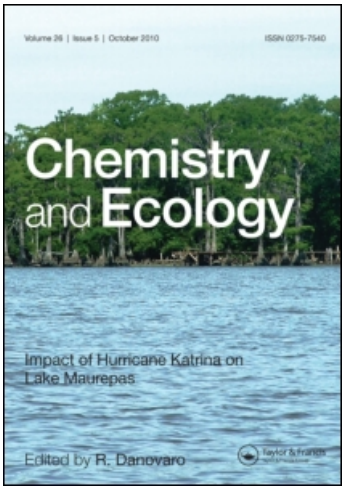

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Munira Sultana[a]; Takashi Asaeda[a]; M. Ekram Azim[a]; Takeshi Fujino[a]
[a] Department of Environmental Science and Human Technology, Saitama University, Saitama-shi, Japan

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Morphological plasticity of submerged macrophyte *Potamogeton wrightii* Morong under different photoperiods and nutrient conditions

Munira Sultana*, Takashi Asaeda, M. Ekram Azim† and Takeshi Fujino

Department of Environmental Science and Human Technology, Saitama University, Saitama-shi, Japan

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The morphological plasticity of the submerged macrophyte *Potamogeton wrightii* under different nutrient conditions and photoperiods was measured in a laboratory controlled experiment for 70 days in Japan. Six treatments were used in this experiment (3×2 factorial design with three replications) which consisted of three photoperiods and two nutrient conditions. Both photoperiod and nutrient condition had a pronounced effect on shoot and leaf morphology in *P. wrightii*. New shoot recruitment, and the length of main and new shoots gradually decreased with shortening photoperiod under both nutrient treatments. Plants under an 8 h photoperiod and high nutrient levels generated significantly more dead leaves (7.42 leaf·shoot^{-1}) and decomposed shoots (1.3 shoots·pot^{-1}) than plants under other treatments. Under short photoperiods (12 and 8 h) plants failed to produce flowering spikes in both nutrient conditions. In high nutrient conditions, *P. wrightii* produced shorter shoots, fewer leaves with shorter and narrower laminas, and smaller petioles compared with plants in the low nutrient condition. This may be adaptive under high nutrient conditions because it lowers foliar uptake and, thus, nutrient toxicity.

Keywords: *Potamogeton wrightii*; petiole; decomposed shoot; flowering spike

1. Introduction

Essential elements for plant growth are usually scattered in a plant's surroundings [1]. Plants may experience stress if essential nutrients are in limited supply or if they occur in excess. In nature, plants frequently come across combinations of stress factors [2]. Some plants are able to develop mechanisms that allow them to acclimate or acquire adequate resources from the adjacent environment. Environment-dependent phenotypic expression is known as phenotypic plasticity [3–5] and may occur by changing physiological processes and altering morphological structure [6]. Many aquatic plants exhibit a higher degree of morphological plasticity which might reduce the need for acclimative changes in physiological processes. Species capable of adjusting to the environment via morphological changes have an improved chance of survival [7] because such plasticity can increase the ecological breadth of the species [2]. If plastic changes are absent, the species might not be able to respond adequately to a changeable environment.

*Corresponding author. Email: munira.sultana@ymail.com
†Present address: Department of Physical and Environmental Sciences, University of Toronto, 1265 Military Trail, Toronto, Ontario M1C 1A4, Canada.

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Nutrients and light are two major controlling factors for plant growth. At lower levels of nutrient availability, plant species mainly compete for nutrients, whereas at higher levels of nutrient availability competition is mainly for light [8]. However, in either condition, morphological plasticity may allow one species to dominate. In general, erect species are primarily regulated by total sediment phosphorus, whereas bottom-dwelling species are largely regulated by surface irradiance [9]. Excessive nutrients often boost die-back in vegetation and alter the species dominance in various aquatic ecosystems [10]. Species characterised by tolerance to environmental variation tend to possess a higher, genetically determined potential for physiological and morphological acclimation, which enables them to shift their metabolism and growth in concert with light [11–14] and nutrient [15–17] availability. The best known morphological responses to nutrients and light are changes in leaf length and width under low photon flux density and in rich nutrient conditions [18–20].

Potamogeton L. (Potamogetonaceae), one of the largest genera of aquatic angiosperms, is ecologically diverse and distributed in various freshwater bodies. The morphological plasticity of various *Potamogeton* species has been investigated and a high degree of plasticity has been revealed [21–26]. *Potamogeton wrightii* Morong is a submerged, rooted species of the genus *Potamogeton* and is distributed in many lakes, rivers and streams in Japan [27]. *P. wrightii* shows three types of growth forms based on habitat: submerged, floating leaves and terrestrial [28]. This plant may have greater plasticity in growth form, which may allow better acclimation to environmental variation.

The rapid expansion of industrialisation and agricultural activities has raised concerns over potential eutrophication problems in Japan [29]. Recently, degradation of habitats because of sedimentation and degraded water quality has been reported for some water bodies in Japan [30–32]. Furthermore, photoperiod or the number of hours of light in a day changes dramatically during the year in temperate regions of the world, as well as in Japan. Photoperiod controls growth and flowering in plants [33]. By knowing how photoperiod affects plant development in photoperiodic species, we can manipulate the natural photoperiod to promote or prevent vegetative growth.

Morphological plasticity is usually measured using an experimental design with the same genotypic plant and these experiments are often conducted under controlled conditions. However, in order to make a credible assessment of the impacts of nutrient condition and different photoperiods on morphological characteristics, a controlled laboratory experiment was performed with *P. wrightii*. A clear impact of nutrient and photoperiod on *P. wrightii* morphology was indeed underlined.

2. Materials and methods

2.1. *Experimental set-up*

We performed a laboratory experiment using 18 glass aquaria (size: $1.6 \times 0.8 \times 0.8$ m) in the Department of Environmental Science and Human Technology, Saitama University, Japan for 70 days. *P. wrightii* plants and sediments were collected from the Hanamuro River (Tsuchiura, Tsukuba, Japan). The Hanamuro River flows into Lake Kasumigaura, which is the second largest lake in Japan, located in central Japan at $\sim 36^\circ$ N and 140.4° E. Open water nutrients such as N and P concentrations were $\sim$30 and 3 μmol·L^{-1}, respectively. Six treatments were arranged in a 3×2 factorial design with three replications which consisted of three photoperiods, 16, 12 and 8 h, and two nutrient levels, 90 μmol N·L^{-1}·d^{-1} and 9 μ mol P·L^{-1}·d^{-1} as the high nutrient condition and 30 μmol N·L^{-1}·d^{-1} and 3 μ mol P·L^{-1}·d^{-1} as the low nutrient condition. Concentrations of N and P observed in the field were used as the 'low nutrient condition' for the experiment. *P. wrightii* (3–4 cm long, and with 2–3 leaves) were planted in individual plastic

pots (7 cm in diameter, 15 cm deep) and then placed in experimental aquaria. The number of pots was 75 per experimental aquarium and stem density per square metre was approximately that observed in the field. Dechlorinated tap water was used to conduct the experiment. Plants were acclimated to the same conditions (nutrient: 30 μmol N·L^{-1}·d^{-1} and 3 μmol P·L^{-1}·d^{-1}, photon: 200 μE·m^{-2}·s^{-1}1 cm below the water surface, photoperiod: 14 h, temperature: 25 °C) for the first four weeks. Light was provided by white fluorescent bulbs, as described by Hootsmans and Vermaat [34] for *Potamogeton pectinatus*. After acclimatisation, three different photoperiods and two nutrient conditions were introduced into the aquarium (regarded as experimental day 1) and continued until day 70. On day 1, the lengths of selected plants were 7–9 cm.

Commercial fertilisers, in the form of ammonium sulfate, potassium nitrate and di- ammonium phosphate, were added on weekly basis to the aquaria. In addition, a commercially available micronutrient solution, 'Tetra flora pride™', was added to all aquaria in equal amounts to maintain a sufficient concentration of micronutrients in the water. A temperature of 25 °C was maintained for all aquaria. The CO_2 concentration in the water in the aquaria was kept at 14–50 μM, as described by Nielsen and Sand-Jensen [35] using CO_2 supplied from a bottle. Water in all tanks was bubbled continuously with air stones to mix the water and minimise CO_2 limitation and O_2 inhibition [36]. All aquaria were covered with thick black screens to maintain a proper and uniform light climate throughout. Within each photoperiodic condition, the position of the planted pots was changed twice a week to avoid any potential heterogeneity in the light field. Treatments that were a combination of high nutrient conditions and different photoperiods were marked with an arithmetic number indicating photo hour and 'HN' (i.e. 16 HN, 12 HN and 8 HN). Conversely, low nutrient conditions were indicated with 'LN' (i.e. 16 LN, 12 LN and 8 LN).

2.2. *Analyses*

After 14, 28, 56 and 70 days of growth, plants from 10 randomly selected pots from each aquarium were measured to determine the plasticity of various morphological characteristics, i.e. shoot length, number of newly recruited shoots, number of live and dead leaves, length of stem internodes, length of leaf petioles, length and maximum width of individual leaves. Only shoot length and number of live leaves were measured for both main shoot and newly recruited shoots separately; others measurements were only for the main shoot. Decomposed shoots appeared after day 42 and were counted on days 56 and 70 for each pot.

All data were checked for the assumption of normal distributions and homogeneity of the variances before statistical analyses. Data for various morphological traits were analysed using a three-way repeated measurements analysis of variance (ANOVA), with photoperiod and nutrient conditions as the 'main factors' and the sampling dates as the 'repeated measures'. A one-way ANOVA was performed for all of the above variables with treatments as the main factor. If the main effect was significant, the ANOVA was followed by Tukey's HSD test. ANOVA tests were performed at a 0.05 significance level using a statistical package, Statistica (v. 5).

3. Results

Nutrient levels and photoperiod affected morphological variables in *P. wrightii*, and these factors also interacted significantly in most of the variables (three-way ANOVA, Table 1).

3.1. *Plastic responses of shoot*

Main and newly recruited shoots and their internodes were 35, 104 and 39% longer, respectively, in the low nutrient condition compared with the high nutrient condition (Table 2 and Figure 1(a)).

Table 1. Results of three-way repeated measures ANOVA with photoperiod and nutrient as main factors and sampling date (not shown) as repeated measures factor for morphological traits of *Potamogeton wrightii*.

	Source of variation		
Variables	Photoperiod	Nutrient	Photoperiod × Nutrient
Length of main shoot (cm)	21.76*	18.23*	13.67*
Number of new shoots per pot	32.56*	5.61***	10.77*
Length of new shoot (cm)	10.75*	28.99*	0.32
Length of internodes (cm)	13.59*	17.21*	13.58*
Number of live leaves per main shoot	40.98*	4.81***	1.62
Number of live leaves of new shoots per pot	5.74**	27.10*	10.42*
Number of dead leaves per shoot	3.11***	0.003	13.50*
Length of leaves (cm)	63.45*	25.55*	36.34*
Maximum width of leaves (cm)	394.59*	259.39*	134.75*
Length of petiole (cm)	14.38*	35.07*	41.90*
Number of decomposed shoots per pot	4.90***	6.40***	15.70*

Notes: F-values are given. Significant at $^{*}p = 0.001$; $^{**}p = 0.01$; $^{***}p = 0.05$.

Table 2. Average values (± SD) of the observed morphological parameters in *Potamogeton wrightii* under different treatments.

	Treatments					
Variables	16 HN	16 LN	12 HN	12 LN	8 HN	8 LN
Length of main shoot (cm)	56.5 ± 35.3^{bc}	111.2 ± 19.6^{a}	45.8 ± 11.6^{bc}	64.0 ± 31.1^{b}	28.5 ± 20.5^{c}	40.8 ± 18.8^{c}
Number of live leaves on main shoot	$7.10 \pm 2.14a^{b}$	8.44 ± 2.05^{a}	6.00 ± 1.63^{bc}	6.03 ± 1.27^{bc}	4.21 ± 1.57^{c}	4.78 ± 1.33^{c}
Number of new shoots per pot	1.45 ± 0.49^{b}	3.00 ± 1.38^{a}	1.20 ± 0.36^{bc}	0.75 ± 0.22^{bc}	0.45 ± 0.10^{c}	0.65 ± 0.10^{bc}
Length of new shoots (cm)	19.5 ± 15.0^{bc}	35.5 ± 27.1^{a}	11.4 ± 5.62^{bc}	22.45 ± 12.36^{b}	7.5 ± 2.50^{c}	20.7 ± 7.34^{b}
Number of leaves on new shoots per pot	3.59 ± 1.10^{b}	5.00 ± 1.95^{a}	3.22 ± 1.70^{bc}	3.13 ± 2.40^{bc}	2.00 ± 1.02^{c}	5.00 ± 0.53^{a}
Length of leaves (cm)	7.20 ± 2.26^{bc}	8.77 ± 1.99^{a}	7.46 ± 2.31^{b}	6.73 ± 1.72^{c}	6.00 ± 1.29^{d}	6.88 ± 1.86^{bc}
Maximum width of leaves (cm)	0.78 ± 0.14^{b}	1.12 ± 0.17^{a}	0.72 ± 0.11^{c}	0.80 ± 0.18^{b}	0.65 ± 0.11^{d}	0.65 ± 0.14^{d}
Number of flowering spikes per pot	0.60 ± 0.57	4.00 ± 1.00	–	–	–	–

Notes: Different superscripts indicate differences at the 0.05 level of significance based on Tukey's test.

The number of newly recruited shoots was also 39% higher in the low nutrient condition than in the high nutrient condition (Table 2). Photoperiod had a significant effect on shoot morphology in *P. wrightii*, as well on new shoot recruitment; the length of main and new shoots decreased gradually with shortening photoperiod (Table 2). Plants under a 16 h photoperiod produced main shoots that were 23 and 98% longer in the high nutrient condition, and 74 and 172% longer in the low nutrient condition, compared with plants under 12 and 8 h photoperiods, respectively. In the high nutrient condition, the number of new shoots in the 16 h photoperiod was 21 and 222% higher per pot than in plants under 12 and 8 h photoperiods. In the low nutrient condition, the number of new shoots in the 16 h photoperiod was 289 and 349% higher per pot than in the 12 and 8 h photoperiods (Table 2). In the case of internodal length of stems, for the high nutrient condition, plants under a 12 h photoperiod had 40 and 29% longer internodes (average length 7.65 cm·individual^{-1}) than plants under 16 and 8 h photoperiods (Figure 1(a)). By contrast, in the low nutrient condition, the 16 h photoperiod resulted in internodes that were 8 and 30% larger than those of 12 and 8 h photoperiodic plants.

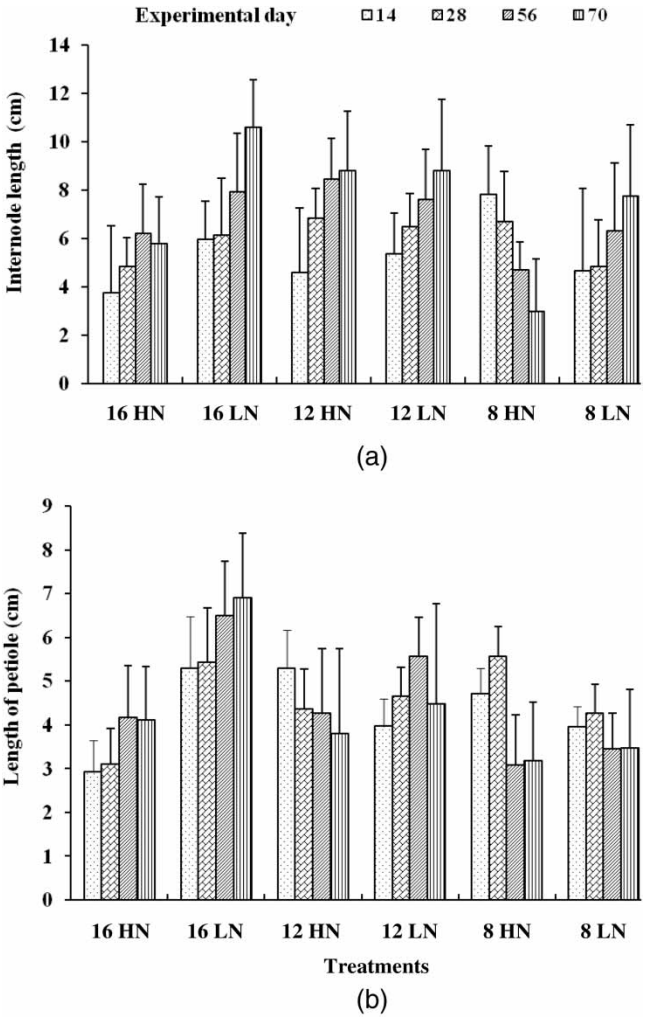

Figure 1. Average (a) length of stem internodes and (b) length of leaf petioles in experimental *Potamogeton wrightii*. Vertical bars indicate ± SD ($n = 10$).

3.2. *Leaf morphology and flowering spike*

Leaf morphology differed significantly among treatments (Table 2). Plants in the low nutrient condition produced more leaves (11% higher in main shoot and 49% in new shoots) with 20% longer petioles, and 19% wider and 9% larger lamina than plants in the high nutrient condition (Figure 1(b) and Table 2). Plants under a 16 h photoperiod in the low nutrient condition produced significantly larger leaf petioles (average 6.03 cm·individual^{-1}) and longer and wider laminas (average length 8.77 and width 1.12 cm·individual^{-1}) than all other treatments (Tukey HSD test) (Figure 1(b) and Table 2). Significant interactions were found between nutrient and photoperiods: main shoots in plants under a 16 h photoperiod produced 18 and 69% more leaves in the high nutrient condition and 40 and 76% more leaves in the low nutrient condition compared with plants under the 12 and 8 h photoperiods. By contrast, new shoots in plants under the 16 h photoperiod produced 11 and 61% more leaves than plants under the 12 and 8 h photoperiods in the high nutrient condition. Whereas, in the low nutrient condition, new shoots in plants under the 16 and 8 h photoperiods produced same number of leaves (average 5.0 leaves·pot^{-1}), which was significantly

higher than in plants under a 12 h photoperiod (Table 2). Average petiole length varied between 2.93 and 5.56 cm·individual^{-1} in the high nutrient condition and 3.46 and 6.90 cm·individual^{-1} in the low nutrient condition (Figure 1(b)).

Under short photoperiods (12 and 8 h) plants failed to produce flowering spikes in both nutrient conditions. However, plants under long photoperiods produced more flowering spikes which were significantly higher in the low nutrient condition (565%) than in the high nutrient condition (Table 2).

3.3. *Decomposed parts of plants*

The number of dead leaves per shoot was not significantly different between the two nutrient conditions, but photoperiod had a significant effect on the number of dead leaves with a significant interaction between two factors (Table 1). Plants under a 8 h photoperiod and high nutrient levels generated significantly more dead leaves (7.42 leaf·shoot^{-1}) and decomposed shoots (1.3 shoots·pot^{-1}) than plants in other treatment combinations (Tukey HSD test) (Figure 2(a),(b)). In the high nutrient condition, plants under a 8 h photoperiod had 86 and 333% more decomposed shoots than plants under a 16 and 12 h photoperiod, respectively. However, in the low nutrient condition, plants under a 16 h photoperiod had 60 and 300% more decomposed shoots than plants under 12 and 8 h photoperiods, respectively (Figure 2(b)). The relative number of new and decomposed shoots per pot in different treatments is compared in Figure 3. In the low nutrient condition, the average proportion of new shoots was 353% and the average proportion of decomposed shoots was 68% per pot under the 16 h photoperiod. The percentage of new shoot production was

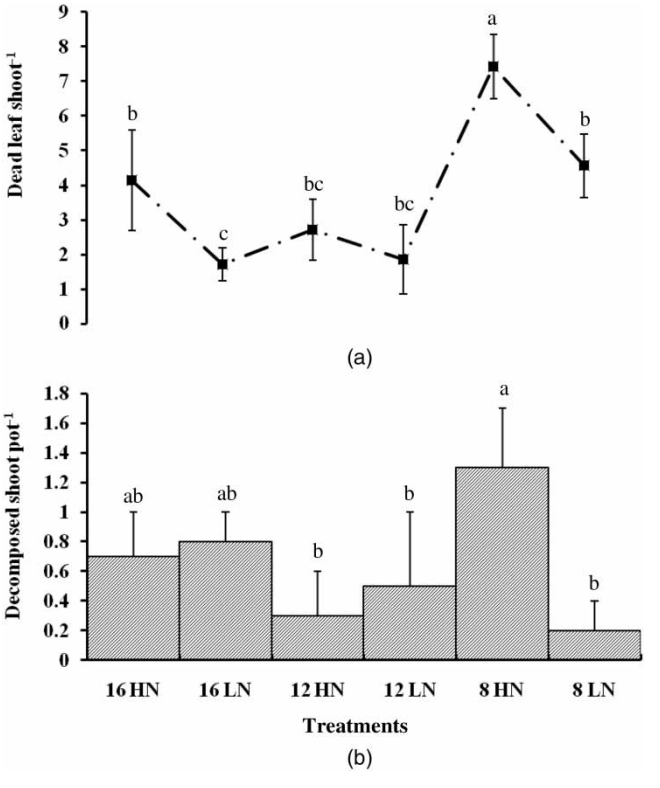

Figure 2. Average number of (a) dead leaves and (b) decomposed shoots per pot. Vertical bars indicate ± SD ($n = 10$).

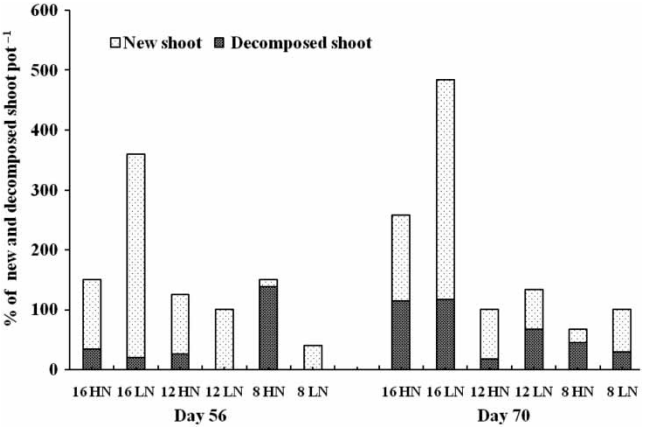

Figure 3. Percentage of new and decomposed shoots of *Potamogeton wrightii* per pot under different treatments.

also higher in 12 h and 8 h photoperiodic plants compared with decomposed shoot production in the low nutrient condition (Figure 3). By contrast, in the high nutrient condition, plants with a 8 h photoperiod (8 HN) produced on average, 91% decomposed and 17% new shoots per pot (Figure 3).

4. Discussion

Experimental plants showed a wide range of plasticity in their leaf and shoot morphology in response to photoperiod and nutrient concentration.

Overall, plants in low nutrient conditions produced more leaves, and larger and wider lamina and shoots than plants in high nutrient conditions. Plasticity in resource-acquiring organs such as leaves is of major importance for plant adjustment to resource availability [37]. In many submerged aquatic macrophytes, light intensity and/or mineral nutrition may have a much greater influence on leaf shape [38,39]. Our findings contradict earlier studies reporting reduced leaf number, smaller and narrower leaves with decreasing nutrient levels. For example, Wang and Yu [40] reported a significant increase in leaf length and width in *Vallisneria spiralis* L. in a nutrient-rich patch (209.85 and 4.13 μmol total N and total P·g^{-1} dry weight sediment) compared with nutrient poor patches (26.40 and 2.48 μmol total N and total P·g^{-1} dry weight sediment) at the State Key Field Station of Freshwater Ecosystem of Liangzi Lake, China. We assume that the plastic response of leaves can vary between plant species. In close agreement with the results of Richards and Ivey [41] for the emergent aquatic macrophyte *Sagittaria lancifolia* L., our results indicate that *P. wrightii* is capable of responding to reduced P and N by increasing petiole length. Further, we noticed that the lengths of both main and new shoots were decreased with reduced photoperiod under both nutrient conditions. However, internode length was greater in 12 h photoperiodic plants than in 16 h photoperiodic plants in the high nutrient condition. Plants in the low nutrient condition did not show the same mechanism. We assume that the greater internode length is a morphological plasticity of *P. wrightii* in high nutrient and 12 h photoperiod conditions. But *P. wrightii* was not capable of expressing this plasticity under a 8 h photoperiod and high nutrient levels. By contrast, under low nutrient levels and 8 h or 16 h photoperiods plants expressed a different type of morphological plasticity; i.e. a greater leaf production in their new shoots.

Plants under a 8 h photoperiod produced more senescent leaves in both nutrient conditions than plants under the 16 and 12 h photoperiods. Moreover, compared with new shoot production, the

number of decomposed shoots was higher in the 8 h photoperiod and high nutrient condition (i.e. 91% decomposed and only 17% new shoot). Our results for the high nutrient condition supported the result of Maeda [42], who noted accelerated senescence and dormancy in the terrestrial plant 'myoga' (*Zingiber mioga* Roscoe) under short photoperiods. He argued that a longer photoperiod prolonged the growth of myoga. This response to photoperiod was also observed in our experiment, plants under a short photoperiod showed more dead leaves and decomposed shoots at a time when was flowering began in plants grown under long (16 h) photoperiods. Again in the current study, plants under a 16 h photoperiod with low nutrient levels had 60 and 300% more decomposed shoots than plants under the 12 and 8 h photoperiods. We observed that the percentage of decomposed shoots (68%) was negligible compared with new shoot production (353%) and the percentage of new shoot production was also higher than the percentage of decomposed shoots in other treatments at low nutrient levels (Figure 3). This indicates that the production of decomposed shoots in the low nutrient condition was not caused by a shorter photoperiod and we suggest that a certain number of dead or decomposed shoots appear as a part of the normal lifecycle in *P. wrightii* after a certain period of growth (in our case after 42 days). This may be triggered by a shorter photoperiod in the high nutrient condition and plants tend to enter a type of dormancy earlier than those under longer photoperiods. Moreover, the number of flowering spikes produced was also significantly higher in plants under a 16 h photoperiod in the low nutrient condition. The importance of photoperiod in flowering is already established for plants [43,44] and our study showed that nutrient conditions are also an important influencing factor for flowering of *P. wrightii* as it produced 565% more flowering spikes in the low nutrient condition than in the high nutrient condition. Our results are also supported by the findings of Mony et al. [45], who found that the production of sexual organs in *Ranunculus peltatus* Schrank tended to be enhanced by low P concentrations in the water.

In the current study, plants in the low nutrient condition grew intensely and significantly increased their shoot length, internodal length, petiole length and had larger and broader leaves, even though they grew in a 16 h photoperiod. By contrast, in the high nutrient condition, plants produced shorter shoots, fewer leaves with shorter and less wide laminas, and smaller petioles compared with the low nutrient condition. This is suggested to be adaptive at high nutrient levels because it reduces the chance of more nutrients being absorbed by the shoot as well as foliage, which would be a risk for survival owing to excessive nutrient stress.

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References

[1] R.B. Jackson and M.M. Caldwell, *The scale of nutrient heterogeneity around individual plants and its quantification with geostatistics*, Ecology 74 (1993), pp. 612–614.
[2] S.E. Sultan, A.M. Wilczek, D.L. Bell, and G. Hand, *Physiological response to complex environments in annual* Polygonum *species of contrasting ecological breadth*, Oecologia 115 (1998), pp. 564–578.
[3] S.M. Scheiner, *Genetics and evolution of phenotypic plasticity*, Annu. Rev. Ecol. Syst. 24 (1993), pp. 35–68.
[4] S.E. Sultan, *Phenotypic plasticity for plant development, function and life history*, Trends Plant Sci. 5 (2000), pp. 537–542.
[5] M. Pigliucci, *Phenotypic Plasticity: Beyond Nature and Nurture*, Johns Hopkins University Press, Baltimore, MD, 2001.
[6] C.D. Schlichting and M. Pigliucci, *Phenotypic Evolution: A Reaction Norm Perspective*, Sinauer, Sunderland, MA, 1998.
[7] D.A. Levin, *Consequences of stochastic elements in plant migration*, Am. Nat. 132 (1988), pp. 643–651.

[8] J.P. Grime, *Plant Strategies and Vegetation Processes*, Wiley, Chichester, UK, 1979.
[9] P.A. Chambers and J. Kalff, *Light and nutrients in the control of aquatic plant community structure. 1.* In situ *experiments*, J. Ecol. 75 (1987), pp. 611–619.
[10] S. Miao, S. Newman, and F. Sklar, *Effects of habitat, nutrients and seed sources on growth and expansion of* Typha domingensis, Aquat. Bot. 68 (2000), pp. 297–311.
[11] W.C. Dennison and R.S. Alberte, *Photosynthetic responses of* Zostera marina *L. (eelgrass) to* in situ *manipulations of light intensity*, Oecologia 55 (1982), pp. 137–144.
[12] P.G. Falkowski and J. LaRoche, *Acclimation to spectral irradiance in algae*, J. Phycol. 27 (1991), pp. 8–14.
[13] E.G. Abal, N. Loneragan, P. Bowen, C.J. Perry, J.W. Udy, and W.C. Dennison, *Physiological and morphological responses of the seagrass* Zostera capricorni *Aschers. to light intensity*, J. Exp. Mar. Biol. Ecol. 178 (1994), pp. 113–129.
[14] A. Bergamini and M. Peintinger, *Effects of light and nitrogen on morphological plasticity of the moss* Calliergonella cuspidate, Oikos 96 (2002), pp. 355–363.
[15] J.C. Crick and J.P. Grime, *Morphological plasticity and mineral nutrient capture in two herbaceous species of contrasted ecology*, New Phytol. 107 (1987), pp. 403–414.
[16] M. Dong, J.H. During, and J.A.M. Werger, *Clonal plasticity in response to nutrient availability in the pseudoannual herb*, Trientalis europaea *L.*, Plant Ecol. 131(20) (1997), pp. 233–239.
[17] L. Wang, P.P. Mou, and R.H. Jones, *Nutrient foraging via physiological and morphological plasticity in three plant species*, Can. J. Forest Res. 36 (2006), pp. 164–173.
[18] H. Smith, *Light quality, photoreception and plant strategy*, Annu. Rev. Plant Physiol. 33 (1982), pp. 481–518.
[19] D.A. King, *Allocation of above-ground growth is related to light in temperate deciduous saplings*, Funct. Ecol. 17 (2003), pp. 482–488.
[20] J. Wang and D. Yu, *Influence of sediment fertility on morphological variability of* Vallisneria spiralis *L.*, Aquat. Bot. 87 (2007), pp. 127–133.
[21] D.F. Spencer and G.G. Ksander, *Influence of planting depth on* Potamogeton gramineus *L.*, Aquat. Bot. 36 (1990), pp. 343–350.
[22] J. Idestam-Almquist and L. Kautsky, *Plastic responses in morphology of* Potamogeton pectinatus *L. to sediment and above- sediment conditions at two sites in the northern Baltic proper*, Aquat. Bot. 52 (1995), pp. 205–216.
[23] J.J. Pilon and L. Santamaría, *Clonal variation in the thermal response of the submerged aquatic macrophyte* Potamogeton pectinatus, J. Ecol. 90 (2002), pp. 141–152.
[24] Y. Xie, D. Yu, X. Geng, Y. Yang, and Y. Huang, *Phenotypic plasticity in submerged plant* Potamogeton crispus *in response to elevated CO_2*, J. Freshwater Ecol. 19 (2003), pp. 701–708.
[25] S. Wolfer and D. Straile, *Spatial and temporal dynamics of clonal architecture in* Potamogeton perfoliatus *L.*, Aquat. Bot. 78 (2004), pp. 307–318.
[26] M. Sultana, T. Asaeda, M.E. Azim, and T. Fujino, *Morphological responses of a submerged macrophyte to epiphyton*, Aquat. Ecol. 44 (2010), pp. 73–81.
[27] G. Wiegleb and Y. Kadono, *Growth and development of* Potamogeton malaianus *in SW Japan*, Nordic J. Bot. 9 (1989), pp. 167–178.
[28] Y. Kadono, *Comparative ecology of Japanese* Potamogeton: *an extensive survey with special reference to growth form and life cycle*, Jpn. J. Ecol. 34 (1984), pp 161–172.
[29] Y. Ahn, S. Mizugaki, F. Nakamura, and Y. Nakamura, *Historical change in lake sedimentation in Lake Takkobu, Kushiro Mire, northern Japan over the last 300 years*, Geomorphology 78 (2006), pp. 321–334.
[30] K.E. Havens, T. Fukushima, P. Xie, T. Iwakuma, R.T. James, N. Takamura, T. Hanazato, and T. Yamamoto, *Nutrient dynamics and the eutrophication of shallow lakes Kasumigaura (Japan), Donghu (PR China), and Okeechobee (USA)*, Environ. Pollut. 111 (2001), pp. 263–272.
[31] K. Hirabayashi, K. Yoshizawa, N. Yoshida, and F. Kazama, *Progress of eutrophication and change of chironomid fauna in Lake Yamanakako, Japan*, Limnology 5(1) (2004), pp. 47–53.
[32] K. Katsuki , Y. Miyamoto, K. Yamada, H. Takata, K. Yamaguchi, D. Nakayama, H. Coops, H. Kunii, R. Nomura, and B. Khim, *Eutrophication-induced changes in Lake Nakaumi, southwest Japan*, J. Paleolimnol. 40 (2008), pp. 1115–1125.
[33] T. Masaki and H. Suge, *Physiological and ecological studies on the pond weed,* Potamogeton distinctus *A. Bennett, a perennial weed of paddy fields: IV. Intraspecific variations in the elongation of winter buds and in the photoperiodic response of winter bud formation*, J. Weed Sci. Technol. 29 (1984), pp. 278–284 [in Japanese].
[34] M.J.M. Hootsmans and J.E. Vermaat, *Light-response curves of* Potamogeton pectinatus *L as a function of plant age and irradiance level during growth*, in *Lake Veluwe: A macrophyte-dominated system under eutrophication stress. Geobotany*, W. Van Vierssen, M.J.M. Hootsmans and J.E. Vermaat, eds., Kluwer Academic, Dordrecht, 1994, pp. 62–118.
[35] S.L. Nielsen and K. Sand-Jensen, *Variation in growth rates of submerged rooted macrophytes*, Aquat. Bot. 39 (1990), pp. 109–120.
[36] W.M. Kemp, M.R. Lewis, and T.W. Jones, *Comparison of methods for measuring production by the submersed macrophyte:* Potamogeton perfoliatus *L.*, Limnol. Oceanogr. 31 (1986), pp. 1322–1334.
[37] M. Dong, H.J. During, and M.J.A. Werger, *Morphological responses to nutrient availability in four clonal herbs*, Vegetatio 123 (1996), pp. 183–192.
[38] J.T.O. Kirk, *Light and Photosynthesis in Aquatic Ecosystems*, Cambridge University Press, Cambridge, UK, 1994.
[39] D.H.N. Spence, *Light and plant response in fresh water*, in *Light as an Ecological Factor: II*, G.C. Evans, R. Bainbridge, and O. Rackham, eds., Blackwell Science, Oxford, 1995.

[40] J. Wang and D. Yu, *Influence of sediment fertility on morphological variability of* Vallisneria spiralis *L*., Aquat. Bot. 87 (2007), pp. 127–133.
[41] J.H. Richards and C.T. Ivey, *Morphological plasticity of* Sagittaria lancifolia *in response to phosphorus*, Aquat. Bot. 80 (2004), pp. 53–67.
[42] K. Maeda, *Physiological and ecological characteristics and cultivation for year-round culture in Mioga* (Zingiber mioga *Roscoe*) *plants*, Spec. Bull. Kochi Agric. Res. Center (Japan) 1 (1994), pp. 1–155.
[43] F.B. Salisbury, *Responses to photoperiod*, in *Encyclopedia of Plant Physiology*, A. Pirson, ed., Springer-Verlag, Berlin, 1981, pp. 135–167.
[44] L. Santamaría and M.J.M. Hootsmans, *The effect of temperature on the growth, photosynthetic performance and reproduction of a Mediterranean submerged macrophyte*, Ruppia drepanensis, Aquat. Bot. 60 (1998), pp. 169–188.
[45] C. Mony, C.G. Thiébaut, and S. Muller, *Changes in morphological and physiological traits of the freshwater plant* Ranunculus peltatus *with the phosphorus bioavailability*, Plant Ecol. 191 (2007), pp. 109–118.