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 bio-

mass 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 *Nymphoides* is described by Ornduff (1970). *N. peltata* is hexaploid ($x = 9$) having $2n = 54$, 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.
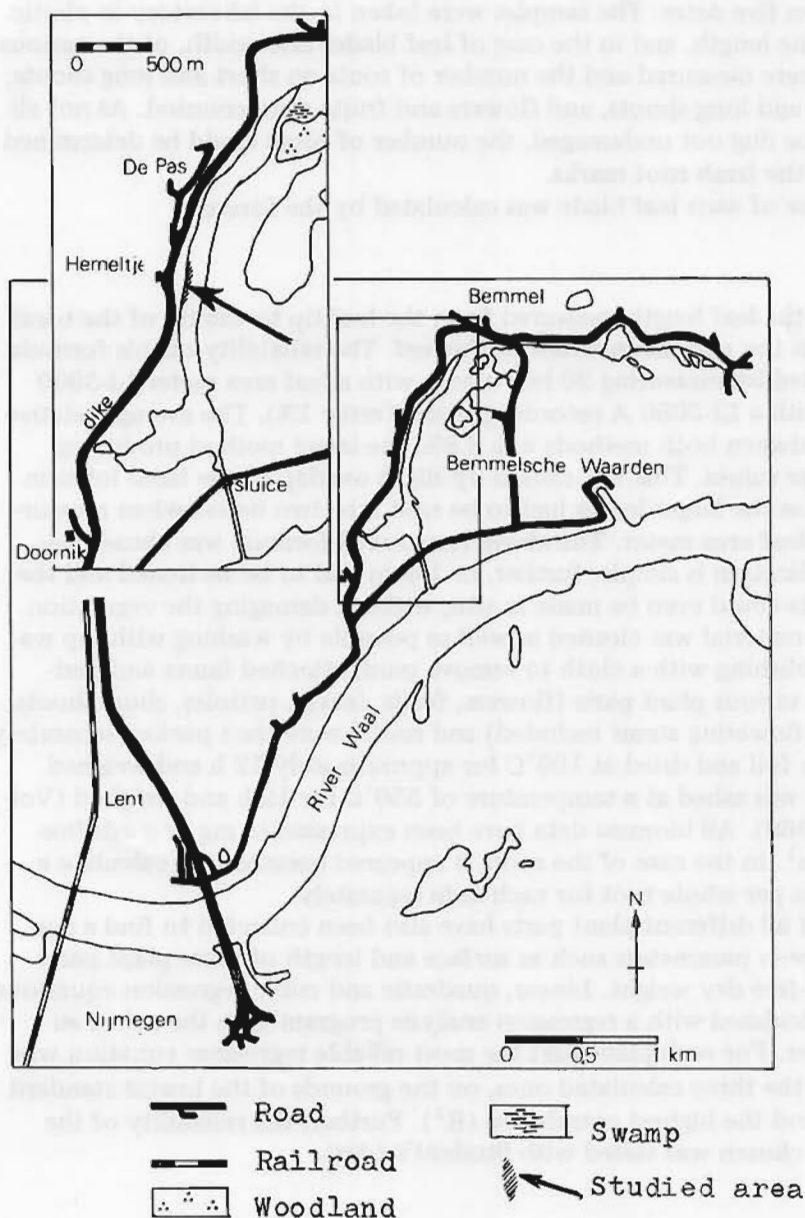

Fig. 1. Map of the study area. The sampling site is marked by an arrow.

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 m² 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/m². 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
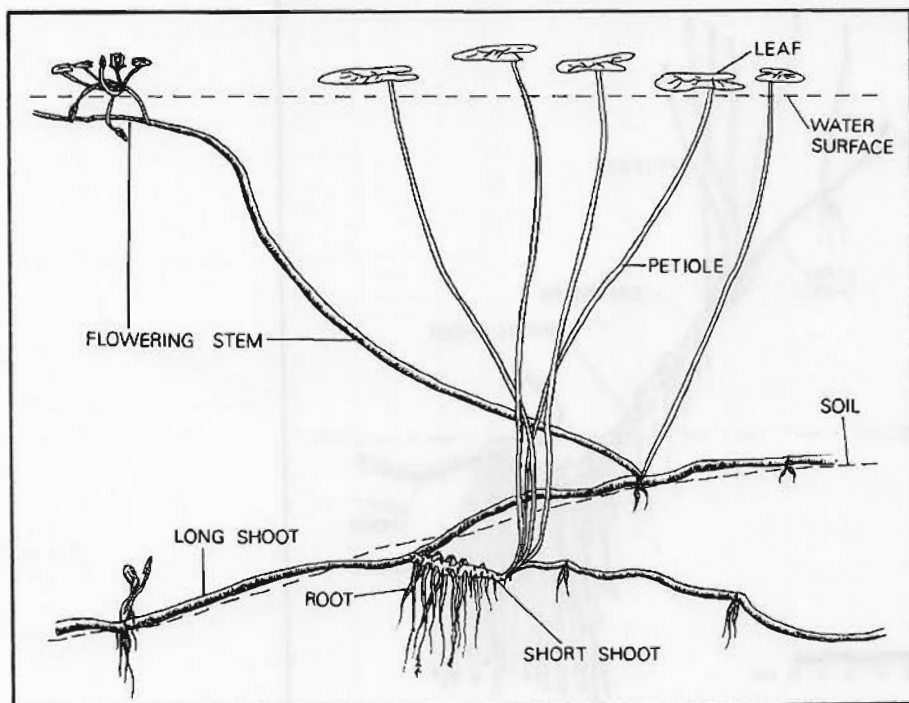

Fig. 2. General structure of *Nymphoides peltata*.

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,
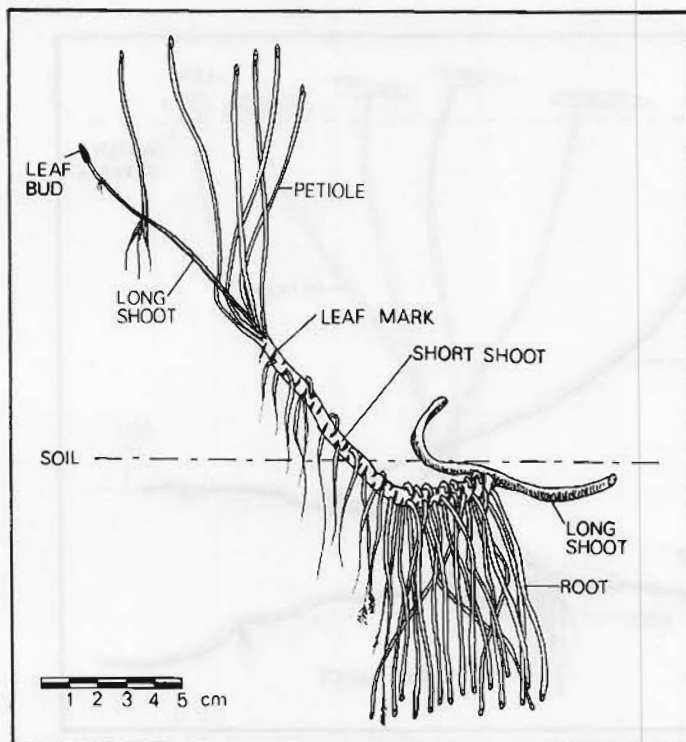

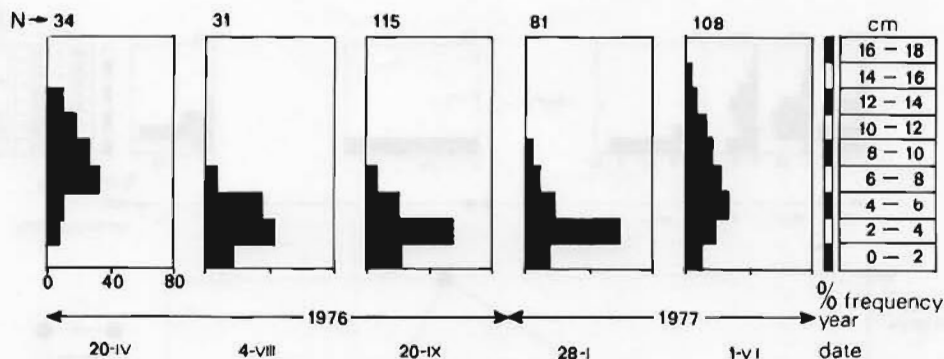Fig. 3. Structure of a hibernating short shoot of *N. peltata*.

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 cm², 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 m² 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.
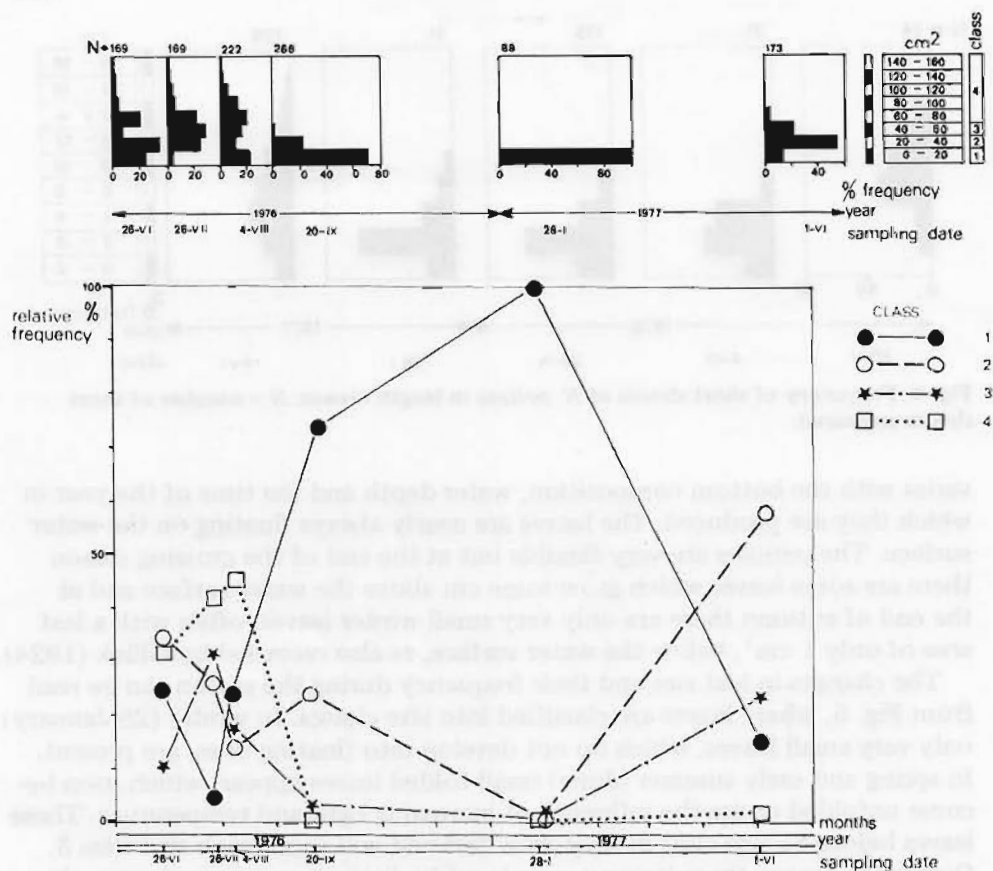
Fig. 5. Frequency of leaves of *N. peltata* in size classes (surface in cm²) during the season.
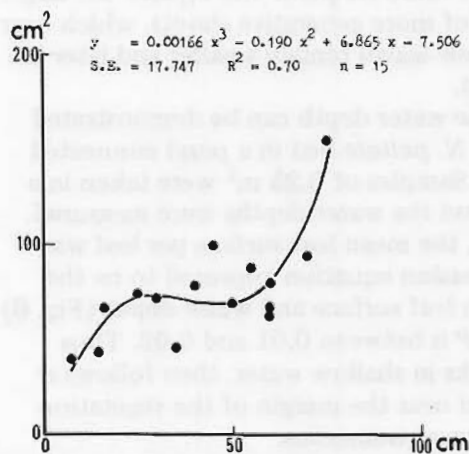*N* = number of leaves measured.

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
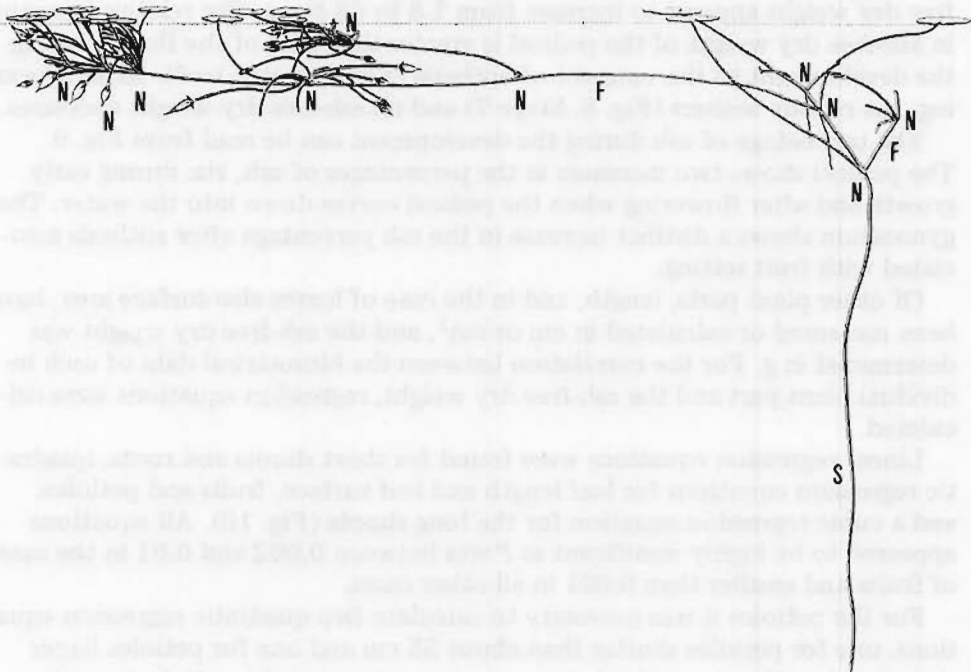

Fig. 7. Structure of a flowering stem of *N. peltata*. N = node, F = flowering stem, S = long shoot.

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,

but when the pedicle further grows and its turgor decreases probably due to cell enlargement, this process is effective for leaves respiration (Else K and Bishma, 1977). Leaves of reed enlarge... the pedicles are usually reach a great length and... high water... (... 1964) but set young plants of N. peltata and... and flies if the young leaves (the old ones less easily do not reach any water... are done about 1 inch during 1 or 2 days (25 mg/day), but a much spread growth of different group could also be recorded. As

TABLE I

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

Developmental stage	Pedicel Length (mm)	Pedicel S.D. (mm)	Bud Length (mm)	Bud S.D. (mm)	Bud Diam. (mm)	Bud S.D. (mm)	Style + ovary Length (mm)	Style + ovary S.D. (mm)	Ovary Length (mm)	Ovary S.D. (mm)	Ovary Max. width (mm)	Ovary 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
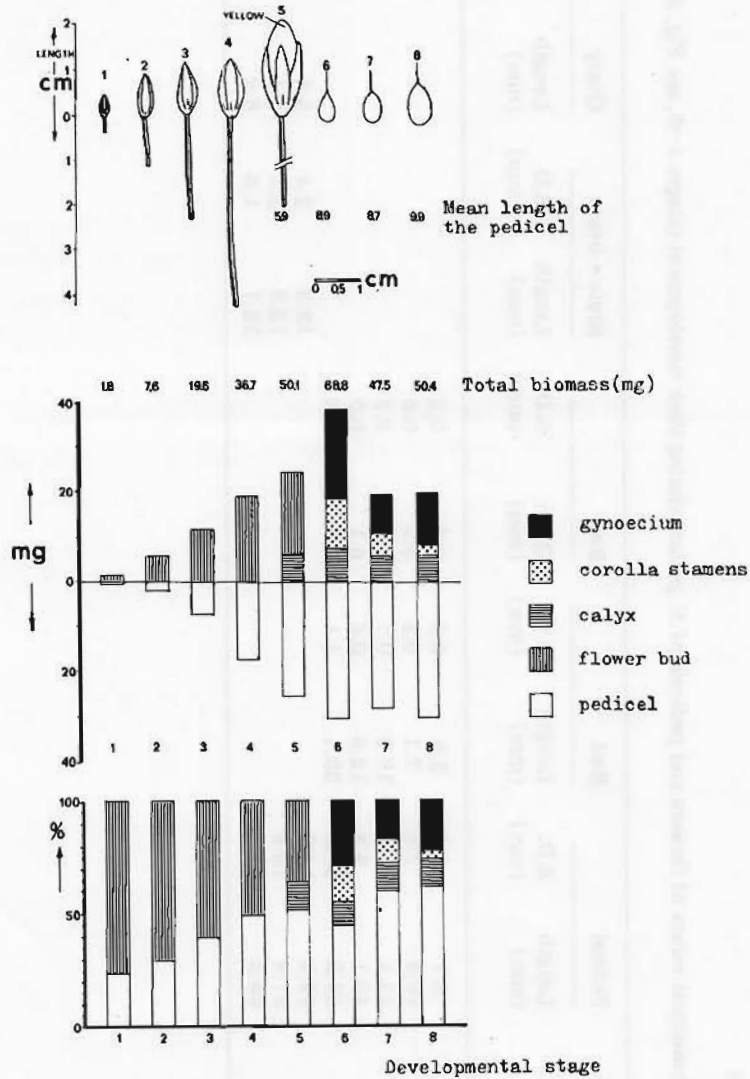

Fig. 8. Developmental stages of the flower of *N. peltata*, the pedicel included (above) (fruit body in stages 6—8 schematically drawn), the ash-free dry weight (middle) and the relative share of different flower parts in the ash-free dry weight (below).
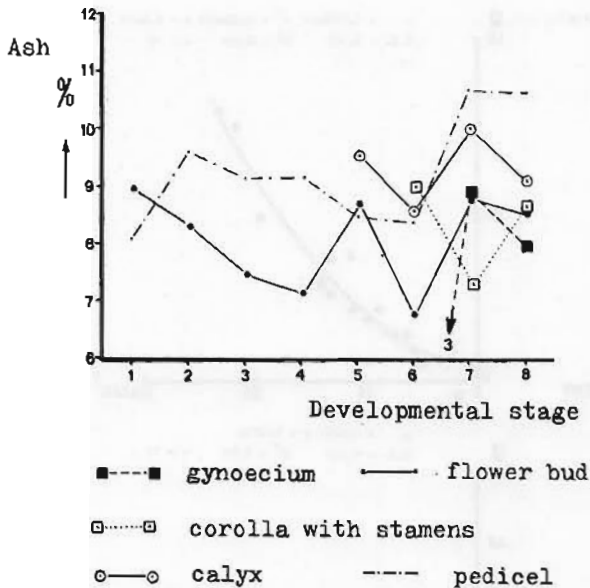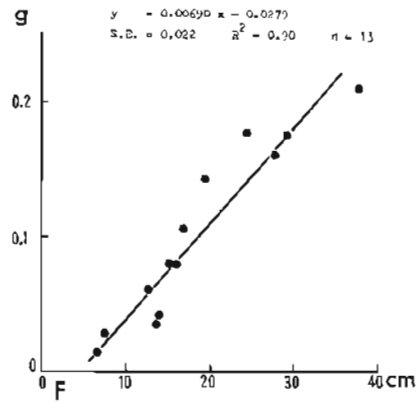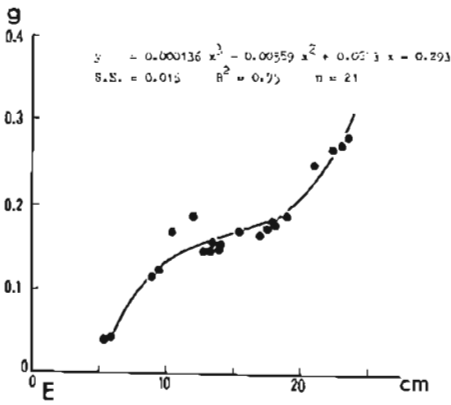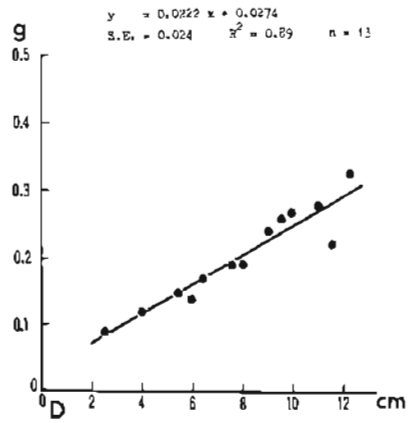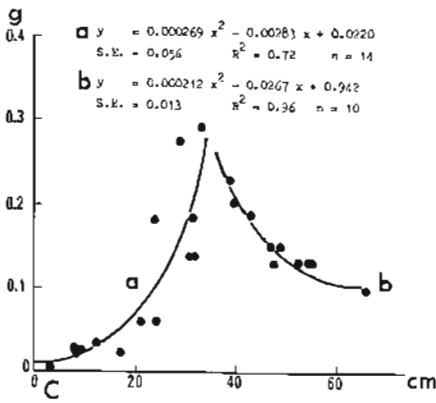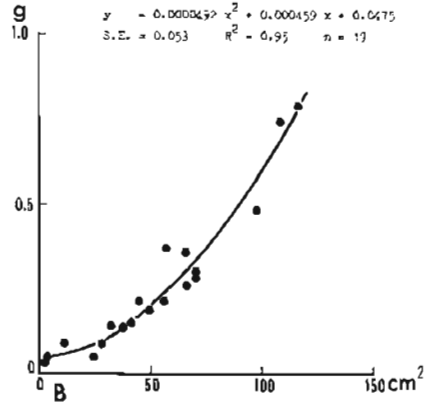
Fig. 9. The percentage of ash of the various flower parts and the pedicel of *N. peltata* related to dry weight during the development of the flower (stages 1—8 corresponding with those in Fig. 8). Flower bud means all flower parts together.

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).

A

g

$y = 0.00869 \ x^2 - 0.0565 \ x + 0.155$

$S.E. = 0.066 \qquad R^2 = 0.92 \qquad n = 19$

B

g

$y = 0.0000492 \ x^2 + 0.000459 \ x + 0.0475$

$S.E. = 0.053 \qquad R^2 = 0.95 \qquad n = 19$

C

g

a $y = 0.000269 \ x^2 - 0.00283 \ x + 0.0220$

$S.E. = 0.056 \qquad R^2 = 0.72 \qquad n = 14$

b $y = 0.000212 \ x^2 - 0.0267 \ x + 0.942$

$S.E. = 0.013 \qquad R^2 = 0.96 \qquad n = 10$

D

g

$y = 0.0222 \ x + 0.0274$

$S.E. = 0.024 \qquad R^2 = 0.89 \qquad n = 13$

E

g

$y = 0.000136 \ x^3 - 0.00559 \ x^2 + 0.0813 \ x - 0.293$

$S.E. = 0.015 \qquad R^2 = 0.95 \qquad n = 21$

F

g

$y = 0.00690 \ x - 0.0279$

$S.E. = 0.022 \qquad R^2 = 0.90 \qquad n = 13$
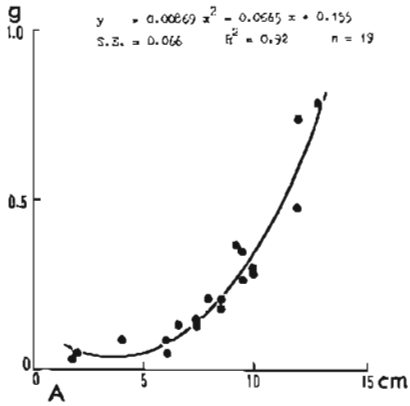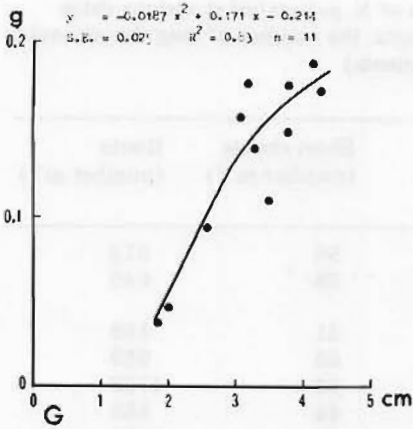
Fig. 10. A, Correlation between the length of a leaf of *N. peltata* and its ash-free dry weight, 20 April 1976. B, Correlation between the surface area of a leaf and its ash-free dry weight, 20 April 1976. C, Correlation between the length of the petiole and its ash-free dry weight, 4 Aug. 1976. D, 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.
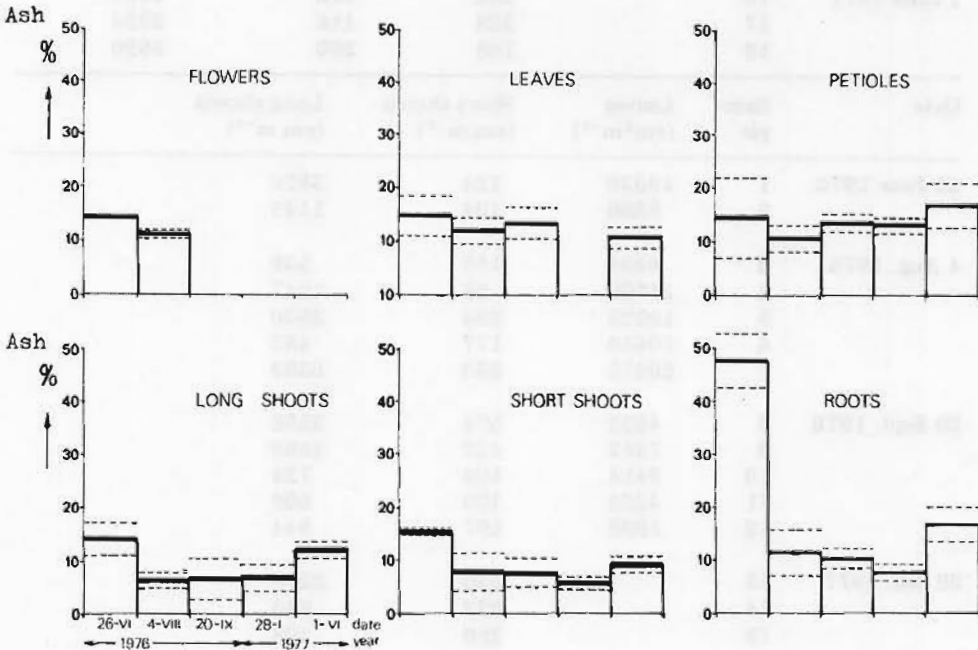

Fig. 11. The percentage of ash of various plant parts of *N. peltata* related to dry weight during the season. Broken lines mean standard deviations.

TABLE II

Numbers and biometrical data of various plant parts of *N. peltata*/m² 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 (cm² 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.

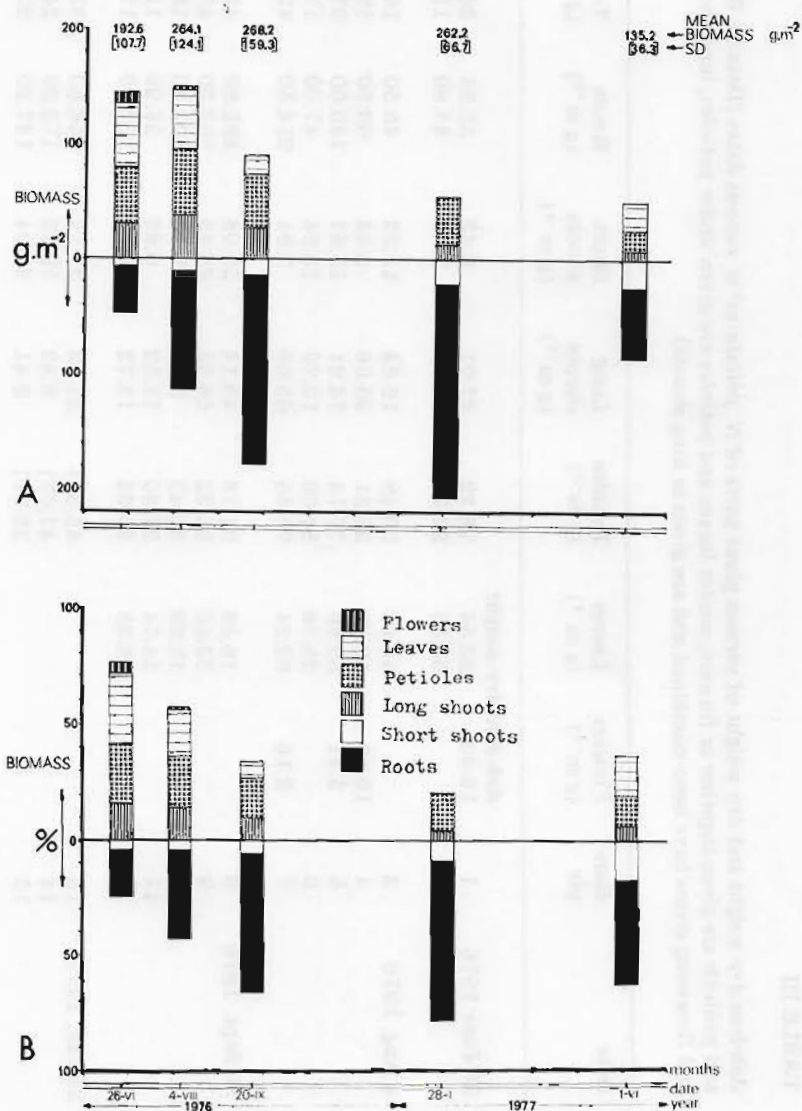Fig. 12. The share (ash-free dry weight) of the different plant parts in total biomass of *N. peltata* at each sampling date and its occurrence above and under the sediment. A = absolute mean values; B = relative mean shares of each plant part to the whole plant biomass/m^2 at each date. Long shoots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

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TABLE III

Ash-free dry weight and dry weight of various plant parts of *N. peltata*/m² 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)
26 June 1976		*Ash-free dry weight*						
	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	28.08	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

Date	Sample							Dry weight
1 June 1977	16	104.88	39.72	12.88	3.72	19.24	29.32	
	17	125.34	54.88	21.68	11.52	15.36	21.90	
	18	175.36	90.88	35.12	12.64	18.36	18.36	
26 June 1976	1	336.32	72.70	9.98	58.51	86.68	94.22	19.23
	2	167.19	80.29	6.47	16.69	25.32	38.42	
4 Aug. 1976	3	183.12	48.20	11.89	11.25	54.81	56.97	12.26
	4	206.37	79.79	3.66	31.36	32.53	46.77	3.85
	5	414.12	158.49	16.49	77.93	88.44	68.92	
	6	136.76	51.76	14.90	14.53	63.68	43.65	
	7	495.38	254.45	9.13	70.96	84.57	73.85	2.42
20 Sept. 1976	8	477.07	327.52	24.51	45.87	59.34	19.83	
	9	501.26	273.43	27.05	64.30	97.70	38.78	
	10	189.30	116.63	6.52	10.12	38.41	17.62	
	11	129.37	61.40	7.20	12.05	32.02	16.70	
	12	198.27	125.33	12.18	12.20	40.64	7.92	
28 Jan. 1977	13	368.36	269.73	22.42	23.50	52.71*		
	14	272.04	188.47	21.33	7.37	54.87*		
	15	219.80	145.96	24.12	9.85	39.87*		
1 June 1977	16	120.69	46.45	14.08	4.24	22.48	33.44	
	17	150.02	68.60	24.16	13.24	19.48	24.54	
	18	200.87	106.75	38.32	14.16	21.44	20.20	

Dry weight

* 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		
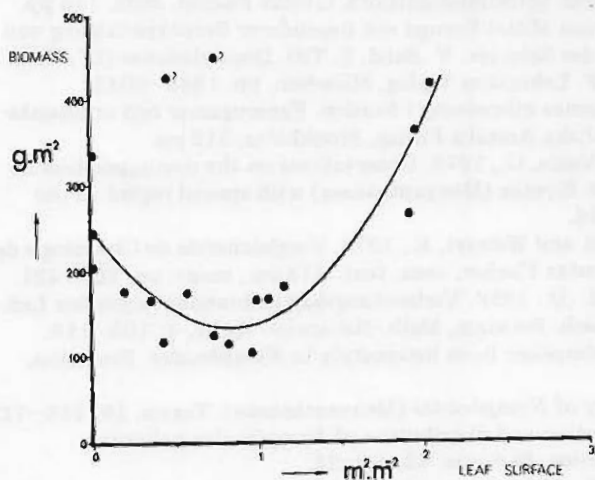
Fig. 13. Correlation between total leaf area/m² and the total biomass (ash-free dry weight)/m² of *N. peltata*. Two values have not been used for the calculation as they clearly fall outside the general picture.

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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REFERENCES

Aston, H.I., 1973. Aquatic Plants of Australia. A Guide to the Identification of the Aquatic Ferns and Flowering Plants of Australia, Both Native and Naturalized. Melbourne University Press, 368 pp.

Black, M. and Edelman, J., 1970. Plant Growth. Heinemann Educational Books Ltd., London, 192 pp.

de Wit, H.C.D., 1966. Aquariumplanten. Hollandia, Baarn, 3rd edn., 359 pp.

Funke, G.L., 1951. Waterplanten. J. Noorduyn and Son, Gorinchem, 250 pp.

Funke, G.L. and Bartels, P.M., 1937. Observations on the growth of water plants. Biol. Jaarb. Dodonaea, 4: 316—344.

Glück, H., 1924. Biologische und morphologische Untersuchungen über Wasser- und Sumpfgewächse IV. Untergetauchte und Schwimmblattflora. Gustav Fischer, Jena, 746 pp.

Hegi, G., 1927. Illustrierte Flora von Mittel-Europa mit besonderer Berücksichtigung von Deutschland, Oesterreich und der Schweiz. V. Band, 3. Teil. Dicotyledones (IV. Teil). Sympetalae. Lief. 100/102, J.F. Lehmanns Verlag, München, pp. 1883—2042.

Hultén, E., 1950. Atlas över växternas utbredning i Norden. Fanerogamer och ormbunksväxter. Generalstabens Litografiska Anstalts Förlag, Stockholm, 512 pp.

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

Meusel, H., Jäger, E., Rauschert, S. and Weinert, E., 1978. Vergleichende de Chorologie der Zentral-europäischen Flora. Gustav Fischer, Jena, text: 418 pp., maps: pp. 259—421.

Müller-Stoll, W.R. and Krausch, H. -D., 1959. Verbreitungskarten brandenburgischer Leitpflanzen. Wiss. Z. Pädag. Hochsch. Potsdam, Math.-Naturwiss. Reihe, 4: 105—115.

Ornduff, R., 1966. The origin of dioecism from heterostyly in Nymphoides. Evolution, 20: 309—314.

Ornduff, R., 1970. Cytogeography of Nymphoides (Menyanthaceae). Taxon, 19: 715—719.

Stuckey, R.L., 1974. The introduction and distribution of Nymphoides peltatum (Menyanthaceae) in North America. Bartonia, 42: 14—23.

van der Voo, E.E. and Westhoff, V., 1961. Limnophytes and helophytes in the area of the large rivers. Wentia, 5: 163—258.

Vollenweider, R.A. (Ed.), 1969. A Manual on Methods for Measuring Primary Production in Aquatic Environments. IBP Handbook No. 12. Blackwell, London, 225 pp.

Wagner, R., 1895. Die Morphologie des Limnanthemum nymphaeoides (L.) LK. Bot. Zt., 53: 189—205, Taf. VIII.