Effects of Water Depth Gradient on Growth and Reproduction of Potamogeton obtusifolius (Postprint)

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Abstract

Water depth is a crucial limiting factor affecting the growth and distribution of wetland plants. This study selected *Potamogeton octandrus* Poir., a species exhibiting typical heterophylly, as the research subject to investigate its adaptive mechanisms and phenotypic plasticity under different water depth conditions by examining seedling growth, biomass, and reproductive strategies across four water depth gradients: shallow water treatments (10 cm and 30 cm) and deep water treatments (50 cm and 70 cm). The results demonstrated that *P. octandrus* developed heterophyllous leaves after reaching the water surface, with relative growth rate decreasing significantly and showing a positive correlation with water depth gradient. Plant height exhibited explosive growth with increasing water depth, while total stem length at 10 cm water depth was significantly lower than in other treatments. Water depth significantly affected internode number, with the 30 cm treatment showing the highest count; conversely, internode length and biomass in deep water treatments were significantly higher than in shallow water treatments. Tiller number displayed significant differences among all four treatment groups, decreasing significantly with increasing water depth. Both total biomass and aboveground biomass allocation increased markedly with water depth. Water depth treatment significantly influenced sexual reproduction indicators, with deeper water inhibiting sexual reproduction. No inflorescences formed under the 10 cm condition, whereas pollen quantity, P/O ratio, and inflorescence number at 50 cm water depth were significantly higher than in other treatment groups, and seed set number and seed set rate in deep water treatments were significantly higher than in the 30 cm group. Comprehensive analysis indicates that *P. octandrus* achieves optimal adaptation to water depth through adjustments in morphological plasticity, biomass allocation, and adoption of different reproductive strategies, with the optimal growth range being approximately 50 cm.

Full Text

Influence of Water Depth on the Growth and Reproduction of *Potamogeton octandrus* Poir.

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Abstract

Water depth is an important limiting factor affecting the growth and distribution of wetland plants. This study selected *Potamogeton octandrus* Poir., a species exhibiting typical heterophylly, to investigate its adaptive mechanisms and phenotypic plasticity under different water depth conditions. We examined seedling growth, biomass, and reproductive strategies across four water depth gradients: shallow water treatments (10 cm and 30 cm) and deep water treatments (50 cm and 70 cm). The results showed that heterophyllous leaves appeared after plants reached the water surface, at which point the relative growth rate decreased significantly and was positively correlated with water depth gradient. Shoot height of *P. octandrus* increased explosively with increasing water depth, with total stem length at 10 cm depth being significantly lower than in other treatments. Water depth also significantly affected internode number, with the 30 cm treatment showing the highest count, while internode length and biomass in deep water treatments were significantly higher than in shallow water treatments. Tiller number differed significantly among all four treatments, showing a significant decreasing trend with increasing water depth. Both total biomass and aboveground biomass allocation increased significantly with water depth. Water depth treatment significantly affected sexual reproduction indices, with deeper water inhibiting sexual reproduction. No inflorescences formed under the 10 cm condition. Pollen production, P/O ratio, and inflorescence number at 50 cm depth were significantly higher than in other treatments, and both seed number and seed set in deep water treatments were significantly higher than in the 30 cm treatment. Comprehensive analysis indicates that *P. octandrus* can optimize its adaptation to water depth by adjusting morphological plasticity, biomass allocation, and adopting different reproductive strategies, with an optimal growth range around 50 cm.

Key words: *Potamogeton octandrus*, phenotypic plasticity, water depth, heterophylly, reproduction strategy, wetland ecology

Introduction

Phenotypic plasticity—the phenomenon where the same genotype produces different phenotypes under different environmental conditions—represents an adaptation of organisms to environmental variability [?]. Water depth is a crucial environmental factor influencing aquatic plant growth and distribution, regulating light availability, substrate conditions, and water transparency. Aquatic plants, which primarily reproduce vegetatively, adapt to depth variations through morphological adjustments, biomass reallocation, and altered reproductive strategies to mitigate stress [?, ?]. Structural traits such as plant size, petiole elongation, stem length, tiller number, and heterophyllous leaf differentiation all exhibit morphological plasticity. For example, *Potamogeton crispus* stems elongate with increasing water depth, elevating photosynthetic organs to the water surface and developing aerenchyma to reduce oxygen limitation [?, ?]. Reproductive changes include modified flowering periods, inflorescence lengths, and the quantity and quality of reproductive organs. *Zizania latifolia* shows significantly reduced basal rhizome tiller numbers with increasing depth, while complete submergence advances flowering dates and increases inflorescence number [?]. *Polygonum hydropiper* reduces rhizome bud number and clonal reproductive biomass under flooding while increasing investment in clonal propagation to adapt to drought stress [?]. As water depth increases, wetland plants allocate more biomass to aboveground parts to facilitate rapid elongation growth and sexual reproduction. The differential responses of various plants to water depth changes reflect their capacity to enhance environmental adaptability, enabling them to overcome heterogeneous environments and maximize growth and reproduction to maintain population stability and persistence [?, ?].

Submerged macrophytes constitute an ecologically important group intimately associated with aquatic environments, and their unique evolutionary history, life history characteristics, and relationships with water environments have become hot research topics [?]. Some submerged plants exhibit heterophylly—a unique form of phenotypic plasticity where different leaf types differentiate under varying water depths [?]. Although numerous studies have examined morphological adaptations of aquatic plants along water depth gradients, research on submerged plants with typical heterophylly remains relatively scarce. Therefore, this study selected *Potamogeton octandrus* Poir., a species in the family Potamogetonaceae that displays typical heterophylly. *P. octandrus* is an annual submerged plant inhabiting ponds and slow-flowing ditches, characterized by strong adaptability and distinct leaf type development between vegetative and reproductive phases during ontogeny. We investigated the effects of four water depth gradients on seedling growth, biomass, and plant reproduction, examining variations in growth and reproductive traits to explore the adaptive mechanisms and phenotypic plasticity of *P. octandrus* under different water depth conditions.

1.1 Materials and Experimental Design

The experiment was conducted in farmland near Heilongtan, Xinhua Village, Dali City, Yunnan Province (26°37 0 N, 100°10 37 E) at an elevation of 2,100

m. The site features a subtropical plateau climate with an average annual temperature of 13.5°C, annual sunshine duration of 2,300.2 h, and mean annual precipitation of 966.4 mm, concentrated primarily in June-August (accounting for over 80% of annual rainfall).

Experimental materials consisted of vigorous young *P. octandrus* plants, which were planted as isolated clonal individuals. Initial aboveground height was (9.93 ± 1.17) cm and initial root length was (6.46 ± 1.16) cm. Plants were individually cultivated in plastic pots (93.5 mm height, 75 mm diameter). Based on the distance from the pot rim to the water surface, we designed shallow water treatments (10 cm and 30 cm) and deep water treatments (50 cm and 70 cm) to observe the optimal depth range. On May 9, 2015, selected seedlings were planted in plastic pots (one plant per pot, 120 pots total). Plants were secured in experimental containers using gravel, which were randomly divided into four groups of 30 pots each and placed in four large plastic barrels (90 cm height, 50 cm diameter), with each barrel serving as a block. After transplanting, plants were pre-cultured for 5 days in barrels at 10 cm depth to allow acclimation and recovery. Following this period, one barrel was maintained at 10 cm depth, while water levels in the remaining three barrels were adjusted to 30 cm, 50 cm, and 70 cm, respectively. During the experiment, water was manually added to maintain depths within 2 cm of target levels. The experiment lasted two months (May 13–July 17, 2015), with water changed on June 11 to prevent interference from excessive growth of phytoplankton and epiphytic algae.

Starting on May 13, 2015, plant height was measured every 3 days by sampling from pots at different depths to monitor height growth changes and heterophyllous leaf development across water depth gradients, with a total of 20 sampling events. On day 70, 30 complete plants from each treatment were collected, rinsed clean of soil, and transported to the laboratory for individual numbering. All inflorescences were first removed, and inflorescence number and fruit set were recorded. Inflorescences together with remaining aboveground parts (stems and leaves) were oven-dried at 65°C for 48 h, with the total dry weight recorded as aboveground biomass. Belowground biomass (roots and rhizomes), individual plant biomass, total stem length (sum of main stem and all lateral branches), total node number (sum of nodes on main stem and all lateral branches), and tiller number on rhizomes were measured, allowing calculation of mean internode length and mean internode biomass for each treatment.

During peak flowering, fresh unopened inflorescences were randomly collected from different plants, with one inflorescence taken from each of the 30 plants per treatment and stored individually in EP tubes fixed with 70% ethanol solution. In the laboratory, one flower was randomly selected from each inflorescence. The stigma and anther of each flower were crushed with a dissecting needle, placed in a 2 mL EP tube, diluted to 2 mL with distilled water, and homogenized into a uniform suspension using a rubber-tipped dropper. A 50 L aliquot of pollen solution was pipetted onto a microscope slide, and total pollen grains in the droplet were counted under an optical microscope. Three replicate counts were performed per flower, and pollen production per flower was calculated based on the dilution factor. *P. octandrus* has single-ovule carpels that are free from one another, so ovule number equals pistil number per flower. The pollen-ovule ratio (P/O) per flower was calculated by dividing pollen production by ovule number.

For each treatment, all naturally fruiting inflorescences were collected from the 30 plants. Total flower number per inflorescence was recorded, and seed set per inflorescence was calculated as the ratio of total seeds to total carpels in that inflorescence.

1.3 Data Analysis

All analyses were performed using SPSS 20.0 software. One-way ANOVA was used to analyze measured indices including plant height, total stem length, and mean internode length for individual *P. octandrus* plants, with each index as the dependent variable and treatment group as the fixed factor. Mean internode biomass was log-transformed to meet homogeneity of variance assumptions before ANOVA analysis. Individual plant biomass data remained non-homogeneous after log transformation, thus non-parametric Kruskal-Wallis tests were applied. When ANOVA results were significant, Tukey's multiple comparison test was used for inter-group comparisons; for significant non-parametric results, Mann-Whitney tests were employed for further pairwise analysis.

Tiller number was log-transformed, while node number, inflorescence number, pollen number, and seed number were analyzed using Generalized Linear Models (GLM) to test for significant differences among water depth treatments. The significance level for all tests was set at $P < 0.05$.

Results

2.1 Growth Variation of *P. octandrus* Under Different Water Depths

Monitoring of *P. octandrus* growth under different water depth treatments revealed significant depth effects. As shown in [Figure 1: see original paper], growth could be divided into two phases: Phase 1 (experimental days 4–44) and Phase 2 (days 44–70). During Phase 1, plants in all four depth treatments showed rapid growth, remaining in the vegetative stage underwater and producing linear or lanceolate submerged leaves that were sessile, with leaf length (36.42 ± 1.46) mm, width (0.87 ± 0.04) mm, and thickness (0.09 ± 0.02) mm, featuring entire margins and acuminate apices ([Figure 1: see original paper]A). In Phase 2, plant height in all treatments exceeded the water depth, after which growth rate decreased markedly as plants transitioned to the reproductive stage. Stems extended to the water surface, where apical meristems formed elliptical or oblong floating leaves with leathery texture, measuring (11.37 ± 0.40) mm in length, (8.15 ± 0.30) mm in width, and (0.26 ± 0.02) mm in thickness, with petiole length (14.75 ± 0.75) mm ([Figure 1: see original paper]B). This transition from vegetative to reproductive stage involved pronounced morphological changes in heterophyllous leaves, with floating leaves showing significantly lower length-to-width ratios (L/W) than submerged leaves, while both thickness and area were greater in floating leaves.

[Figure 1: see original paper] shows that relative growth rate (RGR) in Phase 1 was significantly higher than in Phase 2. The most pronounced height increase occurred in the 70 cm treatment: mean plant height was (11.17 ± 0.27) cm on day 4, (80.7 ± 1.04) cm on day 44, and (91.19 ± 1.79) cm on day 70, yielding average RGRs of 1.74 cm · d ^{1} in Phase 1 and 0.4 cm · d ^{1} in Phase 2. The 10 cm treatment showed the smallest height changes, with average RGRs of 0.75 cm · d ^{1} and 0.07 cm · d ^{1} in Phases 1 and 2, respectively. The 30 cm and 50 cm treatments showed intermediate growth, with Phase 1 RGRs of 1.34 cm · d ^{1} and 1.48 cm · d ^{1}, and Phase 2 RGRs of 0.08 cm · d ^{1} and 0.31 cm · d ^{1}, respectively.

2.2 Effects of Water Depth on Morphological Growth Indices

presents comparisons of six morphological growth indices across water depth treatments. Plant height differed significantly among all four treatments (F , = 215.898, $P < 0.001$), showing explosive growth. Mean total stem length in the 10 cm treatment (271.36 ± 22.43 cm) was significantly lower than in the other three treatments (F , = 10.394, $P < 0.001$), which did not differ significantly from each other. Water depth significantly affected internode number (Wald ^{2} = 23.808, $P < 0.001$), with the 30 cm treatment showing the highest count (157.8 ± 8.69 internodes) and no significant differences among the other treatments. Tiller number differed significantly across all treatments (Wald ^{2} = 51.549, $P < 0.001$), decreasing significantly with increasing water depth. Both internode length and internode biomass differed significantly among treatments (internode length: F , = 37.611, $P < 0.001$; internode biomass: F , = 18.366, $P < 0.001$), with deep water treatments showing no significant differences between them but both significantly exceeding shallow water treatments.

2.3 Effects of Water Depth on Biomass and Allocation

As shown in , individual plant biomass increased significantly with water depth (Kruskal-Wallis ^{2} = 42.948, $P < 0.001$). At 70 cm depth, individual biomass (1.11 ± 0.05 g) was significantly higher than in other treatments, while biomass at 10 cm depth (0.45 ± 0.05 g) was significantly lower than all others.

Water depth significantly affected both aboveground biomass (stems, leaves, and reproductive structures) (Kruskal-Wallis ^{2} = 100.071, $P < 0.001$) and belowground biomass (roots and rhizomes) (Kruskal-Wallis ^{2} = 100.071, $P < 0.001$). With increasing water depth, the proportion of biomass allocated to aboveground parts increased from 90.11% to 93.58%, while allocation to belowground parts decreased from 9.89% to 6.41%.

2.4 Effects of Water Depth on Sexual Reproduction Indices

On day 70, no inflorescences had formed in the 10 cm treatment, so this treatment was excluded from pollen and seed set analyses. Single-flower pollen production differed significantly among treatments (Wald ^{2} = 8.934, $P = 0.011$,), with the 50 cm treatment showing the highest value (37,384.67 ± 2,631.93), significantly exceeding the other two treatments. P/O ratio also differed significantly among treatments (F , = 9.188, $P < 0.001$), peaking in the 50 cm treatment (9,346.17 ± 658.03), followed by the 30 cm and 70 cm treatments, which did not differ significantly.

Total inflorescence number varied significantly among water depth treatments (Wald ^{2} = 143, $P < 0.001$,), with the 50 cm treatment producing the most inflorescences (3.9 ± 0.12), significantly higher than the other treatments. Additionally, water depth significantly affected both seed number and seed set per inflorescence (seed number: Wald ^{2} = 32.362, $P < 0.001$; seed set: Kruskal-Wallis ^{2} = 19.975, $P < 0.001$), with deep water treatments showing significantly higher values than the 30 cm treatment, though not differing significantly from each other.

Discussion

3.1 Effects of Water Depth on *P. octandrus* Growth

Water depth is a critical limiting factor for wetland plant growth and distribution. Aquatic plants that primarily reproduce vegetatively adapt to depth changes through biomass allocation and morphological plasticity to mitigate associated stress [**?**, **?**]. Our findings demonstrate that *P. octandrus* rapidly adjusts morphological plasticity, biomass allocation, and reproductive strategies to optimize local environmental adaptation. Integrating effects on growth, biomass, and reproduction, the optimal depth range for *P. octandrus* is approximately 50 cm, with deeper water inhibiting sexual reproduction.

Although RGR in Phase 1 was significantly higher than in Phase 2 across all depths, the marked reduction in RGR after plants reached the water surface indicates that morphological plasticity adjustments require time [**?**] to adapt to the environment and acquire light resources. RGR in both phases was positively correlated with water depth treatment, peaking at 70 cm depth (1.74 cm · d ^{1} in Phase 1; 0.4 cm · d ^{1} in Phase 2). However, all treatments transitioned from Phase 1 to Phase 2 at day 44, suggesting that while the speed of environmental response was consistent across treatments, stronger depth stress elicited faster responses. During Phase 1, *P. octandrus* produced only submerged leaves underwater, whereas Phase 2 involved stem extension to the water surface and formation of floating leaves at the apex. This production of different leaf types on the same plant—heterophylly—is considered a form of phenotypic plasticity for adapting to aquatic environments [**?**].

Research on heterophyllous *Potamogeton* species has shown that floating leaves contain more chlorophyll per unit area than submerged leaves [?]. Photosynthetic efficiency of floating leaves in air is ten times that of submerged leaves, whereas underwater, submerged leaf photosynthetic efficiency doubles while floating leaf efficiency decreases fourfold. Thus, each leaf type achieves maximal photosynthetic efficiency in its respective habitat, outperforming the alternative leaf type.

With increasing water depth, both shoot height and total stem length of *P. octandrus* increased accordingly. Across all depth gradients, plant height exceeded the water depth by 20–40 cm, with continuous new leaf production and main stem elongation increasing photosynthetic tissue proportion and promoting light absorption, while ensuring that stems extended sufficiently to position floating leaves and inflorescences above water for successful sexual reproduction. Under shallow conditions, *P. octandrus* produced many tillers with short stems, but as depth increased, plants altered their architecture by reducing tiller number and increasing stem length. This rapid stem growth response likely results from cell differentiation and elongation [?, ?, ?]. We observed differences in internode number and mean internode length across depths: the 30 cm treatment had the most internodes, while deep water treatments had fewer internodes but longer mid-stem internodes with increasing depth. Thus, under deep water and low light conditions, *P. octandrus* adapts by increasing internode length rather than internode number. Many aquatic plants share this characteristic of adapting to submergence by increasing internode length [?], as ethylene accumulation in plant tissues promotes cell elongation and division [?]. These results demonstrate that *P. octandrus* possesses strong adaptability to water depth gradients through pronounced morphological plasticity to obtain necessary oxygen and light energy.

3.2 Effects of Water Depth Gradient on Plant Biomass and Reproduction

Water depth variation affects biomass accumulation in aquatic plants [?], and biomass allocation is key to plant ecological strategies, reflecting resource distribution patterns during growth [?]. Our results show that individual total biomass, aboveground biomass, and aboveground allocation ratio increased significantly with water depth, indicating that *P. octandrus* invests more photosynthetically fixed carbon into stems and leaves under deep water conditions.

Belowground biomass and allocation ratio decreased with increasing water depth, suggesting higher resource allocation to root systems under shallow conditions where adequate light enables extensive root growth for nutrient acquisition. Under deep water, plants allocate more energy to aboveground growth to maximize light capture and air contact area, while reducing root expansion to minimize respiratory consumption [?]. The 10 cm treatment produced significantly more tillers but delayed reproductive phenology, directly affecting sexual reproductive capacity. In favorable environments, longer-lived plants produce numerous clonal propagules for vegetative growth while delaying flowering. This plasticity in reproductive timing and allocation ensures population expansion and maximizes adaptability [?]. Conversely, when nutrients or water are limited, short-lived plants flower early to enhance reproductive efficiency [?]. This indicates that excessive investment in vegetative propagation under resource-limited conditions reduces allocation to sexual reproduction, and vice versa.

P. octandrus exhibits clear trade-offs in biomass allocation among aboveground versus belowground tissues and vegetative versus sexual reproduction. Increased investment in one trait necessarily reduces investment in others, and such trade-offs resulting from resource limitation are considered universal principles in life-history trait evolution [?, ?]. These differences in resource allocation patterns across water depths represent integrated phenotypic responses to environmental plasticity for acquiring essential resources [?]. Studies on water depth gradients affecting wetland plant growth, reproduction, and biomass allocation have found that the degree of influence varies among species, depending not only on environmental factors like water but also on plant ecological strategies [?]. Genetic factors also influence the evolution of reproductive strategies, and phenotypes are shaped by the combined effects of genotype, environment, and developmental processes, warranting further research on genetic differentiation among populations in different habitats at the nucleic acid and protein levels.

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