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Production, nutrient dynamics and initial decomposition of floating leaves of *Nymphaea alba* L. and *Nuphar lutea* (L.) Sm. (Nymphaeaceae) in alkaline and acid waters

C.J. KOK, G. VAN DER VELDE & K.M. LANDSBERGEN
Laboratory of Aquatic Ecology, Catholic University Nijmegen, Toernooiveld, 6525 ED Nijmegen, The Netherlands

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Abstract. Production, turnover and nutrient dynamics of floating leaves of *Nymphaea alba* L. and *Nuphar lutea* (L.) Sm. were studied in four aquatic systems in The Netherlands, differing strongly in water quality. Production was 108–447 g AFDW.m^{-2} for *N. lutea* and 319–348 g AFDW.m^{-2} for *N. alba*. Turnover ranged from 3.6 to 4.4 without much difference between the sites and the species. During senescence 60–70% of the N and P from the leaves was resorbed by both of the plant species. The nutrient flow from the floating leaves into the detritus food chain differed considerably between the species and sites studied, mainly because of the differences in production. The data suggest that production is strongly influenced by the environment, whereas turnover and nutrient resorption during senescence seem to be plant characteristics. There was little difference in dynamics of the chlorophyll-α concentration in the leaves of the two species, irrespective of the growing site. Floating leaves of both species lost about 70% of their area due to fragmentation in the alkaline waters, whereas in the acid water very little fragmentation was observed.

Introduction

It is generally accepted that decomposition is one of the key processes in the nutrient and carbon cycles in ecosystems. Degradation and mineralization processes can be considered the counterpart of primary production. Furthermore, a large part of the organisms in an ecosystem have their niche in the decomposition food chain (e.g. Anderson & Sedell 1979).

One of the main processes linked to decomposition in aquatic systems is the cycling of nutrients. The release of nutrients from decomposing macrophyte material has been studied by many authors (e.g. Howard-Williams et al. 1983; Brock 1984; Hemminga et al. 1988).

Most of the studies on nutrient dynamics during decomposition have been carried out using the litter bag technique and material detached from the plant. However, the decomposition of aquatic macrophytes is usually characterized by the fact that this plant material gradually enters the senescence and initial decay stages. Cellulolytic microorganisms can be among the primary colonizers of aquatic plants (Howard-Williams et al. 1978; Robb et al. 1979) and these organisms can cause extensive damage to plant organs (Rogers & Breen 1982).

Thus, the microbial decay of the macrophyte material may start soon after plant parts are formed. It seems quite likely that the plant organs attacked by microorganisms lose nutrients to the surrounding water, because of death of cells and loss of tissue integrity.

Another cause of changes in nutrient concentrations during the life of a plant organ is resorption of valuable components by the rest of the plant during senescence. N and P containing compounds are hydrolysed in the senescence process and the nutrients are transported to vital parts for reuse or to special storage structures (Bidwell 1974). This flow of nutrients can not be detected by the litter bag or leaf pack techniques normally used in decomposition research.

To assess the importance of the decomposition of macrophytes in the carbon and nutrient cycles in aquatic systems, the total input of plant material in the decomposition food chain and the amount of nutrients in this material should be estimated. This can be done by determining the total production and turnover of the aquatic macrophytes and the changes in nutrient concentrations during the life of the plant organs. In this way, the particulate matter and nutrient flow from the macrophytes into the decomposition food chain can be estimated as well as the amount of nutrients reused by the plants.

In this paper results of studies on the production and turnover of floating leaves (i.e. floating leaf blades only) of *Nuphar lutea* (L.) Sm. and *Nymphaea alba* L. are presented. Production and turnover were investigated in four systems, differing strongly in water quality, using a non-destructive leaf marking method. Furthermore, changes in chemical composition of the leaves during the life span were studied. This combination allows estimates of the total input of leaf blade material and nutrient flow into the detritus food chain and of the fraction of the nutrients reabsorbed by the plant during senescence.

Nuphar lutea and *Nymphaea alba* were chosen for this investigation for several reasons. These plants are dominant macrophytes in a large part of the shallow waters in The Netherlands and they are relatively insensitive to both eutrophication and acidification of the environment (Van der Velde et al. 1986; Smits et al. 1988). This allows studies on production and decomposition under a wide range of circumstances. Furthermore a large part of the biomass of these plants consists of floating leaves. These floating leaves are very suitable for this type of study, because they are large, easily marked and observed and their life span is long enough to allow weekly observation and short enough to follow the whole senescence and initial decomposition process of all leaves developed in a plot within one growing season.

Materials and methods

Study sites

Studies on production and senescence were carried out in four different systems. The Oude Waal (municipality of Ubbergen, Province of Gelderland) is a shallow oxbow lake, situated in the river forelands, of the River Waal. 'Pond G' is

Table 1. Chemical characteristics of the water of the studied sites (mean values and pH ranges of monthly measurements).

		Oude Waal	'Pond G'	Haarsteegse Wiel	Voorste Choorven
NH_4^+	$\mu mol.L^{-1}$	13	4	5	75
NO_3^-	$\mu mol.L^{-1}$	4	6	3	13
PO_4^{3-}	$\mu mol.L^{-1}$	0.6	0.5	0.2	0.2
K^+	$\mu mol.L^{-1}$	134	48	69	47
Na^+	$\mu mol.L^{-1}$	1440	708	517	310
Ca^{2+}	$\mu mol.L^{-1}$	1880	1842	1180	230
SO_4^{2-}	$\mu mol.L^{-1}$	660	310	290	380
Cl^-	$\mu mol.L^{-1}$	1980	920	610	340
Alk.	$meq.L^{-1}$	5.2	4.7	1.5	0.07
pH		6.7–8.3	7.8–8.4	7.1–8.5	4.7–5.5

a remnant of the moat of the former fortification Ooy and is located in the direct vicinity of the Oude Waal, but it is protected from flooding by a dike (Van der Velde 1980). The Haarsteegse Wiel (municipality of Vlijmen, Province of Noord-Brabant) is a deep isolated lake which had its origin in floods caused by dike bursts of the River Meuse. The Voorste Choorven is a shallow, isolated, culturally acidified moorland pool near Oisterwijk, Province of Noord-Brabant. In all these water bodies, dense, nearly monospecific nymphaeid stands occur. Chemical characteristics of the investigated systems are given in Table 1.

Production and turnover of floating leaves

Production and turnover of floating leaves were studied using a non-destructive leaf marking method. Plots of 1 m^2 were laid out in the middle of monospecific stands. A square PVC tube frame (1 × 1 m) was held at approximately 15 cm below the water surface by anchoring bricks and cork floats (Fig. 1). Newly developed leaves received a numbered mark (Fig. 2). Observation and marking of new leaves were done weekly, during the whole growing season. The length of each leaf was measured weekly, since some growth takes place after unrolling of the leaves, and damaged or missing areas were estimated visually as the percentage of the area of each individual leaf. The leaves were considered dead if > 95% of the leaf area was missing or if the leaf had lost its buoyancy due to complete decay.

To calculate the biomass in the plots (Ash-Free Dry Weight, AFDW), equations describing the relation between leaf length, leaf area and AFDW were computed. On each location a large number of leaves was harvested at random several times during the growing season. For each site, the relation between leaf length and AFDW was established. Furthermore, the relation between leaf length and leaf area was determined for the undamaged leaves. This relation was used to estimate the potential leaf area (i.e. the area the leaf would have had if undamaged) of damaged leaves. There was a good correlation between the

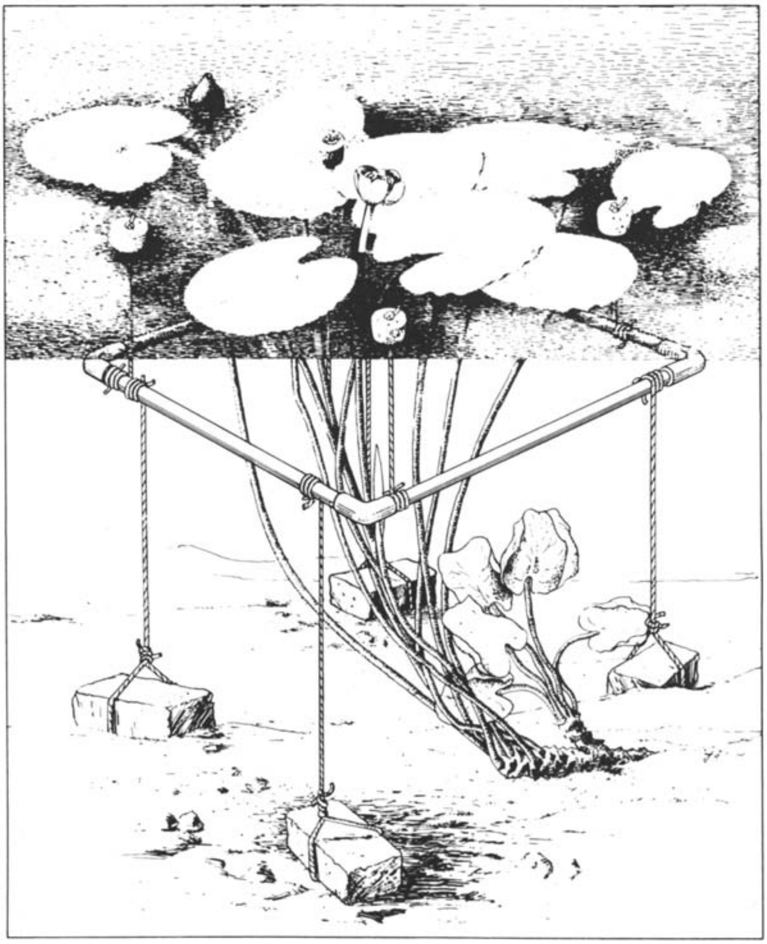

Fig. 1. Plot of *Nuphar lutea* with a 1 m^2 perforated PVC-tubing frame held ca. 15 cm under the water surface by cork floats so that the unfolding of the leaves is not hindered. The frame is anchored at each corner with a string and a brick.

determined parameters, for all locations (Van der Velde & Peelen-Bexkens 1983).

Using the relationship between leaf length, leaf area and AFDW, the potential standing crop in each plot could be calculated. The actual biomass was estimated by subtraction of the biomass of the missing leaf area. The net production was computed by summation of maximal potential biomass of the leaves developed during the growing season. Turnover rates were calculated by means of the formula:

$$\text{turnover rate} = \frac{\text{net production}}{\text{mean potential standing crop}}$$

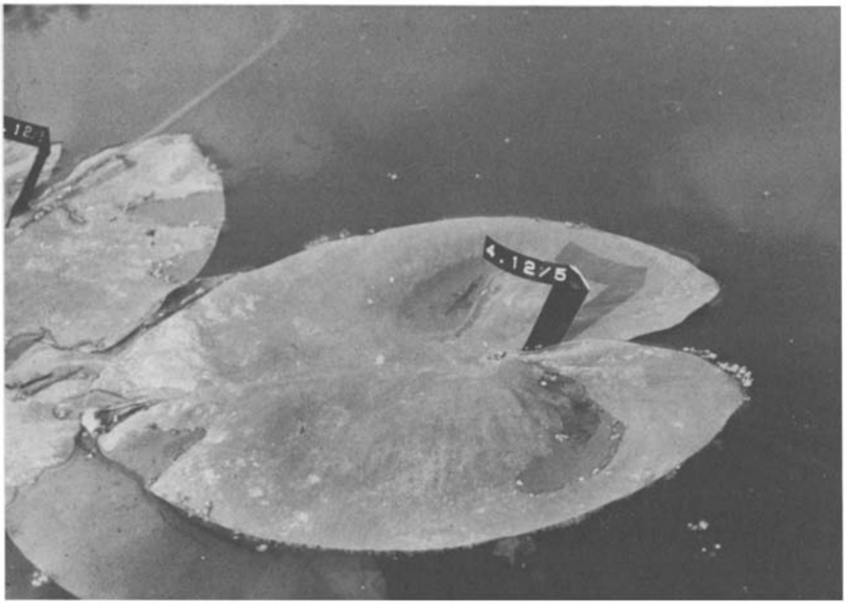

Fig. 2. Floating leaf of *Nuphar lutea* marked with rotex tape on which a number is printed. The covering paper is removed and the tape is fixed around the petiole with a staple, without damaging the petiole. The other end of the tape is drawn through the leaf sinus and bent above the water surface like a flag, so that it can be easily read. Leaves were marked as soon as they unfolded at the water surface.

Observations on production and turnover were carried out in the Oude Waal in 1977 for *Nuphar lutea* and *Nymphaea alba*, in the Haarsteegse Wiel in 1977 for *Nuphar lutea* and in the Voorste Choorven in 1988 for *Nymphaea alba* and *Nuphar lutea*.

Chemical changes and fragmentation during senescence and nutrient input into the detritus compartment

Chemical composition during leaf senescence was determined in a series of 70–90 leaves, which were marked shortly after reaching the surface. Each week seven leaves were harvested at random as long as marked leaves were present. From these leaves, the remaining leaf area, the chlorophyll-α concentration, a parameter to estimate the stage of senescence, and N and P concentrations were determined.

The leaf area was measured in the laboratory using a planimeter (Kontron Messgeräte, MOP.AMO 3). The potential leaf area was calculated from the leaf length as described above. The actual leaf area was expressed as a percentage of the potential leaf area.

Chlorophyll was extracted from triplicate subsamples of the leaves, taking care that the ratio of damaged and undamaged areas in the samples was equivalent to that on the leaves. 80 mg leaf material (fresh weight) was used for each subsample. Chlorophyll-α was measured spectrophotometrically, after extraction in 80% ethanol. 1 ml extractant per 10 mg (fresh weight) of leaf material was used. The acidification method was used to correct for phaeophytin (Moed & Hallegraeff 1978). The fresh weight/dry weight ratio of the remainder of the leaf was used to compute the dry weight of the extracted leaf parts. Calculations of chlorophyll-α concentrations were performed according to Roijackers (1981).

Total N and P concentration in the leaves was determined after grinding and destruction of the dried leaves with H_2SO_4/H_2O_2 (Van Dijk & Roelofs 1988), using triplicate subsamples. Nitrogen was measured as NH_4^+ using salicylate reagent (Grasshoff & Johannsen 1977). Phosphorus was estimated with an ICP emission spectrophotometer.

The N and P input from the floating leaves into the decomposition food chain was estimated by means of the formula

$$\text{nutrient input} = \text{nutrient concentration in senescent material} \\ \times \text{ potential production}$$

The underlying assumptions for this calculation are:

A. The decrease in nutrient concentration during senescence is caused by resorption and not by leaching.

B. The parts of the leaves that are lost by fragmentation have gone through the whole process of senescence.

C. Most of the aquatic herbivorous fauna species feed on leaf material which is senescent. To simplify the calculation damage by specialized herbivores in the early life stages was neglected.

The reasons for these assumptions are considered in the discussion.

The studies on the chemical changes during senescence of *Nymphaea alba* were carried out in the Oude Waal (1986, two series) and in the Voorste Choorven (1988, one series). For *Nuphar lutea*, investigations were carried out in the Oude Waal (1986, two series), ‘Pond G’ (1987, two series) and in the Voorste Choorven (1987 and 1988, one series each year). The calculations of the N- and P-input from the floating leaves were performed on the data sets of the Voorste Choorven and the Oude Waal. It was assumed that the results for the nutrient concentrations in 1986 could be used as estimates for the N- and P-dynamics in 1977, because no data on nutrient levels in the floating leaves for 1977 were available.

Table 2. Production and turnover data for floating leaves of *Nuphar lutea* and *Nymphaea alba*.

Nuphar lutea

Site	Oude Waal	Voorste Choorven	Haarsteegse Wiel
Year	1977	1988	1977
Net production (g AFDW.m^{-2}.yr^{-1})	234	108	447
Max. biomass (g AFDW.m^{-2})			
Potential	105	51	190
Actual	88	50	162
Mean persistence (days)	38.4	48.7	49.9
Turnover ($year^{-1}$)	4.4	3.8	3.8

Nymphaea alba

Site	Oude Waal	Voorste Choorven
Year	1977	1988
Net production (g AFDW.m^{-2}.yr^{-1})	348	319
Max. biomass (g AFDW.m^{-2})		
Potential	154	139
Actual	139	138
Mean persistence (days)	46.2	49.3
Turnover ($year^{-1}$)	3.8	3.6

Results

Production and turnover of floating leaves

The production data for *Nuphar lutea* and *Nymphaea alba* floating leaves are presented in Table 2. Floating leaves of *Nuphar lutea* showed their highest production in the Haarsteegse Wiel and their lowest in the Voorste Choorven. *Nymphaea alba* stands showed far less difference between the studied sites. The actual floating leaf biomass of both nymphaeid species was almost equal to the potential biomass in the Voorste Choorven. In the other systems studied there was far more difference between the actual and the potential biomass. The differences in turnover rates and the mean persistence of the leaves were small compared to the differences in the production data. The results are similar for both species.

Chemical changes and fragmentation during senescence and nutrient input into the detritus compartment

The nutrient dynamics of the floating leaves of *Nuphar lutea* from the Oude Waal and from 'Pond G' were very similar. The results show that there was little

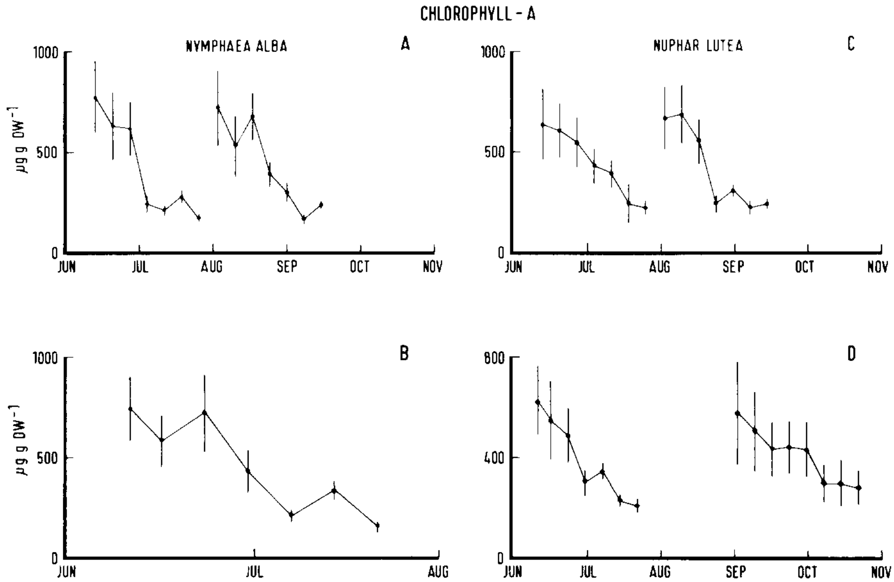

Fig. 3. Mean chlorophyll-α concentrations (μg per g dry weight ± S.D.) in marked floating leaves, which were undamaged at the moment of marking, over a series of sampling dates. Sampling took place until no marked leaves could be found any more. At each date 7 leaves were harvested and subsamples were taken for chlorophyll extraction. (*A*) *Nymphaea alba*, Oude Waal 1986, (*B*) *Nymphaea alba*, Voorste Choorven 1988, (*C*) *Nuphar lutea*, Pond G 1987, (*D*) *Nuphar lutea*, Voorste Choorven 1987/1988.

difference in chlorophyll-α and nutrient dynamics between the two nymphaeid species under investigation. The mean initial N- and P-levels in the leaves from the Voorste Choorven were lower than the mean N- and P-levels from the leaves from the Oude Waal or 'Pond G', for both species. The mean chlorophyll-α concentrations at the start of the experiments were comparable between floating leaves of all the studied sites. Very soon after reaching the surface, the mean chlorophyll-α concentration in the leaves started to decrease. After three to four weeks, the decrease accelerated (Fig. 3). In the Oude Waal and 'Pond G', mean N and P levels of the floating leaves showed the same tendency (Figs. 4 and 5). In floating leaves of the Voorste Choorven, nutrient levels during the summer series were comparable to those of floating leaves in the other systems studied. The results of the autumn observations on *Nuphar lutea* from the Voorste Choorven showed a different pattern of nutrient dynamics and a slower loss of chlorophyll-α from the floating leaves. The ultimate mean levels of chlorophyll-α, N and P were similar in all cases, except for the leaves of *Nuphar lutea* from the autumn series in the Voorste Choorven (Figs. 4 and 5).

In the non-acid systems the remaining leaf area decreased constantly during the period of the life span of the leaves (Fig. 6). In the acid Voorste Choorven,

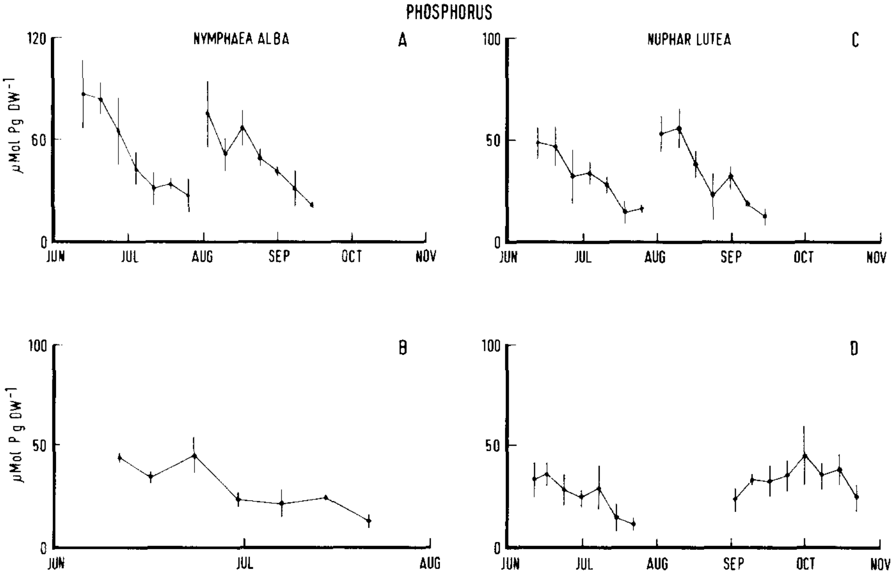

Fig. 4. Mean phosphorus concentrations (μmol per dry weight ± S.D.) in marked floating leaves, which were undamaged at the moment of marking, over a series of sampling dates. Sampling took place until no marked leaves could be found any more. At each date 7 leaves were harvested. (*A*) *Nymphaea alba*, Oude Waal 1986, (*B*) *Nymphaea alba*, Voorste Choorven 1988, (*C*) *Nuphar lutea*, Pond G 1987, (*D*) *Nuphar lutea*, Voorste Choorven 1987/1988.

the decayed floating leaves of both macrophyte species remained almost intact until they disappeared by loss of buoyancy.

The nutrient (N and P) input into the systems through decomposition of floating leaves is presented in Table 3. The nutrient input into the detritus compartment was about 30–40% of the total amount of N and P present in the floating leaves. About 60–70% of the N and P of the floating leaves was resorbed by the plant. The differences in resorption by the studied species were small in all cases. Only the P resorption from the floating leaves of *Nymphaea alba* in the Voorste Choorven was significantly lower than the P resorption from floating leaves in the Oude Waal ($p < 0.05$, Student's t-test).

The total input of nutrients from the floating leaves into the detritus food chain depended on the concentrations in the leaves at the end of the senescence phase and on the total production of floating leaves. The nutrient input, both N and P, from the leaves of *Nuphar lutea* was small in the Voorste Choorven compared to the nutrient input from the floating leaves of *Nuphar lutea* in the Oude Waal. *Nymphaea alba* stands showed less difference in this respect between the sites studied. The N input was higher in the Voorste Choorven while the P input was higher in the Oude Waal.

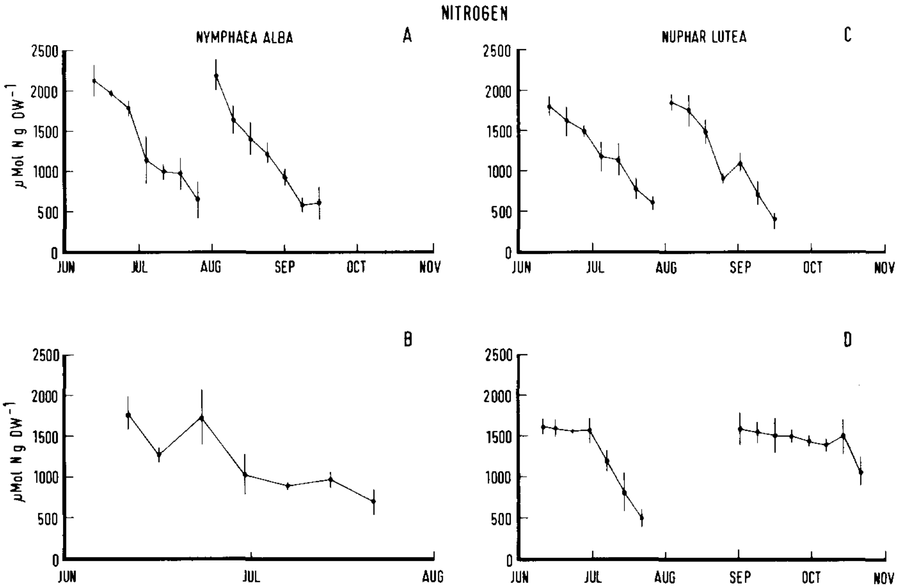

Fig. 5. Mean nitrogen concentrations (μmol per g dry weight ± S.D.) of marked floating leaves, which were undamaged at the moment of marking, over a series of sampling dates. Sampling took place until no marked leaves could be found any more. At each date 7 leaves were harvested. (*A*) *Nymphaea alba*, Oude Waal 1986, (*B*) *Nymphaea alba*, Voorste Choorven 1988, (*C*) *Nuphar lutea*, Pond G 1987, (*D*) *Nuphar lutea*, Voorste Choorven 1987/1988.

Discussion and conclusions

Production and turnover of floating leaves

The production of *Nymphaea alba* in the Voorste Choorven was comparable to that in the Oude Waal. *Nymphaea alba* seems to be fairly insensitive to acidification. The distribution of this species is independent of pH and alkalinity (Van der Velde et al. 1986; Smits et al. 1988). The nutrient levels of the water differed between the systems studied, the Oude Waal showing higher concentrations of P and lower N concentrations than the Voorste Choorven. This did not lead to a major difference in production. It was surprising that the higher N-concentration in the water of the Voorste Choorven did not result in a higher N-level of the floating leaves. It is possible that there is a difference in sediment-based nutrient uptake of the plants at the studied sites, or that the lower N-levels are caused by shortage of P or by some detrimental effect of low pH on the plants.

Nuphar lutea is more sensitive to acidification than *Nymphaea alba*, having its optimum in slightly acid to circumneutral waters with pH values between 6.0 and 7.3 (Van der Velde et al. 1986). Production of this species in the Voorste Choorven was clearly lower than in the non-acid waters. The *Nuphar lutea* vegetation in the Voorste Choorven may be a remnant from the times when the water quality was circumneutral.

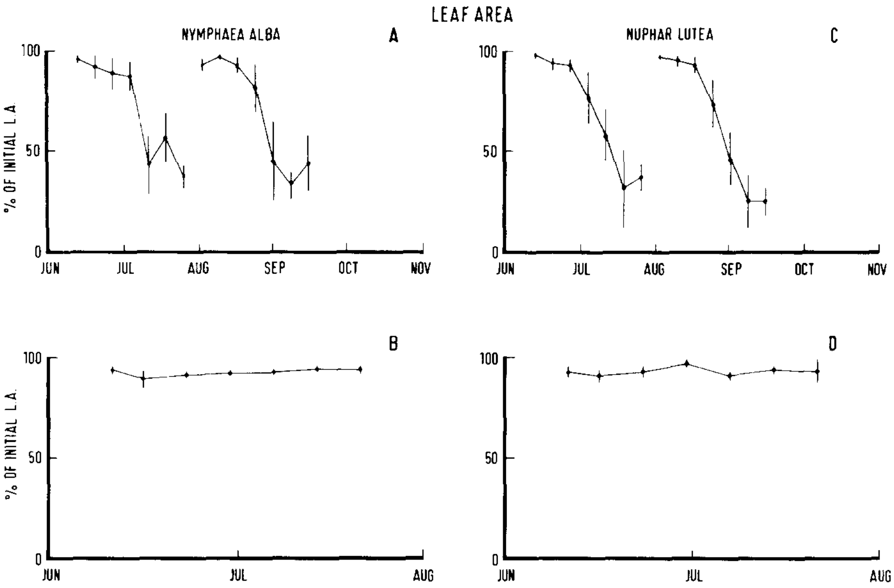

Fig. 6. Mean remaining leaf area of marked floating leaves (percentage of initial ± S.D.), which were undamaged at the moment of marking, over a series of sampling dates. Sampling took place until no marked leaves could be found any more. At each date 7–10 leaves were harvested, their leaf area measured by means of a planimeter and the results expressed as percentage of the pontential leaf area. (*A*) *Nymphaea alba*, Oude Waal 1986, (*B*) *Nymphaea alba*, Voorste Choorven 1988, (*C*) *Nuphar lutea*, Pond G 1987, (*D*) *Nuphar lutea*, Voorste Choorven, 1987/1988.

The high productivity of *Nuphar lutea* floating leaves in the Haarsteegse Wiel can not be explained from the nutrient concentrations in the water layer. Both N and P showed higher levels in the water of the Oude Waal. It is known that nymphaeids can take up their nutrients through their roots as well as through their leaves (Twilley et al. 1977; Brock et al. 1983). Therefore, it is likely that the difference in productivity is caused by differences in the soil nutrient concentrations.

Our production estimates do not take into consideration the excretion of

Table 3. Nitrogen and phosphorus input from the floating leaves into the detritus food chain.

	Oude Waal		Voorste Choorven	
	P	N	P	N
Nuphar lutea				
input into detritus ($mmol.m^{-2}.yr^{-1}$)	11.2	397	4.9	179
resorbed by plant	73%	72%	68%	69%
Nymphaea alba				
input into detritus ($mmol.m^{-2}.yr^{-1}$)	25.2	617	14.1	703
resorbed by plant	71%	70%	61%	65%

organic matter by the leaves. It has been known for a long time that aquatic plants excrete organic matter (e.g. Hough & Wetzel, 1975). This part of the production can not be estimated by the leaf marking method. Wetzel et al. (1972) calculated that 4% of the photosynthetic production of aquatic macrophytes was excreted as dissolved organic matter. Therefore, the error resulting from neglecting the excretion of dissolved organic matter is presumably small.

Determinations of production must take into account the reabsorption of organic matter (Westlake 1982). Correction for resorption was made by means of the equation calculating the biomass of the floating leaves from the length. The reabsorption of organic matter will lead to a lower biomass without changes in the leaf length. The leaves that were harvested to obtain the relationship between leaf length and biomass were randomly sampled several times during the growing season. In this way, the different ratios between leaf length and biomass of senescent leaves and vital leaves are averaged in the resulting equation. The figures presented here are therefore to be considered as conservative estimates, because excretion of organic matter was not taken into consideration.

The mean life span and the turnover rates of the floating leaves of the studied species are little affected by the environmental factors in the various systems. The differences in productivity of the floating leaves are much larger between the studied sites. So it seems that the turnover is under control of the plant rather than environmentally influenced. It is not clear which mechanisms cause the mean leaf age and the turnover to be so constant.

Chemical changes and fragmentation during senescence and nutrient input into the detritus compartment

The resorption of nutrients by the remaining plant parts of both *Nymphaea alba* and *Nuphar lutea* was nearly equal for all the systems studied, indicating that the environmental factors have little influence on the reallocation of nutrients during ageing. It seems that during senescence several processes are under tight control of the plant. The role of this control in the life strategies of nymphaeid water plants will be discussed in a later paper.

For *Nuphar lutea* the N and P input from the floating leaves into the detritus compartment differed considerably between the Voorste Choorven and the Oude Waal. This was mainly due to the large difference in production.

Nymphaea alba showed far less variation in nutrient input in the waters studied. In the Oude Waal the P input was higher, corresponding to a higher P level in the leaves and higher P concentrations in the water. The same tendency was not observed for N in the Voorste Choorven. Here the high N levels in the water did not cause high N concentrations in the leaves and therefore the differences in the N input into the detritus food chain were relatively small.

In the calculations of the nutrient input, it was necessary to correct for the reabsorption of nutrients by the remaining plant parts. The decrease in N and P levels in the floating leaves was unlikely to be due to leaching after cell death, for two reasons:

1. The concentrations of sodium and potassium did not decrease much during most of the experiment. Only at the end of the observation series, greater losses occurred (data not shown). Potassium and sodium are very rapidly lost during leaching (Larsen 1982; Brock 1984). So it is implausible that leaching was important during the ageing of the floating leaves.
2. It is unlikely that a significant part of the phosphorus and nitrogen were lost by leaching out of dead cells, since the remaining N- and P-containing compounds in senescent leaf material of *Nymphaea alba* and *Nuphar lutea* are not very soluble. This is demonstrated by the rise in nitrogen and phosphorus content of *Nuphar lutea* and *Nymphaea alba* floating leaf detritus during the first stage of litter bag experiments (Kok et al. 1990). Similar results have been described in the literature on decomposition (e.g. Howard-Williams et al. 1983; Hemminga et al. 1988).

The second assumption in the calculation of the nutrient input was that leaf parts lost by fragmentation were totally senescent and the nutrients had already been reabsorbed before the loss occurred. Our field observations gave the impression that tears and other physical damage of the leaves not caused by herbivores were mostly restricted to brown or rotten places on the leaves. This makes the assumption acceptable.

The results of studies on the epifaunal community of nymphaeid water plants imply that most of the epifauna which is able to consume macrophytic material, prefers aged leaf material, with the exception of the obligatory herbivores (Van der Velde 1980; Smock & Stoneburner 1982). It was therefore assumed that the nutrient concentrations in the consumed material were equal to the levels at the end of the senescence process. This made it unnecessary to correct the calculations of the resorption of nutrients for herbivore feeding. It is known that the damage from herbivores to floating leaves can be much larger than the actual consumption. The larvae and adults of the beetle *Galerucella nymphaeae* L. feed on the floating leaves of *Nuphar* and *Nymphaea* (Wallace & O'Hop 1985, as *Pyrrhalta nymphaeae*). Their actual consumption is low compared to the extensive damage they can inflict by causing fragmentation of the leaves. The same was observed on the chironomid *Cricotopus trifasciatus* (Meig.) mining the floating leaves of *Nymphoides peltata* (Lammens & Van der Velde 1978; Van der Velde et al. 1982). Fragmentation damage by herbivores in early stages of leaf development was also noticed in our investigations on *Nuphar lutea* and *Nymphaea alba* floating leaves, but it seemed of minor importance in these plant species in the waters studied. So it was disregarded in the calculations.

Data on nutrient resorption during senescence of submerged and floating leaved aquatic macrophytes are scarce, compared to data on emergent macrophytes (e.g. Prentki et al. 1978; Klopatek et al. 1978). Room & Thomas (1986) found that the nitrogen content of leaves of *Salvinia molesta* Mitchell decreased to about 30% of their original value during senescence. Phosphorus levels decreased to 20%. Hocking et al. (1981) found that 30–40% of N and P were still associated with moribund tissue of the seagrasses *Posidonia australis* Hook F. and *Posidonia sinuosa* Cambridge & Kuo. *Ceratophyllum demersum* L. reallocates 23–34% of N and 34–39% of P from senescent parts in the eutrophic Lake Vechten (Best, unpublished data). Garver et al. (1988) reported resorption values of 30–40% for *Typha*-species, but Klopatek (1978) calculated a resorption of 18% for *Typha latifolia* L. Some terrestrial plants are known to resorb 50% or more of the nutrients in their leaves before abscission (Chapin 1980 and literature therein), but other terrestrial species do not seem to recycle any P at all (Richardson et al. 1978). The differences in these figures may be due to the different life strategies of the plants studied, to differences in life span of the organs studied, or perhaps to the nutrient concentrations in the environment. However, methodological differences may well contribute to the discrepancies in the literature. Most investigators in this field study nutrient concentrations in standing crop during the growing season, without gathering information on the age of the investigated material. This approach may yield quite different figures on the resorption of N and P.

It was expected that a large part of the nutrients would be resorbed from the floating leaves of *Nuphar lutea* and *Nymphaea alba*, because these species have extensive root systems which function as permanent storage organs. It is, however, likely that many aquatic plants without storage organs also reallocate nutrients from senescent plant parts to vital, growing sections (Small 1972).

There was a striking difference in the remaining leaf area during the development of the floating leaves between the stands in the acid Voorste Choorven and the other, non-acid systems. Both plant species investigated showed very little loss of leaf area during their whole life span in the acid system. This indicates an inhibition of the microbial degradation of the floating leaves. Lack of fragmentation of *Nymphaea alba* floating leaf material was also observed in litter bag experiments in the Voorste Choorven and in laboratory decomposition experiments under acid conditions (Brock et al. 1985; Kok et al. 1990). This phenomenon seems to be caused by inhibition of cell wall degradation at low pH as shown by the accumulation of hemicellulose components in leaf litter under acid circumstances (Brock et al. 1985) and the low activity of major cell wall degrading exoenzymes in detritus from acid systems (Kok and Van der Velde, submitted).

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References

Anderson NH & Sedell JR (1979) Detritus processing by macroinvertebrates in stream ecosystems. Annu. Rev. Entomol. 24: 351–377

Bidwell RSG (1974) Plant Physiology (pp 483–493). New York

Brock TCM (1984) Aspects of the decomposition of *Nymphoides peltata* (Gmel.) O. Kuntze (Menyanthaceae). Aquat. Bot. 19: 131–156

Brock TCM, Bongaerts MCM, Heijnen GJMA & Heijthuijsen JHFG (1983) Nitrogen and phosphorus accumulation and cycling by *Nymphoides peltata* (Gmel.) O. Kuntze (Menyanthacaeae). Aquat. Bot. 17: 189–214

Brock TCM, Boon JJ & Paffen BGP (1985) The effects of the season and of water chemistry on the decomposition of *Nymphaea alba* L.: Weight loss and pyrolysis mass spectrometry of the particulate matter. Aquat. Bot. 22: 197–229

Chapin FS III (1980) The mineral nutrition of wild plants. Ann. Rev. Ecol. Syst. 11: 233–260

Garver EG, Dubbe DR & Pratt DC (1988) Seasonal patterns in accumulation and partitioning of biomass and macronutrients in *Typha*-spp. Aquat. Bot. 32: 115–128

Grasshoff K & Johannsen H (1977) A new sensitive method for the determination of ammonia in sea water. Water Res. 2: 516

Hemminga MA, Kok CJ & De Munck W (1988) Decomposition of *Spartina anglica* roots and rhizomes in a salt marsh of the Westerschelde Estuary. Mar. Ecol. Prog. Ser. 48: 175–184

Hocking PJ, Cambridge ML & McComb AJ (1981) Nitrogen and phosphorus nutrition of developing plants of two seagrasses *Posidonia australis* and *Posidonia sinuosa*. Aquat. Bot. 11: 245–261

Hough RA & Wetzel RG (1975) The release of dissolved organic carbon from submersed aquatic macrophytes: Diel, seasonal and community relationships. Verh. Internat. Verein. Limnol. 19: 939–948

Howard-Williams C, Davies BR & Cross RHM (1978) The influence of periphyton on the surface structure of a *Potamogeton pectinatus* L. leaf (an hypothesis). Aquat. Bot. 5: 87–91

Howard-Williams C, Pickmere S & Davies J (1983) Decay rates and nitrogen dynamics of decomposing water cress (*Nasturtium officinale* R.Br.). Hydrobiologia 99: 207–214

Klopatek JM (1978) Nutrient dynamics of freshwater riverine marshes and the role of emergent macrophytes. In: Good RE, Whigham DF & Simpson RL (Eds) Freshwater Wetlands. Ecological Processes and Management Potential (pp 195–216). New York, San Fransisco, London

Kok CJ, Meesters HWG & Kempers AJ (1990) Decomposition rate, chemical composition and nutrient recycling of *Nymphaea alba* L. floating leaf blade detritus as influenced by pH, alkalinity and aluminium in laboratory experiments. Aquat. Bot. 37: 215–227

Kok CJ & Van der Velde G (1990) The influence of selected water quality parameters on the decay rate and exoenzymatic activity of detritus of *Nymphaea alba* L. floating leaf blades in laboratory experiments. Oecologia (submitted)

Lammens EHRR & 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

Larsen VJ (1982) The effect of pre-drying and fragmentation on the leaching of nutrient elements and organic matter from *Phragmites australis* (Cav.) Trin. litter. Aquat. Bot. 14: 29–39

Moed JR & Hallegraeff GM (1978) Some problems in the estimation of chlorophyll-α and phaeopigments from pre- and post-acidification spectrophotometric measurements. Int. Rev. ges. Hydrobiol. 63: 787–800

Prentki RT, Gustafson TD & Adams MS (1978) Nutrient movements in lake shore marshes. In: Good RE, Whigham DF & Simpson RL (Eds) Freshwater Wetlands. Ecological Processes and Management Potential (pp 169–194). New York, San Fransisco, London

Richardson CJ, Tilton DL, Kadlec JA, Chamie JPM & Wentz WA (1978) Nutrient dynamics of northern wetland ecosystems. In: Good RE, Whigham DF & Simpson RL (Eds) Freshwater wetlands. Ecological Processes and Management Potential (pp 217–241). New York, San Francisco, London

Robb F, Davies BR, Cross R, Kenyon C & Howard-Williams C (1979) Cellulolytic bacteria as primary colonizers of *Potamogeton pectinatus* L. (Sago pond weed) from a brackish south-temperate coastal lake. Microb. Ecol. 5: 167–177

Rogers KH & Breen CM (1981) Effects of epiphyton on *Potamogeton crispus* L. leaves. Microb. Ecol. 7: 351–361

Roijackers RMM (1981) A comparison between two methods of extracting chlorophyll-α from different phytoplankton samples. Hydrobiol. Bull. (Amsterdam) 15: 179–183

Smits AJM, De Lyon MJH, Van der Velde G, Steentjes PLM & Roelofs JGM (1988) Distribution of three nymphaeid macrophytes (*Nymphaea alba* L., *Nuphar lutea* (L.) Sm. and *Nymphoides peltata* (Gmel.) O. Kuntze) in relation to alkalinity and uptake of inorganic carbon. Aquat. Bot. 32: 45–62

Smock LA & Stoneburner DL (1980) The response of macroinvertebrates to aquatic macrophyte decomposition. Oikos 35: 397–403

Twilley RR, Brinson MM & Davis GJ (1977) Phosphorus absorption, translocation and secretion in *Nuphar luteum*. Limnol. Oceanogr. 22: 1022–1032

Van der Velde G (1980) Remarks on structural, functional and seasonal aspects of nymphaeid-dominated systems. Thesis, Nijmegen (pp 11–58)

Van der Velde G, Custers CPC & De Lyon MJH (1986) The distribution of four nymphaeid species in the Netherlands in relation to selected abiotic factors. EWRS/AAB 7th Symp. Aquat. Weeds (Loughborough): 363–368

Van der Velde G, Van der Heijden LA, Van Grunsven PAJ & Bexkens PMM (1982) Initial decomposition of *Nymphoides peltata* (Gmel.) O. Kuntze (Menyanthaceae) as studied with the leaf marking method. Hydrobiol. Bull. (Amsterdam) 16: 51–60

Van der Velde G & Peelen-Bexkens PMM (1983) Production and biomass of floating leaves of two species of Nymphaeaceae in two Dutch waters. Proc. Int. Symp. Aquat. Macrophytes, Nijmegen, 18–23 September, 1983: 230–235

Wallace JB & O'Hop JH (1985) Life on a fast pad: waterlily leaf beetle impact on water lilies. Ecology 66: 1534–1544

Westlake DF (1982) The primary productivity of water plants. In: Symoens JJ, Hooper SS & Compère P (Eds) Studies on Aquatic Vascular Plants (pp 165–180). Royal Botanical Society of Belgium, Brussels

Wetzel RG, Rich PH & Allen HL (1972) Metabolism of dissolved and particulate detrital carbon in a temperate hard-water lake. Mem. Ist. Ital. Idrobiol. 29: 185–243