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Differential responses of the floating-leaved aquatic plant *Nymphoides peltata* to gradual versus rapid increases in water levels

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ABSTRACT

We compared the growth responses of the floating-leaved species *Nymphoides peltata* to gradual and rapid rising water levels under two nutrient concentrations (1 g and 12 g of slow released fertilizer (N–P–K: 16–8–12) per container filled with 8 kg washed sand), and predicted the population expansion after these floods. The results showed that the capacity for petiole elongation was dependent on leaf age, and only leaves that were no more than five days old had the capability to reach the water surface when the water level increased rapidly from 50 cm to 300 cm. Plants subjected to a gradual rising water level tracked the increase in water depth whose petioles elongated at 3.96 ± 1.70 cm per day and 4.80 ± 0.16 cm per day under low and high nutrient concentrations respectively throughout the experiment period. When water levels were rapidly raised, leaf petioles elongated rapidly at 25.48 ± 1.51 cm per day and 26.64 ± 2.24 cm per day under low and high nutrient concentrations respectively during the first ten days. Plants under a constant water level maintained highest mean leaf recruitment (mean 3.0 ± 0.33 leaves and 24.4 ± 5.87 leaves every ten days under low and high nutrient concentrations, respectively). Therefore, more young leaves existed in the canopy ensuring that when the water level increases, young leaves can rapidly emerge after submergence. Gradual water level rise did not significantly affect biomass and ramet production (4.75 ± 1.41 g and 5.50 ± 1.22 ramets in low nutrient; 48.49 ± 21.45 g and 35.67 ± 11.78 ramets in high nutrient), but rapid water level rise negatively affected ramet production in both nutrient concentrations (3.00 ± 1.26 ramets and 11.25 ± 4.19 ramets in low and high nutrients, respectively). The results indicated that continual leaf recruitment and rapid petiole elongation were both important ways in which *N. peltata* adapted to increasing water levels. Extreme flooding may be a disturbance factor that affects plant growth and the population expansion of *N. peltata*, while small gradual water level rise should not harm this species.

1. Introduction

Wetland plants are regularly or irregularly subjected to flooding which usually causes plant mortality or retards growth (Klimesova, 1994; He et al., 1999; Vervuren et al., 2003) and affects the composition, diversity (van der Valk et al., 1994; Bornette and Amoros, 1996; Riis and Hawes, 2002; Nicol et al., 2003; Van Geest et al., 2005) and distribution (Vervuren et al., 2003; Van Eck et al., 2004; Pennings et al., 2005) of macrophyte communities. The most important constraint for plants subjected to flooding is oxygen deficiency as a result of the slow diffusion rates of oxygen in the water (Crawford and Brändle, 1996; Drew, 1997; Bailey-Serres and Voesenek, 2008), and this leads to the accumulation of deleterious compounds, such as Fe^{2+}, Mn^{2+} and organic acid, which harm the roots (Laan et al., 1990, 1991). As a consequence, plant survival and growth rates under flooding conditions are reduced.

To cope with water stress, flooded plant species develop different adaptive strategies to increase survival during floods. These strategies involve hyponastic growth of leaves, and shoots or leaves elongation to recover contact with the atmosphere (Grimoldi et al., 1999; Voesenek et al., 2003; Pierik et al., 2009). For example, the floating-leaved species *Villarsia reniformis* continually recruits young leaves in the canopy which elongate rapidly to the water surface when flooded (Cooling et al., 2001).

In the past, the magnitude and temporal distribution of floods have changed as a result of human activities, including the destruction of vegetation, land reclamation and siltation, and the construction of levees (Yin and Li, 2001). In the future, it is predicted that global warming scenarios will cause extreme events, such as earlier and higher flooding, to occur more frequently (Houghton et al., 2001), which may have important consequences for plant growth in the floodplains. The severity of flooding is

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affected by flooding duration, submergence depth, and underwater light availability (Vervuren et al., 2003). Though many studies have investigated plant responses to flooding intensities, including flooding depth, duration, and frequency (Miller and Zedler, 2003; Deegan et al., 2006; Geoff et al., 2007), research involving the effect of flood rates on plant growth and adaptive responses are lacking.

Nymphoides peltata, a perennial floating-leaved species, is common to Liangzi Lake, which undergoes seasonal water level fluctuations. This paper investigates the growth responses of *N. peltata* to flooding and the plant's underlying adaptive strategies. We proposed two hypotheses: firstly, *N. peltata* may elongate petioles accordingly to recover contact with the air, and recruit leaves continually to ensure that young leaves always exist in the canopy which elongate faster than older ones when flooded. Secondly, the growth of *N. peltata* will be reduced with increasing flood rates. To test the two hypotheses, we grew *N. peltata* plants under three flooding treatments: constant water level, gradual water level rise, and rapid water level rise. We measured petiole elongation, leaf recruitment, ramet number and plant biomass in response to the gradual and rapid water level rise in interaction with two nutrient concentrations.

2. Methods

2.1. Species description

N. peltata (Gmel.) O. Kuntze (Menyanthaceae) is a perennial floating-leaved plant, which is widely distributed in temperate and subtropical regions of continental Eurasia (Glück, 1924). The species usually occurs in still waters or ponds, lakes, and slow-moving streams, and their petioles hold the leaves floating above the water surface. They can also grow on moist land with leaves and petioles close to the surface of the ground. This widespread species is dispersed by seeds and rhizomes and has a prolific capacity for clonal growth (van der Velde and van der Heijden, 1981).

2.2. Experimental design

The experiment was conducted in The National Field Station of the Freshwater Ecosystem of Liangzi Lake in the Hubei province of China. The plant rhizomes used in our experiment were collected from Liangzi Lake in late July 2008. Homogeneous segments of 36 rhizomes (3.8 ± 0.39 cm length, means ± SD) with developed roots were selected and randomly transplanted into plastic pots (diameter = 22 cm, height = 16 cm) filled with 8 kg washed sand. One plant was potted per pot and 12 pots were placed in each of three concrete ponds (4 m × 4 m × 5 m deep), where they could be individually adjusted vertically by ropes connected to steel bars lying on top of the ponds. All pots were initially suspended at a 50 cm water depth for acclimation growth. The plants were examined every day for 30 days, and newly expanded leaves were labeled and the date recorded. The experiment combined three water levels with two nutrient concentrations in a factorial design and replicated six times. After 30 days, the plants were subjected to three flooding levels: a constant water level of 50 cm, a gradual rising of water level to 300 cm, and a rapid rising to 300 cm. In the constant treatment, the water level was kept at 50 cm depth throughout the whole experimental period. In the gradual rising treatment, the water level was increased from 50 cm to 300 cm by 10 cm every two days during the experimental period. In the rapid rising treatment, the water level was increased to 300 cm on the first day and was kept at this level throughout the experimental period. For the nutrient treatments, the two nutrient concentrations were 1 g (equivalent to 5.61 g N m^{-2} per year, low nutrient concentration) and 12 g (equivalent to 67.38 g N m^{-2} per year, high nutrient concentration) of a slow-release fertilizer (8–9 month Osmocote®, N–P–K: 16–8–12) per container. The pots in each pond were randomly allocated to the six treatments, with two replicates per pond. The water temperatures were 19.8–27.0 °C, pH 7.7–8.4, conductivity 76–127 μs cm^{-1} and the concentration of dissolved oxygen 5.5–8.5 mg l^{-1}. The water was clear with vertical light attenuation coefficient 0.59 m^{-1}.

2.3. Data collection

Leaf length was monitored every ten days. The length of the longest petiole was measured for every plant. Newly expanded leaves were labeled and counted for leaf recruitment measurement. During the first investigation, leaves that were labeled during the previous 30 days and reached the surface were recorded. The experiment was completed late in October 2008, and all the plants were harvested. The number of ramets was then counted, and the plants were dried to a constant weight at 65 °C for three days for dry weight determination.

2.4. Data analysis

All data were log(x) transformed to meet assumptions of normality and homoscedasticity. Repeated measures ANOVA was used to test for differences in petiole elongation, with water level and nutrient concentration as the between-subject main effect and time as the within-subject factor. Two-way ANOVA was used to test for differences in leaf production, ramet number and total biomass, with flooding and nutrient concentration as main factors. If a significant treatment effect was detected, post hoc pair-wise comparisons of means were made to examine differences between treatments using the Student Tukey's HSD for multiple comparisons.

3. Results

3.1. Petiole elongation

The capability for petiole elongation was dependent on leaf age. When water levels increased rapidly from 50 cm to 300 cm, only the leaves that were no more than five days old had the capability of reaching the water surface under both nutrient concentrations, while the older leaves failed to elongate to the surface and died (Fig. 1a and b). Repeated measures ANOVA showed significant water level and nutrient concentration effects (water level: $F = 4134.03$, $P < 0.001$; nutrient concentration: $F = 38.68$, $P < 0.001$). The interaction between water level and time was significant ($F = 209.09$, $P < 0.001$), showing that water level effects differed through time. Plants maintained at a 50 cm water depth mostly kept their leaf petiole lengths constant at 67.6 ± 5.8 cm and 73.2 ± 7.9 cm under low and high nutrient concentrations, respectively. Leaves of plants subjected to gradual water level rise tracked the increase in water depth whose petioles elongated at 3.96 ± 1.70 cm per day and 4.80 ± 0.16 cm per day under low and high nutrient concentrations throughout the experiment period, respectively. When water levels were rapidly raised, leaves emerged within four days and petioles elongated rapidly at 25.48 ± 1.51 cm per day and 26.64 ± 2.24 cm per day under low and high nutrient concentrations during the first ten days, respectively (Fig. 2a and b).

3.2. Leaf recruitment

N. peltata experienced continual leaf recruitment. We determined leaf production during the water level treatments on leaf number basis every ten days during the experimental period. Two-

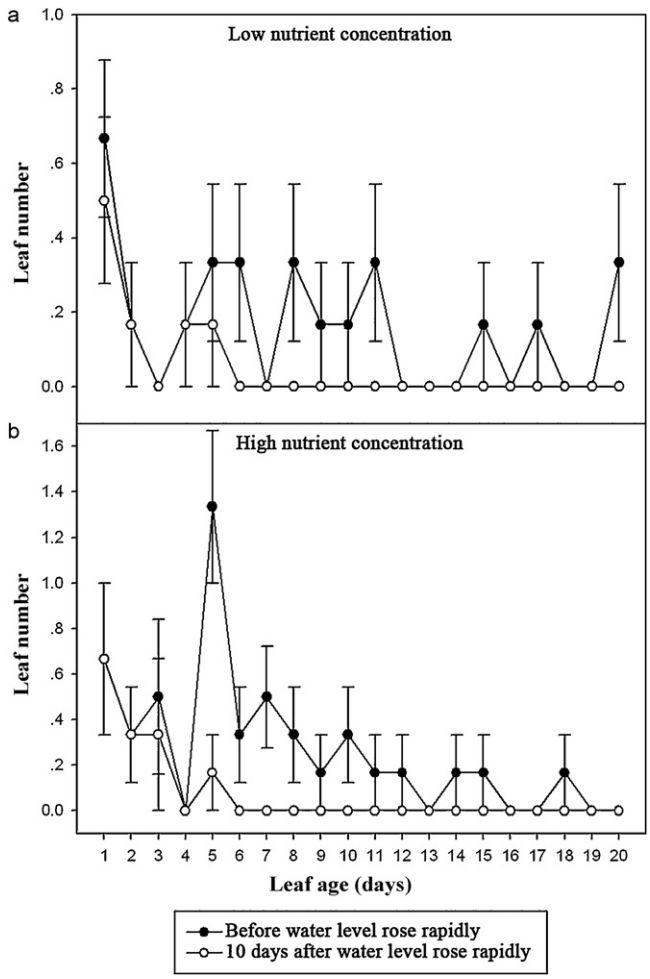

Fig. 1. The number of leaf blades per plant, with different ages, before the water level rose rapidly and leaf blades which could reach the water surface 10 days after the water level rose rapidly under (a) low and (b) high nutrient concentration.

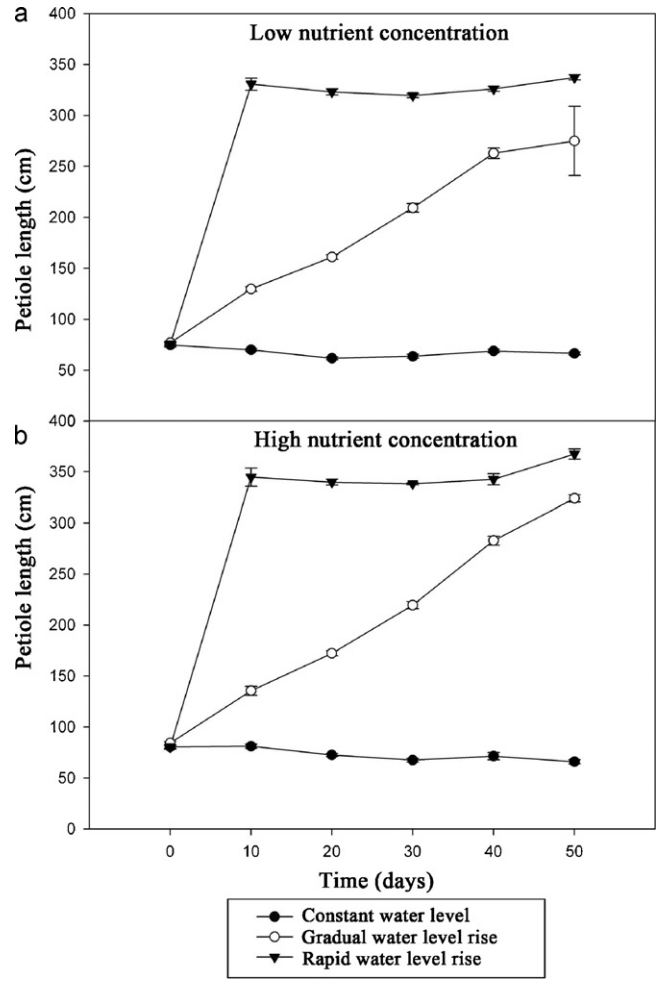

Fig. 2. The length of the longest petiole at constant water level, gradual water level rise, and rapid water level rise treatments under (a) low and (b) high nutrient concentration. Data indicate means ± SE.

way ANOVA indicated that water level, nutrient concentration and their interaction significantly affected leaf production (water level: $F = 169.79$, $P < 0.001$; nutrient concentration: $F = 489.54$, $P < 0.001$; water level × nutrient: $F = 25.27$, $P < 0.001$).

Under low nutrient concentrations, leaf production was highest at the constant water level (mean 3.0 ± 0.33 leaves every ten days), though it decreased slightly after 30 days. Leaf production decreased as the water level increased gradually during the experimental period. Leaf production was lowest at rapid water level rise treatment (Fig. 3a).

Under high nutrient concentrations, leaf production increased continually at the constant water level (mean 24.4 ± 5.87 leaves every ten days), and exceeded the production at the gradually rising water level after 30 days. Leaf production increased as the water level gradually rose during the first 30 days, but then decreased. Similar to the results obtained under low nutrient concentrations, leaf production was lowest at rapid water level rise treatment (Fig. 3b).

3.3. Biomass and ramet number

Ramet number was significantly affected by the water level and nutrient concentration but not by their interaction (Table 1). Under the two nutrient concentrations, ramet number was not affected by the gradual water level rise, but significantly reduced by the rapid water level rise (Fig. 4a). Total biomass was significantly affected by water level, nutrient concentration and their interaction (Table 1). Total biomass did not differ between constant and gradual water level rise treatments in both nutrient concentrations, but was marginally reduced in the low nutrient concentration and significantly reduced under the high nutrient concentration by rapid water level rise (Fig. 4b).

4. Discussion

4.1. Petiole elongation

Petiole elongation in *N. peltata* was closely related to leaf age; this is consistent with the result found by Funke (1951). The result is also true for other floating-leaved plants, such as *Villarsia reniformis* (Cooling et al., 2001) and *Nelumbo nucifera* (Nohara and Tsuchiya, 1990), as well as the wetland-associated *Rumex palustris* (Groeneveld and Voesenek, 2003). Only the leaves of *N. peltata* that were less than 5 days old were capable of reaching the water surface when the water level rose by 250 cm. The older leaves could not reach the water surface and soon died, though some petioles could elongate to some extent. The reduced ability of petiole elongation as leaves age may be caused by an irreversible physiological change in the primary elongation mechanism. Cell elongation becomes the main mechanism for petiole growth in *N. peltata* as a leaf ages (Ridge and Amarasinghe, 1984). Cell walls gradually build up rigidity during maturation and this change can

Table 1
Statistical analysis of the effects of water level and substrate nutrient concentration on ramet number and total biomass of the *Nymphoides peltata* species.

Dependent variables	Source of variation	*df*	MS	*F*	*P*
Ramet number	Water level (*W*)	2	0.889	34.420	**<0.001**
	Nutrient concentration (*N*)	1	3.825	148.015	**<0.001**
	$W \times N$	2	0.032	1.244	0.304
	Error	28	0.026		
Total biomass	Water level (*W*)	2	1.171	30.651	**<0.001**
	Nutrient concentration (*N*)	1	4.941	129.340	**<0.001**
	$W \times N$	2	0.285	7.456	**0.003**
	Error	28	0.038		

Significant *P*-values are presented in bold.

hamper submergence-induced petiole elongation as suggested by Groeneveld and Voesenek (2003) in the *R. palustris* species. Otherwise, young leaves of the floating-leaved plant *Nuphar advenum* are thought to have the capability of sustaining anaerobic respiration in water for several days (Laing, 1940). For *N. peltata*, the young leaves may also be able to survive in water by anaerobic respiration and then rapidly reach the water surface, whereas older leaves lose their ability to respire anaerobically and die quickly.

Plants subjected to gradual water level rise tracked the increase in water depth with petiole elongation. Leaf petioles were always a little longer than the water depth and only elongated when water depth increased. It is possible that when leaves emerged, ethylene accumulation and tension on the leaf petiole, caused by the buoyancy of leaves, decreases and petiole elongation curtails accordingly. However, this strategy reduces the cost of above-ground tissues, as reported in the floating-leaved plant *Villarsia reniformis* (Cooling et al., 2001). If water levels decreased, less expensive shoots could be produced.

N. peltata plants responded to rapid water level rise by rapid elongation of petioles whose young leaves could emerge quickly. Rapid cell elongation is reported to be the dominant effect on petiole elongation in expanded leaves, and this kind of cell elongation results from the interaction between accumulated ethylene in submerged tissues, which increases cell wall extensibility, and the tension in petioles due to their natural buoyancy, which supplies the driving force for cell elongation (Ridge and Amarasinghe, 1984). Cell elongation requires substantial amounts of polysaccharides to

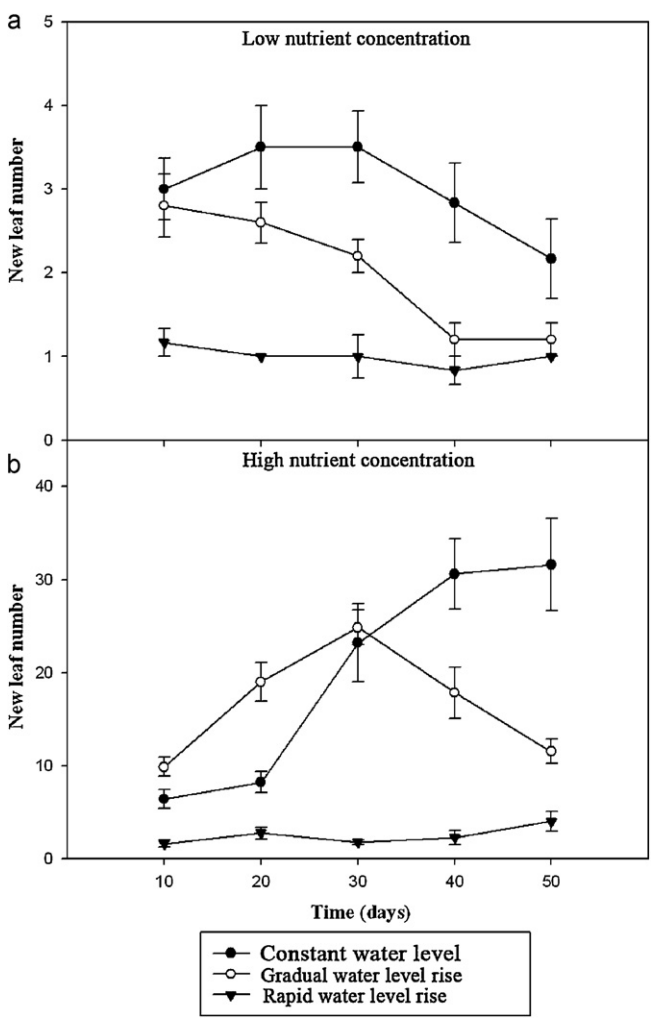

Fig. 3. Leaf recruitment every 10 days for *Nymphoides peltata* growing under two nutrient concentrations and three water levels. (a) low nutrient concentration; (b) high nutrient concentration. Data indicate means ± SE.

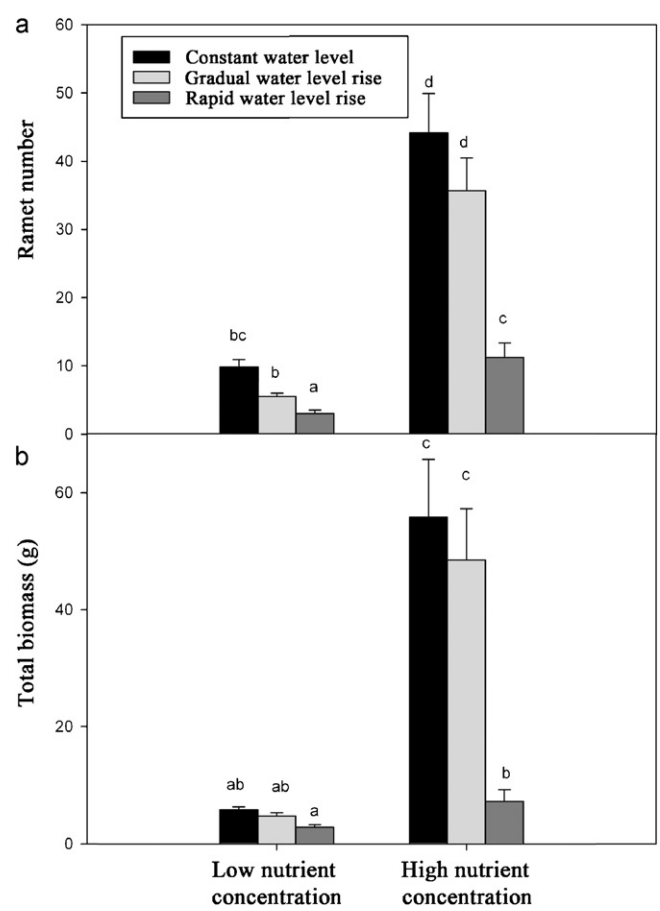

Fig. 4. The effect of the water level and the nutrient concentration on the ramet number and the total biomass of *Nymphoides peltata*. (a) Ramet number; (b) total biomass. Data indicate means ± SE. Significant differences of treatments in each species are indicated by different letters.

expand cell walls during submergence in *Rumex palustris*, so it is concluded that a petiole's elongation ability is partly dependent on the availability of storage compounds (Groeneveld and Voesenek, 2003). The rhizomes planted as experimental materials in our study may supply elongating leaves with storage starch for polysaccharide synthesis in expanding cell walls.

Ridge (1987) divided plant species into two broad groups according to the size and speed of their elongation response under submergence: a rapid elongation response in floating-leaved plants and a smaller delayed response in plants growing in marshes or seasonally flooded grassland. In floating-leaved species, water supports the leaves, reducing the need for lignification and the costs of producing and replacing shoots (Sculthorpe, 1967).

4.2. Leaf recruitment

As leaves aged, their ability to elongate rapidly in response to increased water depth was reduced. Rapid leaf recruitment was necessary to supply continuous young leaves, and these young leaves could track the increase in water depth with petiole elongation. Plants kept at constant water level maintained higher mean leaf recruitment compared to those challenged with changing water levels, such that more young leaves existed in the canopy. This ensures that when water levels increase, young leaves can rapidly emerge after submergence. Similarly, it was helpful for the plants to adapt to the increasing water levels by recruiting relatively high numbers of young leaves in gradual water level rise. However, as water depth increased, the reduced leaf recruitment was probably due to the water depth, which limited leaf recruitment, and more resources were allocated to leaf petiole elongation as in the rapidly rising water level treatment.

Nutrient enhanced leaf recruitment rate (mean 2.0 ± 0.89 leaves every ten days versus mean 16.0 ± 9.68 leaves every ten days in low versus high nutrient concentration) in *N. peltata*, which is consistent with the results reported by Cooling et al. (2001) in *V. reniformis*. High-nutrient supply might provide plant more nutrients which can satisfy the requirement for plant physiological functions, such as photosynthesis, and provides constructive material for leaf recruitment to cope with flooded stresses.

4.3. Biomass and ramet number

Flooding could be an important factor influencing biomass and ramet production in *N. peltata*. Gradual water level rise did not affect plant performance (biomass and ramet number), but rapid water level rise reduced performance. Flooding can reduce plant performance mainly by limiting the amount of light available for photosynthesis and gas exchange between the plant and the environment due to the low gas diffusion rate in water (Armstrong et al., 1994; Vervuren et al., 2003; Mommer et al., 2005). Plants subjected to gradually rising water recruited more new leaves, which reached the water surface for photosynthesis. Therefore, more photosynthates may be available in these plants. In addition, rapid protrusion of leaves above the water surface in response to gradual water level rise should enable the plants to obtain more light for photosynthesis and restore gas exchange quickly between the plant and the air, curtailing inefficient anaerobic respiration in the root system, which causes a rapid depletion of carbohydrate reserves. Although enhanced nutrient supply can offset the negative effects of flooding on plant growth (Xie et al., 2009), it may be too severe for *N. peltata* to recover from the rapid water level rise. However, plant total biomass was not significantly affected by rapid water level rise under low nutrient concentration, but it showed a decreasing trend which may be significantly reduced if the experiment lasted for a longer time.

We compared the responses of the floating-leaved plant *N. peltata* to gradual water level rise and rapid water level rise. In support of our first hypothesis, continual leaf recruitment and rapid petiole elongation are both important ways that *N. peltata* adapted to increasing water levels. The results were consistent with other floating-leaved species, including *V. reniformis*, reported by Cooling et al. (2001). Plants in gradual water level rise displayed similar biomass and ramet production to plants at a constant water level, but were negatively affected by rapid water level rise, which is consistent with our second hypothesis. The results indicated that flooding may be a disturbance factor that affects the plant growth and population expansion of *N. peltata*. It is predicted that extreme flooding would curtail plant performance, while small gradual water level rise would not harm this species.

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