continues living in the same way. Now, however, it becomes hydrophobous and commences normal respiration; its case is now filled with air. The case of the hydrophobous larva is replaced 6—8 times per larval stage, so the damage of the leaves can be great. There are 4 larval stages (2 hydrophilous and 2 hydrophobous). Pupation takes place in June in a cocoon, formed by the case, which is fixed flag-like to a stem, petiole or leaf of the food plant. Air is present in the cocoon (Wesenberg-Lund, 1943). The imago after hatching rises to the water surface by taking up the air from the pupa between its wings.

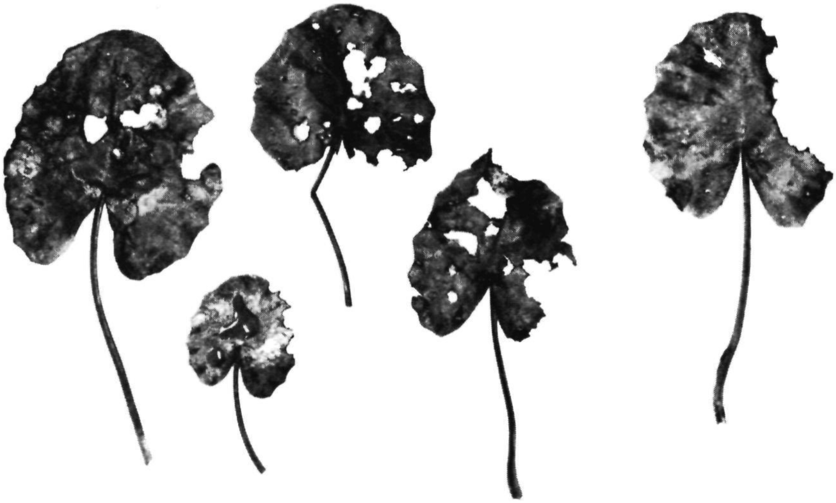
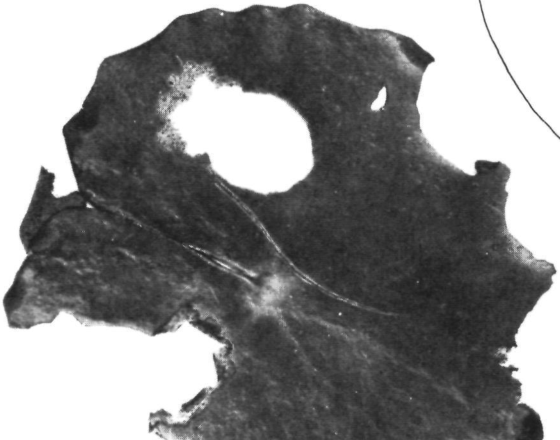


Fig. 6. Leaves of seedlings damaged by *Deroceras laeve*.

A



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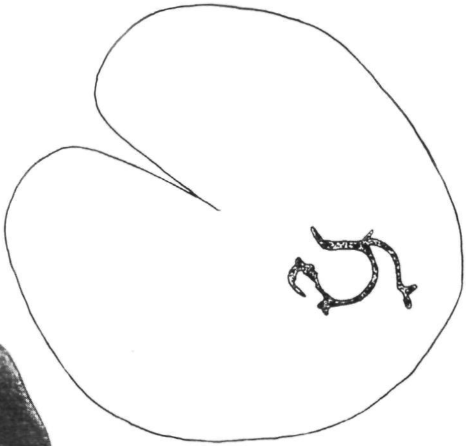

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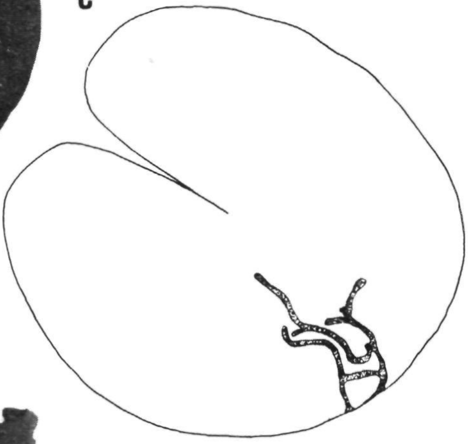

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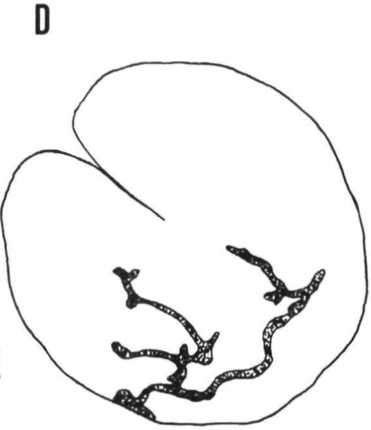

E

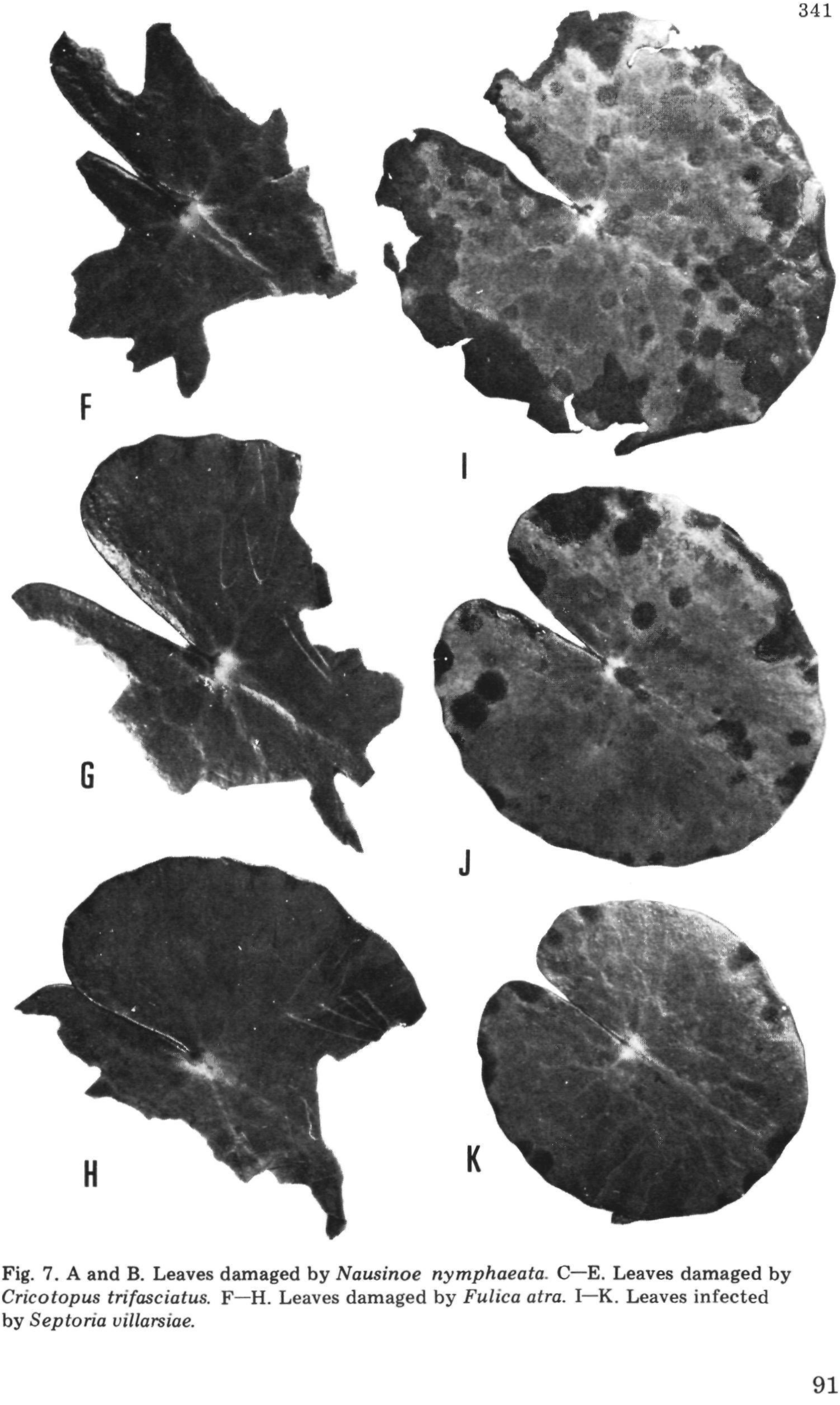

Fig. 7. A and B. Leaves damaged by *Nausinoe nymphaeata.* C—E. Leaves damaged by *Cricotopus trifasciatus.* F—H. Leaves damaged by *Fulica atra.* I—K. Leaves infected by *Septoria villarsiae.*

Cricotopus trifasciatus. Gaevskaya (1969) mentions 6 food plants for *Cricotopus trifasciatus,* all with floating leaves, among which is *Nymphoides peltata.* A description of the various life stages is given by Hirvenoja (1973). A very informative description, which is summarised here, of the biology of the species is given by Kettisch (1936, 1937). The midge lays her eggs together with mucus on a leaf or in old leaf mines, where there is water, or near the edge of the underside of the leaf or their petioles. The larvae live from the mucus until the third moulting. After that time, they begin to mine, mostly from the edge of the leaf, and eat the upper epidermis and palisade tissue and sometimes sponge tissue (halfminer), forming characteristic tracks in the leaf (Fig. 7, C—E). When the mine is broad enough, they build their own case by means of secretions and they make it solid with excrement and diatoms; both ends of this case are open. In the mine the water is steadily refreshed by the activities of the larva which creeps to the edge and makes movements with the anal part of the body or by gnawing the intact under epidermis when the mines are situated in the middle of the leaf. After the seventh moulting the larvae pupate. The development time becomes faster when the temperature rises. During summer, the lifetime of one generation is four to six weeks. There are therefore five or six generations per year. The eggs, which can tolerate low temperatures, probably hibernate (Kettisch, 1937).

Cricotopus larvae can damage the leaves very badly (Fig. 8). By rotting of the mines, leaves easily fragmentate.

Fulica atra. Very extensive information on the life history and habits of the Coot can be found in the works of Glutz von Blotzheim et al. (1973) and Boer et al. (1974). The Coot is an omnivore. The diet of those inhabiting freshwater areas consists mainly of plant material (algae, phanerogams and also decaying plant material) and, to a lesser degree, of animals such as molluscs and insects. The kind of plant material which is consumed depends strongly on time and locality. A great number of aquatic and littoral border plants are mentioned as food by Gaevskaya (1969), Glutz von Blotzheim et al. (1973) and Boer et al. (1974).

In the "Oude Waal" it appears to eat as additional food the leaves of *Nymphoides peltata,* which has not been recorded before as a food plant for the Coot (Fig. 7, F—H). Its main food is young shoots and leaves of *Scirpus* and *Phragmites,* which is available in the area studied. This forms the food in summer. In winter the animals graze in groups on the surrounding grassland, where they eat grass.

Ondatra zibethicus. The Muskrat consumes mainly helophytes such as *Typha* and *Phragmites,* and in particular their root systems. A great number of other plants are known to be eaten occasionally by this species (Gaevskaya, 1969); it also uses animal food (e.g. molluscs). In the "Oude Waal" the Muskrat affects the plants by eating rootstocks, shoots, petioles and leaves and by the use of these plant materials for the building of their "houses". By far the most important, however, is its burrowing activity in spring, by which plants of *Nymphoides* become detached "en masse" from the bottom and float away.

c. Infection by fungi of the living leaves

Two parasitic fungi have been found on the leaves of *Nymphoides* in the "Oude Waal", viz. *Septoria villarsiae* Desm. (Fungi imperfecti) and *Puccinia scirpi* DC (Urediniales). Of these two species, *Septoria* is very important for the decomposition of the leaves while *Puccinia* is too rare to play a role of any importance.

Septoria villarsiae. Septoria villarsiae can be seen as brownish-grey, round spots, with many black points, the pycnidia, on the leaves [see Rabenhorst (1901) and Grove (1935) for a detailed description of the species] (Fig. 7, I–K). In summer the infection occurs very incidentally and when a leaf is infected only one or two large spots can be seen on it. In autumn, the infection becomes very abundant and many spots with diameters of 3–6 mm appear on the leaves. The infection begins at random on the leaf but soon the edge is also infected and from there the infection extends to the centre. The whole infected leaf becomes very weak, begins to fragment and the air spaces become filled with water. Many micro-organisms such as nematodes, ciliates and flagellates are then present on the leaf. The fragments sink to the bottom. After the infection has reached the centre of the leaf, the petiole also becomes infected turning yellowish towards the base; it becomes soft and also begins to fragment.

Fig. 8. Leaves damaged by *Cricotopus trifasciatus*.

In 2 rosettes of *Nymphoides peltata* the appearance and further development of *Septoria* has been followed (Fig. 9). During the growth of the leaf no infection was observed, but when the growth decreased spots of *Septoria* appeared, usually after some weeks. Leaves of the terrestrial form can also be infected by *Septoria.*

Puccinia scirpi. The yellow-orange aecidia of *Puccinia scirpi* were found twice on June 16, 1975, by A.M.J. van der Aa on the leaves of *Nymphoides peltata* (Fig. 10). According to Gäumann (1959) and Wilson and Henderson (1966) the uredo- and teleutospores can be found on *Scirpus lacustris* L. (July—November), the spermogonia and aecidia on *Nymphoides* in July. *Scirpus lacustris* is present in the area studied. A more abundant infection by *Puccinia scirpi* on the leaves of *Nymphoides peltata* has been illustrated in Steinecke (1940, Fig. 32).

DECOMPOSITION OF DECAYING LEAVES

When the dead, rotten leaves and fragments have sunk to the bottom, the detritivores consume this plant material and reduce it to small faecal pellets.

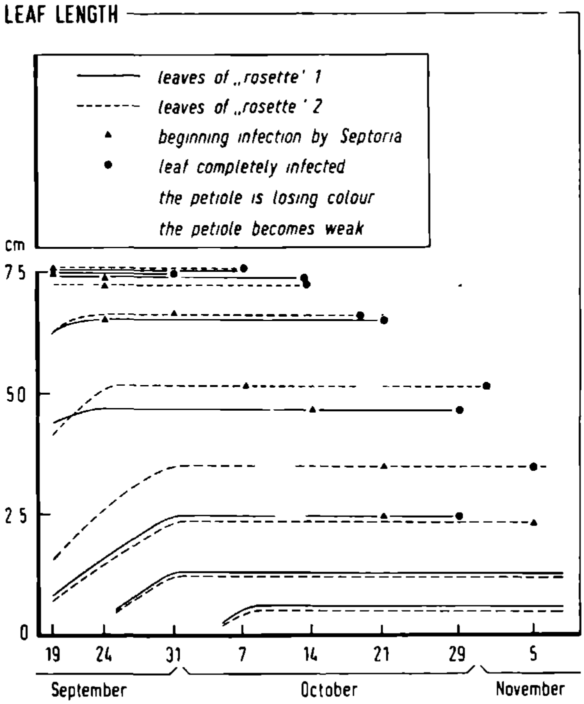

Fig. 9. Development of leaves of two "rosettes". The length of each leaf is plotted against the time. The triangles give the moment that *Septoria* was seen for the first time on the leaf.

To get an impression which animals consume dead plant fragments, litterbags were used. These were made of synthetic material with meshes of 3 mm and were 15 cm long and 10 cm broad. The litterbags were filled with dead leaves of *Nymphoides*, laid on the bottom and every week during autumn the macrofauna attracted by the bags was collected. The following species, in order of decreasing numbers, were caught in this way: *Asellus aquaticus* L. (1982 specimens), *Stylaria lacustris* (L.) (166 sp.), *Cloeon dipterum* L. (78 sp.), *Caenis horaria* (L.) (59 sp.), *Dugesia polychroa* (O. Schmidt) (43 sp.), *Microstomum lineare* (O.F. Müller) (26 sp.), *Piscicola geometra* (L.) (9 sp.), *Haliplus* larvae (8 sp.), *Helobdella stagnalis* (L.) (6 sp.) and *Lumbriculus variegatus* (Müll.) (5 sp.).

Asellus aquaticus appears to be the only important species for the further decomposition of the plant material. Experiments in the laboratory proved that *Asellus* can live exclusively on decayed fragments of *Nymphoides* leaves and also on its faeces. *Stylaria* and *Lumbriculus* feed only on fine particles and possibly depend on the activity of *Asellus* while *Caenis* and *Cloeon* have a preference for detritus and periphyton. The latter can also consume fragments of dead plant tissue (Soszka, 1975). The rest of the fauna found on the litterbags consists of predators and consumers of algae.

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The authors are much indebted to Prof. Dr. C. den Hartog for critical remarks and to Mr. J.G.M. Roelofs for taking the photographs. We also thank the Plantenziektekundige Dienst, Wageningen and Dr. G. van den Ende, Nijmegen for their help with the identification of the fungi.

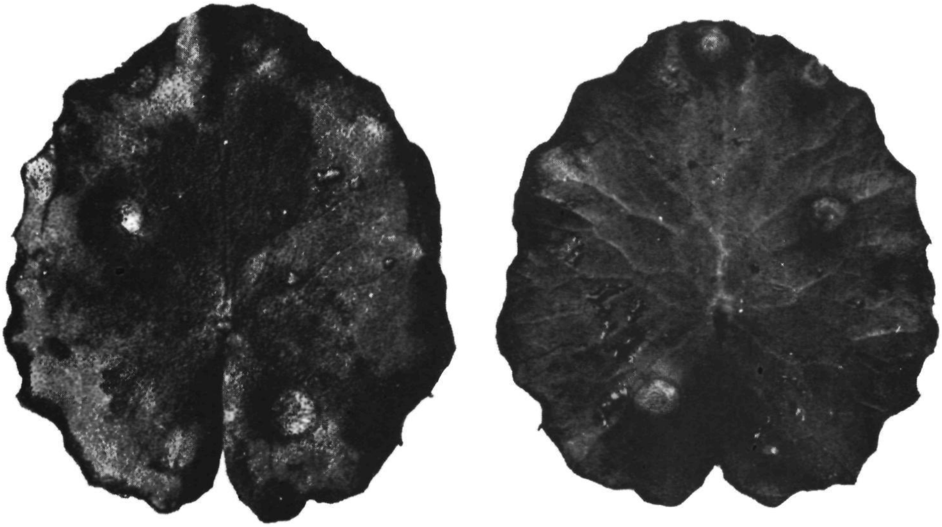

Fig. 10. Aecidia of *Puccinia scirpi* on the upper side of the leaf.

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THE FLORAL BIOLOGY AND SEED PRODUCTION OF *NYMPHOIDES PELTATA* (GMEL.) O. KUNTZE (MENYANTHACEAE).

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ABSTRACT

Van der Velde, G. and Van der Heijden, L.A., 1980. The floral biology and seed production of *Nymphoides peltata* (Gmel.) O. Kuntze (Menyanthaceae).

A study has been made on the prefloral, floral and postfloral biology of *Nymphoides peltata* (Gmel.) O. Kuntze in a former river bed of the Waal and in two concrete tanks situated on the area of the Catholic University of Nijmegen (The Netherlands).

The structure of the flowering stem and the flowering pattern have been described; it grows in such a way that a continuous field of flowers is maintained during a long period in the season. In the development from flower bud to mature fruit 8 stages are distinguished.

The structure of the flower is described. The flowers of *N. peltata* fall within category B of the system of H. Müller who divided the entomophilous flowers in seven categories, as they are not strongly specialized for the visiting of only one insect group, while the nectar is totally hidden. As a specialized feature of the *N. peltata* flower within the genus *Nymphoides* can be considered the u.v. pattern, which is the same as in *N. geminata* (R. Br.) O. Kuntze (also a yellow flowering species), as a primitive feature the heterostyly combined with a weak incompatibility system. *N. peltata* is a day flowering species; the flowers wither within one day. Features of the flower attracting anthophilous insects are: a high flower frequency and long flowering period within the season, the yellow coloured corolla with a characteristic u.v. pattern and an average diameter of 4.60 cm, at average 3.27 cm above the water surface, and a weak sweet odour. Higher temperatures than the surroundings play perhaps no role as attracting feature, as the difference is small.

The flowers have to offer nectar (sheltered by staminodes of 0.5 — 0.6 cm, pollen and perhaps some stigmatic exudate. Further predators are attracted by the insects present. The list of flower visiting animals contains 44 species of which 43 species of Hexapoda and 1 species of Aranea. The possible reasons for flower visiting of the insects and their possible role in pollination are discussed. With respect to pollination species of Apidae, Syrphidae and Ephydridae seem to be most important. Species of Apidae and some species of Syrphidae can reach the nectar by their long tongues (longer than 5—6 mm), most species of Syrphids and all Ephydrid species use pollen and liquid substances, but their tongues are too short to reach the nectar containing fructose and glucose in equal amounts. Apidae and Syrphidae fly from flower to flower while the Ephydridae show an irregular pattern of flower visiting; they are very important by their large numbers. In contrast to the Apidae and Syrphidae the Ephydridae occur also very commonly on the floating leaves of *N. peltata*. Of the 44 species mentioned 30 species were seen only on the flowers while 14 species were also commonly found on the floating leaves. The first category is attracted mostly by the characteristic features of the flower, while the second category is more characteristic for the nymphaeid system. Each flower visitor can cause pollination and in the case of short-styled flowers also self-pollination, by which small capsules are produced with a low number of seeds (mostly below 10—15). The release of developed seeds is 32 — 60 days after the day of anthesis of the flowers. In the field and the concrete tanks where both floral forms occur, distinct differences in the fruit and seed production were observed. The number of fruits and the number of developed seeds per m^2 was much higher in the concrete tanks due to the development of much more flowers than in the Oude Waal, but the average number of seeds per fruit was here much lower and the percentage of fruits with a number of seeds below 15, was higher which indicates that the flowers in the small isolated concrete tanks were not so efficiently pollinated as in the field, possibly because some important Ephydrid species such as *Notiphila brunnipes* were not present in the concrete tanks.

The produced seeds of *N. peltata*, in the Oude Waal more than 3000 per m^2, which are floating at first on the water surface, are dispersed over the water by wind, and by water birds. When the frost period starts nearly all seeds have sunk to the bottom.

INTRODUCTION

Nymphaeids are aquatic plants which root in the bottom, possessing mainly floating leaves; the flowers emerge above or float on the water surface. In shallow fresh water they can form extensive stands; by their structure they characterize the ecosystem to a high degree. In the Netherlands such stands are locally very common.

In 1974 an investigation was started on the structure, dynamics and function of nymphaeid communities in the surroundings of Nijmegen, The Netherlands. The study of the nymphaeid communities is planned as an integrated ecosystem study; aspects of the nymphaeid system are studied separately, but also in relation to each other. The nymphaeid plants themselves are considered to be the frame of the system and all aspects of it has to be studied to understand how the vegetations develops, how it maintains itself, how other organisms can interact with it and how the vegetation influences its surroundings and vice versa.

Nymphoides peltata (Gmel.) O. Kuntze is the dominant species of one of the vegetation types under investigation. Two earlier papers dealt with initial decomposition, distribution and ecology, structure, biomass and seasonal changes in biomass of *N. peltata* (Lammens and Van der Velde, 1978; Van der Velde, Giesen and Van der Heijden, 1979). The present paper will deal with observations on floral biology and seed production of *N. peltata.*

The sexual reproduction of the plant is very important with respect to survival under adverse conditions and for the dispersal of the plant species within and to other localities in the form of seeds. Further there are many interrelations between the flowers and insects for which the flowers offer food, while the insects can play an important role in the pollination of the flowers.

STUDY AREA

Most observations have been made on plants in an former river bed of the river Waal, called "Oude Waal", near Nijmegen. A description of the Oude Waal is given in Lammens and Van der Velde (1978).

The development of flowers was mainly studied in concrete tanks 1.50 x 1.00 m and 50 cm deep, situated on the area of the Catholic University of Nijmegen.

GENERAL STRUCTURE OF THE FLOWERING STEM

The general structure of *N. peltata* is discussed in Van der Velde et al. (1979). As already pointed out there the flowering stem develops from a leaf axil of a long shoot. When the long shoot from which it springs is situated near the bottom the first internode of the flowering stem has a length more or less similar to the water depth; however, often the long shoot itself is growing to the water surface so that the first internode of the flowering stem is rather short with respect to water depth. The flowering stem can branch a few times at its nodes (Fig. 1). The nodes of the flowering stem usually bear no roots. The flowering stem can develop however at its end a short shoot with roots (secondary propagation).

The leaves of the flowering stem differ from the short shoot leaves by being smaller in size (2—5 cm long) and having relatively short petioles, so that these leaves during their development are often held somewhat above the water surface. The leaves stabilize the position of the flower clusters and hold them near the water surface (Fig. 1).

Along the flowering stem two leaves of unequal size nearly opposite to each other are present; from the axil of the largest one the stolon continues sympodially, while from the axil of the smaller one a terminal flower cluster develops. The first internode after this pair of leaves is very short. After another pair of leaves the next internode of the flowering stem is much larger and subsequent internodes become then gradually smaller. The pattern described for the first node is still repeating itself at each node of the flowering stem (Fig. 1 and 2).

Anthesis of the flowers of each cluster takes place in sequence of cluster development, thus in Fig. 2 the flowers of C 1 develop first, then those of C 2 etc. There can be some overlap so that two flowers of subsequent clusters are flowering simultaneous (Table 1). Further a distinct sequence of anthesis takes place per cluster as given by numbers in Fig. 2 and Table 1. According to Wagner (1895) the clusters are cymose and pleiochasial with acropetally diminishing branchings. In our opinion a cluster can be described as a cymose bostryx.

The timing of anthesis in a flower cluster is not totally regular. There are three possibilities with respect to the time in which the anthesis of the next flower occurs (Table 1), viz. the day after the anthesis of the preceeding flower (40% of the cases), two days after the anthesis of the preceeding flower (47%) or 3 days after this (13%) (N = 38).

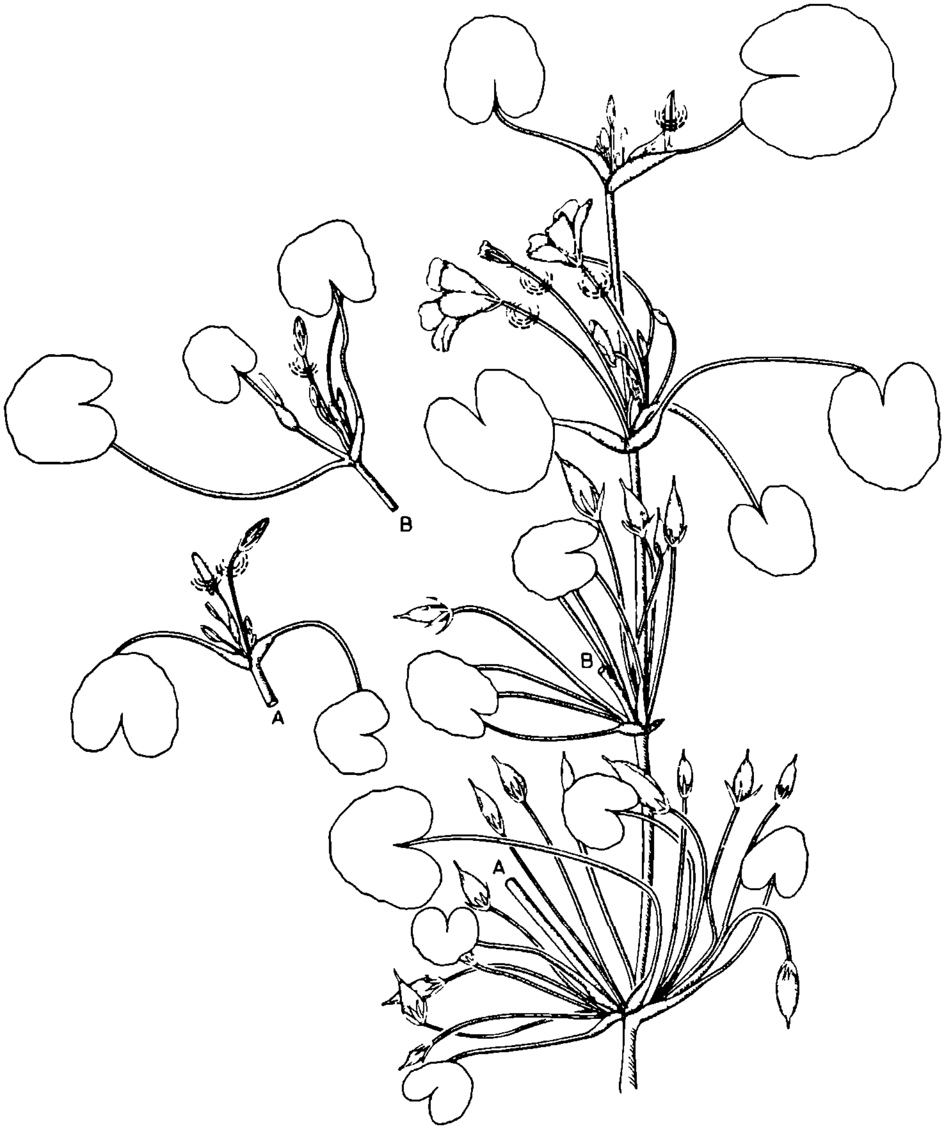

Fig. 1. Flowering stem of *N. peltata* seen from above. Note the various developmental stages of the flowers.

DEVELOPMENT FROM FLOWER BUD TO MATURE FRUIT

During development from flower bud to mature fruit several stages can be distinguished. To follow the development of the flowers two flowering stems in a concrete tank were chosen; each pedicel was marked with Rotex-tape on

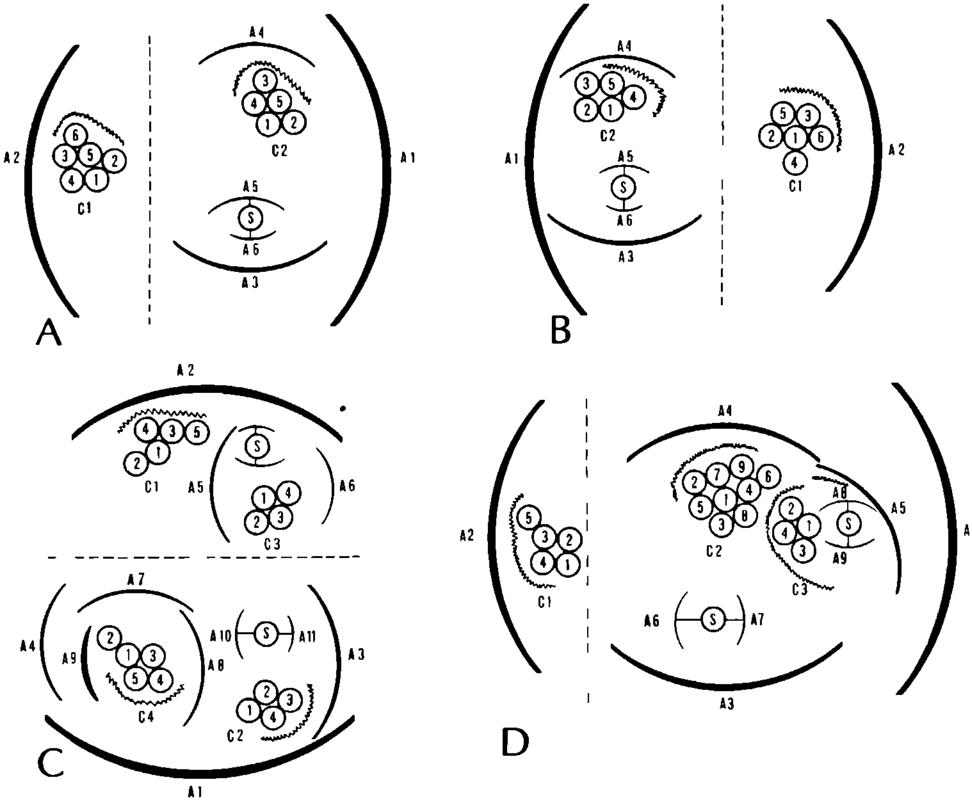

Fig. 2 Schemes of flowering stems of *N peltata* (frontal view), which have been come recently to the water surface. The internodes are still very short
A1 leaf axil of the largest leaf etc., C1 flower cluster 1, S continuing stolon, zickzack lines involucra.

which a number was printed and the length of the pedicel, bud, flower and fruit of each flower of these flowering stems was measured daily.

In this way the development and duration of each stage could be determined. In Fig. 3A and B the development for separate flowers is given. The following stages can be distinguished:

1. A bud stage at which only the green calyx is visible. This situation is maintained till one day before flowering and has a duration of at least 14 days During its development the bud grows on average 0.06 cm per day (SD = 0.02 cm) (Table 2). The buds are usually below the water surface during this stage. During this stage the length of the pedicel increases steadily to about 3.9 cm (Table 3) and the pedicel curves gradually upwards.

2. A bud stage one day before flowering. In this stage the yellow corolla becomes visible. The bud has risen above the water surface. During this stage the pedicel shows a relatively quick growth of approximately 0.67 cm (Table 3).

Table 1

	June						July																														August		
Date	25	26	27	28	29	30	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	01	02	03
Flowering stem 1																																								
C 1	1	2	-	3	-	4	-	5	-	6																														
C 2								1	2	-	3	-	4	5																										
C 3																1	-	2	-	3	4	-	5	-	-	6														
C 4																							1	-	2	-	-	-	3	-	4	-	-	5						
C 5																																					1	-	-	2
Number of open flowers	1	1	-	1	-	1	-	2	1	1	1	-	1	1	-	1	-	1	-	1	1	-	2	-	1	1	-	-	1	-	1	-	-	1	-	-	1	-	-	1
Flowering stem 2																																								
C 1	1	-	-	2	-	3	4	5	6																															
C 2								1	-	2	-	3	-	4	-	5																								
C 3																	1	-	2	3	4	-	5	-	6	-	-	-	7											
C 4																									1	-	-	2												
Number of open flowers	1	-	-	1	-	1	1	2	1	1	-	1	-	1	-	1	1	-	1	1	1	-	1	-	2	-	-	1	1											

Table 1. Sequence of flowering in flower clusters of two flowering stems of *N. peltata*. C1: first flowering flower cluster; 1, 2 etc.: anthesis of flower 1, 2 etc. in one flower cluster (see also Fig. 2).

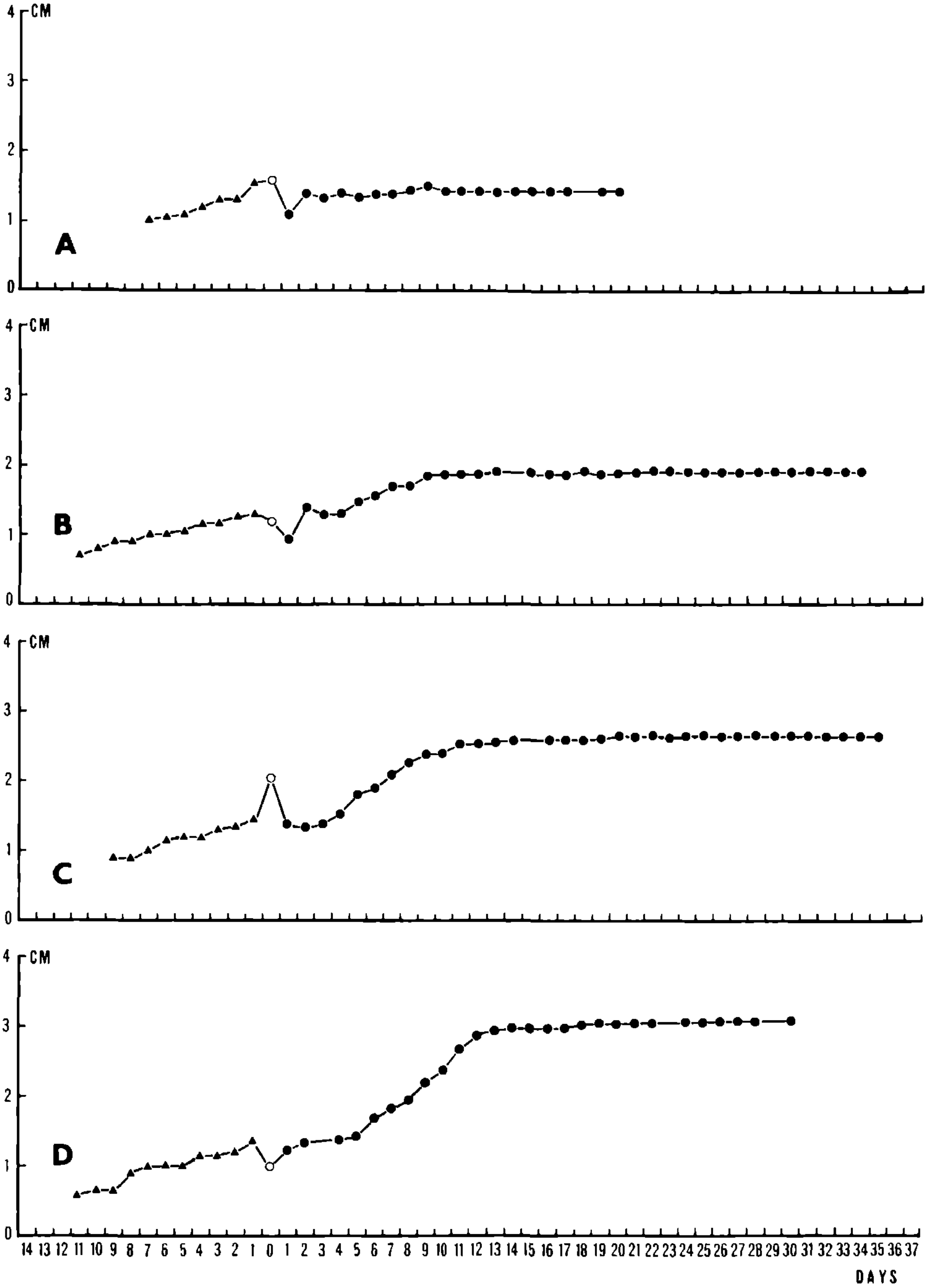

Fig. 3A. Length of the flower bud (triangles), flower (white dot) and fruit (black dot) of *N. peltata* during their development.

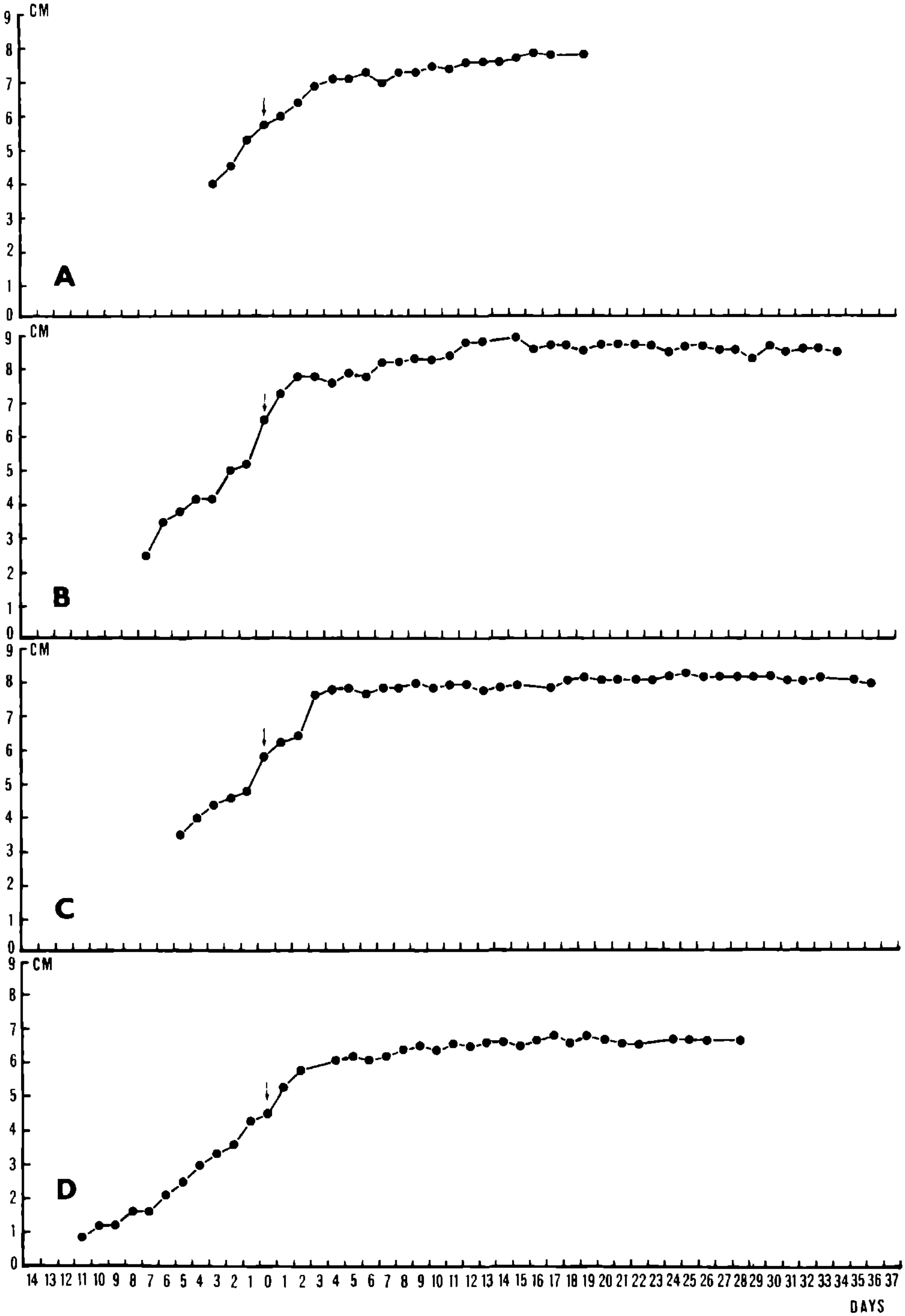

Fig. 3B. Length of the pedicel of flowers of *N. peltata* during the development of the flower (Fig. 3A). The arrows indicate the moment of flowering.

Table 2

Days before flowering	Length flower bud (average) cm	S.D. cm	minimum cm	maximum cm	average growth cm	number of observations
14	0.55	-	-	-	-	1
13	0.59	0.07	0.50	0.70	0.04	6
12	0.68	0.04	0.65	0.75	0.09	8
11	0.71	0.07	0.65	0.90	0.03	12
10	0.77	0.09	0.60	0.90	0.06	14
9	0.84	0.07	0.70	0.95	0.07	21
8	0.89	0.07	0.75	1.00	0.05	30
7	0.96	0.07	0.80	1.10	0.07	35
6	1.03	0.06	0.90	1.15	0.07	37
5	1.10	0.07	0.95	1.20	0.07	38
4	1.16	0.06	1.00	1.30	0.06	39
3	1.22	0.07	1.05	1.35	0.06	40
2	1.25	0.07	1.10	1.45	0.03	41
1	1.43	0.23	1.20	2.65	0.18	42

Table 2. Average, minimum and maximum length and average growth of flower buds of *N. peltata* during their development. S.D. = standard deviation.

Table 3

Days	average pedicel length cm	S.D. cm	minimum cm	maximum cm	average growth cm	number of observations
13	0.65	0.07	0.6	0.7	-	2
12	0.63	0.25	0.4	0.9	— 0.02	3
11	0.86	0.18	0.6	1.1	0.23	8
10	1.05	0.36	0.6	1.9	0.19	10
9	1.22	0.41	0.8	2.2	0.17	18
8	1.46	0.46	0.8	2.6	0.24	27
7	1.75	0.55	1.1	3.0	0.29	31
6	2.06	0.70	1.4	3.6	0.31	32
5	2.49	0.67	1.7	3.9	0.43	34
4	3.00	0.74	2.1	4.5	0.51	34
3	3.52	0.79	2.2	5.4	0.52	34
2	3.96	0.77	2.4	5.9	0.44	36
1	4.63	0.85	3.0	6.8	0.67	38
0	5.63	0.81	4.1	7.2	1.00	38
1	6.09	0.79	4.6	7.9	0.46	36
2	6.34	0.77	4.7	8.2	0.25	39
3	6.72	0.88	4.8	8.4	0.38	38
4	6.80	0.84	5.0	8.8	0.08	43
5	6.97	0.90	5.0	9.0	0.17	42
6	7.07	0.92	5.0	9.3	0.10	40
7	7.09	0.91	5.0	8.9	0.02	41
8	7.20	0.80	5.2	8.8	0.11	41
9	7.24	0.83	5.2	8.9	0.04	41
10	7.23	0.87	5.2	9.0	— 0.01	39

Table 3. Average, minimum and maximum length and average growth of pedicels of *N. peltata* during their development before, during and after anthesis of the flowers. S.D. = standard deviation.

Table 4

Weather conditions	Flowers opening between:	All flowers totally opened between:	Date:
totally clear	8.00 — 8.30 h.	9.30 — 10.00 h.	31 August 1979
changeable with bright periods	8.00 — 10.00 h.	10.00 — 11.00 h.	18 June 1979
	9.00 — 10.00 h.	—	20 June 1979
clouded constantly	12.00 — 13.00 h.	16.00 — 18.00 h.	19 June 1979
	11.00 — 11.30 h.	—	11 September 1979

Table 4. Observations on the time of opening of *N. peltata* flowers in relation with weather conditions.

3. A flowering stage with a duration of one day above the water surface. The pedicel has grown then ca. 1.00 cm (Table 3). *N. peltata* is a day flowering species. Some observations on the time of flowering were made on flowers in the concrete tanks situated on the area of the University of Nijmegen and on flowers of the Oude Waal (Table 4). At 18 June the flowers withered between 18.00 and 24.00 h., but 19 June they lasted to 2.00 — 4.00 h., in the night. We observed in other years that on hot days the flowers are withered before sundown.

It can be concluded from the data gathered, that on clouded days the flowers of *N. peltata* start later with anthesis and are then also flowering at night, in contrast with bright days.

As soon as the flowers start to open insects are visiting them; the stigma is then receptive and the anthers are ripe. This stage will be described more extensively under the next headings.

4. Withered flower stage above the water surface during one day after the flowering. The pedicel grows during that day about 0.46 cm (Table 3). In two cases withered flowers were present till 8.00 h. the second day after anthesis, when they were drawn under water by the recurving pedicel. No distinct flower visiting was observed on withered flowers.

5. Withered flower stage below the water surface during one or three but mostly two days. Remains of the withered corolla are still present. The pedicel has curved down into the water; there is a mean growth of 0.25 — 0.38 cm per day (Table 3). In general the pedicel increases ca. 1.5 cm after flowering.

6. Fruit-setting stage. The pedicel is usually totally fullgrown. When pollination has failed no fruit-setting takes place under water and mostly the gynoecium decays within two or three weeks. In that case the decay of the pedicel starts mostly 8 — 14 days after the day of flowering. When the flower has been pollinated the gynoecium develops into a fruit capsule containing more than 10 seeds, and reaching its maximum length (10) 14 — 16 days after the day of flowering (average after 15 days, SD = 2 days,

Fig. 4. Flower of *N. peltata* (long-styled) showing the general structure.

N = 9). The development of the gynoecium into a fullgrown fruit capsule containing less than 10 seeds takes shorter. In these fruit capsules the maximum length is reached 8 — 14 days after the flowering day (average after 10 days, SD = 2 days, N = 13). See further under the heading Development of fruits and seeds with respect to incompatibility.

7. Stage in which the pedicel decays at the base so that the fruits become floating freely at the water surface. The decay of the pedicel starts mostly 25 — 38 days after the day of flowering (average after 32 days, SD = 5 days, N = 16).

8. Stage of dehiscence of the fruit capsule, enabling the seeds to become released. The fruit capsule bursts open at its base, the fruit flesh becomes soft and decays in the water. According to Wagner (1895) snails can also play a role in this process, so that the release of the seeds goes quicker. The dehiscence of the fruit capsule takes place 32 — 60 days after the day of flowering (average after 45 days, SD = 7 days, N = 24). There is no correlation between the fruit length, the number of seeds and the moment of dehiscence. See further under the headings Production of fruits and seeds per square metre and The seed.

The stages which are distinguished here do not fully correspond with the developmental stages of the flower distinguished with respect to biomass in Van der Velde, Giesen and Van der Heijden (1979); their stage 1—4 correspond with stage 1 in this paper, stage 5 with stage 2, stage 6 with stage 3, stage 7 with stage 4 and stage 8 with stage 5.

THE STRUCTURE OF THE FLOWER

The flowers of *N. peltata* (Fig. 4 and 7) are regular. The calyx is green and consists of five erect lanceolate lobes united at the base into a very short calyx tube. The lobes when fullgrown have a length of 1.35 — 1.40 cm.

The corolla is yellow, showy, opening for one day only, consisting of a basal tube a little shorter than the calyx and (4) 5 spreading lobes. The lobes have each at their base a staminodium consisting mainly of a fringe of hairs, which shelters the nectaria. Each corolla lobe is composed of a central approximately lanceolate section bearing two broad, fringed side wings. The side wings are at first folded inwards to give an induplicate-valvate corolla in bud. There are as many stamens as corolla lobes, which are inserted on the corolla tube at the junction of the lobes; the filaments are short, the anthers two-celled, linear lanceolate, dehiscing introrsely with two longitudinal slits. The ovary is superior to semi-inferior, unilocular, terminated by a single style bearing two somewhat fleshy, papillate stigmata. There are two, sometimes three placentae. The placentae bear numerous ovules; in samples from the Oude Waal the mean number of ovulae per gynoecium was 64 (SD = 14), the maximum number 109, the minimum 25 (N = 40). At the base of the ovary five nectaries sheltered by five staminodes connected with the corolla tube are present.

Heterostyly. The flowers of *N. peltata* are heterostylous. Floral heteromorphism is often associated with a physiological self-incompatibility system, but this appeared to be weak in the case of *N. peltata.* The heterostyly of *N. peltata* can be considered primitive with respect to other *Nymphoides* species where often the heterostyly has been replaced by dioecism, a more effective outbreeding mechanism (Ornduff, 1966).

The two flower types in *N. peltata* differ in the length of the style, the shape of the stigma, the size and height of the anthers (measured from the flower base) and the size of pollen grains (Table 5). Further the stigma of the short-styled form is smaller than that of the long-styled form (Ornduff, 1966). As in the classical example of heterostyly, *Primula vulgaris* Huds., the papillae of the receptive surface of the stigma are longer in the long-styled flowers than in the short-styled flowers (Fig. 5).

The pollen grains of *N. peltata* are triangular in shape and show a typical structure on the exine (Fig. 6). Hegi (1927) mentioned as pollen size for long-styled flowers of *N. peltata* approximately 24 — 37 μm, for short-styled ones 43 — 46 μm. Pollen from 10 flowers of each floral type from the Oude Waal, prepared in Euparal, were somewhat larger than those mentioned by Hegi (1927), as can be seen in Table 4. The same kind of differences in the

Table 5

Floral form		Long-styled	Short-styled
stigma height (mm)	maximum	19.6	11.0
	minimum	17.0	9.0
	average	18.0 ± 0.8	10.5 ± 0.6
stamen height (mm)	maximum	11.0	15.8
	minimum	9.3	11.5
	average	10.3 ± 0.7	13.0 ± 1.2
bases of thecae height (mm)	maximum	8.0	10.0
	minimum	6.0	7.9
	average	7.1 ± 0.6	8.6 ± 0.7
anther length (mm)	maximum	4.7	6.2
	minimum	3.5	5.2
	average	4.4 ± 0.4	5.8 ± 0.4
anther width (mm)	maximum	2.4	2.2
	minimum	1.6	0.9
	average	2.1 ± 0.3	1.8 ± 0.4
pollen diameter (µm)	maximum	47.5	55.0
	minimum	30.0	40.0
	average	40.8 ± 3.4	47.4 ± 3.5

Table 5. Measurements on long- and short-styled flowers of *N. peltata* showing the differences between these flower types. Average values with standard deviation.

size of the pollen grains between long- and short-styled flowers are also known in *N. humboldtiana* (Kunth) O. Kuntze and *N. indica* (L.) Griseb. (Ornduff, 1966).

One plant has only one flower type. In the Oude Waal 52 flowers were gathered at random of which 20 were long- and 32 short-styled, thus a ratio of 0.63. Ornduff (1966) mentioned for 15 populations of *N. peltata* in Britain 13 of only long-styled plants, one of short-styled plants, and only one population with both forms.

ATTRACTION OF THE FLOWERS FOR INSECTS

Typical flower visiting insects are attracted in their search for food at distance by some characters of the flowers, viz.:

1. *A high flower frequency.* The fact that *N. peltata* forms large areas with many flowers during a long period, from the end of June until October, is of importance to many insects and thus for pollination. Stover (1932) mentioned the same flowering period for *N. peltata* in North-America. Bees and bumblebees often fly on a certain time on flowers of one species from

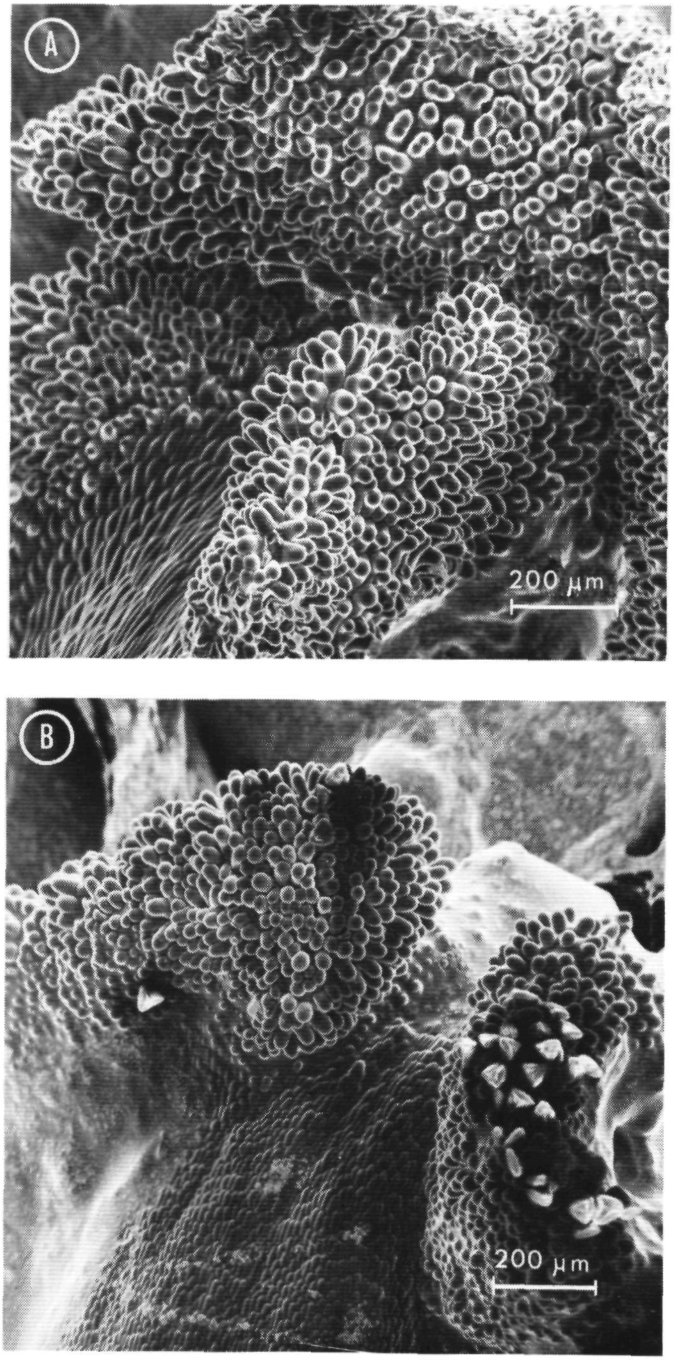

Fig. 5. A. papillae on the receptive surface of the stigma of a long-styled flower, B. idem of a short-styled flower.

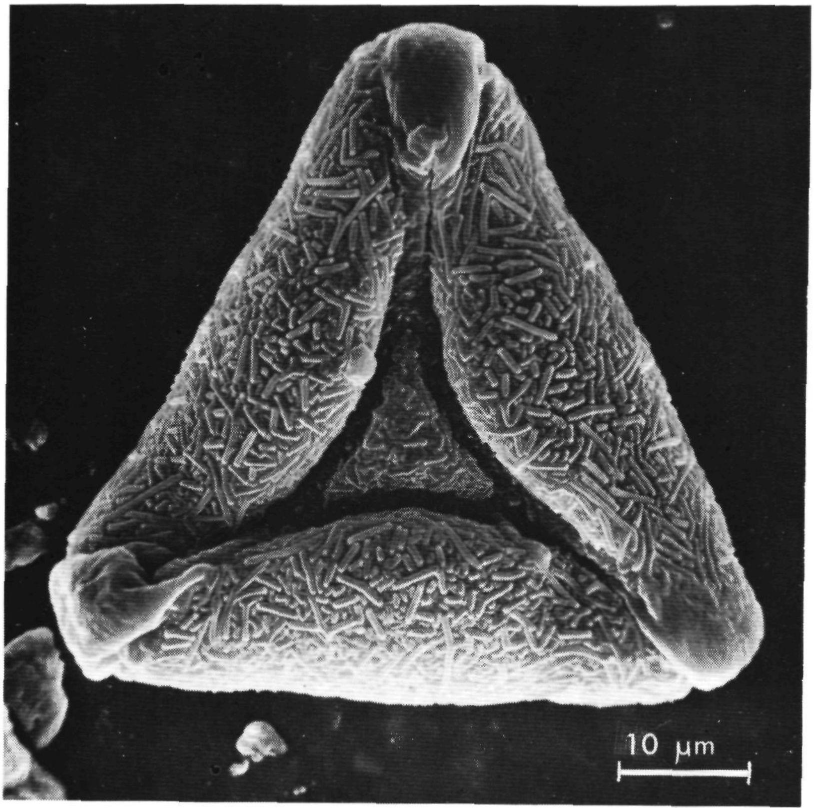

Fig. 6. Pollen grain of *N. peltata* (scanning photograph). Note the typical structure on the exine.

flower to flower.

2. *Flower colour.* The corolla of *N. peltata* is bright yellow. At the base of each corolla lobe two grooves can be observed which are of a darker yellow. Yellow is a colour attracting flies and some species of bumblebees (*Bombus terrestris* L.) (Brantjes, 1979). Ultraviolet reflection and absorption is also an important component of flower colour, as most flower visiting insects are highly sensitive to ultraviolet light (Mazokhin—Porshnyakow, 1959). Spectral qualities of flowers of some *Nymphoides* species have been recorded by Ornduff and Mosquin (1970) viz. for *N. indica* (L.) Griseb., *N. indica* complex (*N. grayana* (Griseb.) O. Kuntze) and *N. geminata* (R. Br.) O. Kuntze.

The ultraviolet reflectance and absorption pattern observed in *N. peltata* flowers from the Oude Waal shows a remarkable resemblance with the pattern in *N. geminata* flowers. The latter species is also yellow flowering. On the u.v. photographs can be seen that there is a well-defined central area of absorption contrasting with a peripheral area of emittance (Fig. 7). This

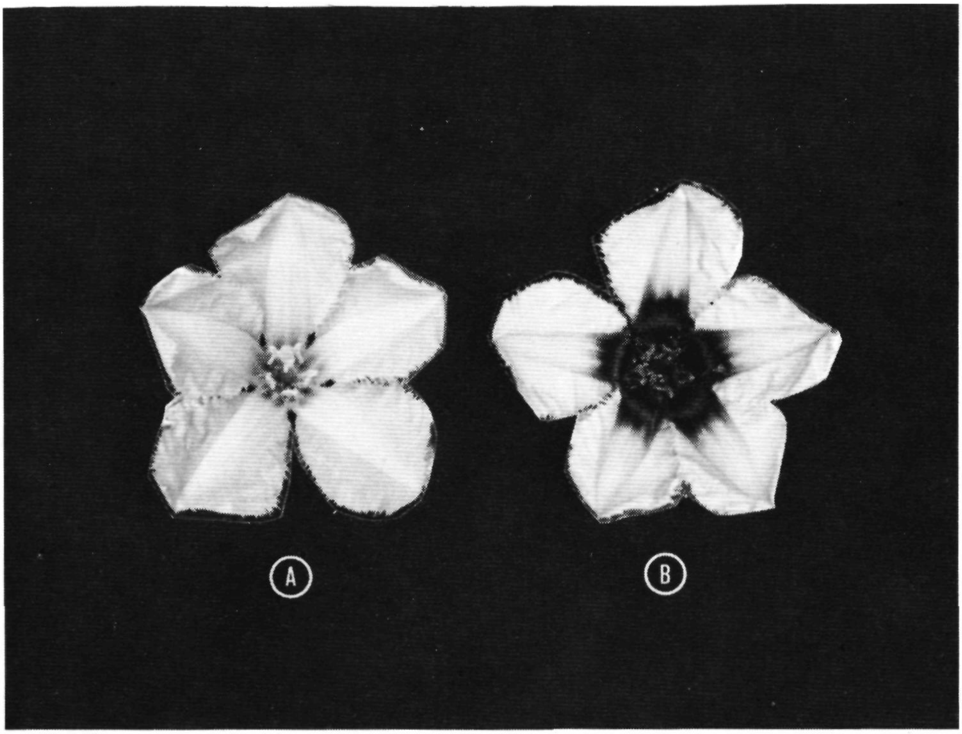

Fig. 7. A: normal photograph of a *N. peltata* flower. B: u.v. photograph of the same flower.

pattern is similar in long- and short-flowers of *N. peltata.* This nectar-guide system of the central area of the flower must be very obvious to the flower visiting insect; the flower contrasts also strongly with the surroundings (Fig. 8).

The very distinct u.v. pattern of the flowers of yellow flowering species (*N. geminata, N. peltata*) can be regarded as specialized with respect to white flowering species of *Nymphoides* of which the flowers show uniform absorption of ultraviolet light (Ornduff and Mosquin, 1970).

3. *Flower shape and flower size.* The shape of flowers of *N. peltata* is radially symmetrical with rounded and fringed broad lobes. The flowers have, according to measurements of 52 flowers from the Oude Waal, a maximum diameter of 4.60 cm (minimum 2.10 cm, average 3.54 cm, SD = 0.48 cm). The total height of the flower is at most 2.90 cm (minimum 1.70 cm, average 2.13 cm, SD = 0.31 cm). The base of the flower is at most 5.50 cm and at least 0 cm above the water surface (average 3.27 cm, SD = 1.15 cm), which is favourable for terrestrial flower visiting insects as the chance to become wet is so diminished.

4. *Odour.* The flower of *N. peltata* has a weak sweet odour, so that attraction at large distances is not very likely.

Fig. 8. Above: normal photograph of a *N. peltata* stand. Below: u.v. photograph of a *N. peltata* stand.

5. *Higher temperatures.* Temperatures in flowers can be higher than in the surroundings which can be attractive to insects for sunning (Brantjes, 1976). Further the flower can form a shelter site e.g. in periods of strong wind. Temperature measurements were carried out deep in the flower on the staminodes which temperatures were compared with those measured 50 cm above the water surface. For this purpose a Wallac oy Universal Thermometer GST 32 was used with the probe Ni—106. Maximum difference between flower temperature and air temperature was 1.3° C due to solar radiation (Table 6). For comparison the maximum difference for *Nymphaea alba* L. flowers was 3.6° C, which larger difference in this species could be explained by the larger size and more complex structure of the flower. Perhaps the temperature on the stigma of *N. peltata* flowers is higher but the surface of these was too small for measurements with the apparatus available.

Thus the corolla has the function to attract insects at large distances by form, colour (u.v. pattern). Hardly any damage to the corolla or calyx caused by animals was observed. It can be concluded that these two flower parts play no role as food resource for the flower visiting insects. The only exception are aphids, which suck here plant fluids.

The food present itself, odour and perhaps high temperatures can attract the flower visiting insects only at small distances. The flowers of *N. peltata* have to offer as food for these insects:

1. *nectar.* There is often a relation between the type of nectar and the insect type, that visits the flower (Proctor and Yeo, 1973). The nectar of *N. peltata* contains the sugars fructose and glucose in equal amounts as appeared from enzymatical tests. As the five nectaria are sheltered by hairy staminodes to

Table 6

Flower temperature	Air temperature	Difference
19.3° C	19.1° C	+0.2° C
19.8	19.2	+0.6
22.1	20.8	+1.3
21.1	20.9	+0.2
21.2	20.9	+0.3
21.8	21.2	+0.6
22.1	21.5	+0.6
22.3	21.9	+0.4
23.0	22.6	+0.4
24.0	22.9	+1.1
23.0	23.0	0.0
23.0	23.0	0.0
24.0	23.0	+1.0
24.0	23.3	+0.7
24.8	24.1	+0.7

Table 6. Flower temperatures of *N. peltata* measured on the staminodes compared with the air temperature measured 50 cm above the water surface.

a height of 0.5 — 0.6 cm only flower visiting insects with a long tongue can reach the nectar.

2. *pollen grains.* Pollen grains contain protein, fat, carbohydrates and various inorganic mineral substances (Percival, 1965). They are an important food for many insects, mixed with honey for larvae of bees and bumblebees. Further most flower visiting flies and beetles eat pollen grains (Proctor and Yeo, 1973). The five stamens of the *N. peltata* flower produce only few pollen grains compared with flowers of other nymphaeids such as *Nuphar* and *Nymphaea.*

3. *stigmatic exudate.* According to Heslop-Harrison and Shivanna (1977), who divided the receptive surfaces of angiosperm stigmata into four main groups, *Nymphoides* has to be placed within the group with wet stigmas and a receptive surface with low to medium high papillae. Stigmatic exudate is important for the germination of pollen grains (Steinecke, 1940). The stigma of *N. peltata* should produce some stigmatic exudate, a perhaps sugar-containing fluid, but we have observed hardly any exudate. It has often been observed by us that flies are licking on the stigma.

4. *corolla fluid.* When the corolla withers, cell fluid is excreted and the surface is so covered with a thin layer of fluid. According to Heukels (1910) this seems to be attractive for flies which are licking there and so can contribute to pollination. It can be questioned however if the stigma is still receptive then.

INSECTS VISITING FLOWERS OF *N. PELTATA*

Very little was known about insects visiting the flowers of *N. peltata.* Heinsius (1890) mentioned the syrphid flies *Platycheirus peltatus* Mg. and *Anasimyia lunulata* (Mg.) (as *Heliophilus lunulatus* Mg.), the muscid fly *Heterostylodes pratensis* (Mg.) (as *Anthomyia pratensis* Mg.) and the bees *Apis mellifera* L. and *Bombus* spp. Knuth (1898) cited Heinsius.

We made the following list of flower visitors of *N. peltata* based on observations in the Oude Waal (0), the concrete tanks (c) and literature data. The flower visitors were collected from May to October 1975 and in August 1979 with the aid of a net; an indication of the relative presence per date was given with the following code: 1. mostly only one specimen; 2. some specimens on some flowers; 3. specimens visiting on a number of flowers; 4. idem on many flowers; 5. many specimens on nearly all flowers.

Hexapoda
Odonata — Zygoptera
Coenagriidae:

Coenagrion pulchellum (Van der Linden)	1	0
Erythromma najas (Hansemann)	1	0
Ischnura elegans (Van der Linden)	2	0

Hemiptera — Homoptera			
Aphididae:			
Rhopalosiphum nymphaeae L.	3	0, c	
Lepidoptera			
Nymphalidae:			
Pieris sp.	1	0	
Aglais urticae L.	2	0	
Pyralidae:			
Nymphula nymphaeata (L.)	1	0	
Noctuidae:			
Autographa gamma (L.)	1	0	
Trichoptera			
Polycentropodidae:			
Holocentropus picicornis Steph.	2	0	
Diptera			
Empididae:			
Hilara sp.	2	0	
Syrphidae:			
Melanostoma mellinum (L.)	2	0	
Anasimya lunulata (Mg.)	3	0,	Heinsius (1890)
Eristalis abusivus Collin	1	0	
Eristalis intricarius (L.)	2	0, c	
Eristalis arbustorum (L.)	1	c	
Eristalis nemorum (L.)	1	c	
Eristalinus sepulchralis (L.)	1	c	)[1]
Eurimyia lineata (F.)	1	0	
Neoascia dispar (Mg.)	1	0	
Neoascia podagrica (F.)	1	0	
Metasyrphus corollae (F.)	3	0, c	
Syrphus vitripennis Mg.	1	0, c	
Episyrphus balteatus (De Geer)	3	0, c	
Platycheirus peltatus (Mg.)	1	0,	Heinsius (1890)
Platycheirus manicatus (Mg.)	1	0	
Helophilus trivittatus (F.)	1	c	
Rhingia campestris Mg.	1	0	)[2]
Sepsidae:			
Themira lucida (Staeg.)	1	0	
Ephydridae:			
Hydrellia griseola (Fallén)	4	0, c	
Hydrellia cochleariae Hal.	3	0	
Notiphila brunnipes R.-D.	5	0	
Scatella stagnalis Fall.	2	0	
Scatomyzidae (= Scatophagidae, Cordyluridae):			
Trichopalpus fraternus Mg.	2	0	
Calliphoridae:			
Melinda sp.	1	0	
Muscidae:			
Heterostylodes pratensis (Mg.)			Heinsius (1890)
Morellia aenescens R.-D.	2	0	
Hymenoptera			
Vespidae:			
Vespa vulgaris L.	1	0	
Apidae:			
Apis mellifera L.	3	0, c	Heinsius (1890), Knuth (1898)

Bombus terrestris L.	3	0, c
Bombus spp.	1	c, Heinsius (1890), Knuth (1898)
Coleoptera		
Nitidulidae:		
Meligethes aeneus (F.)	1	0
Melyridae:		
Dasytes plumbeus Müll.	1	0
Chrysomelidae:		
Pyrrhalta (Galerucella) nymphaeae L. f. aquatica	2	0

)[1] species also observed on *N. peltata* flowers in a water near Kekerdom (The Netherlands).

)[2] species also observed on a *N. peltata* flower in a ditch near Kampen (The Netherlands).

Insects visit flowers for food which can be offered by the flowers themselves, or they prey there on other animals. Further flowers can be used as egg depositing site or as shelter- and sunning site.

The flowers of *N. peltata* attract non-specialized as well as specialized flower visitors. Specialized flower visitors are Lepidoptera, Apidae and Syrphidae.

Only four species of Lepidoptera were observed incidentally in and on the flowers as most species avoid to fly closely over the water surface. *Aglais urticae* was most frequently observed on the flowers. *Autographa gamma*, the only Noctuid species observed, is active at day and was seen sometimes on the flowers. Further *Pieris* sp. must be mentioned. *Nymphula nymphaeata* of which the larva feeds on *Nymphoides* leaves (Lammens and Van der Velde, 1978) was observed once resting on a flower, while the other species of Lepidoptera sack for nectar with their long tongue in the flowers. As pollinators of *N. peltata* the Lepidoptera seem to be unimportant.

The Apidae are mostly collecting nectar in the *N. peltata* flowers. For the Apidae the amount of pollen per flower in the case of *N. peltata* flowers is of less importance as an attractive feature than the presence or absence of nectar in the flower. As soon as the flowers commence to open Apidae are visiting the flowers. As the nectaria are protected by staminodes they must have a tongue longer than 5—6 mm. Percival (1965) mentioned as length for the tongue of *Apis mellifera* 5.7—6.7 mm and for that of *Bombus terrestris* 8.2 mm. Although *Apis mellifera* has been observed very often and must be considered as an important pollinator, *Bombus terrestris* seems to be the most important pollinator of *N. peltata* flowers because of its large hairy body on which pollen can be carried easily, its longlasting visits to *N. peltata* fields and the distinct behaviour by which it flies efficiently from flower to flower. During its visits *B. terrestris* always flies from one flower to the most neighbouring one and in all cases the centre of the flower is visited immediately by using the u.v. nectar-guide system.

Some flowers are refused when *B. terrestris* is flying close near the centre of the flowers possibly due by body scent of bees on the flowers which can be functioning as a signal to other foragers, that the flowers have been recently visited so that the bees sheer off in search of other flowers, which is advantageous for both insect and plant (Van der Pijl, 1954; Faegri and Van der Pijl, 1979).

There is a distinct difference in behaviour of *B. terrestris* on long- and short-styled flowers of *N. peltata.* In long-styled flowers it takes the style between the hind legs and so it circles around in the flower while the nectar from the nectaria situated around the base of the gynoecium is taken up efficiently. In this way *B. terrestris* causes pollination as the tip of the abdomen is moving over the stigma by this behaviour. The style of short-styled flowers is too short for such a behaviour so that the bumblebees crawl around on the weak corolla. In these flowers *B. terrestris* can cause also easily self-pollination as the thecae are situated above the stigma of the style.

Other *Bombus* species have occasionally been observed on *N. peltata* flowers. The only other species belonging to the Hymenoptera which visits the flowers is *Vespa vulgaris*; it makes very short visits during its flights over the water surface, and therefore is not very important for pollination.

With respect to other groups only some species of Syrphid flies have tongues long enough to reach the nectar of the *N. peltata* flowers, e.g. *Rhingia campestris* and perhaps some *Eristalis* species. In the other species the tongues are too short and it is known that Syrphids are mostly pollen eaters and particularly *Anasimyia lunulata, Metasyrphus corollae* and *Episyrphus balteatus* have frequently been observed licking on the anthers of *N. peltata* flowers. Not all Syrphid visits shall result in pollinations as often the flies do not come into contact with the stigma. Further most species are smooth. The larger species such as *Eristalis* species are good pollinators because they have many hairs to which pollen can stick.

Sepsid flies are also known as flower visiting insects, just as the Muscid and Calliphorid flies. These flies eat pollen or liquid substances. The flies mentioned so far are all common species, and visit also many flowers of terrestrial plants.

The species mentioned till now are not resting for a long time in the flowers but fly very active from flower to flower. They are by no means bound to a nymphaeid system. The insects staying for a long time in the flowers are species which are more characteristic for a nymphaeid system and most of them occur also on the floating leaves, e.g. the Ephydridae, which use the flowers also as resting and sunning site.

An important fly with respect to pollination is *Notiphila brunnipes*, which plays also an important role in the pollination of other nymphaeids (Van der Velde and Brock, 1980). *Notiphila brunnipes* deposits its eggs in *Nymphaea* and *Nuphar* flowers but not in those of *N. peltata* and there are several reasons why the flowers of the latter are not very suitable as oviposition site, such as the short flowering period (the moment of hatching of the larvae is at least 5 days after the egg deposition under favourable circumstances) and the fact that withered flowers become submerged ca. 2 days after anthesis, so that the eggs may decay (Van der Velde and Brock, 1980). Larvae and pupae of this Ephydrid species can be found attached to the roots of *Nymphoides peltata. Notiphila brunnipes* can eat pollen, and liquid substances in the *Nymphoides peltata* flowers. Ephydrid flies are often seen licking on the stigma of the style, perhaps feeding on stigmatic exudate. They are also often found deep in the flower where they perhaps are licking on small drops of nectar that remained on the staminodes after visits of nectar feeding insects. *Hydrellia* shows a similar behaviour.

The Ephydrid flies are very numerous and by their irregular visits to flowers they must certainly be important for cross-pollinations.

The *Meligethes* species are well known as pollen eating beetles. *M. aeneus* lives as larva mainly from pollen of Cruciferae. The beetles *Dasytes plumbeus* and *Pyrrhalta (Galerucella) nymphaeae* f. *aquatica* were found in the corolla tube of *N. peltata. Dasytes plumbeus* is known as a flower visitor and is carnivorous. The larvae of this species live from fungi in wood (Reitter, 1911; Freude et al., 1979). *Pyrrhalta nymphaeae* f. *aquatica* was observed in the Oude Waal living together with eggs and larvae on the floating leaves of *Polygonum amphibium* L. f. *natans* and *Rumex hydrolapathum* Huds.

The observation of flower visiting Trichoptera must be considered as accidental. They are very numerous on the floating leaves so that there is a great chance that they come sometimes in the flowers.

The aphid *Rhopalosiphum nymphaeae* has been found regularly in the flowers but plays no role in cross-pollination due to its low activity and by the fact that it is mostly wingless. The aphids are feeding on plant fluids from the flower tissue. In general the aphid was not found very commonly in *N. peltata* flowers in comparison with those of *Nymphaea* and *Nuphar*, probably due to the short flowering time. The aphid is rather commonly found on the floating leaves of *N. peltata.*

Predatory insects such as the Odonata, Empidid and Scatomyzid flies live from small insects such as aphids and *Hydrellia*'s. The Odonata have been seen resting on flower and often they prey there on small flies and caddisflies, but not in the corolla tube. The spider *Erigone atra* Blw. (Micryphantidae) preys in the flowers on small insects and makes here sometimes a primitive web.

All those flower visitors can cause cross-pollination and in the case of short-styled flowers of *N. peltata* certainly self-pollination.

DEVELOPMENT OF FRUITS AND SEEDS WITH RESPECT TO INCOMPATIBILITY

According to Ornduff (1966) the incompatibility system of *N. peltata* is weak, so that self-pollinations invariably result in the formation of small capsules producing 10 to 20 seeds. According to this author capsules resulting from cross-pollination are considerably larger than those produced by self-pollination, and the seed production is approximately four times as high. Seeds from self-pollinations germinate easily, but seedling viability appears to be low (Ornduff, 1966).

We carried out some artificial pollinations to test and to quantify the differences in capsule size and seed production. Flowers of each type were used for self- and cross-pollination and the developed fruits were gathered after 14 days. The results after cross-pollination of long- and short-styled flowers are presented separately (Table 7).

The results confirm the observations of Ornduff (1966) but the number of developed seeds per capsule was not above 10 in the case of self-pollination. As the results with long- and short-styled flowers with respect to cross-pollinations do not differ significantly it is confirmed also that both floral forms are equally hermaphroditic (Ornduff, 1966).

Table 7

	Cross-pollination		Self-pollination
	Long-styled flower with pollen short-styled flower	Short-styled flower with pollen long-styled flower	Long- and short-styled flowers
number of flowers used	11	16	14
decayed without fruit-setting	1	0	2
av. fruit length cm	3.24 ± 0.36	3.11 ± 0.25	2.17 ± 0.45
max. fruit length cm	3.65	3.45	2.90
min. fruit length cm	2.50	2.70	1.50
av. fruit width cm	1.27 ± 0.13	1.31 ± 0.12	0.80 ± 0.19
max. fruit width cm	1.40	1.55	1.00
min. fruit width cm	1.10	1.10	0.35
av. fruit thickness cm	0.47 ± 0.05	0.39 ± 0.06	0.35 ± 0.07
max. fruit thickness cm	0.55	0.50	0.50
min. fruit thickness cm	0.40	0.30	0.25
av. number of developed seeds per fruit	31.8 ± 10.7	31.7 ± 8.0	5.2 ± 2.8
max. number	44	41	10
min. number	12	14	1
av. % developed seeds per fruit	46.9 ± 14.8	50.5 ± 11.2	8.7 ± 4.4
max. % developed seeds per fruit	63.0	65.0	16.6
min. % developed seeds per fruit	16.0	23.7	2.6

Table 7. Fruit and seed development 14 days after an artificial cross- and self-pollination of *N. peltata* flowers. Average values with standard deviation.

In short-styled flowers self-pollination must occur more easily than in long-styled flowers as here the thecae are situated above the stigma. To test this 16 flowers 8 of each type were screened off by gauze (meshes 2 mm). All long-styled flowers decayed without seed-setting but the short-styled flowers produced some seeds due to self-pollination. As can be observed sometimes in the field some flowers are prevented from opening by the withered corolla of a flower which had flowered the day before being stuck to the closed corolla of the next flower. If such flowers are of the short-styled type seed-setting is still possible, due to self-pollination.

Fruits developed after only self-pollination and after cross-pollination in the Oude Waal were distinguished on the capsule size and the number of developed seeds (below or above 15, which number is intermediate between our maximum of 10 in the case of only self-pollination and the maximum found by Ornduff (1966)).

PRODUCTION OF FRUITS AND SEEDS PER SQUARE METRE

An estimation of the production of fruits and seeds has been made at the end of August (31th) 1979 when most fruits were developed and seeds were only at the beginning of becoming released.

Samples were made by means of a 0.25 m^2 frame made of P.V.C.-tubes which was thrown at random in a *Nymphoides* stand. In each sample the average numbers of fruits and seeds were counted and expressed in numbers per m^2.

The mean number of fruits per m^2 was 180 (SD = 76.3, N = 25). The maximum number per sample was 77 fruits, the minimum 12. The average number of developed seeds per fruit was 26.5 (SD = 3.4, N = 11). The average number of developed seeds per fruit per sample ranged from 22.3 — 31.1. The average number of developed seeds per m^2 was 3117 (SD = 858).

The average percentage of fruits with a number of developed seeds below 15, possibly developed after only self-pollination was 23.2% (SD = 5.1%), which produced meanly only 5.3% (SD = 0.6%) of the total seed production.

In the concrete tanks the number of developed seeds per m^2 was 9434 (SD = 5668, only 4 samples). The average number of seeds per fruit was here 17.0 (SD = 2.1); per sample it ranged from 15.4 — 19.3, thus the number of it was much lower than in the Oude Waal. The number of fruits per sample (only three samples) ranged from 283 — 310, thus much higher than in the Oude Waal. The percentage of fruits with a number of seeds below 15 was here higher than in the Oude Waal, viz. 28.5% (SD = 1.7%).

Perhaps the surface of *N. peltata* in the concrete tanks was too small for a more efficient pollination by bees, bumblebees and syrphids. Further *Notiphila brunnipes* was completely absent in the concrete tanks.

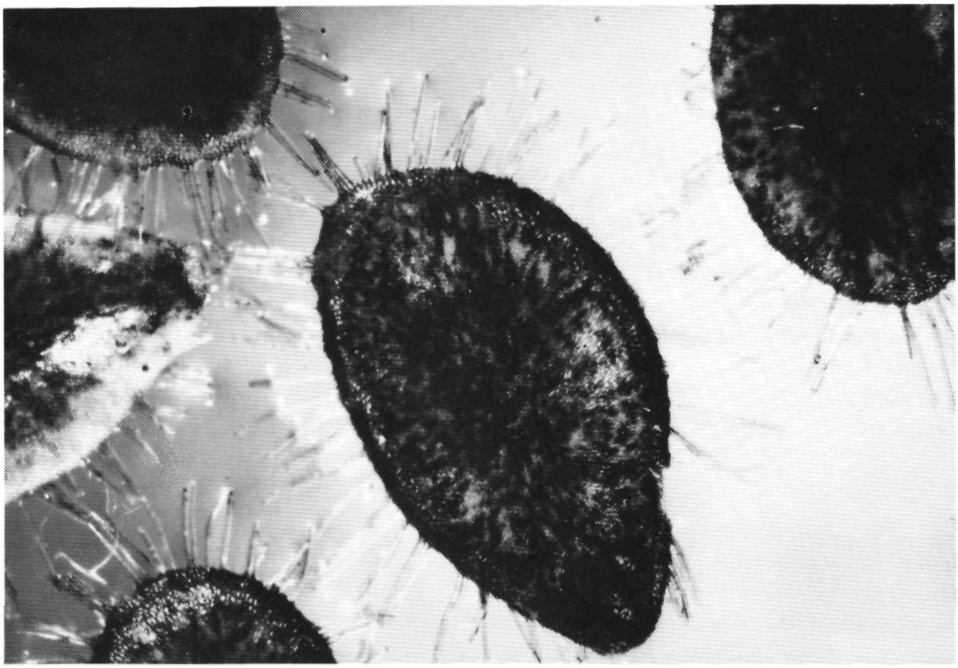

Fig. 9. Seeds of *N. peltata* floating on the water surface. Note the depressions in the water surface at the tips of the large surface projections.

THE SEED

The seeds of *N. peltata* (Fig. 9 and 10) are floating on the water surface. They are flat, broad-elliptical, 3.8 — 5.1 mm long, 2.7 — 3.0 mm broad and 0.4 mm thick; according to Wagner (1895) and Hegi (1927) they are 6 mm long and 3 mm broad. They are light brown. An extensive anatomical description of the seeds is given by Fauth (1903). The seeds are provided with large surface projections at the margins which are 0.07 — 0.35 mm long and ca. 0.02 — 0.06 mm thick. These surface projections are hyaline and hollow and filled with gas thus functioning as floating organs. According to Fauth (1903) seeds of which the large surface projections were removed sank very easily when they were slightly moved. Fauth (1903) suggested that the large surface projections also have a function for dispersal by means of water birds. At the tips of the surface projections small spines are present (Fig. 10 B), so that it can be suggested that by means of these the seeds can be attached more easily to feathers of birds (epizoic dispersal), further the flat form and the fact that the seeds are hydrophobous so that a seed can attach easily even to our hand must be mentioned in this context. The dispersal by migrating birds can explain the many dispersed localities of *N. peltata* (Hegi, 1927; Steinecke, 1940). The surface projections can also function by anchoring the seeds in the mud (Hegi, 1927).

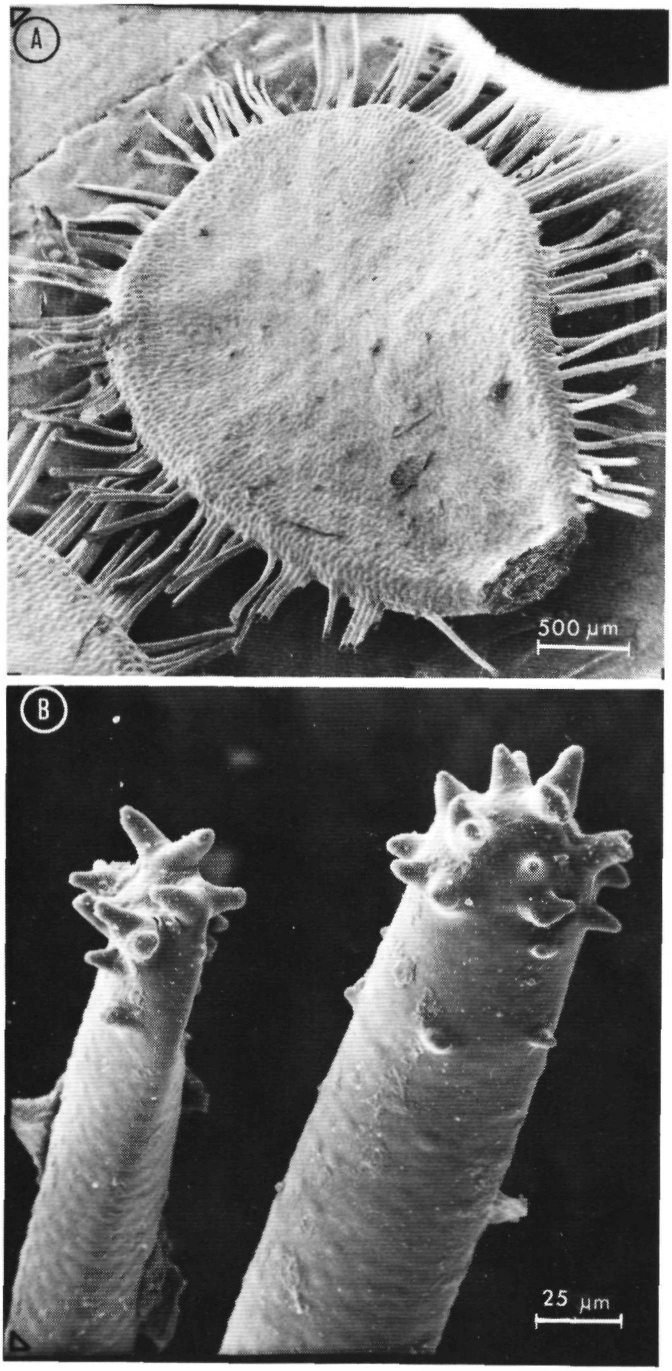

Fig. 10. A: scanning photograph of a seed of *N. peltata.* B: detail of the tip of a large surface projection showing the small spines.

It was very obvious from our observations that the large surface projections by their dense settlement close against each other and the small spines at the tips, hold the seed flat on the water surface with the aid of the surface tension. When a seed was pushed under water it sank in most cases in spite of the air cells of the seed testa, which shows heavy cutinization, and small celled and thinwalled tissues between epidermis and nutritive tissue, which according to Fauth (1903) all have the function to hold the seed floating. As could be observed in petridishes the seeds can float so for at least two months when they are not disturbed. They can be dispersed over the water surface by wind action (hydrochorous dispersal), when the vegetation is diminished strongly, but when they are disturbed too much they sink to the bottom. Anatomical structures for protection of the embryo against frost are not strongly developed, according to Fauth (1903).

CONCLUSION AND DISCUSSION

The structure and manner of growth of the flowering stem is in such a way that a continuous field of flowers is maintained during a long period within the season. An interesting topic for further investigations can be to follow the changes in numbers, in the position of flowers and in the distances between them during a season in permanent quadrats, as this is important for the pollination of flowers and feeding efficiency of insects.

H. Müller (see Heimans et al., 1956) divided entomophilous flowers in seven categories according their degree of specialization to one insect group; the flowers of *N. peltata* fall within the category B, as they are not so strongly specialized for the visiting of only one insect group, while the nectar is totally hidden. The u.v. pattern of the *N. peltata* flower, which is the same as in *N. geminata* (also a yellow flowering species) can be considered as a specialized feature within the genus *Nymphoides*, the heterostyly combined with a weak incompatibility system must be considered a primitive feature. *N. peltata* is a day flowering species; the flowers wither within one day. Features of the flower attracting flower visiting insects are: a high flower frequency during a long period within the season, the yellow coloured corolla with a characteristic u.v. pattern and an average diameter of 4.60 cm, at average 3.27 cm above the water surface, and a weak sweet odour. Higher temperatures than the surroundings play perhaps no role as attracting feature, as the differences are very small. The flowers have to offer nectar containing fructose and glucose in equal amounts, pollen and perhaps some stigmatic exudate. Further predatory insects are attracted by the insects present there.

Knowledge of the amount and the exact chemical composition of the nectar are a desideratum for further research, in combination with the measurements on the distances between flowers, so that the potential efficiency of a nectar collecting insect species in a *N. peltata* stand can be calculated during the season; the same can be done for a pollen collecting flower visitor.

The list of flower visiting animals contains 44 species of which 43 species of Hexapoda and 1 species of Aranea. With respect to pollination species of Apidae, Syrphidae and Ephydridae seem to be most important. Species of Apidae and some species of Syrphidae can use the nectar by their long tongues (longer than 5—6 mm), most species of Syrphids and all Ephydrid species use pollen and liquid substances present, but their tongues are too short to reach the nectar. Apidae and Syrphidae fly from flower to flower while the Ephydridae show irregular flower visits but are very important by their large numbers. In contrast to the Apidae and Syrphidae the Ephydridae occur also very commonly on the floating leaves of *N. peltata.* Of the 44 species mentioned 30 species were visiting only on the flowers while 14 species were also commonly found on the floating leaves (Table 8). The first category is attracted mostly by the characteristic features of the

Table 8 category	A number of species	B number of species
Odonata		
Coenagriidae	-	3
Hemiptera-Homoptera		
Aphididae	-	1
Lepidoptera		
Nymphalidae	2	-
Pyralidae	-	1
Noctuidae	1	-
Trichoptera		
Polycentropodidae	-	1
Diptera		
Empididae	-	1
Syrphidae	17	-
Sepsidae	1	-
Ephydridae	-	4
Scatomyzidae	-	1
Calliphoridae	1	-
Muscidae	2	-
Hymenoptera		
Vespidae	1	-
Apidae	3	-
Coleoptera		
Nitidulidae	1	-
Melyridae	1	-
Chrysomelidae	-	1
Aranea		
Micryphantidae	-	1
Total number of species	30	14

Table 8. The flower visiting animals of *N. peltata* divided into category A, which contains species only occuring on the flowers and category B, which contains species also commonly found on the floating leaves.

flower, while the second category is more characteristic for a nymphaeid system as a whole.

As already mentioned by Den Hartog (1978) the relations of the aquatic community to the surrounding environment are important and many of the organisms participating in the community, including the dominant macrophytes are in one or more stages of their development dependent on the surroundings. This is clearly illustrated by the fact that the pollination of an aquatic plant such as *N. peltata* depends mainly on insects such as Apidae and Syrphidae, which are in no way bound to the nymphaeid system, while *Notiphila brunnipes* which is characteristic for a nymphaeid system depends for completing its life cycle on species of two plant groups viz. *Typha, Acorus* and *Nymphoides* on one side and *Nymphaea* and *Nuphar* on the other side (Van der Velde and Brock, 1980).

Due to these external relations homogenous nymphaeid communities covering extended areas of water are not necessarily richer in species or more characteristic than smaller stands in contact with a variety of other habitats (Den Hartog, 1978).

Further investigations can be made on the frequency of flower visiting by the various species during the season, their changes in numbers during a day and during the season, while more detailed observations on their behaviour in the flowers are necessary to understand the relation between flower visitor and flower more clearly.

Each flower visitor can cause pollination and in the case of short-styled flowers certainly self-pollination; in the case of self-pollination small capsules are produced with a low number of seeds (mostly below 10—15).

The weak incompatibility system makes it possible that *N. peltata* not only maintains itself by extensive vegetative growth on isolated localities when only one floral form is present but that it can also produce seeds which can disperse the plant species further.

In the development from flower bud to mature fruit 8 stages are distinguished; the release of developed seeds is 32—60 days after the day of anthesis of the flowers.

In the field and the concrete tanks where both floral forms occur, distinct differences in the fruit and seed production were observed. The number of fruits and the number of developed seeds per m^2 was much higher in the concrete tanks due to the development of much more flowers than in the Oude Waal, but the average number of seeds per fruit here was much lower and the percentage of fruits with a number of seeds below 15, was higher which indicates that the flowers in the small isolated concrete tanks were not so efficiently pollinated as in the field, also because some important Ephydrid species such as *Notiphila brunnipes* were not present in the concrete tanks. The percentage of flowers which were not pollinated at all, was not determined and is also a gap in the knowledge of pollination efficiency in *N. peltata* flowers.

The seeds of *N. peltata*, in the Oude Waal more than 3000 per m^2, are

first floating on the water surface, they are dispersed over the water by wind when the floating leaves have strongly diminished, and by water birds.
By heavy movements of the water they sink to the bottom, when the frost period starts nearly all seeds have sunk to the bottom.

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THE LIFE HISTORY AND HABITS OF *NOTIPHILA BRUNNIPES* ROBINEAU-DESVOIDY (DIPTERA, EPHYDRIDAE), AN AUTECOLOGICAL STUDY ON A FLY ASSOCIATED WITH NYMPHAEID VEGETATIONS

by

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With 7 figures

ABSTRACT

The life history and some ecological aspects of *Notiphila brunnipes* R.-D. are described. Special attention is paid to the interrelations with the nymphaeid plant species *Nuphar lutea* (L.) Sm., *Nymphaea alba* L., *Nymphaea candida* Presl and *Nymphoides peltata* (Gmel.) O. Kuntze. Observations have been made on phenology, occurrence in space and time, habitat choice, food, general behaviour, sexual behaviour, sex ratio, the deposition of eggs and mortality of the adults. Possible predators are discussed. The eggs are described and the function of the chorion is discussed. Some experiments have been carried out to study the development of the eggs in relation with humidity, oxygen and temperature. The habitat choice, food, mortality of and predation on the larvae are described and discussed. Some data on the puparia are given. Effects of the dry summer of 1976 are described. The geographical distribution is discussed, the absence of *N. brunnipes* north of the limes norrlandicus can be explained from the autecological data gathered during this study.

INTRODUCTION

Nymphaeid-dominated ecosystems, which are very common and show an optimal development in the Netherlands, have been studied by us during several years. Nymphaeids are aquatic plants with floating leaves, which root in the bottom and have flowers above or floating on the water surface. By their structure they characterize the ecosystem. They have an important function as habitat for many organisms, among them semi-aquatic insects such as the Ephydridae.

The species *Notiphila brunnipes* Robineau-Desvoidy, 1830 (syn. *N. stagnicola* Stenhammar, 1844, nec Robineau-Desvoidy, 1830, and *N. chamaeleon* Becker, 1896) occurred abundantly on the nymphaeids we studied and appeared to have many interrelations with *Nymphoides peltata* (Gmel.) O. Kuntze, *Nymphaea alba* L., *Nymphaea candida* Presl and *Nuphar lutea* (L.) Sm. Because of our interest in these interrelations, the life history and habits of *Notiphila brunnipes* were studied in detail and a review was made of data from the literature.

DESCRIPTION OF THE STUDY AREAS

Most observations have been made in the Oude Waal near Nijmegen (municipality of Ubbergen, Province of Gelderland) (fig. 1). The Oude Waal is an old river branch cut off from the river Waal. Here extensive vegetations dominated by *Nuphar lutea*, *Nymphaea alba* and *Nymphoides peltata* occur. The Oude Waal consists of a large shallow water, 1 km in length and about 250 m wide, and three interconnected ponds (D, E and F). The depth of the large shallow water varies from 0.5 to 1.5 m; in the dry summer of 1976 it became almost completely dry. About once every two years this area is flooded in winter or spring by water from the river Waal; summer high waters occur only occasionally. The depths of the three interconnected ponds increase towards the centre to 2.5, 5.5 and 5.5 m, respectively (D, E and F). The bottom of the Oude Waal consists of a pattern of clay and sand, sometimes mixed, covered by a sapropelium layer of varying thickness.

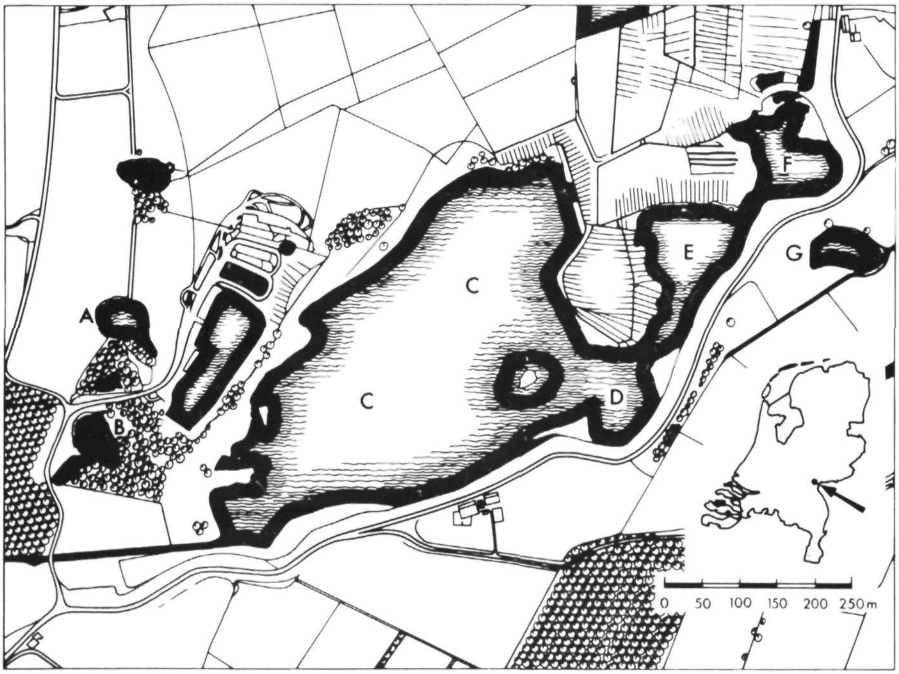

Fig. 1. Map of the Oude Waal.

Some additional observations have been made in the Haarsteegse Wiel (municipality of Vlijmen, Province of Noord-Brabant), which originated from two, but not simultaneous, bursts in the dike of the river Meuse. This water has an area of 17.9 ha and a maximum depth of 17 m. The lake has a vegetation dominated by *Nuphar lutea* and *Nymphaea candida*, which are almost completely restricted to the southern and western parts of the lake and which are sheltered against wave and wind action. *Nymphoides peltata* is very scarce here. The bottom of the Haarsteegse Wiel consists mainly of sand ("wash-over deposits"), but where nymphaeids grow there is a layer of sapropelium, which becomes thicker towards the littoral border. The hydrology of the lake is dependent on rain and ground water only and is more stable than that of the Oude Waal; the water-level shows only small fluctuations.

OCCURRENCE OF ADULTS ON NYMPHAEID LEAVES AND FLOWERS IN SPACE AND TIME

Methods

N. brunnipes (fig. 7) is a small fly with a length of 2.8—4.5 mm, with a remarkable silvery white frons and brownish fore tibiae (see for a description Robineau-Desvoidy (1830), Stenhammar (1844), Grünberg (1910), Becker (1896, 1926), Wahlgren (1927), Séguy (1934) and Dahl (1959)). It can be found in the flowers and on the floating leaves of the nymphaeids mentioned; the fly is not adapted to walk or stay on the water surface, so that they have to fly from leaf to leaf.

To study the changes in numbers during the season an insect-lime method was used. Each week, from June 16th until October 1977, six undamaged floating leaves (five of *Nuphar lutea* and one of *Nymphaea alba*) of the same size were gathered in the Oude Waal, pond F, and covered with insect-lime (Tangletrap or Stikem), which has no odour and consequently does not attract or repel the insects.

These leaves, the petioles of which were removed, were stuck on six other

Fig. 2. Lime-trap for insects. For explanation, see text. The wire netting is kept floating by corks and is attached with a string to the petiole.

floating leaves and then protected from predation by birds by wire netting, with meshes of 3 cm, the netting being supported by cork floaters (fig 2) The wire netting with cork floaters was attached with a string to the petiole of the supporting leaf After 24 hours these leaves were taken to the laboratory in the wire netting in plastic bags, so that the catch remained as undamaged as possible The fauna was washed from the leaves with refined petrol and then fixed in 70% alcohol The leaves were laid in transects from the littoral border vegetation to the open water, so that the distribution of the animals within the nymphaeid zone could also be studied

Three *Nuphar* leaves were laid in the western part of pond F, leaf 1 near the broad littoral border vegetation, consisting of *Typha angustifolia* L , *Rumex hydrolapathum* Huds and *Scirpus lacustris* L , here the floating leaves of *Nuphar lutea* covered up to 60%, leaf 2 six metres from leaf 1 in the centre of the *Nuphar* zone (maximum coverage 70%), leaf 3 twelve metres from leaf 1 at the margin of the *Nuphar* zone with the open water, where *Nuphar* covered up to 60% of the surface Two leaves were laid in a narrow *Nuphar* zone at the eastern side of pond F, leaf 4 near the littoral helophyte vegetation, which borders on grassland, consisting of a narrow zone of the same plant species mentioned for the western side, but also with *Mentha aquatica* L (maximum coverage of *Nuphar* 50%) and leaf 5 at three metres distance from leaf 4 at the margin of the *Nuphar* zone with the open water (maximum coverage 40%) Leaf 6, a *Nymphaea alba* leaf, was laid in an isolated vegetation of *N alba*, surrounded by open water and at six metres distance from the littoral border vegetation at the southern side of the pond (maximum coverage of *Nymphaea* 85%)

The development of floating leaves and flowers was followed in two plots of one square metre, one of *Nymphaea alba* and one of *Nuphar lutea*, as described in Van der Velde (1978) Temperatures of air and water were measured regularly

OCCURRENCE IN TIME

The results with the insect-lime method are summarized in table 1 Among the total catch of approximately 23,158 specimens (of which 99 4% insects, the rest arachnids), 642 specimens were of *N brunnipes*, i e 2 8% of the total catch (see for some other results Van der Velde (1978))

Another *Notiphila* species, *N dorsata* Stenh , was caught in equally large numbers (764 specimens = 3 3% of the total catch) This species has a goldish-yellow frons, so that it cannot be confused with *N brunnipes* *N dorsata* was not observed in the flowers of the nymphaeids and according to Dahl (1959) this species is more or less characteristic for the helophyte zone, although he also observed *N dorsata* in the nymphaeid zone

In fig 3 the water and air temperature, the number of floating leaves and flowers of *Nuphar* and *Nymphaea* per square metre, and the catch of *Notiphila* per week are plotted against time

The highest number of *N brunnipes* was caught on July 28th when flowering of *Nymphaea* and *Nuphar* was at its peak

Adults of *N brunnipes* have been caught by us with a hand net from the floating

Table 1 Catches of *Notiphila brunnipes* with insect-lime (for further explanation, see text)

Date: 1977	numbers of *N. brunnipes* caught leaf number 1	2	3	4	5	6	total	total catch	% *N. brunnipes* of total catch
16.vi	1	-	-	-	-	-	1	1401	0.07
23.vi	-	-	-	-	-	2	2	715	0.28
30.vi	18	-	-	3	-	-	21	1195	1.76
8.vii	19	22	-	6	2	12	61	2234	2.73
12.vii	10	21	2	6	-	23	62	3168	1.96
21.vii	58	5	1	14	4	9	91	2287	3.98
28.vii	89	16	-	11	2	9	127	1284	9.89
5.viii	64	28	-	2	11	15	120	1580	7.59
12.viii	33	5	1	-	-	27	66	1578	4.18
18.viii	49	2	-	-	-	-	51	1322	3.86
25.viii	3	2	-	1	-	1	7	1303	0.54
1.ix	2	6	5	-	2	1	16	1421	1.13
8.ix	6	3	-	-	-	-	9	1876	0.48
15.ix	-	1	-	-	-	-	1	762	0.13
22.ix	3	1	-	-	-	-	4	584	0.68
29.ix	-	-	-	-	-	-	0	448	-
Total number	355	112	9	43	21	99	639	23158	2.76

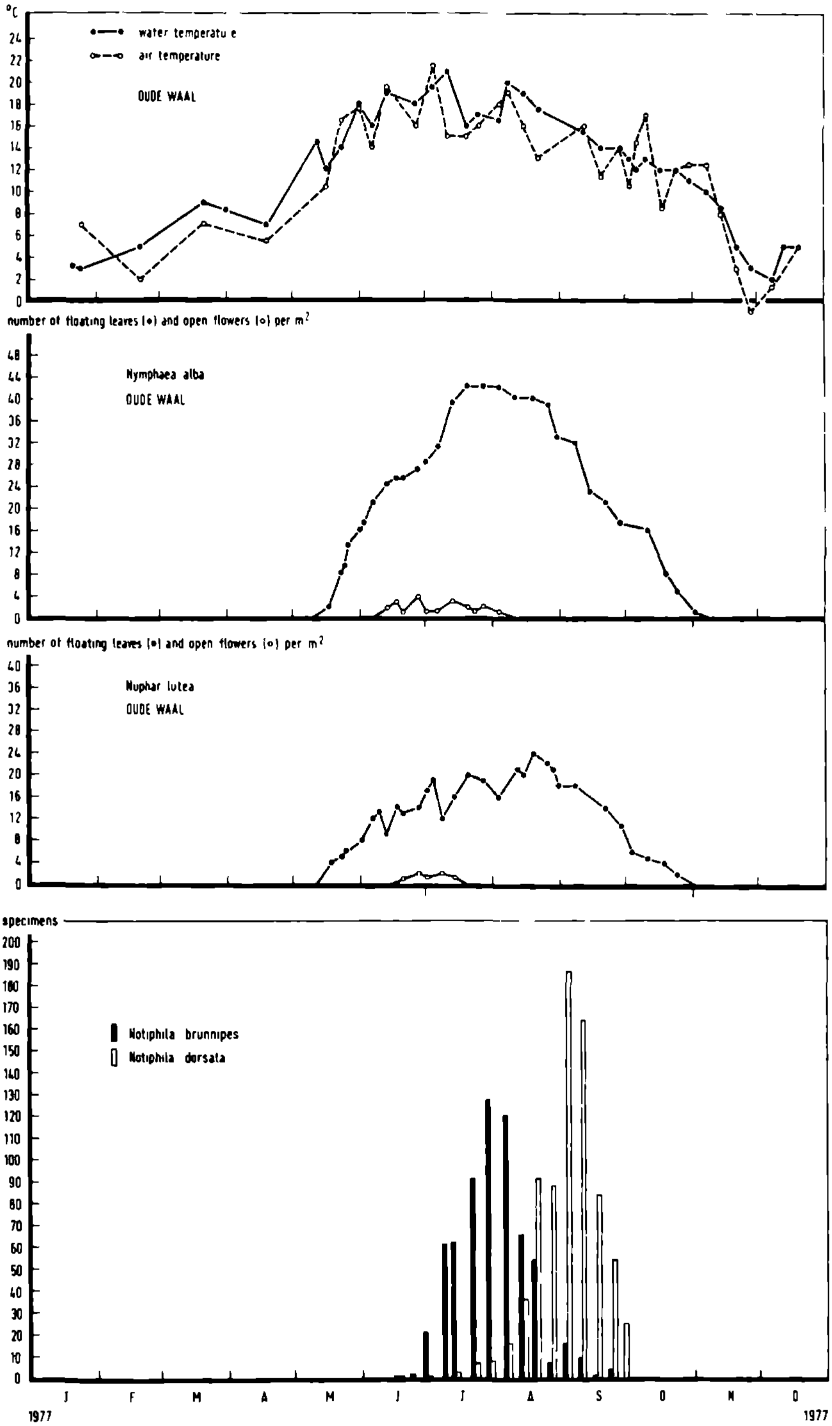

Fig 3 The course of water and air temperatures, the development of floating leaves and flowers of *Nymphaea alba* and *Nuphar lutea* in two plots of 1 m², and the numbers of *Notiphila* species caught per week with insect-lime on the floating leaves on the Oude Waal in 1977

leaves and flowers of nymphaeids between 5 June and 29 September 1975, from 1 June until 29 August 1976 and from 31 May until 22 September 1977. Wahlgren (1927) mentioned the months July and August as the time of occurrence.

Discussion. — From fig. 3 it is clear that the development of numbers of the *N brunnipes* population is highly correlated with the development of the floating leaves and flowers of the nymphaeids mentioned, water and air temperature, the number of floating leaves and flowers and the number of adult *N brunnipes* have their maximum in the same period. *N dorsata*, however, has its maximum on the floating leaves when decomposition dominates over production

From the data obtained with the insect-lime method it can be suggested that both *Notiphila* species have only one generation per year

With respect to the insect-lime method one should keep in mind that the catch is not only dependent on the size of the population but also on changes in the activity pattern of *N brunnipes*, for example caused by weather conditions This also applies to the other insects, so that the percentages of *N brunnipes* with respect to the total catch per date have been calculated The absolute numbers and the percentages show the same trend, so that it is very possible that the catches give a real picture of the development of the numbers in time

OCCURRENCE IN SPACE

The general distribution of the flies over the sampling leaves within the nymphaeid zone can be read from table 1, by comparing the results from the different leaves.

The flies appeared to have a distinctly higher abundance on the floating leaves bordering the littoral helophyte vegetation (leaves 1 and 4), the lowest number of flies has been caught towards the open water (leaves 3 and 5).

Adults of *N brunnipes* also showed to have a higher abundance on the broad *Nuphar* zone (leaves 1, 2 and 3) in comparison with the narrow one (leaves 4 and 5) Relatively more specimens of *N brunnipes* were caught on the *Nymphaea* leaf (leaf 6) which is comparable with the *Nuphar* leaves 3 and 5 because of their similar location near the open water

In the Oude Waal the flies were found abundantly on the floating leaves and in the flowers of *Nymphaea alba, Nuphar lutea* and *Nymphoides peltata* and less so in the littoral border vegetation on *Typha angustifolia, Rumex hydrolapathum* and *Scirpus lacustris* In the Haarsteegse Wiel they were found on the floating leaves and in flowers of *Nuphar lutea* and *Nymphaea candida* and seldom on other plants such as *Acorus calamus* L and *Iris pseudacorus* L. Our data are in accordance with those of Dahl (1959) who studied the ecological distribution of Ephydridae in Scandinavia, he found that *N brunnipes* is characteristic for nymphaeid vegetations and occurs in lesser amounts in the bordering reed vegetation.

Discussion — The higher abundance of adult *N brunnipes* on the nymphaeids bordering the helophyte vegetation may be explained by the fact that the environment is less dynamic (wind- and wave-action) close to the reed-belt than

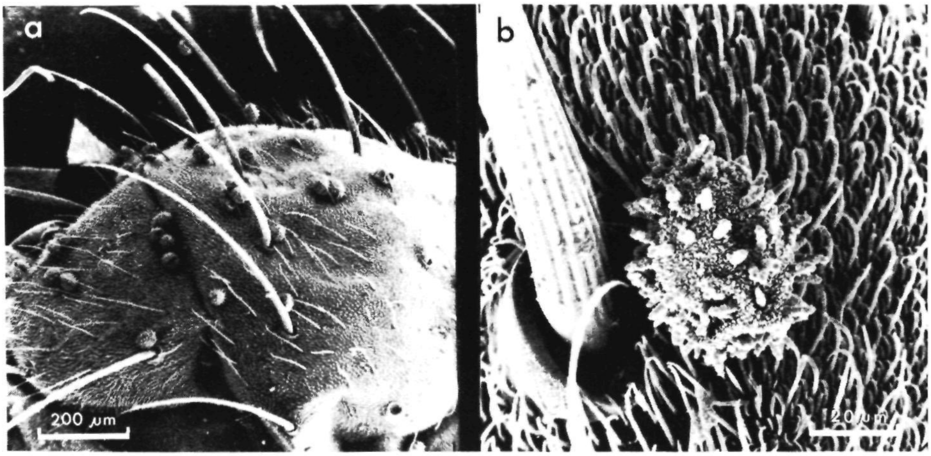

Fig. 4. a, thorax of *N. brunnipes* with attached pollen of *Nymphaea alba*; b, enlarged part of a. Note the many curved hydrophobous hairs on the body which prevent the insect from getting wet.

close to the open water. *N. brunnipes* is, as already mentioned, not able to walk over the water surface, and after a longlasting contact with water it drowns in spite of having numerous curved hydrophobous hairs all over the body (fig. 4).

GENERAL BEHAVIOUR

Generally the flies walk slowly over the floating leaves and fly only short distances to reach other floating leaves or flowers in the neighbourhood. Under warm, sunny weather conditions the flies are more active and fly away sooner than under colder circumstances when they can be captured rather easily by putting a glass tube over them. On a sunny afternoon in July the flies can be found in large numbers on the floating leaves and flowers where they perform several activities like feeding, walking, courting, copulating, polishing, sunning, and depositing eggs.

Under bad weather conditions, for example, heavy rain, they seek shelter in the various flowers, under the aerial leaves of *Nymphaea alba* (leaves of this species often project entirely or partly above the water surface) and between the littoral border vegetation, staying there more or less motionless.

De Meijere (1940b) reports that *N. brunnipes* often forms dense clusters on the leaves of *Nuphar* and *Nymphaea*; the specimens are then situated in a circle with their heads directed to the centre. This behaviour, however, has been noticed by us only sporadically, perhaps because we made observations during day-time while De Meijere (1940b) describes this behaviour for the evening (20.30 h.).

Dahl (1959) has expressed the frequency of a number of activities of the flies in percentages, viz., feeding 8%, polishing 25%, walking 42%, copulating 8%, no movement 17% (the environmental circumstances such as temperature and weather conditions and time of the observation were not mentioned, however).

FEEDING BEHAVIOUR

According to Waitzbauer (1976) the species of the genus *Notiphila* generally feed on fluids of decaying plant material Adults of *N brunnipes* were observed by us obviously feeding on fluids of decaying floating leaves but also on exudates of flowers of the nymphaeid species mentioned, and on the body fluids of dead insects, such as Ephemeroptera, Trichoptera and aphids

In the flowers of *Nuphar*, *Nymphaea* and *Nymphoides* the flies could be seen licking the anthers (even unripe ones) and the stigma The flowers of *Nymphaea alba* and *Nymphaea candida* do not possess nectaria but on the first day of flowering the stigma profusely produces a sweet-tasting exudate containing glucose and fructose as could be proved by enzymatic tests On the second day of flowering this exudate has already disappeared The flowers of *Nuphar lutea* possess nectaria on the outer sides of the petals, which produce nectar, also containing glucose and fructose. The production of nectar occurs especially on the first day of flowering; the flower then has a strong brandy scent while the stigma is sticky or dry and shiny, an extensive description of the development of the flowers of the Nymphaeaceae mentioned is being prepared (Van der Velde, in prep)

The flowers of *Nuphar* and *Nymphaea* have also many anthers which produce abundant pollen. *N brunnipes* can often be found with pollen on its body (fig 4) To check whether the flies also consume pollen the intestines of some of them were studied under the microscope. In some intestines germinated and ungerminated pollen of *Nymphaea alba* could be recognized together with diffuse material and micro-organisms

The flowers of *Nymphoides peltata* possess nectaria which are sheltered by hairy staminodes *N brunnipes* can not reach these nectaria because of the staminodes, although efforts of these flies to reach the nectar can be observed regularly. Furthermore the flies can be observed licking the five anthers and the small stigma of *Nymphoides*, which is papillate and wet according to Heslop Harrison & Shivanna (1977)

This licking behaviour strongly suggests that food is taken up in the form of nectar, stigmatic exudate and pollen in the flowers

On the floating leaves, *N brunnipes* can be seen licking on decaying parts, e g , on decayed tissue around the tracks of the mining larvae of *Hydromyza livens* (Fall) (Scatomyzidae) in *Nuphar* leaves Fungi play an important role in the decomposition of the leaves of nymphaeids. By feeding on the fluids of leaf parts infected by fungi the flies can be vectors of these fungi, e g , via the passage of spores in the digestion canals or by chance presence of spores on their body

According to Fischer & Gaumann (1929) small flies such as *Drosophila* species can be vectors of the spores of *Glomerella cingulata* (Ston) Spauld et Schrenk, which is known from many plant species and also occurs on the floating leaves of *Nymphaea alba* and *Nymphaea candida*, this may well apply to *N brunnipes* and also to *N dorsata*.

SEXUAL BEHAVIOUR AND SEX RATIO

The flies can regularly be observed in copulation on the floating leaves and in the flowers of the nymphaeids mentioned. Many of the flies which are found on and in first-day flowers of *Nuphar* and *Nymphaea* are in copulation; sometimes masses of the flies were present on these flowers.

N. brunnipes shows a distinct mating behaviour. This behaviour was described by Dahl (1959) as follows: "During the posturing phase of courtship the male approaches the female from behind and after performing encircling movements around her with his head directed towards her, he stops in front of her head, tapping her antennae with his own. After this phase the partners have been observed slowly circling round face to face. If the female accepts the invitation, she spreads her wings permitting the male to mount. During the insemination the female continues feeding and walking".

It appeared from our field and laboratory data that the mating behaviour as described by Dahl (1959) is not always so elaborate. Sometimes the female spreads her wings immediately when a male approaches her and so copulation is allowed directly. It also has been observed that a male approached a female in a more aggressive way leading to copulation.

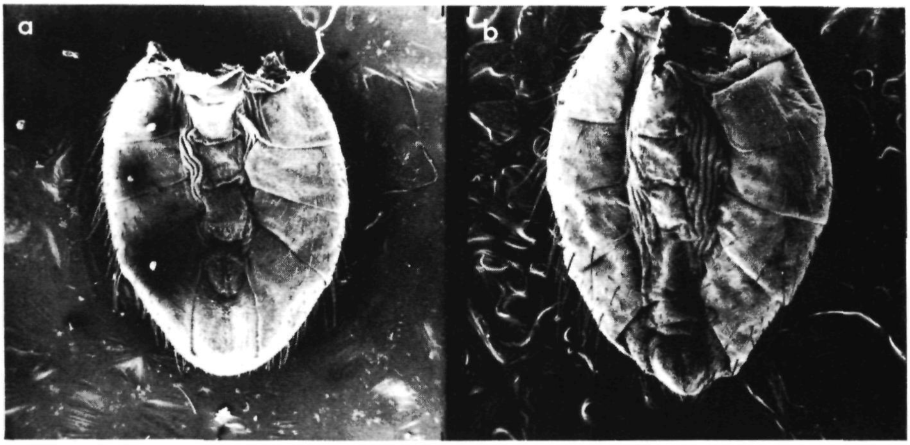

Fig. 5. a, abdomen of *N. brunnipes*, male; b, abdomen of female; ventral aspects.

Males and females of *N. brunnipes* can easily be separated from each other because they differ in size and in the position of the genital aperture. Males have a length of 2.8—3.7 mm, so they are smaller than the females which measure 4.0—4.5 mm in length (10 specimens of each sex were measured). The genital aperture is situated on the ventral side of the abdomen in the males and at the caudal tip of the abdomen in the females (fig. 5).

Some samples from the insect-lime catch on the floating leaves were studied for calculating the sex ratio. The results are summarized in table 2. More males than females were caught on the floating leaves in July and more females than males in

Table 2. Sex ratio of *Notiphila brunnipes* in samples caught with insect-lime.

Date: 1977	number of specimens examined	males	females	sex ratio percentage of males
30.vi	14	5	9	35.7
12.vii	18	17	1	94.4
21.vii	53	31	22	58.5
28.vii	66	44	22	66.7
5.viii	72	33	39	45.8
12.viii	43	21	22	48.8
18.viii	45	19	26	42.2
Total	311	170	141	54.7

June and August. Perhaps the females occur more often in flowers during July when also flowering is at its peak; the deposition of eggs in flowers can be mentioned in this respect. Another explanation can be that males are more active in this month than the females because of their mating behaviour.

DEPOSITION OF EGGS

As described by Rousseau (1919) and De Meijere (1940a, b) the females of *N. brunnipes* deposit eggs in the flowers of *Nymphaea alba* and *Nuphar lutea*; we found the eggs also in the flowers of *Nymphaea candida* ancally observed them, during the dry summer of 1976, in the flowers of *Nymphoides peltata*, further on floating leaves of the various nymphaeids of which the margins were curled up and desiccated. The eggs are especially deposited in first-day flowers. The flowers of *Nymphaea candida* in the Haarsteegse Wiel contained relatively few egg clusters because these flowers were very often half-filled with water (Van der Velde et al., 1978).

When the numbers of *N. brunnipes*, and also flowering, are at their peak in the Oude Waal, nearly all *Nuphar* (when intact) and *Nymphaea* flowers contain egg clusters. The number of eggs per flower varies with the population size from year to year; in July 1975 hundreds of eggs could be found per flower of *Nymphaea alba* and *Nuphar lutea*. The maximum number of eggs found in an ovarium of a *N. brunnipes* female was 24.

According to Müller (1921) *Notiphila riparia* Meigen also deposits its eggs on *Nymphaea* (also cited by Hennig, 1943, and De Meijere, 1944), but this has not been confirmed in the present study. With the insect-lime method only one specimen of *N. riparia* was caught on a *Nuphar* leaf. *N. riparia* is more characteristic for a reed vegetation according to Dahl (1959).

MORTALITY AND PREDATION

Especially after heavy rain the population of *N. brunnipes* seems to be diminished. The flies drown easily when they become wet for a long time.

Fig. 3 shows that the numbers of *N. brunnipes* decrease at the end of the summer. Then mortality of adults may have several reasons, e.g., competition with *N. dorsata*, falling temperatures, and lack of food from flowers.

Although predation on the flies has not been observed by us, the following species must be taken into consideration with respect to possible predation: the spider *Pirata piraticus* (Cl.) (Lycosidae), some of the larger Dolichopodid species, the fly *Hydrophoria conica* Wied. (Muscidae), some species of Gerridae, Odonata (*Coenagrion pulchellum* Van der Linden, *Erythromma najas* Hansem., *Ischnura elegans* Van der Linden) and the green frog *Rana esculenta* L. It has been observed that specimens of *Hydromyza livens* approached *N. brunnipes* in an aggressive way, but they were never consumed or killed by this predatory fly. In the flowers the flies have a smaller chance to be caught by large predators such as Odonata.

DESCRIPTION OF THE EGGS

The eggs of *N. brunnipes* have a length of 1.1—1.3 mm and a width of 0.4—0.5 mm (fig. 7); they are white in colour and possess a short toadstool-like micropylar protuberance on the rostral end. The other end of the egg is rounded (fig. 6).

The eggs are deposited in the flowers in rows of usually 2—7 eggs but larger rows are not exceptional. Usually the eggs can be found on the bases of the petals, sepals and even on the anthers of *Nymphaea alba*, *Nymphaea candida* and *Nuphar lutea*. The eggs are attached to the substrate, but not very strongly so; they are, however, very well attached to each other, in such a way that it is impossible to separate the eggs without damaging the chorion.

Eggs have been studied by means of scanning electron microscopy; in this way regular netlike structures and pores could be recognized on the chorion (fig. 6). The eggs of *N. brunnipes* show a striking bipolarity, because they possess different structures on the dorsal and ventral side. The structure on the dorsal side can be described as "wall"-structure, a structure in which concavities are flanked by walls. The structure on the ventral side can be described as "island"-structure; here island-like structures are flanked by canal-like concavities. The "wall"-structure was already described by De Meijere (1940a). On fig. 6 a possible glue substance can be recognized at the margins of the "islands"; this side of the chorion was fixed to a petal.

To study the internal structure of the chorion the eggs were sliced with a razor blade and examined with the scanning electron microscope. The chorion appeared to possess cavities which are in contact with the pores in the external walls of the chorion (fig. 6). The surface structures of the chorion, described as "wall"- and "island"-structure, coalesce on places where the eggs are attached to each other; in this way the eggs support each other so that they maintain their position between the floral leaves.

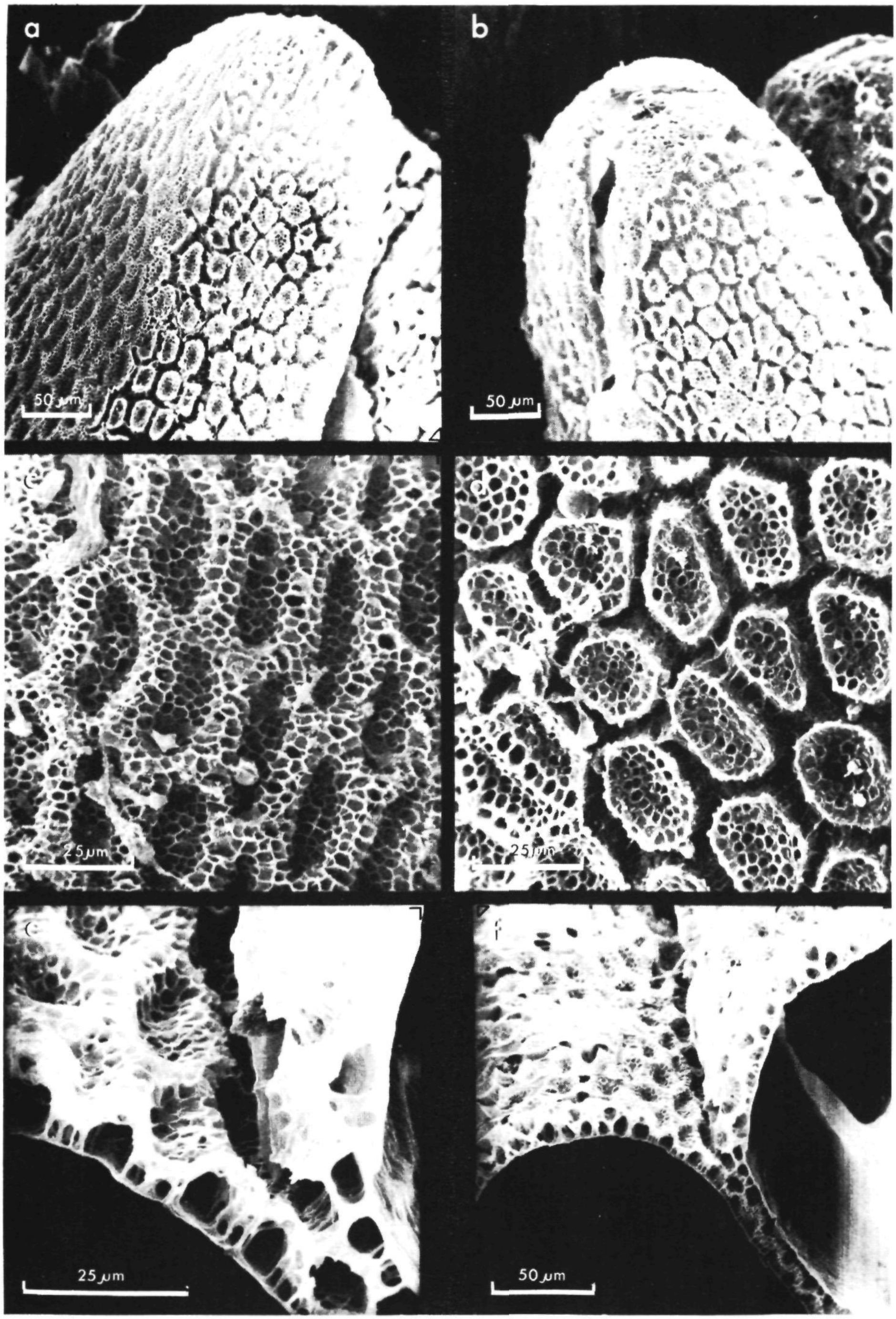

Fig. 6. a, caudal part of *N. brunnipes* egg showing both structures; b, rostral part of the egg (note the micropylar protuberance and the beginning hatching split); c, wall-structure (dorsal); d, island-structure (ventral); e and f, coupe of the chorion showing cavities and the attachment of two eggs by means of both structures.

THE FUNCTION OF THE CHORION

The distinct structures of the chorion of the *N. brunnipes* egg were suspected to hold an air layer which functions as a plastron. Hinton (1960, 1969, 1971) has shown that structures such as a network of walls and pores on the egg surface have the function to hold air, so that the egg can continue with respiration when becoming wet, e.g. by a rain shower. According to this author a system of hydrofuge structures can form the architecture for a permanent or unshrinkable, physical gill which is called a plastron. An egg with a plastron can remain immersed indefinitely and obtains the oxygen it requires from the ambient water, provided that the water is well-aerated.

The flowers of *Nymphaea* close at night and when they close they sink somewhat, to a third, under water, so that the eggs of *N. brunnipes* regularly become wet (Rousseau, 1919; De Meijere, 1940b); the flowers of *Nuphar* do not close at night and during flowering they are always above the water surface (Van der Velde, in prep.).

When the eggs are held under water an air-film around them can be observed; De Meijere (1940b) pointed out, however, that the eggs cannot tolerate a longlasting contact with water, but in that case soon decay.

In the laboratory some experiments were carried out to study the development of eggs with regard to the functioning of the air-layer in and around the chorion as a plastron. For the experiments young first-day flowers of *Nuphar* and *Nymphaea* were collected which contained eggs of *N. brunnipes*; the eggs in these flowers had nearly the same age and thus could be regarded as being in the same developmental stage.

For the first experiment four *Nuphar* flowers with eggs were placed in jars at room temperature (25° C). Flower 1 was placed upright in a jar with water so that the flower was some centimetres above the water surface; flower 2, was placed as flower 1, but was sprayed two times per day with water; flower 3 was placed upside down in aerated water, held in this position with wire netting; flower 4 was treated as flower 3, but the water was not aerated. Furthermore some eggs were taken out of a flower and placed in a dry petridish. Observations were made daily during 2 weeks.

After 4 days there were larvae in the water from the eggs in flower 1 and 2, after 6 days from those of flower 3. The eggs of flower 4 decayed instead of developing into larvae. The eggs in the petridish also did not develop into larvae but desiccated.

It can be concluded that eggs develop into larvae in a relatively dry environment (flower 1), in a dry but temporarily wet environment (flower 2) and in well-aerated, oxygen-rich water (flower 3). Eggs decay in water poor in oxygen (flower 4) and desiccate in a dry environment outside the flower (petridish); probably the air within a flower is humid enough to prevent desiccation. It can also be concluded that the development of the eggs under dry but air-humid conditions goes faster than in water and that the structures of the chorion hold an air-layer which functions as a plastron as the eggs developed in well-aerated water, so that they must have obtained oxygen from this medium.

Table 3 Development of eggs into larvae under three different conditions (for further explanation, see text).

Time	Number of larvae in jar A	B	C
4 days	0	0	14
5 days	0	0	87
6 days	0	75	96
10 days	0	83	96

A second experiment has been carried out to study the development of the eggs more quantitatively. Three-hundred eggs were collected from first-day flowers and used for this experiment. In each of three flowers of *Nymphaea alba* 100 eggs were deposited. In jar A a *Nymphaea* flower with eggs was held upside down in non-aerated water by wire-netting, in jar B the same was done in well-aerated water and in jar C the flower was placed upright (only its stem was in contact with water). The experiment was carried out at room temperature (25° C) and the development of the eggs into larvae was followed by daily observations until the remainder of eggs was disintegrating. The results are summarized below (table 3).

This experiment confirms the results of the first experiment; furthermore the number of eggs not developing into larvae is larger in water (B) than under air-humid conditions (C).

DEVELOPMENT OF EGGS IN RELATION WITH TEMPERATURE

To measure the influence of temperature on the development rate of eggs an experiment was carried out in the laboratory. In the field a number of first-day flowers of *Nuphar* and *Nymphaea* were collected in which eggs had been deposited by *N. brunnipes*. A cluster of eggs attached to the innerside of a sepal or petal was placed in a petridish with a layer of water in order to maintain high humidity and to prevent desiccation of eggs. The petridishes were placed in different climate chambers which had constant temperatures of 5°, 10°, 14°, 18°, 20°, 24° and 30° C, respectively. By daily observations the development of the eggs into larvae was followed.

At temperatures of 5° and 10° C the eggs had not yet developed into larvae after 30 days. At 14° C larvae hatched after 13 days and at 18°, 20°, 24° and 30° C after 5, 6, 4 and 6 days, respectively.

It can be concluded from the experiment that the eggs develop well and fast into larvae at temperatures between 18—30° C.

Temperatures within this range indeed occurred in the flowers of *Nymphaea alba* and *Nuphar lutea*, as measured in the field with the aid of a Wallac oy Universal Thermometer (GST 32; probes Ni-101x and Ni-106). By day light, temperatures in flowers can be several degrees higher than the surroundings, due to solar radiation

Table 4. Temperature measurements in °C in flowers and surroundings of *Nymphaea alba* and *Nuphar lutea*

Nymphaea alba	Tw	Tl	Tf	Ts	Tf - Ts
Date: 23.vi.1977	22.5	26.0	29.0	24.5	4.5
Time: 14.30 h.	22.0	26.1	28.2	24.5	3.7
Sunny, unclouded	21.5	26.0	28.4	25.0	3.4
	22.9	26.1	29.4	24.0	4.9
	22.5	26.1	29.5	24.5	5.0
Date: 7.vii.1977	22.9	23.2	22.1	21.1	1.0
Time: 14.45 h.	23.0	23.8	22.8	22.1	0.7
Heavily clouded	23.0	23.5	23.1	22.9	0.2
	22.9	25.2	22.0	21.8	0.2
	23.4	22.8	23.0	22.0	1.0
Nuphar lutea					
Date: 8.vii.1977	22.0	25.4	27.2	22.6	4.6
Time: 14.30 h.	23.5	28.0	29.8	26.5	3.3
Sunny, unclouded	23.2	25.0	27.1	24.1	3.1
	23.2	26.0	27.8	25.8	2.0
	23.4	26.5	28.0	26.2	1.8
Date: 29.vi.1977	19.0	19.4	18.8	18.8	0
Time: 13.45 h.	19.5	19.5	18.6	17.8	0.8
Heavily clouded	19.1	19.1	19.1	18.4	0.7
	19.2	19.2	17.9	18.0	-0.1
	19.0	19.0	18.0	17.2	0.8

Tw = water temperature, Tl = temperature upper surface floating leaf, Tf = temperature innerside of the floral leaves, Ts = temperature outerside of the sepals of the flower

(table 4). Table 4 also shows that under clouded weather conditions the differences in temperature between the inner and outer side of flowers are not as spectacular in comparison with those under sunny weather conditions.

A fast development of the eggs into larvae within 4—6 days also has to take place under natural conditions. The flowers of *Nymphaea alba* and *Nymphaea candida* flower 4—6 and 4 days, respectively, before they become definitively closed (Van der Velde, in prep.); the larvae cannot leave the flower in case the development should be longer. This is in accordance with the fact that adult females of *N. brunnipes* deposit their eggs especially in young first-day flowers

The flowers of *Nuphar* remain open after the flowering so that the larvae can always leave.

MORTALITY AND PREDATION

The experiments prove, that the eggs cannot develop into larvae when they are too long in water poor in oxygen; then the eggs soon decay.

In both study areas, the Coot (*Fulica atra* L.) consumes most of the petals and sepals of the flowers of *Nuphar lutea*. In this way many eggs of *N. brunnipes* attached to these floral leaves must be either consumed or lost into the water. The oviposition substrate is thus strongly diminished in size. The floral leaves of *Nymphaea* were seldom consumed by waterfowl. These facts might explain the higher numbers of *N. brunnipes* adults and eggs on *Nymphaea alba* flowers in comparison with *Nuphar lutea*.

A possible consumer of the eggs might be the fly *Hydromyza livens*, a regular visitor of flowers of *Nuphar lutea*. In the laboratory this fly appeared to consume the eggs but this could not be confirmed by field observations; it is difficult to see, without disturbing them, what these flies are doing in the flowers. It is not known whether there are other consumers of the eggs but in the flowers of *Nymphaea alba* and *Nuphar lutea* some Braconid species have been collected, which are suspected of this.

HATCHING OF THE LARVAE

De Meijere (1940b) described the hatching of larvae as follows (translated from Dutch): "The eggs, on the time of hatching, were dark gray in colour and one saw the larva moving in the egg-shell when using the pocket-lens. Then the egg-shell at once tore cleft-like open on one end and the larva, which was situated with the blackish headtop in front of the developed aperture, crept out. When that had happened, the walls of the egg-shell came together again, so that a flat membrane of white colour was left". From the scanning photographs (fig. 6b) it is obvious that the egg-shell splits open in the surroundings of the micropylar protuberance.

After the larvae have left the egg-shell through this opening, they also creep out of the flower and drop themselves in the water to reach the bottom (see for a description of the larvae, De Meijere (1940b), Hennig (1943), and further fig. 7).

HABITAT CHOICE OF THE LARVAE

When the larvae have reached the bottom they make tracks in detritus and mud as already described by De Meijere (1940b), which could be confirmed by us.

An experiment was carried out to test the response of the larvae to light. Hundred larvae were placed in a petridish with water. The petridish was half covered with aluminum foil and placed under a lamp. After an hour 87 larvae were present in the covered half and only 13 in the uncovered half. Thus the larvae are negatively phototactic and seek dark places.

The detritus, however, is poor in oxygen. It is known that larvae of certain *Notiphila* species obtain oxygen from aquatic and littoral border plants; the larva pierces its pointed caudal stigmata in the plant tissue and so oxygen is obtained from the intercellular cavities (Grünberg, 1910; Varley, 1937; De Meijere, 1940b; Berg, 1950; Oldroyd, 1964).

De Meijere (1940b) and Hennig (1943) recorded puparia of *N. brunnipes* from the roots of *Typha angustifolia* and *Typha* spec.; we inspected various aquatic and littoral border plants in May and July 1977 to find out if larvae or puparia occurred on their roots or root stocks. The plant species *Nymphaea alba*, *Nymphaea candida*, *Nuphar lutea*, *Nymphoides peltata*, *Rumex hydrolapathum*, *Typha angustifolia*, *Glyceria maxima* (Hartm.) Holmb., *Iris pseudacorus*, *Acorus calamus*, *Phragmites australis* (Cav.) Trin. ex Steud. and *Mentha aquatica* were investigated.

In spite of investigations over two years we never found the larvae on roots or other aquatic parts of *Nymphaea alba*, *Nymphaea candida* or *Nuphar lutea*, as also recorded by De Meijere (1940b). Large numbers of puparia and some larvae, however, have been found pierced with their stigmata in roots and short shoots of *Nymphoides peltata* from the Oude Waal. A large number of puparia and full-grown larvae (7—10 mm long) were found on the roots and root-stocks of *Acorus calamus* in the Haarsteegse Wiel (*Acorus* does not occur in the Oude Waal and in the Haarsteegse Wiel *Nymphoides* is very scarce). Furthermore a number of pupae was found on the roots of *Typha angustifolia* at both localities. Some pupae have hatched in the laboratory so that a definite identification of *N. brunnipes* was possible. From the roots of *Typha angustifolia* also a specimen of *N. dorsata* hatched.

It is clear that *Nymphaea* and *Nuphar* are important for *N. brunnipes* to complete its life cycle, but also such plants as *Nymphoides peltata*, *Acorus calamus* and *Typha angustifolia*.

In the Netherlands *Nymphaea alba* also occurs in oligotrophic, dystrophic moorland pools. Here *N. brunnipes* also occurs although the above-mentioned plants do not. Possibly *Typha latifolia* L. fulfills a similar function in these habitats.

Although larvae are observed having pierced their stigmata in roots of plants, it is so far unknown whether the larvae remain attached to one root or plant-individual only or whether they move from one plant to another. It is clear that the larvae do not need to be always pierced with their stigmata in plant roots. They may creep from *Nymphaea* or *Nuphar* to *Nymphoides*, *Acorus* or *Typha*; the distance between these groups of plants can be several metres.

It is possible that the younger larvae can remain longer in detritus poor in oxygen (skin-respiration) and creep larger distances than the full-grown ones without having pierced the stigmata in plant tissue.

How long the development of the larvae takes is not exactly known; in spring full-grown larvae can be found, so that *N. brunnipes* certainly hibernates as a larva. Furthermore it is very likely that *N. brunnipes* has only one generation per year.

FOOD OF THE LARVAE

According to Dahl (1959) De Meijere (1940a) has written that the larvae of *N. brunnipes* mine in the roots of *Nymphaea alba*, but, in fact, De Meijere (1940a, b) denied this. His papers are written in Dutch, which may have caused the misunderstanding. De Meijere (1940b) who studied the young larvae in petridishes with detritus reports that some specimens showed a green or brownish mass in their body and thus concluded that they had fed obviously on fresh plant material or detritus; most of the larvae however were totally colourless, crept restlessly around and did not feed.

To study the feeding habits of the larvae some experiments were carried out. A number of newly hatched larvae were put in petridishes with water; green filamentous algae (1), detritus from the Oude Waal (2), fresh submerged *Nuphar* leaves (3) and decaying floating leaves of *Nuphar* (4), *Nymphaea* (5) and *Nymphoides* (6) were offered as food. Only some larvae kept in the petridishes with detritus (2) and decaying leaves (4, 5, 6) had material in their intestines after a day. Probably the larvae feed on material from the detritus and decaying plant parts or on organisms occurring there, such as bacteria, fungi and protozoa.

Under laboratory conditions the larvae, however, could not be kept alive for a long time. They also tried to creep out of the petridishes via the condensation water; lack of oxygen may have caused this behaviour.

Mortality and predation

When the larvae drop themselves in the water they have a great risk to be eaten by fish; furthermore they can get lost when they creep in wrong directions, when they find no suitable root for attaching and die by lack of oxygen.

PUPA

The puparia of *N. brunnipes* (fig. 7) have been described by De Meijere (1940b) and Hennig (1943). As already mentioned, the puparia can be found pierced with their stigmata in the roots, root stocks or short shoots of *Nymphoides peltata*, *Acorus calamus* and *Typha angustifolia*, possibly in order to obtain oxygen from these plants. The puparia remain attached to the same root.

Puparia were found in spring, thus *N. brunnipes* hibernates also as puparium. After the hatching under water the flies must reach the water surface quickly; it is thus favourable that the puparia occur in shallow water.

EFFECTS OF THE DRY SUMMER OF 1976

By the prolonged drought during the summer of 1976 the broad of the Oude Waal became nearly completely dry and also the interconnections between the ponds, so that the littoral border plants and especially *Nymphoides peltata* suffered badly. In 1977 the coverage and vitality of *N. peltata* in the Oude Waal had strongly diminished, in 1978 the vegetation had regained its vitality.

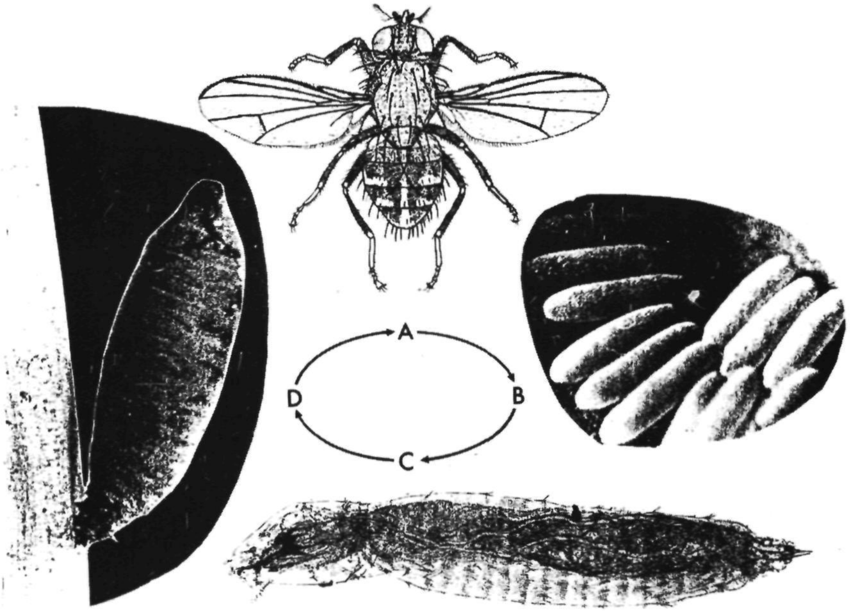

Fig. 7. Life stages of *N. brunnipes*. A, imago; B, eggs; C, larva; D, pupa (pierced in root).

As a result the population of *N. brunnipes* of 1977 remained very small in numbers with respect to other years, which supports the suggestion that there is only one generation per year.

GEOGRAPHICAL DISTRIBUTION

N. brunnipes has been recorded from Central Europe (Becker, 1926), Italy (Torelli, 1922, according to Hennig, 1943), France (Séguy, 1934), Belgium (Rousseau, 1919), The Netherlands (De Meijere, 1940a), North Germany, Silesia (Grünberg, 1910), Great-Britain (Oldroyd, 1975) and Fennoscandia (Dahl, 1959). Dahl (1978) gives the following rough distribution area in Limnofauna Europaea: Iberian Peninsula, Eastern Balkans, Western lowlands, Central lowlands, Baltic Province, England, Boreal highlands, Northern Sweden and Taiga. The second author of the present paper observed the species also in the Republic of Ireland in 1978.

According to Dahl (1959) the species is not found north of the limes norrlandicus (about the 16° C isotherm of July); from Finland there are only some southern records. He writes that both the ecological and phenological distribution is governed by the species' affinity for *Nuphar* and *Nymphaea*, but the geographical distribution of *N. brunnipes* does not appear to include the northern parts of the *Nymphaea* and *Nuphar* area of Fennoscandia.

Our investigations have shown that *N. brunnipes* occurs during its life cycle in two different habitats and is bound indeed to *Nuphar* and *Nymphaea* but also to *Typha angustifolia*, *Acorus calamus*, *Nymphoides peltata*, and probably *Typha* *latifolia* Both the *Typha* species, as well as *Acorus* and *Nymphoides* have a distribution south of the limes norrlandicus (Hultén, 1950), which may explain the similar distribution of *N brunnipes*

SUMMARY

As can be concluded from the data in this paper there are direct relations between *N brunnipes* and the nymphaeids *Nuphar lutea*, *Nymphaea alba*, *Nymphaea candida* and *Nymphoides peltata*

Adults of *N brunnipes* visit the flowers of *Nymphaea* and *Nuphar* for

(a) food in the form of stigmatic exudate, nectar or pollen,
(b) the deposition of eggs, the development of eggs is favoured by the temperatures and the air-humid or alternately dry and wet environment in the flowers,
(c) protection and shelter against bad weather conditions and certain predators such as Odonata,
(d) copulation site, especially first-day flowers attract many specimens and copulation often occurs there,
(e) resting site, e g for warming up the flight muscles, because of the higher temperatures their digestion probably goes faster inside the flowers

The flowers of *Nymphoides peltata* have these functions only partly (not b) The flies play an important role in the pollination of all the nymphaeids mentioned

Adults of *N brunnipes* occur on the floating leaves of *Nuphar*, *Nymphaea* and *Nymphoides* for

(a) food, viz , directly for consumption of fluids of decaying leaf parts and indirectly to consume body fluids of dead insects,
(b) copulation site,
(c) resting site, also for sunning,
(d) shelter or protection under aerial leaves or leaf margins which have been curled up and dried out,
(e) sporadical egg-deposition on sheltered sites By their behaviour adults of *N brunnipes* can function as vectors of spores of fungi, occurring on the floating leaves

The larvae and puparia seem to be restricted to the roots of *Typha*, *Acorus* and *Nymphoides*, and obtain oxygen by means of pointed stigmata from the intercellular cavities The larvae feed there most likely on detritus and decaying plant material

The fact that *N brunnipes* is bound to at least two different plant species during its life cycle may explain the geographical distribution of the species

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Onderzoek naar door nymphaeiden gedomineerde systemen.

SAMENVATTING

Nymphaeiden zijn waterplanten die in de bodem wortelen, met hoofdzakelijk drijfbladeren en met bloemen die boven water uitsteken of op het water drijven. De nymphaeide groeivorm is karakteristiek voor stilstaand zoetwater, waar de nymphaeiden tot in ongeveer 3 m diep water kunnen voorkomen.

In de Nederlandse zoetwatergebieden zijn nymphaeiden vaak de dominante groeivorm en het ligt voor de hand te veronderstellen dat deze planten niet alleen een belangrijke hoeveelheid biomass kunnen vertegenwoordigen maar ook door hun strukturele (morfologische) opbouw vele mogelijkheden voor gebruik door en vestiging van vele andere organismen bieden. Daarnaast beïnvloedt de nymphaeide vegetatie zijn omgeving op karakteristieke wijze o.m. door het wegvangen van licht door de drijfbladeren en het dempen van golfslag.

Als voorbeelden van nymphaeiden kunnen waterlelies (*Nymphaea alba* L., *Nymphaea candida* Presl) en de Gele plomp (*Nuphar lutea* (L.) Sm.) behorende tot de familie van de Nymphaeaceae, en de Watergentiaan (*Nymphoides peltata* (Gmel.) O. Kuntze) behorende tot de familie van de Menyanthaceae, genoemd worden. Gemeenschappen gedomineerd door deze soorten vormen het onderwerp van onderzoek vanaf 1974; een deel van de resultaten is in dit proefschrift verwerkt waarbij vooral de door *Nymphoides peltata* gedomineerde gemeenschappen aan de orde komen.

De nymphaeide vegetatie kan als het frame van een oecosysteem beschouwd worden. Met betrekking tot de ruimtelijke opbouw kunnen door de structuur van de vegetatie zelf verschillende compartimenten onderscheiden worden (Fig. 1):
A. het plantenweefsel, B. de bloemen, C. de luchtbladeren, D. de bovenzijde van de drijfbladeren, E. de onderzijde van de drijfbladeren, F. opgerolde bladeren onder water, G. bloemstelen onder water, H. bladstelen onder water, I. onderwaterbladeren, J. rhizomen of stolonen en K. wortels.
Daarnaast kunnen een aantal compartimenten van de direkte omgeving van de vegetatie onderscheiden worden: L. het luchtruim boven de nymphaeiden en het wateroppervlak, M. het wateroppervlak, N. de waterruimte onder de drijfbladeren, O. de bodem.

Naar de wijze waarop de verschillende mogelijkheden binnen het nymphaeide systeem benut kunnen worden, zijn minstens 16 strukturele hoofdelementen te onderscheiden (tussen haakjes worden hier de compartimenten vermeld waar ze zich bevinden): 1. de nymphaeide plant zelf, 2. geassocieerde macrofyten (compartiment L—O), 3. fytoplankton (N), 4. epifyton (E—J), 5. endofyten (A), 6. microbiële organismen (A—O), 7. mineerders (A), 8. sessiele aquatische epifauna (E—K), 9. vagiele aquatische epifauna (E—K), 10. terrestrische fauna (C, D, B), 11. neuston (M), 12. de

boven de nymphaeiden en het wateroppervlak vliegende fauna (L), 13. zoöplankton (N), 14. nekton (N), 15. benthische infauna (O), 16. vagiele bodemfauna (O).

Gezien de komplexiteit van het nymphaeide systeem en de grote variatie in ruimte en tijd konden gedurende het onderzoek niet alle compartimenten en strukturele elementen bestudeerd worden; tijdens het onderzoek hebben de drijfblad- en bloemcompartimenten de meeste aandacht gekregen temeer daar deze strukturen voor nymphaeiden het meest karakteristiek zijn. De algemene lijn van het onderzoek wordt behandeld in het eerste hoofdstuk waarbij tevens desiderata voor verder onderzoek vermeld worden. De daaropvolgende hoofdstukken zijn deelstudies, waarbij *Nymphoides peltata* als voorbeeld gekozen is. In het tweede hoofdstuk wordt de algemene oecologie, de verspreiding, struktuur en biomassa van *Nymphoides peltata* behandeld. In dit hoofdstuk wordt de mogelijkheid behandeld om de biomassa en de veranderingen in biomassa per m^2 in een zuivere vegetatie van *N. peltata* te meten, terwijl tevens correlaties zijn berekend tussen biometrische gegevens en biomassa. Correlaties zijn berekend tussen parameters zoals bladoppervlak en lengte van de verschillende plantenonderdelen met hun asvrij drooggewicht. Voor de bloemen werd een gemiddeld asvrij drooggewicht bepaald voor elk ontwikkelingsstadium tezamen met de bloemstelen.

Biomassamonsters werden gedurende een geheel jaar genomen in het midden van een *Nymphoides* vegetatie, zodat de seizoensveranderingen in biomassa per vierkante meter konden worden gevolgd. In tegenstelling tot andere plantenonderdelen vertoonden de wortels een zeer hoog aspercentage in juni terwijl de wortelbiomassa dan het laagst was; in de winter vertegenwoordigden de wortels absoluut en relatief de hoogste biomassa. De verhouding biomassa bovengrondse plantendelen / biomassa ondergrondse plantendelen was het hoogst eind juni (3.20) en het laagst in januari (0.27).

De correlatie tussen het bladoppervlak per m^2 ('Leaf area index') en de totale biomassa per m^2 kan worden beschreven als een regressievergelijking van de tweede graad.

Met behulp van de correlaties tussen biometrische gegevens en biomassa kan een schatting worden gemaakt van de plantenmassa in het veld en het verlies door decompositie worden bepaald door eenvoudige metingen in het veld zonder de vegetatie te beschadigen.

Het derde hoofdstuk handelt over de diverse processen van initiële decompositie in het bijzonder van de drijfbladeren van *N. peltata.* De verschillende beschadigingspatronen worden beschreven en afgebeeld zodat ze in het veld herkend kunnen worden. De verschillende wijzen van initiële decompositie kunnen naar hun oorzaken als volgt ingedeeld worden: 1. door de planten zelf gereguleerde decompositie (a. veroudering van bladeren, b. massa decompositie na de vruchtzetting), 2. biotische afbraak (a. consumptie door dieren, b. beschadiging door dieren, c. infektie door schimmels en bacteriën), 3. abiotische faktoren (wind- en golfslag, vorst, uitdroging).

Gedurende het gehele groeiseizoen van *N. peltata* vindt afbraak plaats. Met betrekking tot de biotische afbraak is de schimmel *Septoria villarsiae* Desm. zeer belangrijk. De schimmel treedt met name massaal op vanaf begin augustus. Een andere schimmel, *Puccinia scirpi* DC, waarvan de aecidia op de drijfbladeren voorkomen, werd gevonden in juni maar speelt bij het decompositieproces geen belangrijke rol. Het rotte plantenmateriaal, afkomstig van de fysiologische afbraak door de plant zelf en van schimmelinfekties, speelt een belangrijke rol voor detritivore organismen. Materiaal dat op de bodem terechtkomt wordt door detritivore bodemdieren, waarbij met name de zoetwaterpissebed (*Asellus aquaticus* L.) genoemd moet worden, verwerkt tot fijne faecesdeeltjes terwijl een deel van het materiaal verteerd wordt. Hierdoor wordt een enorme oppervlaktevergroting bereikt zodat schimmels en bacteriën de verdere afbraak kunnen verzorgen.

Onafhankelijk van deze processen vindt ook decompositie plaats door dieren die van het levende plantenmateriaal eten. Deze afbraak wordt veroorzaakt door longslakken, zoals de poelslak (*Lymnaea stagnalis* (L.), de rups van *Nymphula nymphaeata* (L.), de muggelarve *Cricotopus trifasciatus* (Mg.), de meerkoet (*Fulica atra* L.) en de muskusrat (*Ondatra zibethicus* (L.)). Kiemplanten op tijdelijk droge modderbodems werden gegeten door landslakken zoals *Deroceras laeve* (Müller), gedurende vochtige weersomstandigheden. De verschillende schadebeelden beschreven in dit hoofdstuk geven de mogelijkheid om de schade in permanente kwadraten te volgen en per schadetype te kwantificeren.

In het vierde hoofdstuk wordt de bloembiologie en de zaadproduktie van *N. peltata* behandeld. De struktuur van de bloeistengel en het bloeipatroon zijn bij deze soort zodanig dat een groot veld van bloemen gedurende een lange periode gedurende het groeiseizoen gehandhaafd blijft. In de ontwikkeling van bloemknop tot gerijpte vrucht kunnen acht stadia worden onderscheiden.

De bloemen van *N. peltata* vallen in de caterogie B van de indeling van H. Müller, die de entomofiele bloemen verdeelde in zeven categorieën, aangezien de bloemen van *N. peltata* niet sterk voor het bloembezoek van een bepaalde insektengroep zijn gespecialiseerd, terwijl de nektar totaal verborgen is. Als een gespecialiseerde eigenschap van de bloemen binnen het geslacht *Nymphoides* kan het ultraviolet patroon beschouwd worden, welke hetzelfde i als bij *N. geminata* (R. Br.) O. Kuntze (ook een geelbloeiende soort), als een primitieve eigenschap de heterostylie gekombineerd met een zwak incompatibiliteitssysteem. De bloemen van *N. peltata* bloeien overdag en verwelken binnen een dag. Eigenschappen die bloembezoekende insekten aantrekken zijn: een hoge bloemfrekwentie en een lange bloeitijd gedurende het groeiseizoen, de geelgekleurde bloemkroon met een karakteristiek ultraviolet patroon en een gemiddelde doorsnede van 4.60 cm, die zich gemiddeld 3.27 cm boven het wateroppervlak bevindt, en een zwakke geur. Hogere temperaturen dan de omgeving spelen waarschijnlijk geen rol als eigenschap om insekten aan te trekken aangezien het verschil erg klein is. De bloemen bieden de insekten voedsel in de vorm van nektar, die echter afgeschermd wordt door staminodiën van 0.5—0.6 cm lengte, stuifmeelkorrels en misschien wat stempelvloeistof. Verder worden predatoren aangetrokken door de insekten die in de bloemen aanwezig zijn. De lijst van dieren die op of in de bloemen zijn aangetroffen bevat 44 soorten waarvan 43 insekten en 1 spinnensoort. De mogelijke redenen voor het bloembezoek van de insekten en hun mogelijke rol bij de bestuiving van de plant worden behandeld. Met betrekking tot de bestuiving schijnen bijen, zweefvliegen en vliegen van de familie Ephydridae het meest belangrijk. De bijen en sommige soorten zweefvliegen bezitten lange tongen (langer dan 5—6 mm) waarmee ze de nektar in de bloemen kunnen bereiken. De meeste soorten zweefvliegen en andere vliegen zoals de Ephydridae gebruiken stuifmeelkorrels en vloeistoffen, maar hun tongen zijn te kort om de nektar, die de suikers fructose en glucose in gelijke hoeveelheden bevat, te bereiken. Bijen en zweefvliegen vliegen van bloem tot bloem terwijl de Ephydridae de bloemen op onregelmatige wijze bezoeken; de Ephydridae zijn enorm talrijk op de drijfbladeren. Van de 44 soorten dieren die in en op bloemen zijn aangetroffen werden 30 soorten alleen op de bloemen gezien terwijl 14 soorten algemeen op de drijfbladeren voorkomen. De eerste categorie wordt geheel door de karakteristieke eigenschappen van de bloemen aangetrokken, terwijl de tweede categorie karakteristiek is voor het nymphaeide systeem. Elke bloembezoeker kan bestuiving veroorzaken. In kortstijlige bloemen gaat dit wat betreft zelfbestuiving zeer gemakkelijk aangezien hier de meeldraden boven de stempel gesitueerd zijn in tegenstelling tot de langstijlige bloemen, waarbij dus minder gauw zelfbestuiving zal optreden. Bij zelfbestuiving ontstaan kleine vruchten met weinig zaden, meestal minder dan 10—15, bij kruisbestuiving grote vruchten met gemiddeld 32 zaden. Het vrijkomen van de zaden gebeurt 32—60 dagen na de bloei.

In het veld en betonnen bakken waarin beide bloemvormen aanwezig waren werd de produktie van vruchten en zaad onderzocht. Het aantal vruchten en het aantal zaden per vierkante meter was veel hoger in de betonnen bakken dan in het veld hetgeen te danken was aan de ontwikkeling van veel meer bloemen dan in het veld gevonden werd, maar het gemiddelde aantal zaden per vrucht was hier veel lager evenals het percentage vruchten met minder dan 15 zaden, hetgeen betekent dat de bloemen in de kleine geïsoleerde betonnen bakken niet zo efficiënt bestoven werden als in het veld, waarschijnlijk mede dank zij het feit dat sommige in het veld belangrijke bestuivers zoals de Ephydride vlieg *Notiphila brunnipes* R.-D. niet aanwezig waren in de betonnen bakken.

De geproduceerde zaden van *N. peltata*, in het veld meer dan 3000 per m^2, drijven eerst op het wateroppervlak en worden vervolgens door de wind en door watervogels verspreid. Wanneer de vorstperiode inzet zijn bijna alle zaden naar de bodem gezonken.

De vlieg *Notiphila brunnipes*, die in nymphaeide systemen zeer talrijk en karakteristiek is brengt een groot deel van zijn levenscyclus op nymphaeiden door en speelt behalve voor de bestuiving van *N. peltata* ook een belangrijke rol voor de bestuiving van andere nymphaeiden. Dit was de aanleiding tot een autoecologische studie van deze vliegensoort, die hoofdstuk vijf van dit proefschrift vormt. Er zijn direkte relaties tussen *Notiphila brunnipes* en de nymphaeide soorten *Nuphar lutea, Nymphaea alba, Nymphaea candida* en *Nymphoides peltata.*

De volwassen vliegen bezoeken de bloemen van *Nymphaea* en *Nuphar* om de volgende redenen:

a) voedsel in de vorm van stempelvloeistof, nektar en stuifmeelkorrels
b) het afzetten van eieren; de ontwikkeling van de eieren wordt begunstigd door de temperaturen en de luchtvochtigheid of afwisselend droge en natte omgeving in de bloemen
c) bescherming tegen bepaalde predatoren zoals libellen en als schuilplaats voor slechte weersomstandigheden
d) copulatieplaats; vooral eerstedagsbloemen trekken vele exemplaren aan en copulatie vindt hier dikwijls plaats
e) rustplaats, waarschijnlijk ook om de vliegspieren op te warmen; vanwege de hogere temperaturen in de bloemen gaat hun spijsvertering hier waarschijnlijk sneller.

De bloemen van *Nymphoides peltata* vervullen deze funkties maar ten dele. Deze bloemen zijn niet geschikt voor de eiafzetting.

De volwassen vliegen komen om de volgende redenen op de drijfbladeren van *Nymphaea, Nuphar* en *Nymphoides* voor:

a) voedsel, n.l. direkt voor de consumptie van vloeibare substanties van rottende bladdelen en indirekt om de lichaamssappen van dode insekten te consumeren
b) copulatieplaats
c) rustplaats, ook om te zonnen
d) schuilplaats of bescherming onder luchtbladeren of bladranden die opgekruld zijn en opgedroogd
e) sporadische eiafzetting op schuilplaatsen, zoals bovengenoemde bladranden.

Door hun gedrag kunnen de vliegen fungeren als vectoren van sporen afkomstig van schimmels die op de drijfbladeren aanwezig zijn.

De larven en poppen schijnen beperkt te zijn tot de wortels van Lisdodde (*Typha angustifolia* L., waarschijnlijk ook *T. latifolia* L.), Kalmoes (*Acorus calamus* L.) en de Watergentiaan (*Nymphoides peltata*), en betrekken hier via gepunte stigmata zuurstof van de intercellulaire holten. De larven leven van detritus en rot plantenmateriaal.

Het feit dat *Notiphila brunnipes* gedurende zijn levenscyclus gebonden is aan tenminste twee verschillende plantensoorten kan de geografische verspreiding van deze soort, die boven de zgn. limes norrlandicus niet voorkomt, verklaren.

CURRICULUM VITAE G. VAN DER VELDE

Gerard van der Velde werd op 7 september 1946 te Groningen geboren. Reeds vroeg had hij belangstelling voor de natuur en op 12-jarige leeftijd werd hij lid van de Nederlandse Jeugdbond voor Natuurstudie (N.J.N.), waarvan hij tot zijn 23e jaar lid was.

In 1966 behaalde hij het einddiploma H.B.S.-B aan het Gemeentelijk Lyceum te Delft. Zijn militaire dienstplicht vervulde hij van 21 september 1966 tot 21 september 1967. Vervolgens liet hij zich met ingang van het studiejaar 1967/68 inschrijven aan de Rijksuniversiteit te Leiden als student in de biologie. Het kandidaatsexamen behaalde hij aan dezelfde universiteit op 29 februari 1972 in de studierichting B 5 (hoofdvakken biologie en geologie).

Van het academiejaar 1970/71 tot en met het jaar 1973/74 vervulde hij een student-assistentschap op de afdeling Systematische Dierkunde en Evolutiebiologie te Leiden. In het jaar 1971/72 vervulde hij bovendien een student-assistentschap bij het Rijksherbarium te Leiden.

Voor zijn doctoraalexamen bewerkte hij onderwerpen in de Systematische dierkunde, de Bijzondere plantkunde en de Evolutiebiologie, namelijk:

1. Systematiek, verspreiding en oecologie van platwormen (Turbellaria) in Nederland bij Prof.Dr. J.T. Wiebes (afd. Systematische Dierkunde en Evolutiebiologie) onder de direkte leiding van Dr. J. van der Land (Rijksmuseum van Natuurlijke Historie, Leiden).
2. Biologische waardering van de Vijfheerenlanden onder supervisie van Prof.Dr. C. Kalkman (Rijksherbarium, Leiden) en onder direkte leiding van Drs. J. Mennema en Prof.Dr. C. den Hartog.
3. Sex-attractantia bij vlinders (Lepidoptera) in Meijendel onder supervisie van Prof.Dr. J.T. Wiebes (afd. Systematische Dierkunde en Evolutiebiologie, Leiden) en onder de direkte leiding van Dr. W.M. Herrebout.

Het doctoraalexamen werd afgelegd op 18 juni 1974 aan de Rijksuniversiteit te Leiden. Op 1 juli 1974 werd hij benoemd tot Wetenschappelijk Medewerker bij het Laboratorium voor Aquatische Oecologie van de Katholieke Universiteit te Nijmegen.

Onder leiding van Prof.Dr. C. den Hartog werd een promotie-onderzoek verricht naar de oecologie van door nymphaeiden gedomineerde gemeenschappen, waarvan een deel van de resultaten in dit proefschrift is verwerkt.

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Stellingen bij het proefschrift van G. van der Velde.

I

Binnen nymphaeide systemen in de terrestrische fauna meer karakteristiek dan de aquatische fauna.

Dit proefschrift

II

Vrijwel alle zoetwateroecosystemen zijn in hoge mate open systemen. Het is zeer de vraag of zoetwateroecosystemen zich onafhankelijk van hun omgeving kunnen handhaven.

R. Lingeman, 1980. Analysis and interpretation of the diel and annual oxygen regimes in two ecosystems. A macroscopic approach to ecosystem research. Thesis Amsterdam. 132 pp.

III

De studie van semipermanente zoete wateren en moerassen verdient meer aandacht van aquatische oecologen.

IV

Drassige boezemlanden en kleine rietmoerassen dienen ook als hun floristische waarde gering is, vanwege hun karakteristieke aquatische fauna in het landschap gespaard te blijven.

H P.J.J. Cuppen, H. de Priester en G. van der Velde.
The habitat choice of adult aquatic and semi-aquatic Heteroptera and aquatic Coleoptera in a Dutch polder area-“De Vijfheerenlanden”.
manuscript. 34 pp.

V

In vele studies betreffende de decompositie van aquatische macrofyten houdt men te weinig rekening met de wijze waarop decompositie in het veld verloopt.

C. Howard-Williams en W. Howard-Williams, 1978.
Nutrient leaching from the swamp vegetation of lake Chilwa, a shallow African lake. Aquat Bot., 4. 257-267.
G.L. Godschalk en R.G. Wetzel, 1978. Decomposition of aquatic angiosperms. III. *Zostera marina* L. and a conceptual model of decomposition Aquat. Bot., 5 329-354.

VI

Waterkevers zijn door hun grote mobiliteit en diversiteit betere milieu-indicatoren dan slakken.

H.P J.J. Cuppen en G. van der Velde, ongepubliceerd.

VII

Voor het oplossen van problemen in de oecologie is een grondige kennis van de systematiek en van de Nederlandse flora en fauna noodzakelijk. In de prekandidaatsstudie dient men hieraan meer aandacht te besteden.

VIII

In de besliskunde beslist men beslist beter dan de beslisser in zijn beslissingssituatie beslist.

IX

De New Orleans jazz bereikte zijn muzikale hoogtepunt in de jaren 1925-1930 (opnamen van o.a. King Oliver, Louis Armstrong, Johnny Dodds, Clarence Williams, Jelly Roll Morton, Luis Russell en Fletcher Henderson); de muzikaliteit en technische vaardigheid van de bands in deze periode worden door de huidige revivalbands niet geevenaard.

X

Een nietmachine en een loterij hebben vele nieten gemeen.