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INITIAL DECOMPOSITION OF *NYMPHOIDES PELTATA* (GMEL.) O. KUNTZE (MENYANTHACEAE), AS STUDIED BY THE LEAF-MARKING METHOD

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INTRODUCTION

Communities dominated by nymphaeids have been studied by the Laboratory of Aquatic Ecology (Catholic University of Nijmegen) during several years. The aims and goals of this ecosystem study on nymphaeid-dominated communities are explained by VAN DER VELDE (1980, 1981).

The aspect presented here concerns the relation between production and decomposition of nymphaeids, and the role of the nymphaeids in the grazer and detritus food chain. Particularly with respect to the floating leaves, one of the most characteristic features of nymphaeids, many causes of initial decomposition can be recognized in the form of damage types and infection or decomposition patterns. They have been described extensively for *Nymphoides peltata* (Gmel.) O. Kuntze (Menyanthaceae) by LAMMENS and VAN DER VELDE (1978) and VAN DER VELDE (1979, 1981). The other organs of this nymphaeid are consumed or used for several purposes by some mammalian vertebrates such as muskrats (*Ondatra zibethicus* (L.)), but the effect of these animals is very local and difficult to quantify because their activity is mainly under water (LAMMENS and VAN DER VELDE, 1978; HEINE and VAN DER VELDE, 1978). Certainly most of the plant mass under water disintegrates under the influence of detritivorous animals and saprotrophic organisms and can be studied by the litter bag technique (BROCK *et al.*, 1982).

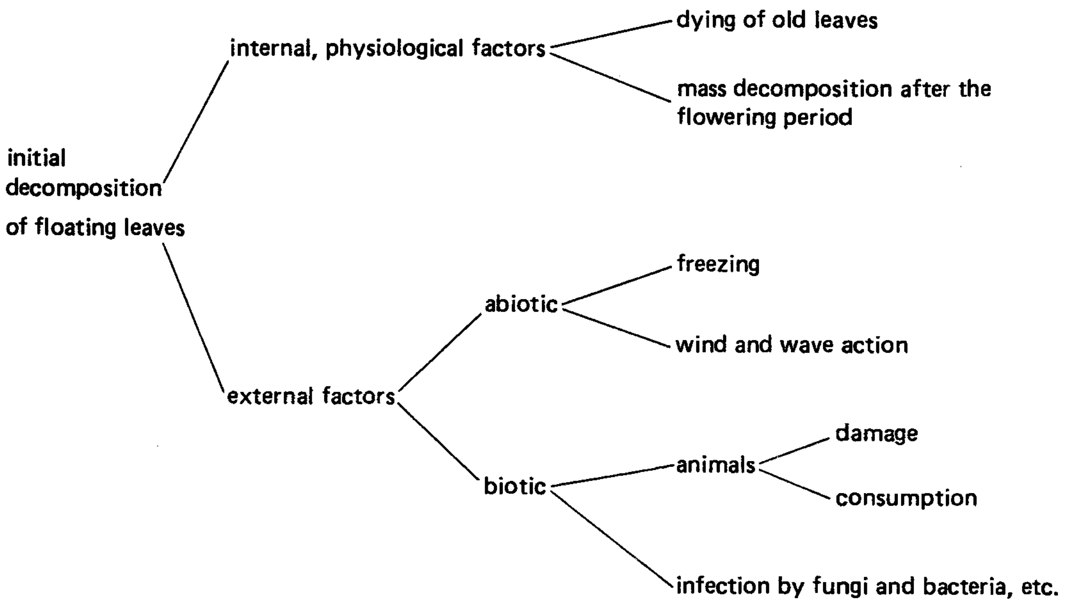

Table I. Classification of initial causes of decomposition of floating leaves.

The factors which cause initial decomposition of the floating leaves can be divided into biotic and abiotic factors; they often influence each other, but also can act totally independent. The biotic factors, in their turn, can be divided into (1) internal, physiological factors, regulated by the plant itself by means of hormones, such as ageing of old leaves, mass decomposition by exhaustion after the flowering period, and (2) external factors such as consumption and damage caused by animals, and infection by bacteria and fungi. (Table I). The main abiotic factors causing decomposition are wind- and wave action, desiccation and frost damage. There are temporal and spatial patterns of initial decomposition; examples will be presented here for *Nymphoides peltata*, based on data obtained by the leaf-marking method within plots. Advantages and disadvantages of the method will be discussed. Furthermore some general results are presented for *N.peltata*, based on data obtained from some concrete tanks where certain external factors causing initial decomposition could be excluded, and from a field situation (Table II), so that a relatively simple situation can be compared with a much more complex one.

SITE AND METHODS

The development and initial decomposition of floating leaves of *N.peltata* were followed in two concrete tanks of 80x150 cm and 60 cm deep situated outside on the area of the Catholic University of Nijmegen during 1978 -1979, and in two plots in the Bemmelse Strang (Fig. 1), an old branch of the river Waal situated in the northern river forelands between Lent and Bemmel, north of Nijmegen, during 1980.

In the concrete tanks a layer of heavy river clay and mud of about 10 cm is present; the water is alkaline and eutrophic. *N.peltata* has developed itself here for three years, so that the concrete tanks are filled with this plant species. In concrete tank 1 *Glyceria fluitans* (L.) R. Br. and *G.maxima* (Hartm.) Holmb. are also present; in tank 2 only *N.peltata* occurs. The water depth in both tanks was very stable and fluctuated only by evaporation and rain fall between 40 -50 cm.

The Bemmelse Strang has in summer a depth of up to 2-3 m. In this alkaline and eutrophic water body the water depth varied very much due to high or low water levels of the river. In plot 1 (BS 1), which was laid out in the centre of a *Nymphoides* bed, it fluctuated during the growing season from 30 -106 cm (average 67 cm, S.D. = 22 cm). In plot 2 (BS 2), which plot was laid out at the margin of the *Nymphoides* bed bordering the open water, it fluctuated from 56 -154 cm (average 117 cm, S.D. = 22 cm). Minimum depths of both plots were recorded on 1980 -10 -20, while the maximum depths occurred on 1980 -08 -07. Each plot with an area of 0.25 m2 was laid out by means of a square, perforated P.V.C.-tubing frame. The frames were anchored at each edge by stones and were held approximately 15 cm under the water surface by cork floaters so that the unrolling of floating leaves at the water surface was not hindered (see VAN DER VELDE, 1980).

Newly developed, unrolled leaves in the plot were marked by means of Rotex tape (12 mm) in the case of the tanks or with small aluminium strips, in which a number was scratched, in the case of the Bemmelse Strang. The latter method is cheaper. The strips can be suppressed very easily around the petiole near the base of the leaf blade, while the Rotex tape has to be fixed around the petiole by means of a staple. No printer is necessary for the leaf marking method with strips.

Observations were made twice a week. In this way the fate of each individual leaf could be followed. At each observation date length (l) and width (w) of each leaf were measured. The surface area of each leaf at each date was calculated by means of the formula

$$1.028\,\left(\frac{l + w}{4}\right)^2$$

in which 1.028 is a correction factor as the leaves are not totally circular in shape. In this way the growth of each leaf at the water surface could also be followed. The surface area of each leaf was correlated with its biomass according to the regression equation $y = 3.018\,x + 6.500$ (S.E. = 13.81; $r^2 = 0.91$; $n = 100$; Student t-test $p < 0.001$) for leaves in the tanks and $y = 3.925x - 26.572$ (S.E. = 26.06; $r^2 = 0.91$; $n = 106$; $p < 0.001$) for leaves in the Bemmelse Strang (y is biomass in mg

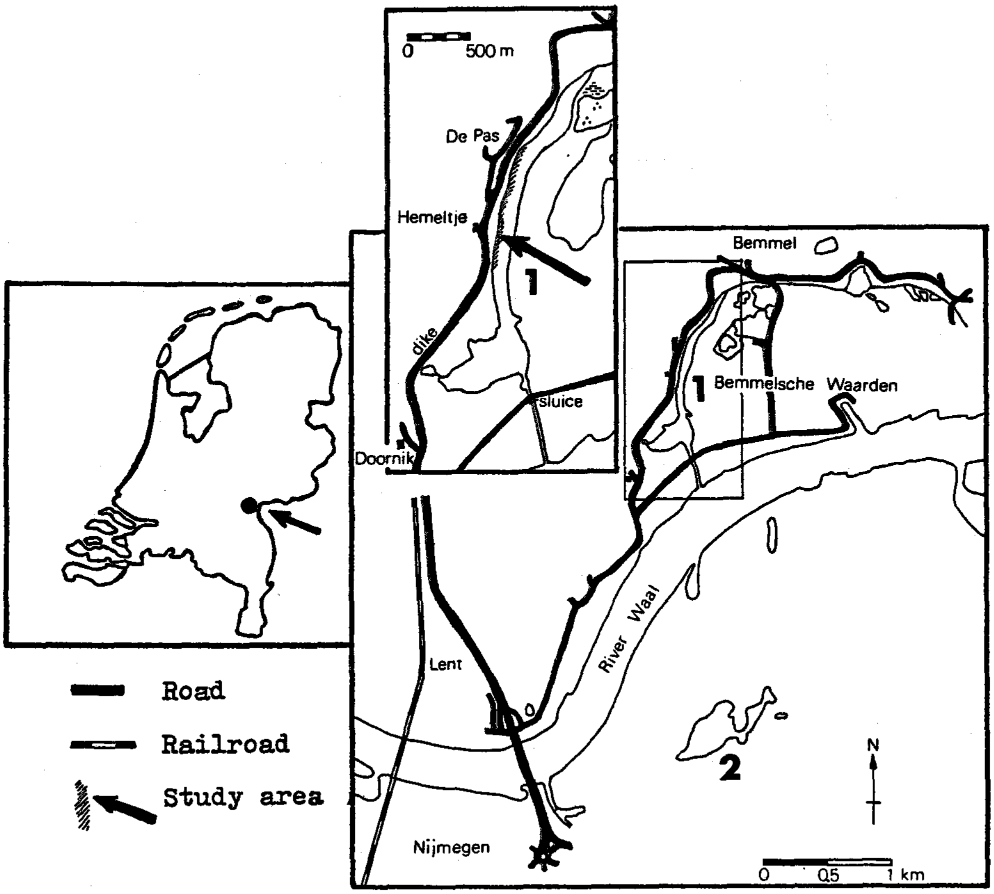

Fig. 1. Map of the study areas. 1. the Bemmelse Strang, 2. the Oude Waal.

animals:		Bemmelse Strang	concrete tanks
Chironomidae	*Cricotopus trifasciatus* (Mg.)	+	–
Lepidoptera	*Nymphula nymphaeata* (L.)	+	–
	Cataclysta lemnata (L.)	–	+
Gastropoda	*Lymnaea stagnalis* (L.)	+	–
	Radix peregra (Drap.)	(+)	(+)
	Radix auricularia (L.)	(+)	–
	Galba turricula (Held)	(+)	(+)
Aves	*Fulica atra* L.	+	–
Mammalia	*Ondatra zibethicus* (L.)	+	–
Fungi	*Septoria villarsiae* Desm. .	+	+
wind and wave action		+	–

Table II. External factors causing decomposition of floating leaves of *Nymphoides peltata* (Gmel.) O. Kuntze present in the Bemmelse Strang and in the concrete tanks (+ = present, (+) = present but not very important, – = absent).

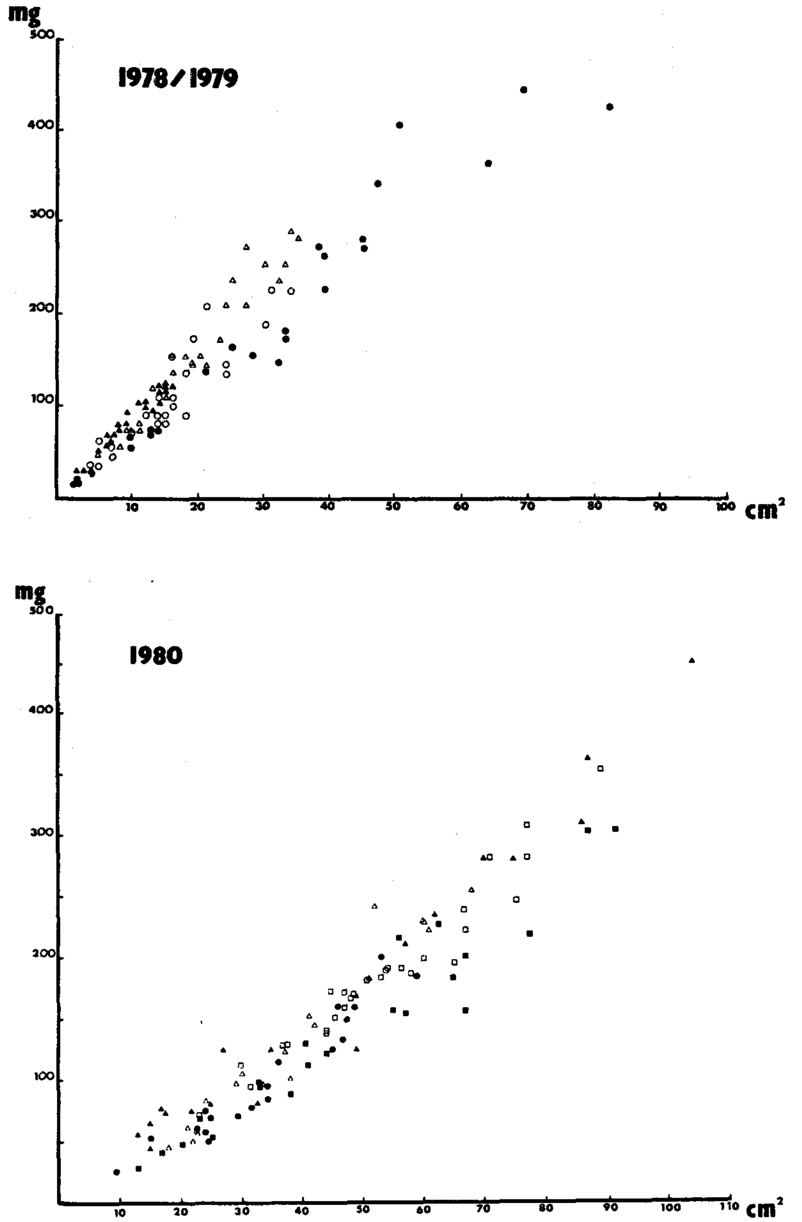

Fig. 2. The relation between the area of a leaf of *Nymphoides peltata* (Gmel.) O. Kuntze and its ash-free dry weight.
Above: for the concrete tanks (symbols: filled circles leaves from May-June; open triangles July; open circles August; filled triangles September-October).
Below: for the Bemmelse Strang (symbols: filled circles leaves from June; open triangles July; filled triangles August; open squares September; filled squares October).

concrete tanks					
month	n	equation	S.E.	r^2	p
May-June	25	y = 2.956 x − 2.120	13.66	0.96	< 0.001
July	25	y = 4.265 x − 7.135	9.00	0.95	< 0.001
August	25	y = 3.267 x + 1.033	11.79	0.85	< 0.001
September-October	25	y = 3.610 x + 1.573	3.06	0.97	< 0.001
Bemmelse Strang					
May-June	20	y = 3.625 x − 21.815	14.02	0.93	< 0.001
July	18	y = 4.439.x − 37.529	15.81	0.96	< 0.001
August	19	y = 4.375 x − 21.450	30.99	0.95	< 0.001
September	28	y = 3.901 x − 27.868	15.40	0.95	< 0.001
October	21	y = 3.386 x − 21.746	21.97	0.93	< 0.001

Table III. List of monthly regression equations of floating leaves of *Nymphoides peltata* (Gmel.) O. Kuntze (y is biomass of a leaf in mg ash-free dry weight; x is leaf area in cm^2). All equations have been tested with the Student t-test.

plot	year	leaf biomass produced in $g.m^{-2}$		difference A - B	rel. difference % of B
		A	B		
concrete tank 1	1978	139.0	134.5	+ 4.5	3.3
concrete tank 2	1978	148.0	146.1	+ 1.9	1.3
Bemmelse Strang 1	1980	231.6	226.9	+ 4.7	2.1
Bemmelse Strang 2	1980	185.7	188.9	− 3.2	1.7

Table IV. Leaf biomass of *Nymphoides peltata* (Gmel.) O. Kuntze produced during a whole growth season as calculated with monthly regression equations (A), and with general equations (B) the difference between them and relative difference with respect to B.

ash-free dry weight, x is the leaf area of a leaf in cm^2) (Fig. 2). In order to test the reliability of the general equations regression equations have been determined also monthly (Table III). The difference between results obtained with monthly and with general regression equations was very small (Table IV), so that all further calculations have been made with the general regression equations.

The contribution of different damage and decomposition types was estimated visually as a percentage of the area per leaf at each date. To test the reliability of these estimations 40 leaves from the Bemmelse Strang were taken to the laboratory of which the total damage and leaf area in decomposition were estimated visually (number of estimations 97) as well as measured by a Kontron Messgeräte GmbH planimeter MOP-Am 03. There was a distinct tendency to estimate somewhat too high, especially with respect to smaller damage. The average difference between the estimations by eye and the measurements by the planimeter was 1.84 % (S.D. = 1.50 %), so that visual estimations can be considered to be reliable.

Further maximum and minimum temperatures were measured at a depth of 10 cm below the water surface. In the Bemmelse Strang the water level has been followed at each observation date. All data have been coded for elaboration with the computer (Table V). A computer program was developed by the Department of Statistical Consultation of the Catholic University of Nijmegen.

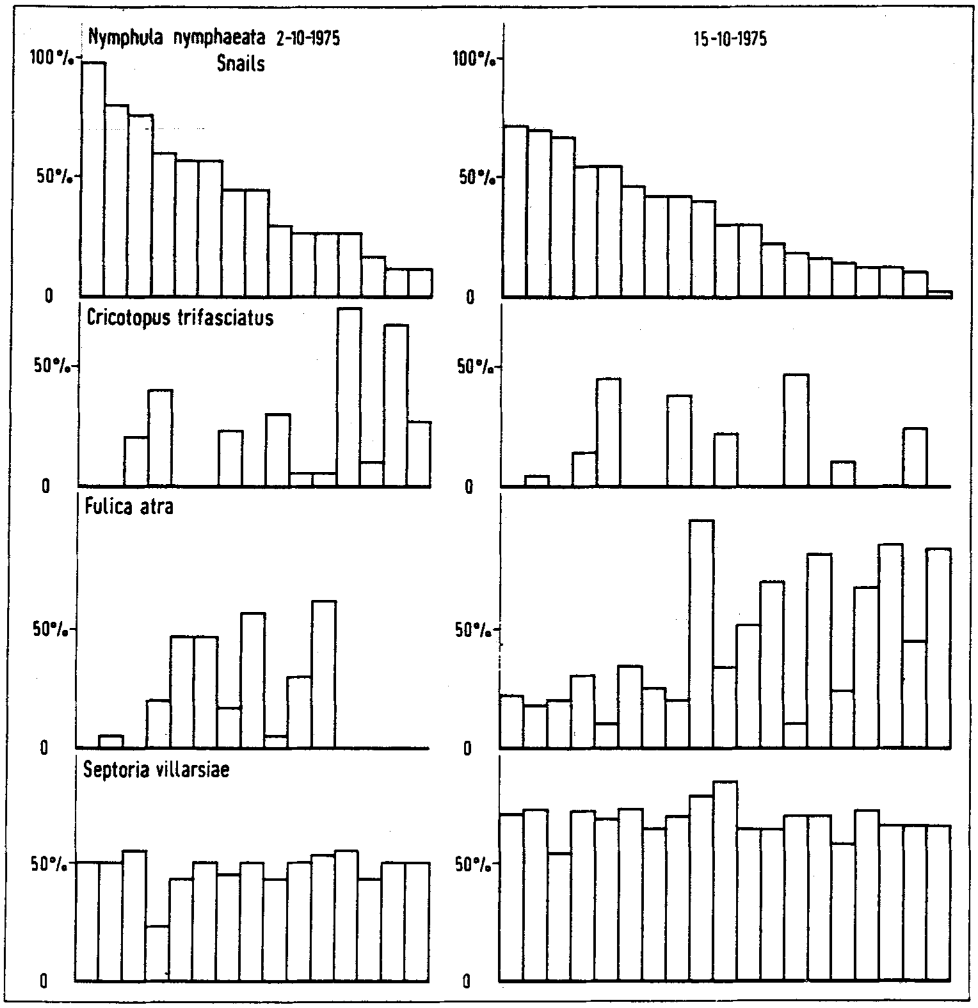

Fig. 3.

Results from 34 samples of floating leaves of *Nymphoides peltata* (Gmel.) O. Kuntze from different sites in the Oude Waal in 1975.
Vertically: the percentage of leaves affected by a certain damage or infection type in each sample. Horizontally: the samples arranged for each sampling date with respect to the combined damage caused by *Nymphula nymphaeata* (L.) and snails from high to low damage percentages.

RESULTS

Some general results obtained with the leaf-marking method are presented in Table VI. The following remarks can be made with respect to each indicated cause of initial decomposition.
Animals.

1	2	3	4	5	6	7	8	9	10	11	12
1	1978-05-25	9	61	57	281	0	0	0	0	0	0
1	1978-05-29	9	62	57	286	0	0	0	0	0	0
1	1978-05-30	9	62	57	286	0	0	0	0	0	0
1	1978-06-01	9	62	58	291	0	0	0	0	0	0
1	1978-06-05	9	62	58	291	0	0	0	0	0	0
1	1978-06-09	9	62	58	291	0	0	0	0	0	0
1	1978-06-13	9	62	58	291	2	0	2	0	0	0
1	1978-06-16	9	62	58	291	8	0	2	5	1	0
1	1978-06-20	9	63	58	296	22	0	2	5	5	10
1	1978-06-23	9	63	58	296	62	0	2	10	20	30
1	1978-06-27	9	63	58	296	62	0	2	10	20	30

Table V. Data on development and initial decomposition from a floating leaf of *Nymphoides peltata* (Gmel.) O. Kuntze, (concrete tank 1, 1978) such as used in the computer program. 1. means short shoot leaf; 2. observation dates (1978-05-25 is the date on which the unrolled leaf number 9 was observed for the first time at the water surface, on 1978-06-27 it was observed for the last time); 3. number of the leaf; 4. leaf length in mm; 5. leaf width in mm; 6. leaf surface in mm^2; 7. total percentage of leaf area damaged or in decomposition; 8. damage by *Cataclysta lemnata* (L.) (% of leaf area); 9. idem by snails (%); 10. idem by microbial decay (%); 11. idem by *Septoria villarsiae* Desm. (%); 12. yellow leaf area (% of leaf area).

Animals affect the floating leaves by consumption and/or damage by which they cause leaching, fragmentation and decay of the leaf biomass. The larvae of the chironomid *Cricotopus trifasciatus*, which are halfminers, were very important with respect to the disintegration of the floating leaves in the Bemmelse Strang. The percentages of the leaf area disappearing from the plots due to their activity include the combined effect of mining (consumption), microbial decay of the mines and subsequently fragmentation by wind and wave action. Certainly consumption of the leaf material by *C.trifasciatus* is much lower than the loss of material due to decay of the mines and successive fragmentation. Pyralid caterpillars (*Cataclysta lemnata, Nymphula nymphaeata*) played a relative minor role with respect to the disintegration of the leaves. In this case the percentages of leaf area loss represent the combined effect of consumption of leaf material and damage as these caterpillars also cut out pieces from the leaf margin to construct their cases.

For snails and coots (*Fulica atra*) the percentages represent consumption only. The effect exercized by snails on the total leaf area was small, in the field as well as in the concrete tanks.

Fungi.

Fungi can affect fresh, green but also yellow leaves. In general fungi play an important role in the gradual disintegration of the leaves from the flowering period to the end of the vegetation period. In this period infection spots of *Septoria villarsiae* present on floating leaves extend and cause the leaves to loose their hydrophobous character, resulting in decay and fragmentation. *S. villarsiae* played an important role with respect to the initial decomposition of leaves in concrete tank 1, where *Septoria* was present for several years. In tank 2 *S.villarsiae* established itself during our observations in 1978 so that the leaf area infected here was lower than in tank 1; moreover it started later. In the Bemmelse Strang *S.villarsiae* was relatively unimportant in 1980 due to the strong vegetative growth and poor flowering of *N.peltata*, which was certainly an effect of the high water level of the river in summer (June-July) that disturbed the normal development of floating leaves.

Autolysis with microbial decay.

Normal decay starts with autolysis by which the leaves become yellow and loose their

hydrophobous character. This process is gradually followed by microbial decay; the leaves become brown, submerged and finally fragmentary. Autolysis followed by microbial decay was important in all situations studied.
Not exactly known cause.

This category was relatively low in the case of the concrete tanks, but high in the case of the Bemmelse Strang. This is certainly due to the method used; it is not known, what happened exactly with a leaf between the last date on which it was observed and the date at which it was no longer present. Decaying leaf-blades can easily fragmentate, particularly by wind and wave action, and move out of the plots or sink under water. Furthermore petioles can break off by various causes resulting in leaves being washed out of the plots. During the high water of the river in June in the Bemmelse

concrete tank	1	2
total number of leaves/m^2	2608	2524
short shoot leaves/m^2	2204	1676
flowering stem leaves/m^2	404	848
total leaf area in m^2/m^2	3.90	4.30
total biomass in g/m^2	134.5	146.1
decomposition in % caused by:		
Cataclysta lemnata	0.30	0.29
snails (*Radix peregra, Galba turricula*)	2.27	1.02
fungi (*Septoria villarsiae*)	31.85	11.86
autolysis and microbial decay of old leaves	50.12	72.32
not exactly known	15.46	14.51

Bemmelse Strang	1	2
total number of leaves/m^2	1712	1108
short shoot leaves/m^2	1664	1096
flowering stem leaves/m^2	48	12
total leaf area in m^2/m^2	6.96	5.56
total biomass in g/m^2	226.9	188.9
decomposition in % caused by:		
Cricotopus trifasciatus	16.59	18.82
Nymphula nymphaeata	0.49	0.20
snails (*Radix peregra, R.auricularia*)	1.38	0.55
(*Lymnaea stagnalis*)		
Fulica atra (consumed)	3.53	2.55
idem (beak impressions)	0.12	0.08
fungi (*Septoria villarsiae*)	0.31	0.29
autolysis and microbial decay of old leaves	29.36	37.99
not exactly known	48.22	39.52

Table VI. The production of floating leaves of *Nymphoides peltata* (Gmel.) O. Kuntze in the concrete tanks during the growth season of 1978 and in the Bemmelse Strang during the growth season of 1980 and the percentages of the total leaf area disintegrated by damage, infection and decomposition types.

Strang, 16.81 and 8.63 % of the total leaf area produced during the whole growth season in plot 1 and 2, respectively, disappeared under water and could not be observed further.

It is very well possible that all this disappearing leaf material entered the detritus food chain. Then the percentages for microbial decay were in all plots studied about the same, *viz.* 65.58 and 86.83 % for the concrete tanks (1 and 2) and 77.58 and 77.51 % for the plots 1 and 2 in the Bemmelse Strang.

DISCUSSION

It can be questioned to what extent the results obtained from the plots with an area of a quarter of a square meter are representive for the *Nymphoides* vegetation as a whole. Certainly there can be differences in the spatial distribution of damage types particularly in those caused by animals (Fig. 3) as was found in the Oude Waal (Fig. 1), a former river bed of the river Waal near Nijmegen where extensive stands of *N.peltata* occurred along all borders. The fungus *Septoria villarsiae* occurs here randomly distributed over the leaves within a *Nymphoides* bed (Fig. 3). Coots appeared to cause damage of the floating leaves particularly in sheltered habitats near the banks, while damage by *Cricotopus trifasciatus* was especially important at the margins of the stands directed to the open water. The damage caused by *Nymphula nymphaeata* was spread over the vegetation, but lowest at the open-water margin, while snails caused most damage in the shallower parts near the littoral border vegetation. It can be concluded that in an extensive area such as the Oude Waal more plots are necessary for a quantitative description of the decomposition types over a large area covered by *N.peltata.* In the Bemmelse Strang, however, sheltered *Nymphoides* beds do not occur. Cows consumed here *Nymphoides* in the shallower parts, so that the *Nymphoides* beds are separated from the littoral border vegetation by a belt without vegetation. There were some minor differences between the results from the two plots in the Bemmelse Strang, and these are in accordance with the tendencies in spatial distribution of animal damage types such as found in the Oude Waal.

The weather conditions during the growth season form also a factor of great importance. They may cause flooding of the vegetation in one and emersion in another year. Particularly the occurrence of the fungus *Septoria villarsiae* is influenced by the weather conditions. Protracted heavy rain caused flooding of the river in 1980 by which the leaf area got lost under water, and a strong vegetative development with poor flowering occurred. In other years flowering can be very rich, and then *Septoria villarsiae* plays a more important role at the end of the season. *S.villarsiae* can also be important in other parts of the growth season as was observed in other years in the concrete tanks. In a period with constant cloudy weather, rain and low temperatures during early summer *S.villarsiae* infected all leaves causing a strong decrease of the leaf area. Also fluctuations in the size of the various insect generations can cause fluctuations in the damage during the growth season in one year, but also from year to year. Such fluctuations in leaf damage and infection are well-known for common field crops such as potatoes, in which in one year fungi and in an other year chrysomelid beetles are very important. It can be concluded that several plots must be followed for several years to gain insight in the causes of such yearly fluctuations.

SUMMARY

In this paper the leaf-marking method as used for the study of the development and initial decomposition of floating leaves is described and the reliability of the various measurements is tested and/or discussed. Some general results obtained with *Nymphoides peltata* (Gmel.) O. Kuntze in tanks and in the field are presented and critically discussed. Autolysis followed by microbial decay was in all cases the most important factor by which leaves disintegrated. In the field plots animals were responsible for the disappearance of 22 % of the total leaf area produced during a growth season. This is, however, the combined effect of consumption and damage succeeded by microbial decay. Real grazing can be estimated to be no more than 10 % of the production of floating leaves. Fungi can have an important role in initial decomposition, especially after the

flowering period, as is demonstrated for *Septoria villarsiae* Desm. All damage types show temporal and, in the case of animals, also spatial distribution patterns.

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