

Can small water level fluctuations affect the biomass of *Nymphaea alba* in large lakes?

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Abstract

In this study we investigated above-ground biomass and morphological responses of a floating-leaved plant species, *Nymphaea alba*, to small spring water level manipulations (0.1–0.5 m) in a large, shallow lake over a 9-year period (1995–2003). A year effect was found in mean annual above-ground plant biomass with higher values found in years of low water levels, 275–339 g DW m⁻² in 1995 and 2003 against 143–198 g DW m⁻² in 1996–2002 (no data transformation). No significant changes in biomass patterns were observed within each season (one summer peak), except in 1995 when a summer decline in biomass occurred. The amplitude and duration of exposure to high water levels affected the spring and annual above ground biomass of *N. alba*. The plant responded to high spring water levels by producing longer and thinner petioles to preserve leaves from flooding while no significant changes in leaf surface area (except in May) and leaf/petiole biomass ratio were obtained. The results are interpreted with regard to plant adaptations to changing environments (biomass allocation patterns in the different plant organs and stem density) and the effects of other abiotic factors relevant to the size of the system. We concluded that small deviations in spring water level can be driving forces in a large system in controlling the above-ground biomass of this floating-leaved plant.

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1. Introduction

The importance of water level fluctuations in regulating aquatic plant distribution and composition has been demonstrated in numerous lakes (e.g. Wallsten and Forsgren, 1989; Van der Valk, 1990; Papastergiadou and Babalonas, 1992; Blindow et al., 1993; Gacia and Ballesteros, 1996; Hertzman and Larsson, 1999). Water level directly affects plants through changes in for example net photosynthesis. It also indirectly affects plants through changes in sediment characteristics, water clarity and wind/wave exposure (e.g. Scheffer, 1998). In practice the water level is rarely constant over a year. Facing these dynamic conditions, notably when large increases in water level occur, plants must exhibit morphological responses (e.g. changes in stem biometrics) and changes in biomass allocation patterns in above- and below-ground organs (e.g. increased biomass allocation to rooting systems) to survive (Coops et al., 1996; Blanch et al., 1999; Vretare et al., 2001).

Currently, compared to submerged and emergent plants, little research has been conducted on morphological and biomass responses of floating-leaved plants to water level fluctuations (but see for example Nohara and Tsuchiya, 1990; Sinden-Hempstead and Killingbeck, 1996). Floating-leaved plants, particularly nymphaeids, are often the dominant vegetation in shallow waters (Brock et al., 1983; Van der Velde and van der Heijden, 1985; Wallsten and Forsgren, 1989). The dominance of nymphaeids in a large range of water depths (0.5–3 m, e.g. Wetzel, 1975; Spence, 1982; Brock et al., 1987; Testard, 1995) has led to them being considered as tolerant of significant water level changes, partly due to their characteristic growth form. Nymphaeids form dense canopies of floating leaves, not hindered by turbidity. To a certain degree of water level increase, these plants stay anchored in the sediment thanks to a well-developed rooting system, and young leaves can remain at the water surface by petiole elongation (Brock et al., 1987). However, little is known about the response of nymphaeids to relatively small changes in water level in natural habitats.

In our case, the extensive beds of floating-leaved macrophytes of the large, shallow Lake Grand-Lieu, and more particularly the dominant *Nymphaea alba*, have resulted in the

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lake becoming endangered by a large accumulation of organic matter (Rofès et al., 1993; Marion and Brient, 1998). Standard techniques used for controlling aquatic plants (cutting, harvesting) cannot be applied in the lake because of its high conservation interest (site of international significance for the conservation of floating vegetation-nesting bird species). The alternative of a slight increase in spring water levels (without interfering with agricultural and conservation interests) has been chosen for limiting the growth of *N. alba*, despite its known adaptation to water level fluctuations (Brock et al., 1987). In the present study, we intended to test the hypothesis that relatively slight increase in water level during spring leaf emergence of *N. alba* could be an important driving force in this large lake, influencing biomass and morphology of this floating-leaved plant. The specific objectives of the study were: (1) to determine whether biomass patterns of the above-ground organs of *N. alba* were affected by small variations in water regime (0.1–0.5 m) over a 9-year period (1995–2003) and explore the modelled response of *N. alba* above-ground biomass in relation to water level parameters (amplitude, timing and duration of exposure to low/high water levels), and (2) to evaluate the morphological responses and biomass allocation patterns of *N. alba* with respect to water level fluctuations.

2. Study area and methods

2.1. Study area

Lake Grand-Lieu is a large, shallow, turbid, eutrophic and macrophyte-dominated freshwater ecosystem in western

France (47°05'N, 1°39'W). It covers 4000 ha in summer and extends to 6300 ha in winter as a result of flooding of surrounding peaty marsh grasslands (Fig. 1). Half of the summer area is composed of a peat fen with *Phragmites*, *Salix* and *Alnus*, which becomes progressively exposed in early summer and thus isolated from the water area. The special feature of Lake Grand-Lieu is the presence of extensive beds of floating-leaved plants (770–978 ha), mainly nymphaeids, which covered from 24 to 42% of the permanently flooded area (2000 ha) during the study period (Paillisson and Marion, 2001; Boret and Reeber, 2002). Such a Nymphaeid cover is unusual in European lakes and ranged at the top, for instance, of the recent compilation of Van Geest et al. (2003) on Nymphaeid cover of a large set of shallow Dutch lakes. The central 1000 ha of open-water at Lake Grand-Lieu lacks vegetation except for small patches of submerged and emergent macrophytes covering less than 10 ha.

2.2. Water level manipulations

Water level manipulations were restricted to the months during which critical life cycle stages of *N. alba* occur, i.e. emergence and spring development (May–July). Winter flooding is unlikely to have much direct impact on *N. alba* in temperate lakes since the plant overwinters in the form of dormant underground structures. Furthermore water level fluctuations in Lake Grand-Lieu follow the seasonal cycle of rainfall in the catchment and high inflows occur from November to April when the daily discharges from the two rivers entering the lake are highest. Consequently water levels

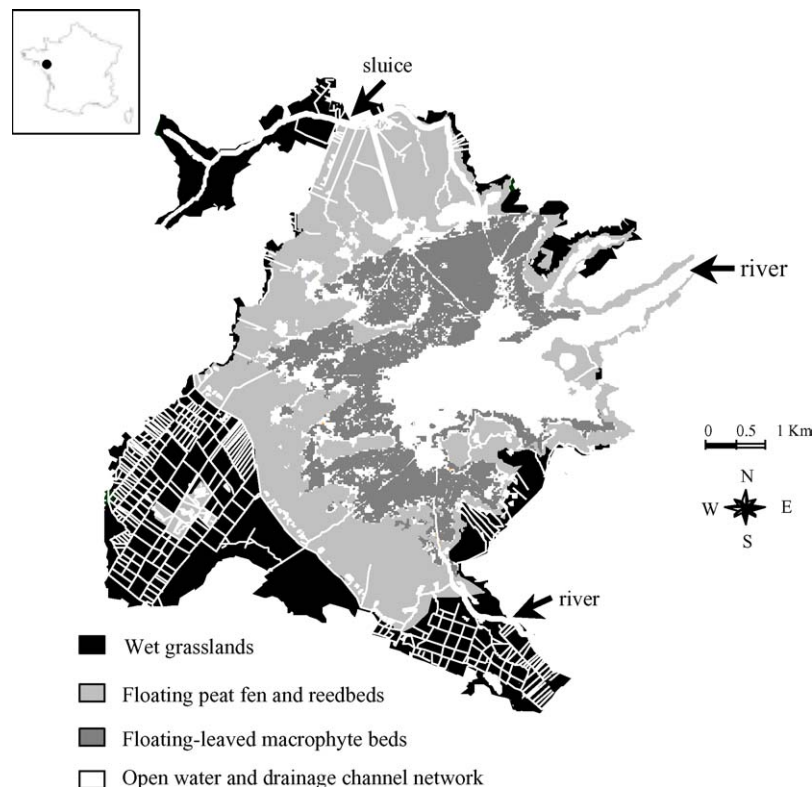


Fig. 1. Map of Lake Grand-Lieu with the different vegetation zones.

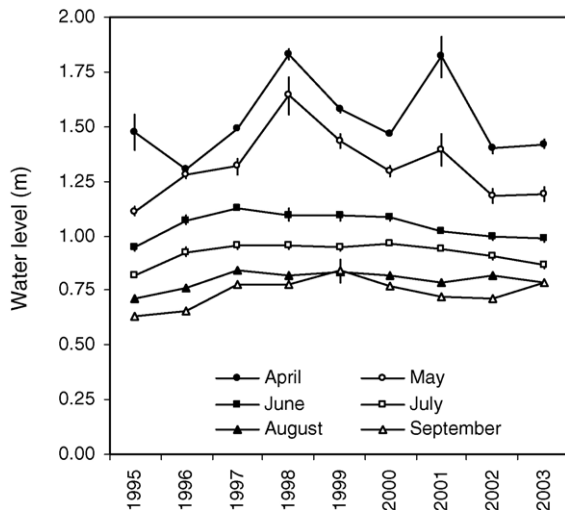


Fig. 2. Monthly water level (mean values with a 95% confidence interval) in the floating-leaved macrophyte area from April to September in all 9 years.

cannot be regulated effectively by the sluice gate in this period and large between-year fluctuations in water level occur (see water levels in April in all 9 years, Fig. 2). The low spring water levels in 1995 (May–June) were typical of the situation over the past 30 years (Marion, 1999) before a new water regime was introduced from 1996 to 2001: +0.20 m in May (1.30 m) in the *N. alba* area and +0.10 m in June and in July when compared with 1995 (1.10 and 0.95 m, respectively), accentuated in some years (1998, 1999 and 2001) by additional flooding in May (+0.10–0.30 m compared to 1996, 1997 and 2000, Fig. 2). In 2002 and 2003, a third water regime, intermediate between the ones in 1995 and 1996–2001, was applied with 1.20, 1.00 and 0.90 m in May, June and July. Overall water levels slowly decreased in summer (August to September) as a result of evapotranspiration and agricultural pumping.

2.3. Plant monitoring, environmental variables chosen and data processing

N. alba, like other floating-leaved plants, has a small biomass relative to high primary productivity (Van der Velde and Peelen-Bexkens, 1983; Tsuchiya et al., 1990). This results from numerous successive leaf cohorts produced during the growing season. Leaf longevity ranges from 22 to 26 days in Lake Grand-Lieu (Marion et al., unpublished data) compared to 46–49 days in other sites (Kok et al., 1990), and turnover rates of above-ground leaves are about four times (Kok et al., 1990) to nine times a year (Lake Grand-Lieu, unpublished data). In the present study, we focused on instantaneous biomass and did not estimate primary productivity since leaf longevity was rather constant over the season. A monthly sampling was used to document the biomass pattern of *N. alba* as in other works (e.g. Twilley et al., 1985). Additional biomass data (two harvests per month, unpublished data) showed similar results for the biomass pattern of *N. alba* and supported the monthly sampling interval design.

Samples of the above-ground parts of *N. alba* were harvested using the standing crop method (Brock et al., 1987) once a

month from May to October. A 1 m² area was harvested each month at 6 (1995–1997) and 10 (1998–2003) stations. These stations were located in monospecific stands far enough distant from the shore (>150 m) to minimize differences in wind and wave exposure known to affect plant development (e.g. Wallsten and Forsgren, 1989; Blindow et al., 1993; Coops et al., 1994; Scheffer, 1998). Sampling was not a repeated measurements design (not the same individuals sampled) since it consisted in harvesting not the same 1 m² area but a nearby area at each station over the season (see longevity parameters and a relevant possible bias in studying *N. alba* growth pattern). The leaves and petioles of a fraction of the fresh material (500 g) were dried separately at 80 °C for 6 days and weighed. All biomass data were reported as grams dry weight per square metre (g DW m⁻²) and mean values were defined with a 95% confidence interval. From 1998, biomass of the plant was derived from the linear regression of fresh (FM) and dry standing crop (DM) from data collected in the 1995–1997 period and older unpublished data (DM = 0.096FM + 2.70, R² = 0.97, P < 0.001, n = 156). All biomass data were square-root transformed to meet the assumptions of normality. Normality was tested with the Kolmogorov–Smirnov/Lilliefors test. Analysis of variance (one-way ANOVA) was used to test for differences in mean annual above-ground biomass over the 9 years (year factor). ANOVA was also used to compare the biomass pattern of *N. alba* (phenology) between months (month factor) and within each season (i.e. pooled across years). Multiple comparisons were performed using the Tukey HSD procedure.

To document morphological responses and plasticity in biomass allocation patterns of *N. alba* in relation to water level manipulations, at harvest we recorded changes in stem density from 1995 to 1997, and some additional biometric measurements in the laboratory in 1996: length and weight of petioles (expressed in cm and g DW m⁻², respectively), leaf surface area using a planimeter (cm²), leaf area index (LAI) derived from the density and surface area of leaves, and leaf/petiole biomass ratio. One-way ANOVA was used to test for differences in stem density over the 3 years (1995–1997, year factor), and in all biometric variables in 1996 (month factor). Monthly biomasses were related to changes in stem density using a linear regression.

Water level is a dynamic factor changing temporally. Consequently, not only the amplitude and the seasonal maximum water level affect plants, but also the duration, frequency and the period in the life cycle in which high water levels occur (Ostendorp, 1991; Coops and Hesper, 2002; Paillisson and Marion, 2002). In the present study, daily water levels in the floating plant area were compiled (mean value) for each year for various critical life cycle stages of the plant, including emergence (May and April–May) and spring development (May–June, May–July, April–June, April–July). Furthermore we determined water-level duration curves based on the 9-year period to describe the duration and continuity of exposure to various water levels as used by Bodensteiner and Gabriel (2003). From these cumulative frequency duration curves, we calculated the number of days at low and high water levels using respectively the 10, 25, 75 and 90th percentiles at four periods (April–May, April–June, May–June and May–July).

Changes in *N. alba* biomass (May, May–June, May–July, May–October and maximum seasonal biomass) were related to these various water level scenarios (mean water levels and number of days at low/high water levels) using linear regression.

3. Results

3.1. Biomass patterns in *N. alba*

The ANOVA tested on the mean annual above-ground biomass of *N. alba* showed a year effect ($F = 12.44$, $P < 0.001$, $n = 462$, Fig. 3). Biomass values (squared-root transformation) were the highest in 1995 and 2003 (16.0 – 18.0 g DW m⁻²) compared to values ranging from 11.6 to 13.6 g DW m⁻² in 1996–2002. At the same time, seasonal biomass patterns of *N. alba* did not vary greatly between years (Fig. 4). One peak of biomass was the rule over the time series although a threshold of maximum biomass lasting four and five consecutive months occurred in 1999, 2000 and 2002. Some delays in the seasonal maximum biomass appeared depending on years. In 1995, a somewhat different biomass pattern occurred. Two non-consecutive maximum biomass values were recorded (June and September) and a lower biomass was found in mid-summer (July and August).

3.2. Biometric variables

The results of the one-way ANOVA on stem densities in the 1995–1997 period showed a year effect ($F = 6.67$, $P = 0.002$, $n = 123$). The stem densities were significantly higher in 1995 (49.1 ± 5.6 stems m⁻²) than in the two other years (37.1 ± 5.0 and 38.7 ± 4.9 stems m⁻², respectively in 1996 and 1997, pairwise comparisons with $P < 0.01$). Moreover changes in plant biomass were highly related to stem densities ($0.72 < r^2 < 0.80$, $P < 0.001$, $n = 39$ and 41 , respectively in 1995 and 1996, and 1997).

Some morphological responses of *N. alba* to water level fluctuations were found during the growing season in 1996 (Fig. 5). The stem density was lower in May and October and a significant peak in the stem density was noted in June ($F = 81.7$, $P < 0.001$, $n = 32$, results of pairwise comparisons are reported in Fig. 5). Longer and thinner petioles were noted in spring when water levels were high compared to what was found from August or September according to the two relevant

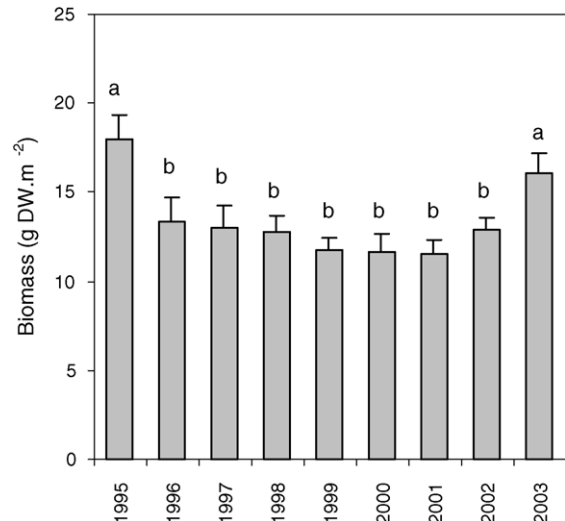


Fig. 3. Annual biomass of *N. alba* (mean square-root values with a 95% confidence interval) over the time series (1995–2003). Values with the same letter are not significantly different at $P \leq 0.05$ from pairwise comparisons using a Tukey HSD test.

biometric variables ($F = 32.14$, $P < 0.001$, $n = 27$ for petiole length, and $F = 5.64$, $P < 0.01$, $n = 30$ for biomass per petiole metre, see related pairwise comparisons in Fig. 5). However the resulting energy allocated by the plant to petiole biomass did not show any fundamental changes according to months, although a significant difference in total petiole biomass was noted between June and August ($F = 3.34$, $P = 0.05$, $n = 27$, and related pairwise comparisons in Fig. 5). At the same time, the leaf surface area tended to peak in June and July ($F = 6.80$, $P < 0.001$, $n = 35$) and LAI significantly peaked in these months ($F = 23.84$, $P < 0.001$, $n = 35$, Fig. 5). In spite of some changes in the morphology of the plant according to water level fluctuations, the major part of the investment of *N. alba* in biomass of above-ground organs was always devoted to leaves (Fig. 5). The leaf/petiole biomass ratio ranged from 1.32 to 2.01 and did not show any particular pattern over the season.

3.3. Relationships between water level manipulations and biomass changes in *N. alba*

The spring and annual biomass of *N. alba* were related to the water regimes occurring during its emergence and development stages, using either mean water levels or duration of exposure to

Table 1
Water level parameters (mean water levels, WL, and duration of exposure to extreme water levels, D) in regressions that significantly predicted changes in biomass of *N. alba* (B , square-root transformed) according to different life cycle stages of the plant over the 1995–2003 period

Dependent variable	Factor	r^2	P	Slope \pm S.E.	Intercept \pm S.E.
$B_{\text{May-June}}$	$D < 25\text{th percentile}_{\text{May-June}}$	0.44	0.05	1.00 ± 0.42	-2.10 ± 0.62
$B_{\text{May-July}}$	$D > 75\text{th percentile}_{\text{May-July}}$	0.51	0.04	-0.22 ± 0.08	17.59 ± 1.68
$B_{\text{May-October}}$	$WL_{\text{May-June}}$	0.44	0.02	-15.15 ± 5.34	31.42 ± 6.34
$B_{\text{May-October}}$	$D < 10\text{th percentile}_{\text{May-June}}$	0.47	0.04	1.67 ± 0.67	4.23 ± 0.37
$B_{\text{May-October}}$	$D < 25\text{th percentile}_{\text{May-June}}$	0.58	0.02	0.79 ± 0.25	2.02 ± 0.37
$B_{\text{May-October}}$	$D > 75\text{th percentile}_{\text{May-June}}$	0.56	0.02	-0.28 ± 0.09	16.24 ± 1.06
$B_{\text{May-October}}$	$D < 25\text{th percentile}_{\text{May-July}}$	0.54	0.02	0.51 ± 0.18	3.02 ± 0.36
$B_{\text{May-October}}$	$D > 75\text{th percentile}_{\text{May-July}}$	0.65	0.01	-0.23 ± 0.06	17.51 ± 1.19

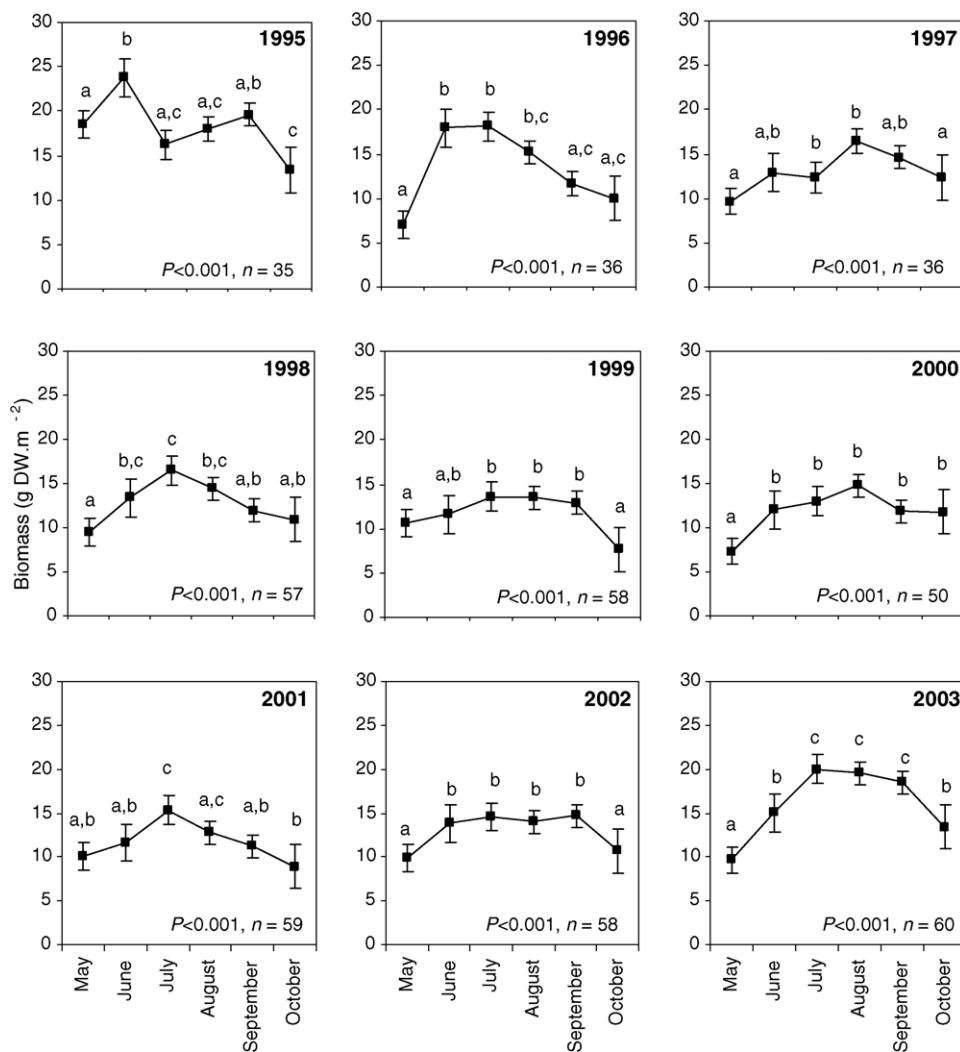


Fig. 4. Biomass patterns of *N. alba* among months within each season over the 1995–2003 period. All biomass values (mean with 95% confidence interval) are square-root transformed. Results of the one-way ANOVA (month factor) are indicated. Data with the same letter are not significantly different at $P \leq 0.05$ from pairwise comparisons using a Tukey HSD test.

spring water levels over the time series (Table 1). High spring water levels and durations of exposure to high water levels (75th percentile) significantly affected *N. alba* biomass. At the same time, the less the plant was subjected to high spring water levels (10th and 25th percentiles), the less its growth was affected. We failed to detect any significant relationship between water level parameters and *N. alba* biomass during the other life cycle stages of the plant (seasonal maximum and summer period). Among all water level scenarios including water levels in April no significant relationship was found with plant biomass.

4. Discussion

Although large variations in mean annual above-ground biomass of *N. alba* were found over the study period (143–339 g DW m⁻², non-transformed data), these values were lower than reliable biomass values reported in previous studies: 400–500 g DW m⁻² (Smart, 1980; Malthus et al., 1990). Conditions in Lake Grand-Lieu are probably less favourable than in other sites for the growth of *N. alba*. The mean annual

above-ground biomass of the plant was significantly higher in years characterised by low spring water level (1995 and 2003). All the years, except 1995, did not show significant changes in biomass pattern of *N. alba* among months. Van der Velde and Peelen-Bexkens (1983) also mentioned one summer peak in *N. alba* above-ground biomass in two Dutch waters. In our study, a summer depression in biomass values was observed in 1995 after a very large spring biomass (maximum biomass over the time series, 517 g DW m⁻²). A probable self-shading mechanism resulting from the high density and surface area of leaves could have occurred and resulted in foliage depletion. Indeed high leaf density increases competition for light and may limit photosynthetic capacity. Such a mechanism of self-shading has also been described by other authors (Sand-Jensen, 1989; Lodge, 1991) as explaining plant density limitation. New cohorts of leaves and petioles resulted in the recovery of a high *N. alba* biomass in September.

In the present study, a lower *N. alba* above-ground biomass occurred in the years when high water levels were experienced (Fig. 3). Above-ground organ production should incur cost of

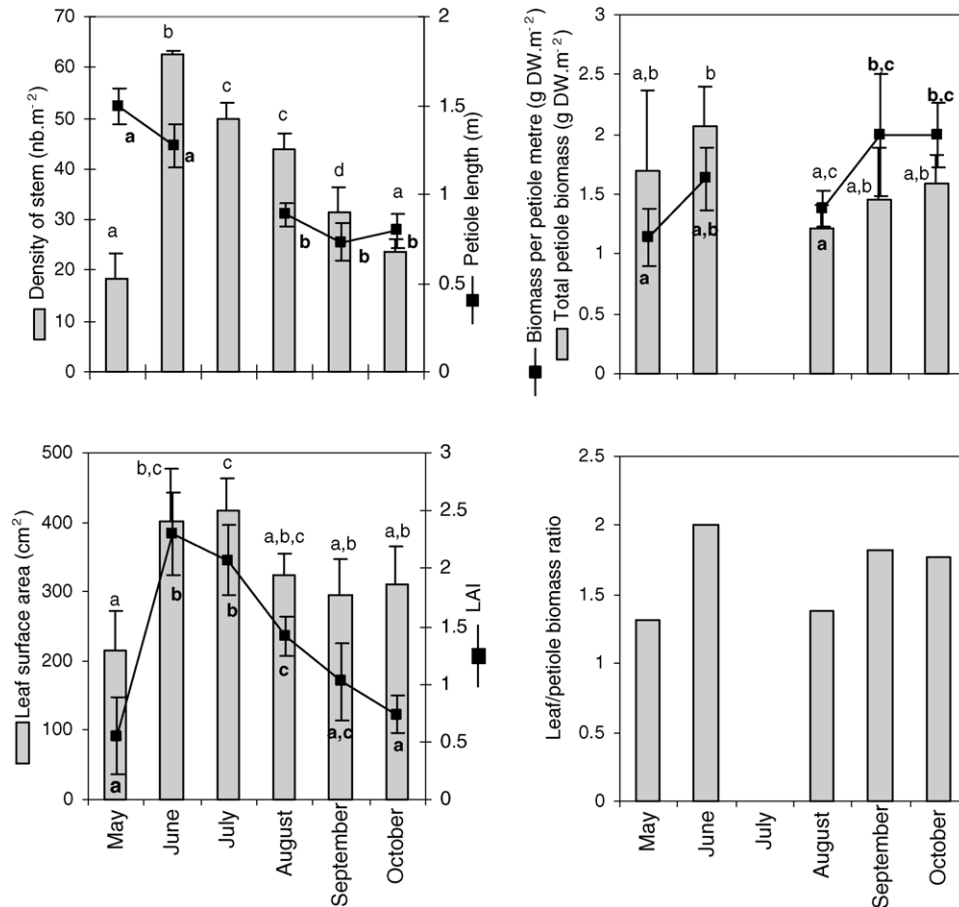


Fig. 5. Seasonal changes in biometrics of *N. alba* in 1996: stem density (No. m⁻²), petiole length (m), biomass per petiole metre and total petiole biomass (g DW m⁻²), leaf surface area (cm²), LAI and leaf/petiole biomass. Values with the same letter are not significantly different at $P \leq 0.05$ from pairwise comparisons using a Tukey HSD test.

both leaf and petiole, whose cost increases in proportion to water depth. Leaf surface area, which is an integrative measure of resource allocation and photosynthetic capacity, could decrease with increasing water depth to compensate for the increased cost of producing a longer petiole. In the present study, there was no consistent pattern of change in leaf surface area in relation to the water level variations experienced (except in May, Fig. 5). This suggests that petiole elongation compensates for water level increase without affecting biomass allocation to leaves. Indeed *N. alba* responded to high water levels by producing longer and thinner petioles to preserve leaves from flooding but there was no significant change in biomass allocation between petioles and laminae (Fig. 5). However the balancing of costs of the plant is more complicated, since the other organs of the plants (flowers and under-ground structures) must be taken into account. These latter organs constitute significant amounts of biomass: around 15% of the above-ground biomass for flowers (Brock et al., 1987) and 28–74% for rhizomes and roots (Brock et al., 1987; Malthus et al., 1990; Marion et al., unpublished data). Thus the increased mobilization of nutrients to above-ground organs with high water levels without any balancing of costs in petioles versus leaves is probably provided from resource translocation from large below-ground organs (Brock et al., 1987; Malthus

et al., 1990) as has been found for other species (e.g. Clevering and Hundscheid, 1998; Blanch et al., 1999; Vretare et al., 2001).

Only a few studies have investigated the effect of water level fluctuations on the growth of floating-leaved macrophytes and most have focused on the role of flooding in the maintenance of wetland species (e.g. Brock et al., 1987; Papastergiadou and Babalonas, 1992). The impact of high water levels on plants must be evaluated with respect to their amplitude, duration and timing. For example, Brock et al. (1987) showed that extremely high water levels (at least 3 m) in summer led to the disappearance of wetland species that were flooded for several weeks. However they noted only a slight decrease in the abundance of *N. alba*. Our results showed that a slight increase in water levels in the emergence/development phases of the plant (<0.5 m over the time series) significantly affected plant biomass even if these rises in water level were low. These apparently conflicting results must be interpreted with respect to the size of the wetlands studied (19.7 ha in the oxbow lake in the Netherlands, Brock et al. (1987) compared to 2000 ha in the central part of Lake Grand-Lieu) and relevant environmental factors and feed-back mechanisms. For instance, it is well known that wave and wind stresses vary according to size and morphology of water bodies (e.g. Scheffer, 1998; Coops and

Hosper, 2002). In the case of Lake Grand-Lieu these factors are likely to be severe in spring when high water levels and sparse vegetation occur. Furthermore wave impact has probably increased in Lake Grand-Lieu since the almost complete disappearance of beds of *Scirpus lacustris* and *Typha angustifolia*: currently 2–3 ha and only a few stands of these emergent species persist in the central open-water area instead of 60 and 26 ha, respectively in the early 1980s (Marion and Marion, 1992). These emergent plants played a key role in the absorption of wind/wave action. Even if wave action can be severe during the first part of the growing period when the vegetation is sparse and may cause mechanical damage to *N. alba* organs at least in exposed areas (i.e. near the open central area), wind/wave action is inhibited later in the season due to dense floating-leaved plant beds. Moreover no significant changes in wind velocity occurred over the study period (mean annual wind velocity ranged from 23 to 26 km h⁻¹, data from the Bouguenais meteorological station located at 5 km near the lake).

Our results also showed the importance of timing (emergence and spring development phases) and duration of exposure to extreme water levels in spring but also annual above-ground biomass of *N. alba*. These findings were in accordance with those found by Blindow et al. (1993, 1998) on submerged plants. They observed shifts in the coverage and biomass of submerged vegetation in two large, shallow lakes in Sweden (Lake Tåkern and Lake Krankesjön) on several occasions, coinciding with deviations from the average water level (amplitude and duration in spring). They concluded that high spring water level was the most probable cause of the relatively low biomass of submerged vegetation.

In nutrient-enriched shallow lakes, the recovery or maintenance of a vegetated state is a major objective from both ecological and restoration points of view (e.g. Moss et al., 1997; Scheffer, 1998). In contrast, in some water bodies dense macrophyte-covered areas can be a nuisance for recreational activities (Cooke et al., 1993; Coops et al., 2002), but also represent a real threat for systems by strongly contributing to silting (e.g. Dutartre et al., 1989; Wallsten and Forsgren, 1989; Testard, 1995). The results of the present study showed that a slight increase in water level in a large system at key life cycle stages of a floating-leaved plant can be regarded as a potential alternative for controlling its biomass when normal control techniques cannot be used because of local constraints.

Acknowledgments

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