

## Growth characteristics of *Nelumbo nucifera* Gaertn. in response to water depth and flooding

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Three experiments on the effects of water depth and flooding on *Nelumbo nucifera* Gaertn. were made in the artificial environment of concrete ponds. First, plants were harvested in autumn after growing under seven different water levels ranging from 0.2–3 m. The number of floating leaves, the total number of leaves and the leaf area index of emergent leaves were greatest in the tanks at 0.5 m depth. The petiole dry weight per unit length of emergent leaves and the ratio of aboveground to belowground biomass rose with increasing water depth up to 2 m. In contrast, that of floating leaves was constant at about 10 mg dry weight cm<sup>-1</sup>. The proportion of biomass in tubers fell from 20% at 0.2 m to 6% at 2 m. Second, petiole elongation responses to the amplitude of flooding were investigated in early summer. The maximum rate of petiole elongation was 25 cm per day at 2.4 m water depth. This was the maximum depth at which *N. nucifera* could grow. No petioles could elongate from 3 m to 5 m depth. Finally, the effects of timing of flooding on growth were investigated. At the end of growing season, the belowground biomass of plants in the flooding treatment in late summer was smallest among the flooding treatment plants ( $P < 0.05$ ), and was most severe when flooding occurred in this season. Based on the results of these experiments, the growth characteristics of *N. nucifera* in relation to petiole elongation, biomass allocation, and flooding tolerance were discussed.

**Key words:** biomass allocation; floating leaf; flooding; heterophylly; petiole elongation; water depth.

### INTRODUCTION

One of the central issues in aquatic plant ecology is what environmental or biological factors determine the distribution and abundance of plant species in a lake. The mechanisms leading to lakeshore zonation are poorly understood (Spence 1982). It is well known that water levels and flooding influence the composition of wetland plant communities (Brock *et al.* 1987; Blom *et al.* 1990; Nohara 1991). Flooding during the growing season is a critical factor for the survival of most species of aquatic plants (Crawford 1982). Plant growth may be especially affected by the amplitude and timing of flooding (Nohara & Tsuchiya 1990). The effects of flooding on primary productivity have been investigated in many wetland ecosystems. Some emergent

plants have characteristics to adapt to flooding (Vergara 1985; Blom *et al.* 1990). Floating-leaved plants in the littoral zone must overcome water level fluctuations (flooding) to keep laminae on the water surface. Temporarily submerged leaves of these aquatic plants can accommodate their petiole length to rising water levels and thus maintain the laminae at the water surface. Although various studies have illustrated that water depth has a pronounced regulatory effect on the distribution and abundance of emergent plants (Ikusima 1972; Hutchinson 1975; Spence 1982; Grace 1989; Squires & van der Valk 1992), only a few studies have been made on the relationships of floating-leaved plants to water depth and flooding (Brock *et al.* 1987; Chambers & Kalff 1987).

In Lake Kasumigaura in Japan, floods with a water level increase greater than 1 m occur once every few years, most commonly in July (the rainy season) and September (the typhoon season). One of

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the main floating-leaved plants in Lake Kasumigaura is *Nelumbo nucifera* Gaertn. *Nelumbo nucifera* is a very large aquatic perennial plant with both a slender, horizontal, vegetative stolon and a thickened storage tuber. It usually has two different leaf forms: floating and emergent leaves. All the leaves float early in the season when the plant is immature; later in season some leaves float and others are raised high above the water. *Nelumbo nucifera* is widely distributed in Japanese eutrophic waters (Sastroutomo 1973, 1982; Sakurai 1981; Kunii & Maeda 1982; Kunii *et al.* 1985) and has been widely cultivated in fields around Lake Kasumigaura (Minamikawa 1963; Tano 1983; Tezuka 1983). In Lake Kasumigaura, the distribution of *N. nucifera* seems to be restricted to sites of a water depth less than 1.5 m (Nohara 1991). In other lakes, natural stands of *N. nucifera* are distributed in sites 3 m deep (Unni 1971, 1976; Kunii & Maeda 1982). The maximum water depth reported for floating-leaved plants ranges from 3.5 m in northern Europe to 4 m in East Africa (Spence 1982). Why is the range of distribution of *N. nucifera*, a floating-leaved plant, so shallow?

The relationship among environmental factors is complex and it is difficult to isolate the effects of water level and flooding on plant performance in field conditions. As part of the ecological studies of *N. nucifera* in a lake, experiments on the effect of water depth and flooding on *N. nucifera* were conducted in outdoor concrete ponds to investigate the following two questions: (i) what is the maximum water depth at which *N. nucifera* can grow; and (ii) what is the effect of the amplitude and timing of flooding on *N. nucifera*?

## METHODS

### Experimental conditions

The following three experiments were conducted (Fig. 1): (i) growth responses under different water levels; (ii) petiole elongation responses to the amplitude of flooding; and (iii) effects of timing of flooding on growth. A cylindrical concrete pond (6 m in diameter  $\times$  5 m deep) near Lake Kasumigaura was used. The pond was filled with water overflowing from the lake during the experiments. Polycarbonate tanks (100 l, 0.39 m<sup>2</sup> surface area)

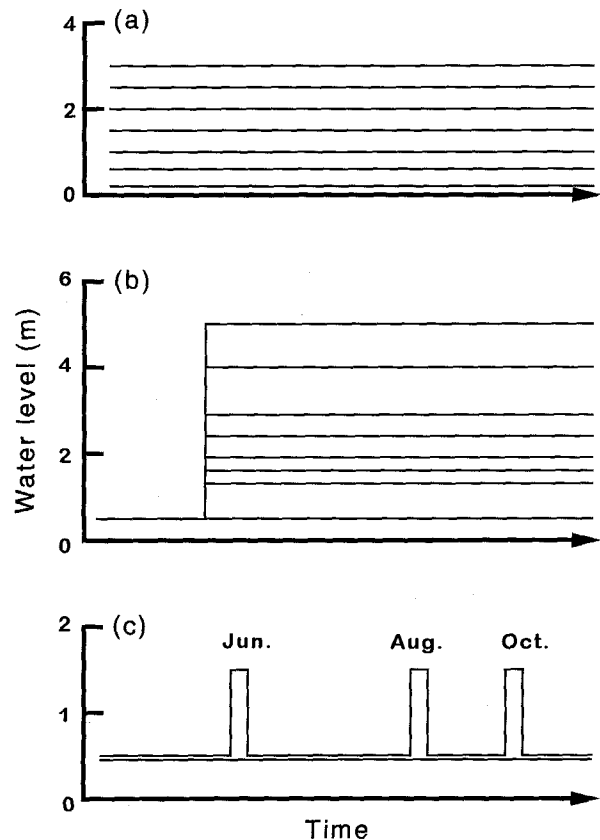


Fig. 1. Experimental regimes of water level change in (a) experiment 1, (b) experiment 2 and (c) experiment 3.

were filled with mud from Lake Kasumigaura to a depth of about 15 cm and suspended in the pond to cultivate the plants. The plants harvested from the tanks were brought to the laboratory and washed with tap water on the final day of each experiment. Stolon length was measured from photographs. Lamina width and petiole length were measured directly. Fresh plants were separated into the lamina, petiole, flower, stem, bud, stolon, tuber and root. Dry weight after freeze-drying was determined to within 0.1 g.

### Experiment 1: Growth responses under different water levels

Several tubers ( $201 \pm 10$  g dry weight per tank, mean  $\pm$  SD) were transplanted into each tank and fixed in the mud with netting (5 cm mesh opening) and bricks on 23 April 1991. Duplicate tanks were suspended by rope at 0.2, 0.5, 1.0, 1.5, 2.0, 2.5 and

3.0 m depth. These plants were harvested on 20 September 1991. Leaf number was counted, and leaf area was measured to determine the leaf area index (LAI) for all surviving plants.

### Experiment 2: Petiole elongation responses to the amplitude of flooding

Two tubers of 481 g mean fresh weight ( $225 \pm 50$  g dry weight per tank, mean  $\pm$  SD) were transplanted into each tank on 27 April 1989. Chemical fertilizer (15 g N, 15 g P, 15 g K) was added to the mud in each of the eight tanks. The tanks were suspended by rope at 0.5 m depth in the pond. The plants in these tanks were allowed to grow undisturbed in 1989. On 12 June 1990, the eight tanks were suspended at depths of 0.5, 1.3, 1.7, 1.9, 2.4, 2.9, 4.0 and 5.0 m, respectively. Before being placed at the new depth and about 1 week later (20 June), lamina width and petiole length were measured. The plants were harvested on 6 December 1990.

### Experiment 3: Effects of timing of flooding on growth

Twelve tanks were suspended by rope at 0.5 m depth in the pond. Two tubers of 280 g mean dry weight per tank were transplanted into each tank on 17 May 1992. Three groups of three tanks were lowered to 1.6 m depth on one of the following three dates in 1992 to simulate flooding: 19 June, 22 August and 25 September. After 1 week of treatment, the tanks were pulled up to their original depth, and lamina width and petiole length of plants in the three groups of 'flooded' tanks and the three control tanks were measured. The plants were harvested on 26 November 1992.

## RESULTS

### Effect of water depth

The plants in all tanks at 1.5, 2.5 and 3.0 m depth and those in one of the two tanks at 2 m depth in experiment 1 soon died under submerged conditions. The mean leaf area of emergent leaves increased markedly with depth (Fig. 2a). The mean leaf area of floating leaves increased with increasing

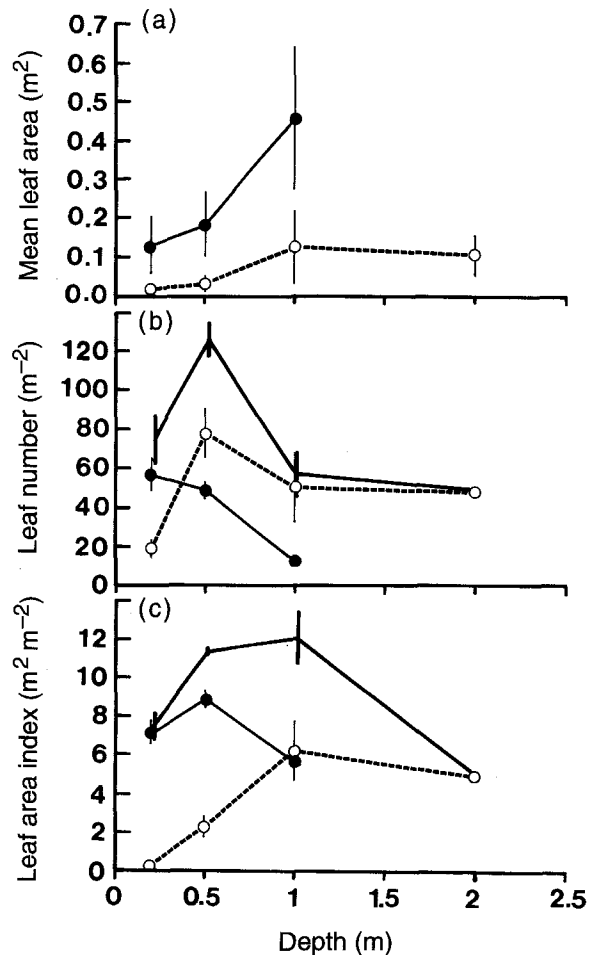


Fig. 2. Mean leaf area (a), leaf number (b) and leaf area index (c) in September 1991 for plants grown at each depth in experiment 1. —●—, emergent leaves; ---○---, floating leaves; +, total leaves. Vertical bars indicate SD.

water depth up to 1 m, beyond which it was constant at about  $0.1 \text{ m}^2$ . The number of emergent leaves decreased with increasing water depth. Emergent leaves were not borne by the plants in the 2 m deep tank (Fig. 2). The number of floating leaves, the total number of leaves and the LAI of emergent leaves were greatest in the tanks at 0.5 m depth. In contrast, the LAI of floating leaves increased with increasing water depth up to 1 m. Total LAI was greatest at about  $12 \text{ m}^2 \text{ m}^{-2}$  in the tank at 1 m water depth.

Petiole length of emergent leaves at 0.2 and 0.5 m water depth was longer than that of floating leaves (Fig. 3a, Cochran-Cox test,  $P < 0.01$ ). The specific petiole weight (petiole dry weight [d.w.] per unit length) of emergent leaves rose with increasing

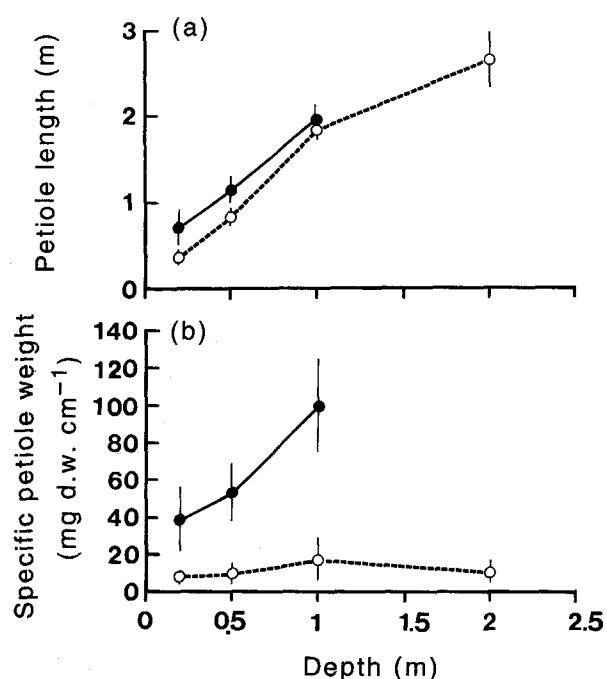


Fig. 3. Petiole length (a) and specific petiole weight (b) at each depth in experiment 1. —●—, emergent leaves; ---○---, floating leaves. Vertical bars indicate SD.

water depth up to 1 m (Fig. 3b). In contrast, the specific petiole weight of floating leaves was constant at about 10 mg d.w. cm<sup>-1</sup> between 0.2 and 2 m water depth. The specific petiole weight of emergent and floating leaves differed significantly ( $P < 0.01$ ) for each depth.

Water depth had a large effect on biomass distribution (Fig. 4a). Biomass was maximum for plants grown at 0.5 m water depth. There was a marked increase in the ratio of aboveground to belowground biomass (T/R ratio) with increasing water depth (Fig. 4a). The biomass distribution of the laminae of emergent leaves decreased while that of floating leaves increased with increasing water depth (Fig. 4b). The distribution of aboveground biomass rose from 45% at 0.2 m to 68% at 2 m water depth. The proportion of biomass in tubers fell from 20% at 0.2 m to 6% at 2 m.

#### Effect of flooding amplitude

The leaves of *N. nucifera* were submerged temporarily in the flooding experiment. Some petioles of temporarily submerged leaves could elongate above

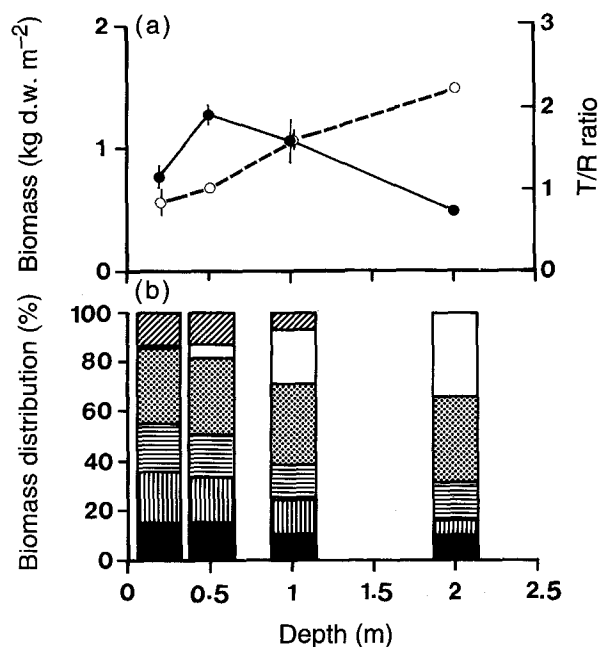


Fig. 4. Biomass, T/R ratio (a) and biomass distribution (b) for each depth in experiment 1. —●—, biomass; ---○---, T/R ratio. Vertical bars indicate SD. ▨, lamina of emergent leaves; □, lamina of floating leaves; ▩, petiole; ▤, stolon; ▥, tuber; ■, root.

the water surface, while others could not elongate and eventually died (Fig. 5). Several plants submerged at a greater depth of 3–5 m died as they could not elongate their petioles to the water surface. The maximum rate of petiole elongation was 25 cm day<sup>-1</sup> at 2.4 m depth. The maximum water depth at which *N. nucifera* could grow was 2.4 m. The mean petiole length of both floating and emergent leaves after 1 week of flooding was about 30 cm greater than the depth at which the respective plants were grown from 0.5–2.4 m water depth. The elongated petioles became very fragile after flooding. The belowground biomass in December was about 400 g d.w. per tank at each depth from 0.5–2.4 m.

#### Effect of timing of flooding

The maximum leaf number for control plants during the seasonal flooding experiment was 28 per tank during August (Fig. 6). Following the flooding, about half of the living leaves of plants flooded in late June or late August remained submerged and were relatively old and soon died. The other half of

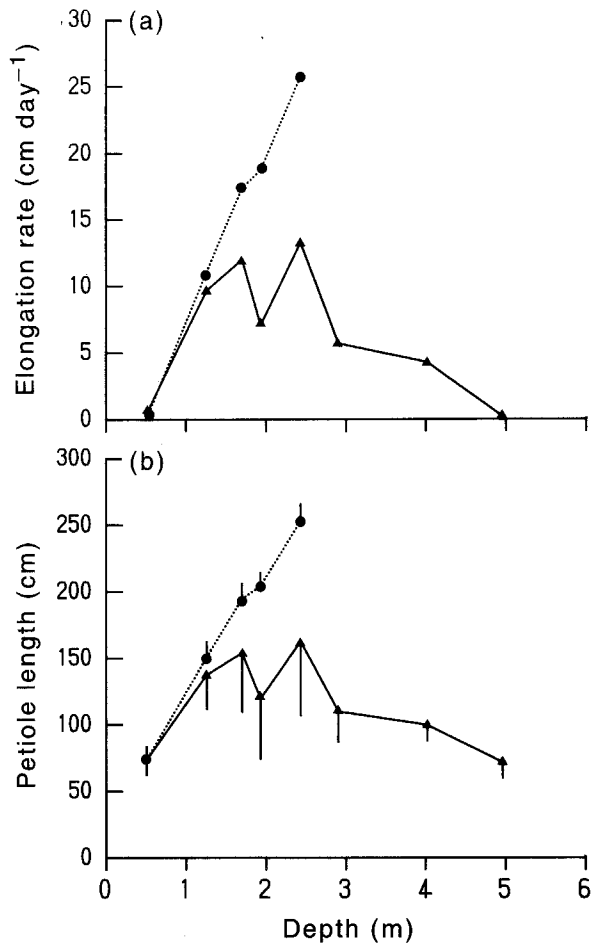


Fig. 5. Elongation rate of (a) petiole and (b) petiole length at each depth in experiment 2. Vertical bars indicate SD. ---●---, floating and emergent leaves; —▲—, total of floating, emergent and temporarily submerged leaves.

the floating and emergent leaves whose petioles could elongate over the water surface were relatively young and survived. In early October, all leaves were relatively old and they remained submerged after 1 week of flooding.

Mean petiole length of flooded plants was longer than that of control plants (Fig. 7,  $P < 0.01$ ). Mean petiole length of floating leaves after the flooding in late June or late August was 1.0 m longer than that of control leaves ( $P < 0.01$ ). The length of petioles of emergent leaves after flooding in late August was 0.8 m longer than that of control leaves ( $P < 0.01$ ). In early October, the petioles of floating and emergent leaves were less elongated, and all these leaves were submerged. After flooding in June, August and October, mean petiole length of temporarily

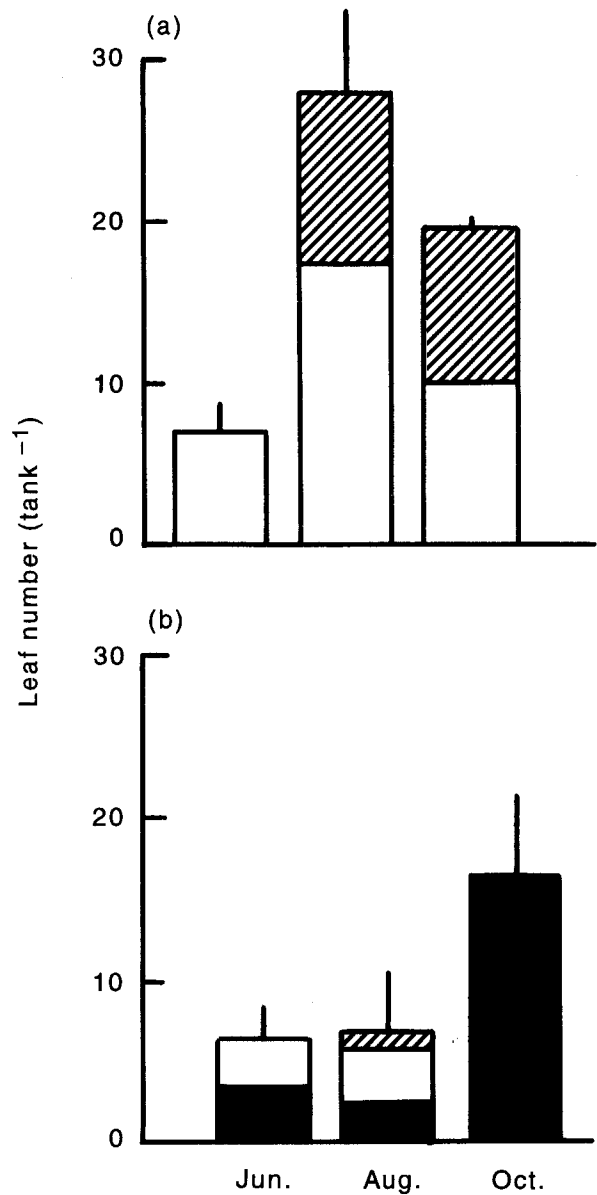


Fig. 6. Seasonal changes in leaf number in (a) control and (b) flooding during experiment 3. Vertical bars indicate SD. □, floating leaves; ▨, emergent leaves; ■, temporarily submerged leaves (living).

submerged leaves were longer than that of floating and emergent leaves of the control.

At the end of the growing season, the mean belowground biomass of control plants was  $305 \pm 96$  g d.w. per tank (Fig. 8). The belowground biomass of plants flooded in late August was smallest ( $150 \pm 65$  g d.w. per tank) among the flooding treatments plants and about half of control plants ( $P < 0.05$ ).

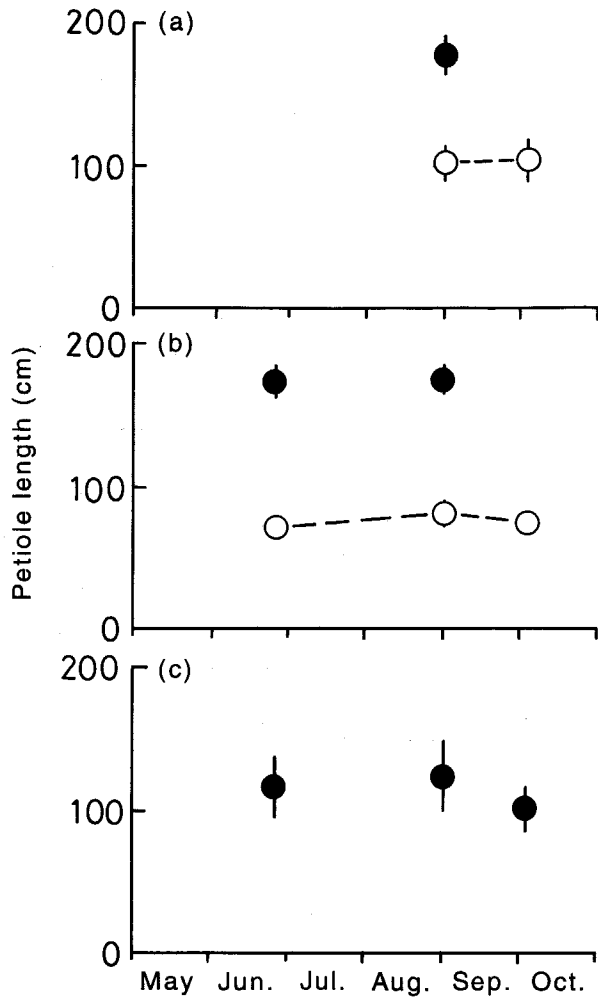


Fig. 7. Petiole length in experiment 3 for (a) emergent leaves, (b) floating leaves and (c) emergent leaves. Vertical bars indicate SD. ○, control; ●, flooding.

## DISCUSSION

### Petiole elongation

Heterophylly, or the occurrence of more than one leaf form within a single plant individual, is common among aquatic plants (Arber 1920; Sculthorpe 1967). *Nelumbo nucifera* also has heterophylly of floating and emergent leaves. At shallow sites, *N. nucifera* is predominant over other floating-leaved plants because its emergent leaves can shade the leaves of these other plants. At deep sites, *N. nucifera* is predominant over submerged plants because its floating leaves can shade the water surface above other submerged plants. Therefore,

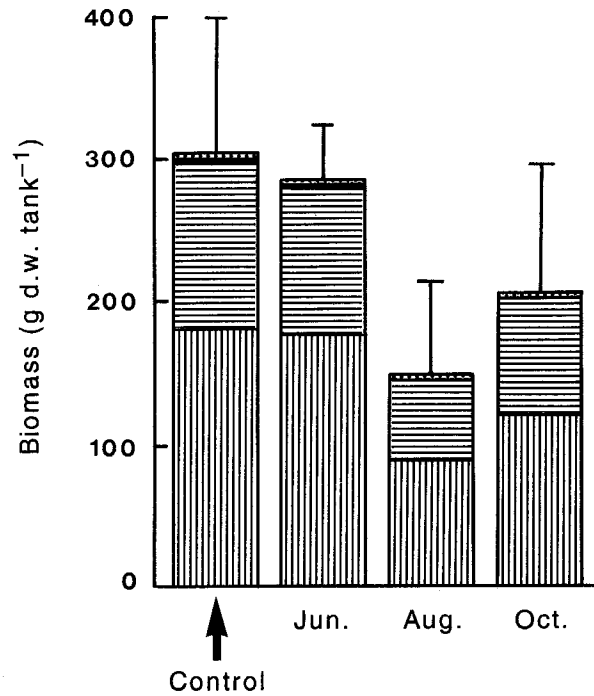


Fig. 8. Belowground biomass on 26 November in relation to timing of flooding. Vertical bars indicate SD. ▨, petiole and young lamina; ■, stem bud; ▩, stolon; ▤, tuber.

the control of petiole length of heterophyllous leaves is very important for predominance of *N. nucifera*.

Ridge (1987) described a number of species in which the petiole could elongate to be 4–6 times longer under water than in air. Floating leaves of *N. nucifera* at the deep sites have longer petioles than leaves at the shallower sites (Nohara & Tsuchiya 1990). When water level fluctuation was small, the mean petiole length exceeded the mean water depth by 10–80 cm for floating leaves and by 50–100 cm for emergent leaves (Fig. 3). When plants of *Ranunculus sceleratus* L. are submerged, the rate of petiole elongation of recently extended leaves is increased until such time as each leaf blade reaches the surface of the water (Samarakoon & Horton 1981). *Nelumbo nucifera* grown at 1 m depth had emergent leaves with petioles of 200 cm long, but emergent leaves were not borne on plants grown in the tank at 2 m depth. Only floating leaves were able to elongate their petioles sufficiently to allow their lamina to reach the water surface in plants grown in tanks over 2 m deep (Fig. 3). *Nelumbo nucifera* is able to adapt to deeper sites by elongating the petioles of its floating leaves. Many floating-leaved plants have increasingly longer petioles with

increasing water depth (Sculthorpe 1967; Wooten 1986). Deep water rice is grown in the flood plains where flood waters may reach a height of 6 m. It will elongate up to 25 cm day<sup>-1</sup> in rapidly rising water (Vergara 1985). In the present study, the maximum rate of petiole elongation of *N. nucifera* was the same as 25 cm day<sup>-1</sup> at 2.4 m depth. This adaptive mechanism for increases in plant height is an important part of the plant's ability to grow in a wide range of water depths.

In Lake Kasumigaura the habitat of these floating-leaved plants is restricted to shallower sites by other environmental factors such as waves and the wind (Nohara 1991; Nohara 1993; Tsuchiya *et al.* 1993). The greater fetch of large wetlands and their tendency in most years to contain surface water exposes shoreline vegetation to extensive wave action (Spence 1982; Keddy 1983; Wetzel 1983). These physical disturbances on the shoreline make a vegetation zone narrower than that when there is no disturbance.

### Biomass allocation

The change in biomass allocation to floating and emergent leaves with the increase of water depth can be explained from a cost/benefit relationship as follows (Fig. 9). The construction cost of a leaf was considered to be construction energy depending on the leaf weight that increased with the increase of water depth (Fig. 3). Since the slope of the weight increase of an emergent leaf with an increase of water depth was larger than that of a floating leaf, the construction cost of an emergent leaf ( $C_e$ ) was assumed to increase more rapidly than that of a floating leaf ( $C_f$ ). On the other hand, the benefit ( $B_e$ ,  $B_f$ ) such as the primary production per leaf during the leaf life span was expected to remain almost steady with the increase of water depth. The photosynthetic rates per unit of structural material of emergent leaves seemed to be almost the same as that of floating leaves, and leaf life span for an emergent leaf is only 2.6 times longer than that for a floating leaf in the sites at all depths (Tsuchiya & Nohara 1989). Therefore, line  $C_f$  crosses line  $B_f$  at  $D_f$  and line  $C_e$  crosses line  $B_e$  at  $D_e$ . In addition, the slope of  $C_f$  was assumed gentler than that of  $C_e$  (Fig. 3), so  $D_f$  was expected to be deeper than  $D_e$ . Since floating leaves were supported by water, the physical strength of petioles could be minimized.

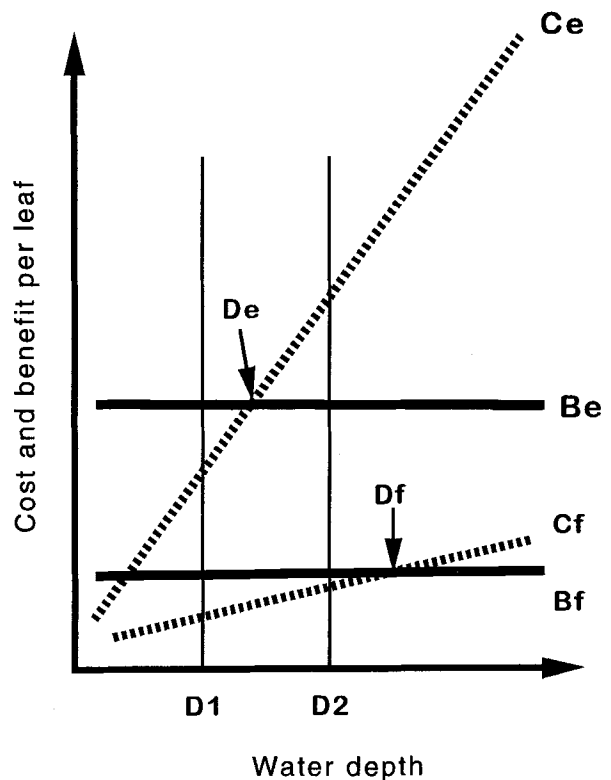


Fig. 9. Relationship between water depth and the leaf construction cost/benefit. Line  $C_f$ , the construction cost of a floating leaf;  $B_f$ , the benefit from a floating leaf during leaf life span;  $C_e$ , the construction cost of an emergent leaf;  $B_e$ , the benefit from an emergent leaf during leaf life span;  $D_f$ , the depth at the point of intersection of  $C_f$  and  $B_f$ ;  $D_e$ , the depth at the point of intersection of  $C_e$  and  $B_e$ ;  $D_1$ , some depth;  $D_2$ , the depth at the two times of  $D_1$ .

*Nelumbo nucifera* seemed to reduce the construction cost of petiole formation to a minimum by making a floating leaf at the deeper sites than  $D_e$  of water depth. At the sites ( $D_2$ ) deeper than  $D_e$ , the construction cost for an emergent leaf from the benefit left a negative value. Therefore, it was inferred that there were no emergent leaves at deeper sites than  $D_e$ .

Plants alter their resource allocation to above-ground and belowground tissues along environmental gradients of disturbance and resource availability (Grime 1979). Lieffers and Shay (1981) reported that *Scirpus maritimus* var. *paludosus* L. plants were taller in deeper water despite the fact that total biomass declined. Grace and Wetzel (1982) found that for two *Typha* species plants showed a modest increase in height with increasing depth and that the species capable of growing in

deeper water had taller leaves. In the present study, there was a marked increase in the ratio of aboveground to belowground biomass with increasing water depth up to 2 m (Fig. 4a). The distribution of aboveground biomass rose from 45% at 0.2 m to 68% at 2 m water depth. The biomass distribution of lamina of emergent leaves decreased while that of floating leaves increased with increasing water depth (Fig. 4b). Allocation shifts occurred along the gradient of water depth. Especially at the deep site, the survival and production of laminae in the present growing season was more important for *N. nucifera* than the investment in tuber growth in the next growing season.

### Flooding tolerance

The effects of water level change on the growth of *N. nucifera* differed with times of flooding. The leaf birth rate of floating and emergent leaves in late September is very low (Tsuchiya & Nohara 1989). Most petioles are found to reach full length within 2 weeks after they begin unrolling (Nohara & Tsuchiya 1990). These findings suggest that most leaves in experiment 3 during October were mature or old leaves which could not respond to abrupt flooding by elongation of their petioles. In the case of other floating-leaved plants (Brock *et al.* 1987) only the petioles of younger leaves still had the capacity to elongate in order to allow the laminae to reach the surface of the water after flooding.

The amplitude, duration and timing of flooding events are important factors regulating primary productivity in wetlands (Crawford 1982; Nohara & Tsuchiya 1990; Megonigal & Day 1992). *Nelumbo nucifera* has organic matter in its tubers until July (Nohara & Tsuchiya 1990; Nohara 1996). If flooding leading to destruction of aboveground parts occurs at a time when the reserves in the tubers are abundant (in August), *N. nucifera* regenerates some biomass using stored organic matter; otherwise the vegetation is much diminished (Nohara & Tsuchiya 1990). In experiment 2, flooding occurred at a time when there were still energy reserves in the tubers. *Nelumbo nucifera* that grew at a shallower site than about 2 m responded to flooding by regenerating its biomass using stored organic matter. Although *N. nucifera* can transfer oxygen-rich air from emergent or floating leaves to young submerged leaves via its stolons and tubers

(Mevi-Schutz & Grosse 1988a,b), the duration of flooding in experiment 2 was long enough for mature leaves not to survive under submerged conditions. Under submerged conditions, the oxygen concentration in the shoots can be expected to differ substantially from oxygen concentration in non-submerged shoots because of the low diffusion of oxygen in water, the low solubility of oxygen and the diminished convective movements in aquatic media. When the shoots of some emergent plants submerge under water the oxygen in the aerenchyma may be consumed very quickly (Sale & Wetzel 1983).

Rhizomes of several species were killed by anaerobic incubation at 22°C for 7 days, while others survived and showed normal shoot extension on return to aerobic conditions (Barclay & Crawford 1982). In the present study, several tubers in the deeper site were killed in submerged conditions and could not elongate their petioles to water surface. Since the intercellular air apices of submerged leaves filled with water in all the sites deeper than about 3 m, there is a need to consider the effects of water pressure on the growth of *N. nucifera*. Further studies are necessary to clarify the relationship between duration of flooding and the growth of *N. nucifera*.

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