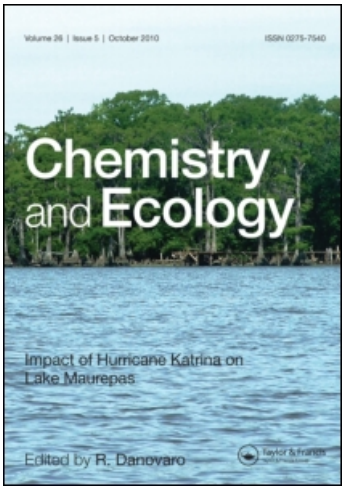

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Munira Sultana[a]; Takashi Asaeda[a]; M. Ekram Azim[ab]; Takeshi Fujino[a]
[a] Department of Environmental Science and Human Technology, Saitama University, Saitama, Japan [b] Department of Physical and Environmental Sciences, University of Toronto, Toronto, Canada

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Photosynthetic and growth responses of Japanese sasabamo (*Potamogeton wrightii* Morong) under different photoperiods and nutrient conditions

Munira Sultana[a]*, Takashi Asaeda[a], M. Ekram Azim[a,b] and Takeshi Fujino[a]

[a]*Department of Environmental Science and Human Technology, Saitama University, Saitama, Japan;* [b]*Department of Physical and Environmental Sciences, University of Toronto, Toronto, Canada*

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Controlled laboratory experiments were conducted to examine how photosynthesis and growth occur in *Potamogeton wrightii* Morong under different photoperiods and nutrient conditions. The experiment was based on a 3×2 factorial design with three photoperiods (16, 12 and 8 h) of 200 $\mu E \cdot m^{-2} \cdot s^{-1}$ irradiance and two nutrient conditions, high (90 $\mu mol\ N \cdot L^{-1} \cdot d^{-1}$ and 9 $\mu mol\ P \cdot L^{-1} \cdot d^{-1}$) and low (30 $\mu mol\ N\ L^{-1} \cdot d^{-1}$ and 3 $\mu mol\ P \cdot L^{-1} \cdot d^{-1}$). After 14, 28, 56 and 70 days of growth, plants were harvested to determine net photosynthesis rate and various growth parameters. Above- and below-ground biomass were investigated on days 56 and 70 only. Plants under low nutrient conditions had greater leaf area, more chlorophyll *a*, a higher rate of net photosynthesis and accumulated more above- and below-ground biomass than plants in the high nutrient condition. Plants with an 8 h photoperiod in the low nutrient condition had a significantly higher rate of net photosynthesis, whereas 8 h photoperiod plants in the high nutrient condition had a lower rate of net photosynthesis and their photosynthetic capacity collapsed on day 70. We conclude that *P. wrightii* has the photosynthetic plasticity to overcome the effects of a shorter photoperiod under a tolerable nutrient state.

Keywords: *Potamogeton wrightii*; nutrient; dark respiration; photoperiod

1. Introduction

For any primary producers, photosynthesis is the key physiological process and is primarily governed by the availability of nutrients and lights. In the case of submerged macrophytes, photosynthesis is directly related to light [1,2] and nutrient availability [3], and these variables combine to modify the photosynthetic characteristics. Rooted submerged macrophytes absorb nutrients from both water and sediment [4,5], and their uptake and accumulation of nutrients depend largely upon the nutrient concentration in the water [6]. If nutrients in the water are insufficient for growth, macrophytes may be able to continue to grow by root uptake of P and N [7]. Nutrient availability in water often limits aquatic plant growth and resolves species dominance and abundance [8]. Worldwide, the massive use of fertilisers in agriculture and industry has led to an exponential increase in nutrient input into natural waters. One of the most serious threats to aquatic ecosystems is an overabundance of nutrients, particularly nitrogen and phosphorus. With increasing N and P

*Corresponding author. Email: munira.sultana@ymail.com

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loading, many shallow freshwater ecosystems have undergone dramatic changes, and a decline in aquatic macrophytes has been reported worldwide [9–12], e.g. enrichment of water-column nitrate (NO_3^-) has caused the death of the seagrass *Zostera marina* [13].

Similarly, light is the ultimate energy source for photosynthesising organisms. Photoperiod or the length of light availability also has a large impact on many aspects of plant life [14]. The general hypothesis related to submerged macrophytes is that a decrease in light availability reduces effective photosynthesis, ultimately leading to plant death. Perennial submerged macrophytes exhibit distinct growth periodicity, with growth initiated after a period of overwintering. This distinct periodicity suggests that the growth and development of perennial submerged macrophytes may be affected by photoperiod. The effect of photoperiod on terrestrial plants and several grass species has been studied previously [15–17]. Data on the effects of photoperiod on growth in submerged plants are scarce.

The ecological quality of freshwater ecosystems in temperate zones is strongly related to the integrity of submerged vegetation, which is important for the maintenance of clear water in shallow lakes [18–20]. Macrophyte species are replaced or become extinct when one or more of the ecological parameters that govern their growth rate are changed. Predicting the effects of such impacts is crucial for the management and conservation of ecosystems, and managers need to predict the effects of their actions if they wish to achieve desired goals [21].

Potamogeton wrightii Morong (Sasabamo) is a common submerged perennial macrophyte in lakes, ditches and rivers in central and south-western Japan. It is also distributed throughout east and south-east Asia, including the Indonesian Archipelago and some Pacific islands [22]. Even though *P. wrightii* is very common and is abundant in many places in the world, no detailed information about its biology and ecology is known to date. Human development and industrialisation throughout Japan have led to changes in nutrient loading and hydrology within the habitat of *P. wrightii*. It is uncertain whether this anthropogenic nutrient loading influences submerged plant species. Furthermore, *P. wrightii* shows distinct periodicity in its growth cycle, representing a resting period or dormancy over the winter season [23]. From this distinct periodicity, we assume that the growth and development of *P. wrightii* may be affected by photoperiod.

The ability of plants to adapt to variations in environmental factors are species specific and the most instantaneous effects occur at the biochemical and physiological levels. Photosynthesis shows an immediate response to changes in environmental conditions [24]. For the management of submerged species, it is important to know about conditions that favour and/or limit growth, for example, by estimating the photosynthetic rate. In this study, it is hypothesised that *P. wrightii* may take advantage of increased nutrients under longer photoperiods to successfully invade. Controlled laboratory experiments were conducted to examine how photosynthesis and dark respiration occur under different photoperiods and nutrient conditions. The information may have ecological implications and practical use in developing management strategies.

2. Materials and methods

2.1. *Experimental design and set-up*

The experiment was conducted over 70 days in the Environmental Science and Human Technology Laboratory, Saitama University, Japan. The set-up consisted of 18 glass aquaria ($1.6 \times 0.8 \times 0.8$ m) and was based on a 3×2 factorial design with three photoperiods (16, 12 and 8 h) of $200\ \mu E \cdot m^{-2} \cdot s^{-1}$ irradiance and two nutrient conditions (high and low, described below), each with three replications.

P. wrightii and sediments were collected from the River Hanamuro, 2 km upsteam of the mouth, which flows into Lake Kasumigaura (36° 05′ N, 140° 12′ E), the second largest lake in Japan.

The concentrations of N and P were ∼30 and 3 $\mu mol \cdot L^{-1}$, respectively, in open water. Single shoots of *P. wrightii* with rhizomes (3–4 cm long, with 2–3 leaves) were carefully selected for uniformity and planted in individual plastic pots (diameter: 7 cm, depth: 15 cm) filled with collected river sediment. Seventy-five pots (each planted with a single shoot) were then transferred to each of the 18 aquaria filled with de-chlorinated tap water. We tried to keep approximately the same stem density per square metre as observed in the field. During the first four weeks, plants were maintained with the same amount of commercial nutrient, photon irradiance (200 $\mu E \cdot m^{-2} \cdot s^{-1}$, 1 cm below the water surface), a 14 h photoperiod and 25 °C temperature to acclimatise them to the new environment. Hootsmans and Vermaat [25] used the same light level (200 $\mu E \cdot m^{-2} \cdot s^{-1}$) in a growth experiment on *Potamogeton pectinatus*. Light was provided by white fluorescent bulbs. After four weeks, three different photoperiods and two nutrient conditions were introduced and that date was considered as experimental day 1; the experiment continued to day 70. On experimental day 1, the lengths of selected plants were 7–9 cm.

Within each photoperiodic condition, the position of the planted pots was changed twice a week to avoid any potential heterogeneity in the light field. A temeprature of 25 °C was maintained for all aquaria. Water in all tanks was bubbled continuously with air stones for mixing and to minimise CO_2 limitation and O_2 inhibition [26]. The CO_2 concentration of the water in the aquaria was kept at 14–50 μM CO_2, as described by Nielsen and Sand-Jensen [27], by supplying from a CO_2 bottle. All aquaria were covered with thick black screens to maintain a proper and uniform light climate throughout the aquaria.

Commercial fertilisers in the form of ammonium sulphate, potassium nitrate and di-ammonium phosphate, containing equal amounts of NO_3^-, NH_4^+ and P, were added (N/P ratio 10:1) on a weekly basis to the aquaria (90 $\mu mol\ N \cdot L^{-1} \cdot d^{-1}$ and 9 $\mu mol\ P \cdot L^{-1} \cdot d^{-1}$ as the high nutrient condition and 30 $\mu mol\ N \cdot L^{-1} \cdot d^{-1}$ and 3 $\mu mol\ P \cdot L^{-1} \cdot d^{-1}$ as the low nutrient condition). The amount of N and P used for 'low nutrient treatments' was equal to the N and P concentration recorded in water from the River Hanamuro (the origin of experimental macrophytes). In addition, a commercially available micronutrient solution, Tetra Flora Pride™, which is normally used for aquarium plants, was added to all aquaria in equal amounts to maintain sufficient concentrations of micronutrients in the water. The water was changed every week to avoid shading effects created by phytoplankton and filamentous algae. Treatments combination with high nutrient level and different photoperiods were marked with the number of photo hours and 'HN' (i.e. 16 HN, 12 HN and 8 HN). In the case of low nutrient treatments, the symbol indicating the nutrient condition was 'LN' (i.e. 16 LN, 12 LN and 8 LN).

2.2. *Sampling*

After 14, 28, 56 and 70 days of growth, plants were harvested to determine leaf area, concentration of chlorophyll *a*, *b*, and rates of net photosynthesis and dark respiration. Plants from 15 randomly selected pots (three per parameter) from each of the aquaria were used. To maintain the same stem density in all aquaria, a similar number of pots with approximately the same sized plants from the stock tank was placed in the aquaria every sampling day. The newly placed plants were marked and excluded from subsequent sampling. Only the main shoot from each pot was considered for the above measurements. For biomass (above- and below-ground) analysis, plant materials were dried in an oven at 70 °C for 48 h, cooled and weighed on days 56 and 70. Relative growth rate (RGR) was calculated for that time (from day 56 to day 70) as described by Hunt [28]:

$$\mathrm{RGR} = (1\mathrm{n}B_2 - \ln B_1)/t_2 - t_1,$$

where B_2 = total biomass at day 70, B_1 = total biomass at day 56, and $(t_2 - t_1) = 14$ days (because t_2 is day 70 and t_1 is day 56).

To calculate the per cent variation or the difference between two factors, in every case, we first calculated the average or mean value of the data for each factor for the entire experimental period (those average values are not shown here), and then used the following formula:

$$\frac{\text{High-valued factor} - \text{Low-valued factor}}{\text{Low-valued factor}} \times 100.$$

2.3. *Laboratory analyses*

On each sampling day, the fully opened fourth leaf (from the top) of the main shoot from three pots was taken for chlorophyll *a* (chl. *a*) and chlorophyll *b* (chl. *b*) analysis. After grinding the leaves with a tissue grinder using 90% acetone, the sample was transferred to a 15 mL graduated centrifuge tube and kept in the dark at room temperature for 10 min. Samples were then centrifuged at 3000 rpm for 10 min and the supernatant was used for spectrophotometer analysis according to the method of Jeffrey and Humphrey [29].

Net photosynthesis and dark respiration rates for *P. wrightii* were measured using the dissolved oxygen (O_2) method. In both cases, oxygen concentration was estimated using a standard Winkler technique [30]. One 10 cm long shoot tip (from the main shoot, consisting of 4–5 full leaves) was placed in each of the three 'light' (for photosynthesis) and three 'dark' (for dark respiration) bottles (300 mL) for 3 h at a depth of 1 cm below the water surface of each aquarium. Moreover, each treatment comprised three blank bottles (without shoot tips and with non-filtered aquarium water). Light and dark bottles were filled with filtered aquarium water before incubation, and the results from the blank bottles without shoot tips were subtracted from those from bottles with shoot tips to allow for any changes resulting from phytoplankton in the water. Shoots were washed carefully before incubation to remove loose epiphyton.

2.4. *Statistical analyses*

All data were checked for the assumption of normal distributions and homogeneity in the variances before statistical analyses. Leaf area, chl. *a*, chl. *a*/*b* ratio, net photosynthesis, dark respiration and biomass (above- and below-ground) data were analysed using a three-way repeated measures analysis of variance (ANOVA) with photoperiods and nutrient conditions as the main factors and the sampling dates as the repeated measures factor. 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 significance level of 0.05 using the statistical package Statistica (v. 5).

3. Results

Sampling dates, photoperiods and nutrient conditions had significant effects on leaf area, chl. *a* and chl. *a*/*b* ratio in leaves, rates of net photosynthesis and dark respiration, and above- and below-ground biomass of the experimental *P. wrightii*. There were also significant differences among all combinations in the interactions of sampling dates, photoperiods and nutrient conditions on the above parameters (three-way ANOVA, presented in Table 1).

3.1. *Leaf area*

Leaf area in plants with 16 and 12 h photoperiods increased gradually from the beginning to the end of the experiment, whereas in 8 h photoperiod plants leaf area reduced over time under both

Table 1. Results of three-way repeated measures analysis of variance (ANOVA) with photoperiod (P) and nutrient (N) as the main factors, and sampling date (T) as the repeated measures factor for some variables of *Potamogeton wrightii*.

	Source of variation						
Variables	P	N	T	P×N	N×T	P×T	P×N×T
Leaf area (cm^{-2})	79.71*	64.04*	16.24*	20.84*	12.28*	17.78*	2.69**
Chlorophyll *a* ($mg \cdot g^{-1}$ DW)	6.29*	14.22*	20.61*	3.85***	0.21NS	3.73*	4.83*
Chl. *a*/*b* ratio	3.25**	7.24*	10.45*	1.75***	1.27***	2.00**	2.17**
Photosynthesis ($mg\ C \cdot g^{-1}\ DW \cdot h^{-1}$)	10639.5*	16957.9*	28885.2*	15005.4*	11108.4*	7797.8*	2862.0*
Dark respiration ($mg\ C \cdot g^{-1}\ DW \cdot h^{-1}$)	3646.33*	2279.04*	4341.09*	27.44*	201.70*	3467.18*	644.69*
Above ground biomass ($g\ DW \cdot m^{-2}$)	106884.7*	113211.6*	1643.3*	49657.9*	19053.8*	1984.1*	3825.7*
Below ground biomass ($g\ DW \cdot m^{-2}$)	1699.28*	4708.58*	468.47*	1202.92**	670.00*	78.79*	22.94*

Note: F-values are given. Significant at * $p = 0.001$; ** $p = 0.01$; *** $p = 0.05$. NS, not significant.

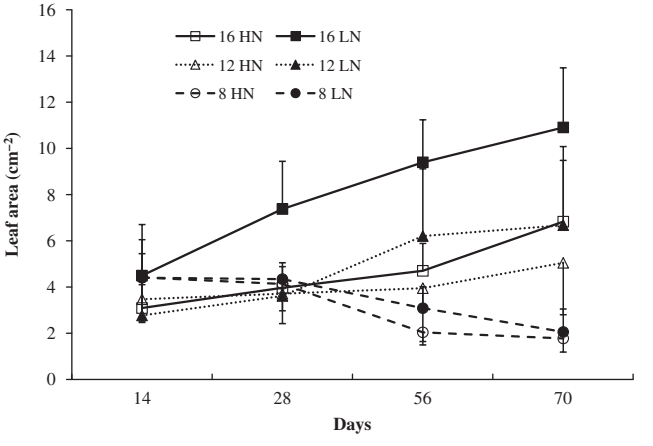

Figure 1. Average leaf area of *Potamogeton wrightii* under different treatments on different sampling days. Vertical bars indicate ±SD ($n = 15$) for leaf area.

nutrient conditions (Figure 1). Again, plants grown under low nutrient conditions expressed 39% greater leaf area than plants grown under high nutrient conditions. A significant interaction was also noticed between nutrients and photoperiods, with 42 and 132% increased leaf area obtained respectively from 16 h photoperiod plants in high and low nutrient treatments compared with plants with the 8 h photoperiod. These values were 22 and 67% for 16 h plants, compared with 12 h plants (Figure 1). However, 12 h plants achieved 17 and 39% greater leaf area in high and low nutrients treatments compared with 8 h plants (Figure 1).

3.2. *Chlorophyll content*

The experimental plants in all treatments showed a trend towards increasing synthesis of leaf chl. *a* throughout the experimental period (Figure 2(a)). Values ranged between 4.23 and 16.23 $mg \cdot g^{-1}$ DW in 16 h plants in the high nutrient treatment (16 HN). By contrast, 8 h photoperiod plants in the high nutrient treatment (8 HN) initially showed a sharp increase in chl. *a* synthesis (from day 14 to 28); thereafter chl. *a* synthesis did not increase by much (range 4.57–4.93 $mg \cdot g^{-1}$ DW). In the

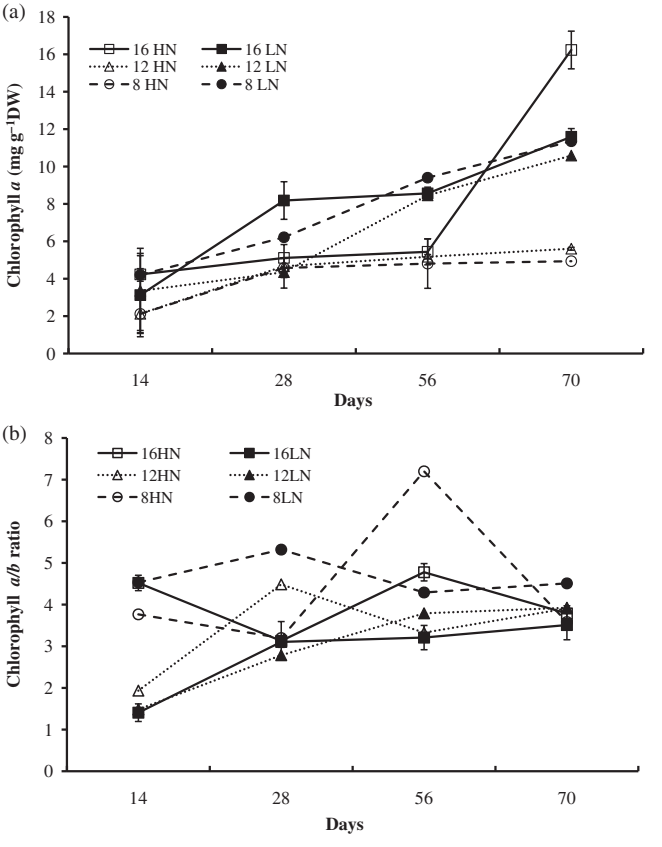

Figure 2. Concentration of (a) chlorophyll a and (b) the chlorophyll a/b ratio in *Potamogeton wrightii* leaves under different treatments in the experimental period. Vertical bars indicate $\pm$SD ($n = 3$).

high nutrient treatment, chl. a content was not significantly different among the three photoperiods until day 56 (Tukey HSD test). After day 56, plants with a 16 h photoperiod suddenly showed a sharp increase in the chl. a concentration in their leaves (Figure 2(a)). Overall, 16 h plants had 89 and 77% more chl. a than plants with 8 and 12 h photoperiods in the high nutrient treatments (Figure 2(a)). By contrast, in the low nutrient treatments, there were no significance differences among the three photoperiods (Figure 2(a)). The chl. a/b ratio varied among treatments and 8 HN plants showed a significantly higher chl. a/b ratio than all other treatments (Tukey's HSD test). Plants under the 8 h photoperiod in the high nutrient treatments showed the highest chl. a/b ratio on day 56 and treatment 16 LN expressed the lowest chl. a/b ratio (Figure 2(b)).

3.3. *Net photosynthesis rate and dark respiration*

The net photosynthesis rate for experimental *P. wrightii* was 108% greater in the low nutrient condition than in the high nutrient condition. It showed a decreasing tendency in all treatments except for plants under the high nutrient condition with a 12 h photoperiod (treatment 12 HN). Net photosynthesis rate showed a significant interaction between nutrient condition and photoperiod. Plants with an 8 h photoperiod in the low nutrient condition (treatment 8 LN) had a significantly higher rate of photosynthesis (average 1.49 mg C $\cdot$ g^{-1} DW $\cdot$ h^{-1}) than all other treatments except for 12 LN (Tukey's HSD test). By contrast, 8 h plants in the high nutrient condition had a lower

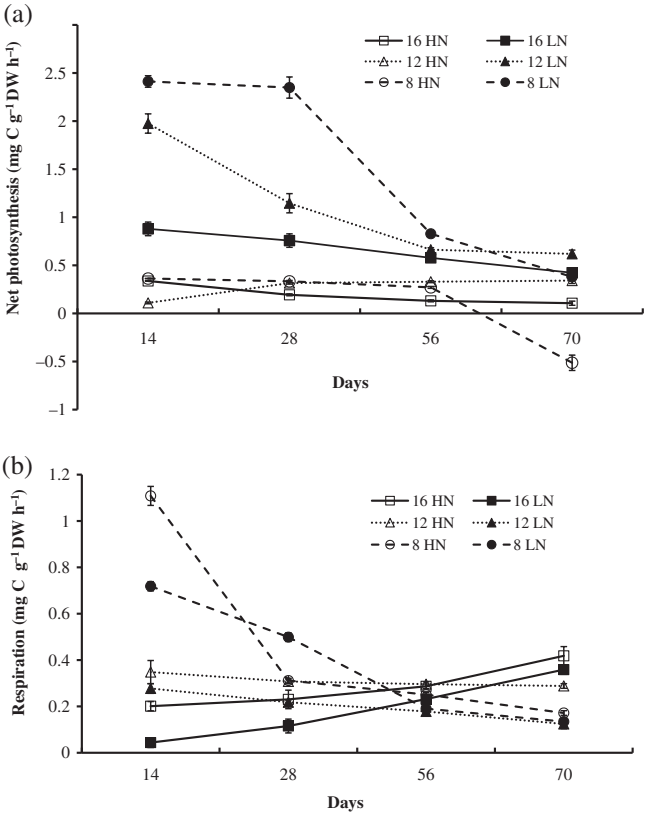

Figure 3. Rates of (a) net photosynthesis and (b) dark respiration in experimental *Potamogeton wrightii* in different treatments. Vertical bars indicate ±SD ($n = 3$).

rate of net photosynthesis (average 0.11 mg C · g^{-1} DW · h^{-1}) and their photosynthetic capacity collapsed on day 70 (Figure 3(a)).

Dark respiration increased over time in longer photoperiodic plants (16 h) in both nutrient conditions (Figure 3(b)). By contrast, in shorter photoperiodic plants (both 12 and 8 h) respiration rate reduced day by day (Figure 3(b)). Plants with an 8 h photoperiod and low nutrient conditions (treatment 8 LN) showed higher levels of dark respiration than 16 and 12 h photoperiodic plants under low nutrient conditions until day 28. However, 12 h plants behaved differently under the two nutrient treatments. For example, in the high nutrient condition, the average rate of dark respiration was more or less the same in 12 and 16 h plants (Figure 3(b)), allthough the 12 h plants expended 46% more oxygen through dark respiration than 16 h plants in the low nutrient condition (Figure 3(b)).

3.4. *Biomass*

Below-ground biomass accumulation showed a tendency to increase in experimental plants in all treatments from experimental day 56 to day 70 (Figure 4(b)). However, a negative RGR in above-ground biomass was found in the high nutrient treatments (i.e. 16 HN, 12 HN and 8 HN; Figure 4(c)). Plants accumulated 147% greater above- and below-ground biomass under the low nutrient conditions than under high nutrient conditions (Figure 4(a),(b)). The RGR of plants in the low nutrient condition was 691% greater than in the high nutrient condition. Plants with a 16 h

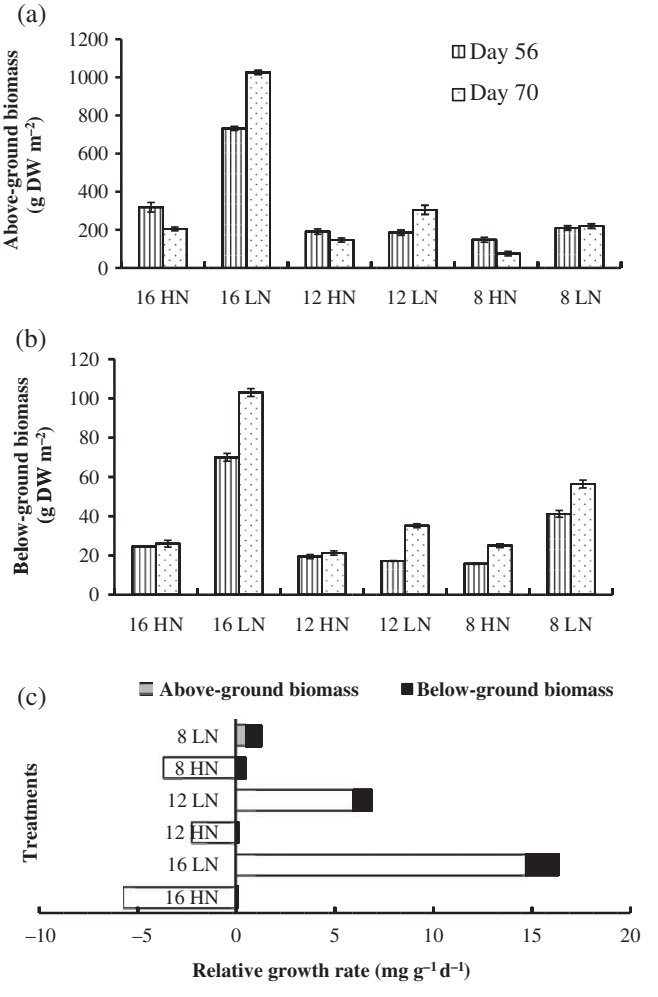

Figure 4. Average (a) above-ground biomass, (b) below-ground biomass and (c) relative growth rate (RGR) for above- and below-ground biomass of *Potamogeton wrightii* populations in different treatments. Vertical bars indicate ±SD ($n = 3$).

photoperiod accumulated more above- and below-ground biomass than 12 and 8 h plants in both nutrient conditions. However, 12 h plants accumulated 51 and 15% more above-ground biomass than 8 h plants under high and low nutrient conditions. In the case of below-ground biomass, 8 h plants were able to produce more dry matter than 12 h plants in both nutrient conditions (Figure 4(a),(b)).

4. Discussion

The chl. *a* concentration per unit biomass was significantly higher in the low nutrient condition than in the high nutrient condition. A sharp increase in photosynthetic pigment (chl. *a*) in plants under high nutrient levels and a longer photoperiod (treatment 16 HN) on day 70 in this experiment might be an adaptive mechanism to overcome filamentous algal shading which grew due to excess nutrients and co-existed with macrophytes, even though the water was replenished

on a weekly basis. Lippert et al. [31], described how the chlorophyll content in leaves of an emergent macrophyte, *Phragmites australis*, increased with higher N availability in a eutrophic lake (Lake Templiner, Germany). An increase in chlorophyll production by algae and phytoplankton due to the addition of nitrogen has also been reported by White and Payne [32] and Callaway et al. [33]. However, plants with shorter photoperiods in high nutrient conditions (treatments 12 HN and 8 HN) were not able to adopt the increase. Normally, acclimation to low irradiance involves a decreases in the chl. a/b ratio [34] and indicates a higher investment in the light-harvesting complex which contains more chl. b. However, in the current experiment, short photoperiodic plants in the high nutrient treatment (8 HN) expressed a significantly higher chl. a/b ratio. Plants grown under constant short-day photoperiods might exhibit substantially lower photochemical efficiency in the high nutrient condition. By contrast, in low nutrient conditions, short photoperiodic plants may be able to increase their photosynthetic pigment up to end of the experiment, which was not significantly different from plants with a longer photoperiod (Figure 2(a)), although their photosynthetic performance decreased over time (Figure 3(a)). The different responses of photosynthetic pigments to low nutrient conditions measured in this study indicate that experimental *P. wrightii* was strongly influenced by different nutrient conditions; as a result, plants showed different phenotypic adaptations in different nutrient conditions even though they grew under the same irradiance or photoperiod. Moreover, we found a negative RGR in above-ground biomass in all high nutrient treatments from experimental day 56 to day 70 (Figure 4(c)). This indicates that the plants did not grow at the end of the experiment, possibly because of high levels of P and N. For example, Mony et al. [35] reported a negative RGR for a freshwater, submerged macrophyte, *Ranunculus peltatus* Schrank, in a controlled experiment with $9.67\,\mu\text{mol}\cdot\text{L}^{-1}$ P.

A similar trend was seen for net photosynthesis rate. When plants grew under an 8 h photoperiod and high nutrient level, their average rate of photosynthesis was significantly lower (0.11 mg $\text{C}\cdot\text{g}^{-1}\,\text{DW}\cdot\text{h}^{-1}$) than plants with an 8 h photoperiod and low nutrient level (average photosynthesis rate 1.49 mg $\text{C}\cdot\text{g}^{-1}\,\text{DW}\cdot\text{h}^{-1}$; Figure 3(a)). This indicates that *P. wrightii* could not acclimatise properly to short irradiance when grown under high nutrient conditions. As a result, photosynthetic capacity collapsed after day 56 (Figure 3(a)). In other studies, photosynthetic capacity increased at decreasing photoperiods, as seen for the submerged aquatic macrophyte *Ruppia drepensis* [36] and for terrestrial plants [37]. In contrast to photosynthesis rate, plants with an 8 h photoperiod had a higher rate of dark respiration and those with a 16 h photoperiod under both nutrient conditions. These results correspond with those of Pilon and Santamaria [14] who reported that a decrease in photoperiod (13 h) resulted in significantly higher rates of dark respiration for two submerged *Potamogeton pectinatus* clones. In our investigation we also observed that the respiration rates are quite high compared with photosynthesis. This type of trend, not commonly observed, may be an important characteristic of *P. wrightii* and requires further investigation.

A reduction in the photoperiod from 16 h to 12 and 8 h resulted in a decrease in above-ground biomass under both nutrient conditions (Figure 4(a)), indicating that the increase in photosynthesis rate was insufficient to compensate fully for the decrease in daily irradiance at shorter photoperiods. We observed that leaf area gradually decreased in plants with a shorter photoperiod (8 h), whereas leaf area increased in plants with 16 and 12 h photoperiods (Figure 1). Although the net photosynthesis rate of plants with a 16 h photoperiod was lower, leaf area was significantly higher (Figure 1). These plants were able to fix more carbon because of their larger leaf area, longer exposure (16 h) to irradiance, and with their lower dark respiration rate, they reduced their energy loss, eventually resulting in a significantly higher biomass than seen in plants with shorter photoperiods. However, in the case of below-ground biomass, a reduction in the photoperiod from 12 to 8 h did not result in a decrease in plant biomass (Figure 4(b)). Santamaria and van Vierssen [36] showed a significant decrease in plant biomass as a result of the combined effect of shorter photoperiod and lower temperature.

Indeed, photosynthesis is an immediate response to changed environmental conditions, whereas plant biomass and productivity are the end result of photosynthesis. *P. wrightii* showed considerable plasticity in photosynthetic responses as an effect of different nutrient and photoperiod conditions when temperature was constant. Plants grown in the shorter photoperiod and low nutrient condition exhibited average maximum photosynthesis, but were not able to allocate more biomass. We suggest that the lower productivity (less biomass at the end) was due to the higher rate of dark respiration in these plants (treatment 8 LN).

Our hypothesis, that *P. wrightii* might take advantage of increased nutrient levels under a longer photoperiod, is not supported by our observations. We observed that *P. wrightii* has phenotypic plasticity within a certain range of nutrient concentrations in water to metabolically compensate for changes in the environment. Overall, rate of net photosynthesis was significantly higher in plants given a short photoperiod and low nutrient levels (treatment 8 LN), suggesting that *P. wrightii* has the photosynthetic plasticity to overcome the effects of shorter photoperiod when the nutrient state remains tolerable. Unless the photosynthetic rate is very low under high nutrient conditions and after some days of exposure to excessive nutrients, photosynthetic capacity collapses. These results may constitute valuable information concerning the existence and ecological significance of freshwater-submerged macrophytes.

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