



Egeria najas Planchon (Hydrocharitaceae) responses to abiotic short-term environmental changes

Maura Maria Pezzato · Marcela Bianchessi da Cunha-Santino · Antonio Fernando Monteiro Camargo · Irineu Bianchini Jr.

Received: 31 August 2023 / Revised: 12 December 2023 / Accepted: 29 January 2024 / Published online: 13 March 2024
© The Author(s), under exclusive licence to Springer Nature Switzerland AG 2024

Abstract Understanding the factors that control the growth of macrophytes is of paramount importance in predicting their distribution and management. This study describes the effect of short-term variation of pH, light intensity ($10\text{--}390 \mu\text{mol m}^{-2} \text{s}^{-1}$), and temperature ($15\text{--}30 \text{ }^\circ\text{C}$) over the gross photosynthetic rate, respiration rate and net photosynthetic rate (NP) of *Egeria najas* in nutrient limited condition, and high nutrient availability. The light and dark bottles method was utilized to measure photosynthesis. The pH increase from 4.0 to 8.5 promoted a continuous decrease in NP. Temperature had an important effect

on the NP value, with variations in Q_{10} from 1.42 to 2.23. Although maximum NP rates occurred under low light intensity ($158\text{--}204 \mu\text{mol m}^{-2} \text{s}^{-1}$), in short-term, the availability of light can represent the main factor controlling photosynthesis in rooted *E. najas*; nevertheless, dissolved nutrients can highly induce the growth of free-float specimens. Our results facilitate the understanding of *E. najas* potential to colonize since it easily adapts to changes in environmental conditions.

Keywords Narrow-leaf elodea · Net photosynthetic rate · Temperature · pH · Light intensity · Nutrients availability

Handling editor: Julie Coetzee

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10750-024-05496-4>.

M. M. Pezzato
Instituto de Permacultura da Bahia, Rua Fonte do Boi, 131,
1° andar. Rio Vermelho, Salvador, BA CEP: 41940-360,
Brazil
e-mail: mauramp02@gmail.com

M. M. Pezzato · M. B. da Cunha-Santino · I. Bianchini Jr.
Programa de Pós-Graduação em Ecologia e Recursos
Naturais (PPG-ERN), UFSCar, Rod. Washington Luiz, km
235, São Carlos, SP CEP: 13565-905, Brazil

M. B. da Cunha-Santino · I. Bianchini Jr. (✉)
Departamento Hidrobiologia, Universidade Federal de
São Carlos (UFSCar), Rod. Washington Luiz, km 235,
São Carlos, SP CEP: 13565-905, Brazil
e-mail: irineu@ufscar.br

M. B. da Cunha-Santino
e-mail: cunha_santino@ufscar.br

A. F. M. Camargo
Instituto de Ciências Biológicas, Universidade Federal
do Rio Grande (FURG), Av. Itália, km 8, Rio Grande,
RS CEP: 96203-900, Brazil
e-mail: antoniofmcamargo@gmail.com

A. F. M. Camargo
Departamento de Biodiversidade, Universidade
Estadual Paulista (UNESP), Av. 24/A, 1515, Rio Claro,
SP CEP: 13506-900, Brazil

Introduction

The biomass development of submerged aquatic plants varies both inter-specifically (Gillard et al., 2021) and intra-specifically among macrophyte communities (Dumont et al., 2019). The variability depends on geographic location, seasonality, and local controlling factors such as temperature, light availability, pH and trophic state (Dar et al., 2014). Temperature is usually considered the main factor that determines the rates of metabolic processes (Berry & Björkman, 1980; Li et al., 2020), influencing the distribution of plants in aquatic and terrestrial ecosystems. In aquatic environments with low thermal variations (e.g., tropical and subtropical aquatic systems), environmental factors affecting macrophyte growth such as light availability and trophic state can prevail over the effect of temperature (Madsen & Sand-Jensen, 1991; Riis et al., 2012; Ersoy et al., 2020).

In aquatic environments exposed to anthropogenic actions, temporal variations in light intensity, temperature and chemical properties of water (e.g., availability of nutrient elements, presence of toxic elements or substances, turbidity, pH) also result from artificial processes, which can directly interfere with the selection and growth of macrophytes (Cristofor et al., 2003). Various factors that contribute to the failure or low growth of submerged aquatic plant species include: high water turbulence, low acidity, high turbidity, extreme temperatures, and low redox potential. The frequency and duration of these factors reduce biodiversity and select species that are not always the most favorable to keep ecosystem services untouched (Thomaz, 2023). Environments with more stable physical and chemical conditions, in turn, tend to favor the establishment of species with more predictable characteristics, making the selection of control actions more objective, specific and simplified.

Photosynthetic rates of submerged macrophyte species are susceptible to several short-term events: (1) passage of turbidity plumes (usual causes: vertical water circulation, effluent adductions, rainfall and surface runoff); Hall Jr. et al. (2015); (2) changes in the intensity of photosynthetically active radiation (PAR) due to the passage of clouds and change of solar radiation angle (circadian and seasonal variations); Barko & Smart (1981); (3) PAR absorption and blocking of the electron transfer by colored dissolved compounds

(e.g., humic substances); Padial & Thomaz (2008); Steinberg et al. (2008); (4) pH changes (e.g., the introduction of organic and inorganic residues, the addition of deep water due to breakdown of thermal stratification); (5) temperature variations (daily and seasonal), thermal pollution (e.g., effluent supply from a thermoelectric power plant), water supply from thermal sources (Majewski & Miller, 1979) and (6) water level changes (Hussner et al., 2008; Taveira, 2022). Although various natural or anthropogenic adducts are rich in nutrient elements, there is a possibility that they contribute to the inhibition of photosynthetic rates due to the predominant composition (e.g., metals, toxic compounds) and the possible presence of color (Gimenes et al., 2020; Machado et al., 2020). These events, which constitute the forcing functions of photosynthesis, modulate plant growth, expressed in temporal variations of growth rates (Carr et al., 1997; Yoshida et al., 2022).

Aquatic plants have a doubling time of a few days to a few weeks (Bianchini Jr. et al., 2015) and the knowledge of environmental changes on a low time scale (e.g., day, week) may be necessary to understand or predict successful establishment and maintenance of species. Short-term environmental alterations and the respective response time of macrophytes are also important information to properly establish the time interval of the algebraic equations that deal with the growth of aquatic plants, to derive more accurate results (Chapra & Canale, 2010). In a short-term time scale, environments with changes in the physical and chemical characteristics of water due to anthropogenic actions (e.g., hydroelectric reservoirs, aquatic environments impacted by agricultural activities, aquatic ecosystems exposed to erosion processes) may not provide adequate support for the desired establishment of a native species, to the detriment of another, not always desired (e.g., invasive species). Ultimately, the chemical and physical variability of the aquatic environment, resulting from anthropogenic actions, can induce the establishment of undesirable species, with negative repercussions on native biodiversity (Salgado et al., 2019).

The distribution, richness and density of aquatic species can be mapped using satellite imagery and field assessments. This is useful information for the protection and management of aquatic plants. In addition, mathematical models that deal with the growth of these organisms provide information on

the bathymetric and chemical characteristics of sediments and water. To perform simulations, besides information on the physical and chemical characteristics of the environment, it is necessary to know the ecophysiological parameters of the target species, such as: (1) range of variation of growth rates; (2) tolerance limits for solar irradiation, temperature and pH; (3) growth dependence relationships on nutrient elements; (4) relations of the effects of elements and toxic substances on growth rates (Bowie et al., 1985; Jørgensen & Fath, 2010). Mathematical models that deal with the growth of phytoplankton and submerged aquatic plants tend to discriminate temperature from other variables, considering it to be the most important factor (e.g., Eq. 1; Bowie et al., 1985; Carr et al., 1997).

$$NP = NP_{max}(T_{ref}) \times f(T) \times f(L, P, N, C, Si) \quad (1)$$

where NP=Net photosynthetic rate ($\text{mg O}_2 \text{ g}^{-1} \text{ DM h}^{-1}$); $NP_{max} \times (T_{ref})$ = maximum net photosynthetic rate at particular reference temperature (T_{ref}) under optimal conditions of saturated light intensity and excess nutrients ($\text{mg O}_2 \text{ g}^{-1} \text{ DM h}^{-1}$); $f(T)$ = temperature function for growth; T =temperature ($^{\circ}\text{C}$); $f(L, P, N, C, Si)$ = growth limiting function for light and nutrients; L =light intensity; P =available inorganic phosphorus concentration (mass volume^{-1}); N =available inorganic nitrogen concentration (mass volume^{-1}); C =available inorganic carbon concentration (mass volume^{-1}); Si =available inorganic silicon concentration (mass volume^{-1}).

Beyond the use of mathematical models in management programs for aquatic plants, they have been used to describe scenarios involving: (1) potential dispersal (local and regional) of macrophytes (Strange et al., 2019; Cordeiro et al., 2020; Jetter et al., 2021); (2) the management of populations to provide raw material for methane production (Kuar et al., 2018); (3) changes in water quality due to nonpredatory mortality (or decomposition) and herbicide use (e.g., release of colored organic compounds and nutrients, dissolved oxygen consumption; Bianchini Jr. et al., 2014; Song et al., 2021); (4) establishment of the biomass mechanical removal effort and the respective costs (e.g., raw materials, fuel, equipment sizing and hours of work; Mahujchariyawong & Ikeda, 2001; Weber et al., 2021); (5) assessment of changes in ecosystem services in the aquatic environment due to

different degrees of incidence of macrophytes (Janssen et al., 2021); (6) evaluation of the macrophyte interferences in the multiple uses of aquatic environments (Verhofstad & Bakker, 2019; García-López et al., 2023) and (7) mapping of potential areas that may harbor disease vectors (Mackay et al., 2016).

Mathematical models are also essential tools for the monitoring and proper management of aquatic environments given the effects of climate change on macrophytes growth (e.g., changes in temperature, euphotic zone, intensities and regime of water supply, trophic state) and, consequently, on biodiversity (Silveira & Thiébaud, 2017; He et al., 2018; Reitsema et al., 2018). Due to its use in wide-ranging activities, the theoretical basis of the models that describe the growth of aquatic plants is already well established (Carr et al., 1997); however, the parameters that address the physiology of various macrophyte species often still need to be determined.

Egeria najas Planchon 1849 (narrow-leaf elodea) is a submerged and rooted angiosperm native to the tropical region of South America and cultivated in Europe (Cook & Urmi-Körnig, 1984). This species is adapted to low light intensities ($120\text{--}300 \mu\text{mol m}^{-2} \text{ s}^{-1}$) and can live under conditions of low availability of free CO_2 and high pH (Tavecchio & Thomaz, 2003). *E. najas* can obtain nutrients from sediments when concentrations are low in the water column. This species presents a greater affinity for nitrogen than phosphorus and has competitive advantages in low-fertility environments (Thomaz et al., 2007). As described for *Egeria densa* Planch. (Morgan et al., 2023), it is usually rooted in the bottom mud but can be found as a free-floating mat or as fragments with stems near the surface of the water (Duarte et al., 1994). The growth of *E. najas* with and without sediment showed similar growth coefficients, suggesting that this species uses both the nutrients available in the sediment and in the water (Bianchini et al., 2006), a trait that has been verified for other species of this genus (Yarrow et al., 2009). This species is widely distributed and plays a crucial role in several Neotropical aquatic systems (lakes, oxbow lakes, artificial lakes, floodplains).

For species of the Hydrocharitaceae family (e.g., *E. densa*, *Hydrilla verticillata* (L.f.) Royle and *Elo-dea canadensis* Michx.), the participation of C_4 cycle enzymes (NADP-ME and PEPC) in CO_2 fixation, under high light intensities and temperatures

(300 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and 30 °C), and low carbon concentrations, confer adaptive advantages on the metabolism of these plants (Casati et al., 2000; Lara et al., 2002). The Hydrocharitaceae family has great invasive potential and worldwide distribution, thus subsidizing several trophic chains in different environments. Due to its great potential for growth and dispersal, *E. najas* often causes problems in artificial reservoirs, reducing multiple uses and interfering with the operation of hydroelectric plants (Martins et al., 2003; Verhofstad & Bakker, 2019; Florêncio et al., 2021). Even though several ecophysiological aspects have already been addressed for the Hydrocharitaceae family, this study specifically aims to describe the effects of short-term variations of abiotic factors (i.e., pH, light, nutrient availability, and temperature) that occur in aquatic ecosystems on the photosynthetic activity of *E. najas*. We hypothesize that among the four abiotic factors that control *E. najas* growth, in the short-term, temperature will be the most determinant for defining the intensity of photosynthetic activity (i.e., small temperature variations will lead to expressive changes in photosynthetic rates, more than the changes in other variables).

Material and methods

E. najas plants and water samples were collected in the summer (December to February) at Óleo Lagoon (21° 36' S and 47° 49' W), an oxbow lake sited in the floodplain of the Mogi-Guaçu River, located at the Ecological Station of Jataí, municipality of Luís Antônio, (São Paulo State, Brazil). Plants were taken to the laboratory (Bioensaios e Modelagem Matemática, DHb, UFSCar) and washed with tap water to remove periphyton and adhered material. Then, after 1 day, the plants were used in experiments related to photosynthetic activity. The biomass of *E. najas* was estimated from linear regression between length and dry mass (DM); for this purpose, 70 stem fragments (between 2.0 and 32.0 cm) were used. After determining the lengths, the fragments were dried (60 °C) until constant mass.

Incubation time of *Egeria najas*

To estimate a suitable time to measure the gross photosynthetic rate (GP), respiration rate (R) and net

photosynthetic rate (NP) of *E. najas*, pre-tests with the light and dark bottles method (Vollenweider, 1971) were employed. The plants (apical shoots \approx 7 cm long \equiv 31 mg DM) were incubated under non-limiting light intensity (i.e., 177 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PAR; Tavecchio & Thomaz, 2003) for 0.5, 1, 2, 3, 4, and 5 h at 25 °C (temperature value within the variation range of Óleo Lagoon ($\bar{x} = 23.5 \pm 4.2$ °C), and close to the optimal growth temperature of *E. najas* (26.3 °C); Pezzato et al., 2023). The water sample from Óleo Lagoon was used in the photosynthetic assays (pH: 4.16 ± 0.08 ; electrical conductivity: 17.0 ± 0.0 $\mu\text{S cm}^{-1}$; total alkalinity: 0.07 ± 0.01 meq l^{-1} ; dissolved inorganic carbon: 1.16 ± 0.08 mg l^{-1} ; free CO_2 : 1.06 ± 0.07 mg l^{-1} ; HCO_3^- : 0.10 ± 0.00 mg l^{-1} ; Total nitrogen (TN): 0.40 mg l^{-1} ; N-NH_4 : 0.02 mg l^{-1} ; Total phosphorous (TP): 0.03 mg l^{-1} ; Fe: 3.22 mg l^{-1} ; Mg: 0.40 mg l^{-1} ; K: 0.61 mg l^{-1}).

Three incubations (i.e., BOD bottles; volume \approx 300 ml; 177 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PAR) were employed for each experimental period (i.e., 0.5, 1, 2, 3, 4, and 5 h). For each time, three incubations were also prepared and kept in the dark to determine the respiration rates. Dissolved oxygen concentrations (DO) were determined by the Winkler titrimetric method (Golterman et al., 1978), and calculations of GP, NP, and R were made according to the equations described by Littler & Arnold (1985). The same mass of apical shoots (\approx 31 mg DM) and number of incubations (3 light and 3 dark bottles for each experimental condition) were also used in the photosynthetic assays where the effect of different light intensities, pH and temperature were evaluated.

For the selected experimental conditions (i.e., plant species, biomass, temperature, and light intensity), net photosynthesis rates were significantly higher when incubated from 1 to 5 h ($p < 0.001$) compared to half an hour of incubation. Variations in NP values between 1 and 5 h were not significant (Fig. 1 and supplementary material section; S1). Based on these results, the exposure time of 1 h was adopted for the experiments with pH, light intensity and temperature.

Photosynthetic rate and light intensities

The response of photosynthetic rates of *E. najas* to light was assessed with incubations ($n=3$) with different light intensities (PAR: 10, 16, 27, 45, 75, 100, 177, 275, 390 $\mu\text{mol m}^{-2} \text{s}^{-1}$) at 25 °C and an

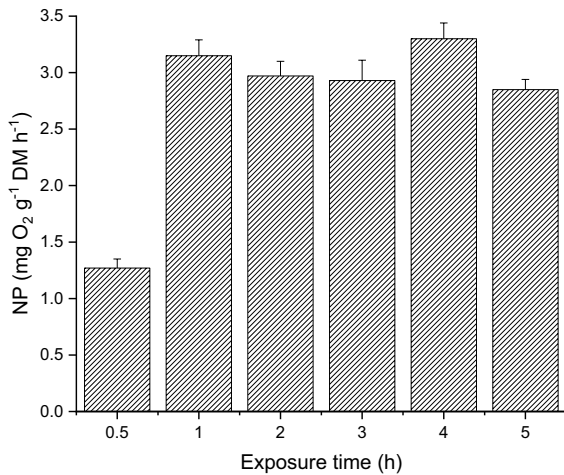


Fig. 1 Average values of the net photosynthesis rates of *Egeria najas* as a function of incubation time (at 25 °C and 117 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PAR); bars refer to standard deviations

exposure time of 1 h. Light intensities were obtained using four 9 w led tubular lamps and a black polyethylene net (Menendez & Sanches, 1998). In addition, to compare the availability of the nutrients on photosynthetic rates, two media were used in these evaluations: (1) water sample from the Óleo Lagoon and (2) diluted (10%) nutrient medium: pH 5.87 ± 0.05 ; electrical conductivity: $190 \pm 0.05 \mu\text{S cm}^{-1}$; total alkalinity: $0.14 \pm 0.01 \text{ meq l}^{-1}$; dissolved inorganic carbon: $0.85 \pm 0.10 \text{ mg l}^{-1}$; free CO_2 : $0.70 \pm 0.11 \text{ mg l}^{-1}$; HCO_3^- : $0.15 \pm 0.03 \text{ mg l}^{-1}$; TN: 21.0 mg l^{-1} ; N- NH_4 : 1.40 mg l^{-1} ; TP: 3.10 mg l^{-1} ; Fe: 0.07 mg l^{-1} ; Mg: 4.80 mg l^{-1} ; K: 23.4 mg l^{-1} (Hoagland & Arnon, 1950). The nutrient medium was used to determine the NP of unrooted *E. najas* without the limitations due to nutritional deficiencies of the lagoon water. Six incubations were also prepared with apical shoots of *E. najas* (3 with a water sample from the Óleo Lagoon and 3 with Hoagland-Arnon medium) to be kept in the dark to determine respiratory rates in the 2 different trophic conditions.

The results referring to the experiment of photosynthetic rates and light intensity were fitted to the formulation proposed by Steele (1965). For this purpose, the NP values were adjusted to Eq. 2 with an iterative algorithm (Fylstra et al., 1998). GP, NP and R calculations were derived from DO concentrations (Littler & Arnold (1985) that were measured by the titrimetric method (Golterman et al., 1978).

$$NP = NP_{\max} \times \frac{I}{I_s} e^{\left(1 - \frac{I}{I_s}\right)} \quad (2)$$

where NP = net photosynthetic rate; NP_{\max} = maximum value of NP; I = light intensity; I_s = optimum (saturating) light intensity.

pH response experiment

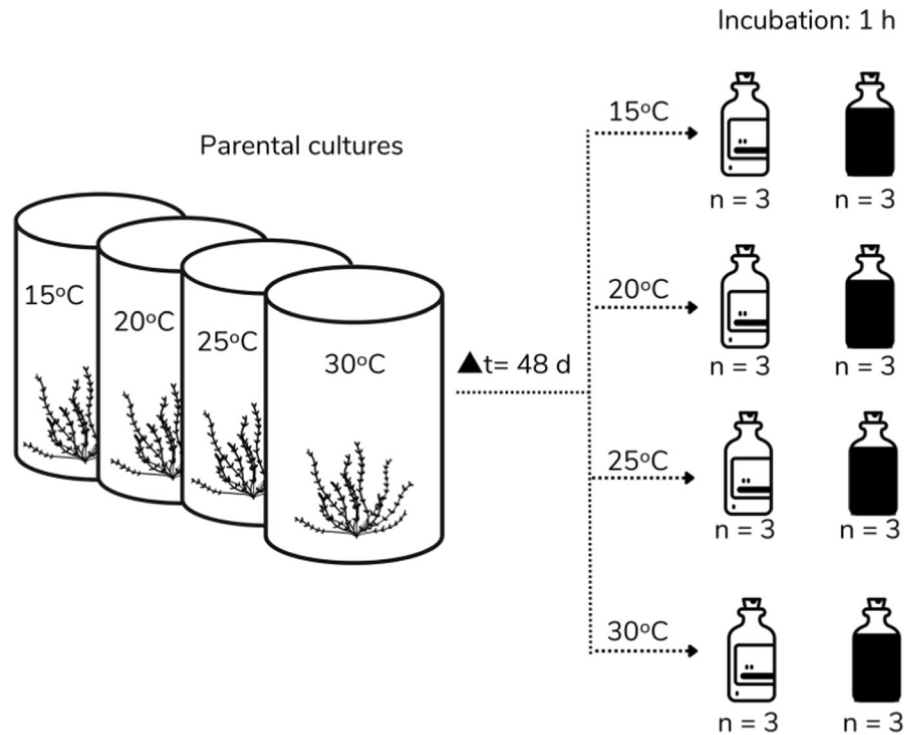
To verify the effect of pH on NP, incubations ($n=3$) with the Óleo Lagoon water sample and apical shoots ($\approx 31 \text{ mg DM}$) were maintained at 25 °C and $177 \mu\text{mol m}^{-2} \text{s}^{-1}$ (PAR), respectively (Tavecchio & Thomaz, 2003). The experiment was conducted with three pH values (4.0, 6.5 and 8.5). Hydrochloric acid (HCl) or potassium hydroxide (KOH) 0.5 M solutions were added to the water samples to adjust the pH. For each pH value, 3 incubations with apical shoots of *E. najas* were also prepared to be kept in the dark to determine respiratory rates.

Photosynthetic rate for plants acclimatized at different temperatures

Four cultures of *E. najas* were maintained for ca. 7 weeks at 15, 20, 25 and 30 °C to assess the short-term effect of temperature on NP (Fig. 2). These parental cultures were prepared, with plants harvested in the Óleo Lagoon, and planted in borosilicate containers (area: 250 cm^2 ; volume: 6.0 L) containing diluted (10%) nutrients medium (Hoagland & Arnon, 1950). Parental cultures were kept under controlled conditions (germination chamber Tecnal, model TE-401) of temperature, and 12 h photoperiod, in non-limiting light intensity [$177 \mu\text{mol m}^{-2} \text{s}^{-1}$ (PAR); Tavecchio & Thomaz, 2003]. Parental cultures were prepared and maintained according to the experimental procedures suggested by Machado et al. (2020). Medium nutrients were replenished every ten days.

Using the light and dark bottles method, three plants ($\approx 31 \text{ mg DM}$ apical shoots) from each temperature treatment (15, 20, 25 and 30 °C) were incubated to measure NP. These values were used to calculate the parameters of the optimum temperature function (Shugart et al., 1974): Q_{10} (ratio of reaction rates at 10 °C temperature increments; Sierra, 2012), T_{opt} (optimum temperature); T_{max} (maximum temperature; the temperature at which NP is null); therefore, an iterative algorithm (Fylstra et al., 1998) was used

Fig. 2 Experimental design to assess the short-term effect of temperature on the net photosynthetic rate, gross photosynthetic rate and respiratory rate of *Egeria najas*; where n is equal to the number of flasks (light and dark) used in each 1-h incubation (at 15, 20, 25 and 30 °C)



to calculate these parameters. The optimal temperature curve describes the increments of NP and GP with increasing temperature until the respective optimal temperatures are reached, after which the rates decrease. The temperature function parameters (i.e., Q_{10} , T_{opt} and T_{max}) were calculated from the NP values of 1-h incubations (at 15, 20, 25 and 30 °C) of apical shoots of plants from parental cultures. R was also used to calculate Q_{10} (temperature coefficient) due to respiration; therefore, the Arrhenius approach was used (Eq. 3; Jones, 2014).

$$Q_{10} = \left(\frac{k_2}{k_1} \right)^{\left(\frac{10}{(T_2 - T_1)} \right)} \quad (3)$$

where k_1 =reaction rate (e.g., R) at temperature T_1 ; k_2 =reaction rate at temperature T_2 ; Q_{10} =ratio of reaction rates at 10 °C temperature increments.

Data analysis

Statistical tests were performed to evaluate differences in incubation time, light intensity, nutrient availability, temperature, and pH conditions. The normalities of the NP datasets were verified by

normality of each NP data set was verified using the D'Agostino-Pearson test. Once the normality of the data was confirmed, the analysis of variance (ANOVA) was performed to verify the occurrence of significant differences between pH, nutrient availability and light intensity and NP. For optimal temperature curve comparisons, the Kruskal–Wallis test was performed once normality was not confirmed. A P -level of 0.05 was considered to be statistically significant in this case. The post hoc used for multiple comparisons was Dunn multiple comparison tests for temperature differences. The Tukey post hoc was performed according to incubation time, light intensity, nutrient availability, and pH conditions. Statistical analyses were performed using the open-source software PAST (version 4.03).

Results

The increase in pH (4.0, 6.5 and 8.5) promoted a highly significant continuous decrease in net photosynthesis rates ($P < 0.001$); NP=4.22, 1.74 and 0.0 mg O₂ g⁻¹ DM h⁻¹, respectively. Compared to incubations carried out at pH 4, the NP at pH 6.5

decreased by ca. 60% and at 8.5, by 100%. *E. najas* showed greater affinity for free CO_2 and illustrated a reduction in the photosynthetic performance when the inorganic carbon form was 50% free CO_2 and 50% HCO_3^- (i.e., pH 6.5) and showed NP null when the HCO_3^- was predominant (Fig. 3a).

The fitting of NP as a function of light intensity using water from Óleo Lagoon resulted in an optimum light intensity (I_s) of $157.6 \mu\text{mol m}^{-2} \text{s}^{-1}$ and a maximum net photosynthetic rate (NP_{max}) of $1.06 \text{ mg O}_2 \text{ g}^{-1} \text{ DM h}^{-1}$ (Fig. 3b). In contrast,

when *E. najas* was placed in the Hoagland–Arnon medium, these values were significantly increased with $I_s = 204.2 \mu\text{mol m}^{-2} \text{s}^{-1}$ and NP_{max} of $3.05 \text{ mg O}_2 \text{ g}^{-1} \text{ DM h}^{-1}$ (Fig. 3c). Similarly, NP of *E. najas* was also higher in the medium solution. The light response curves were significantly different ($F = 8.9$; $df = 9$; $P \leq 0.005$). However, when excluding the effect of nutrient availability (i.e., dividing NP by NP_{max} in each condition), the light and $\text{NP}/\text{NP}_{\text{max}}$ curves (ranging from zero to 1) were similar ($F = 1.1$; $df = 15$; $P \leq 0.005$; $P > 0.05$), showing that

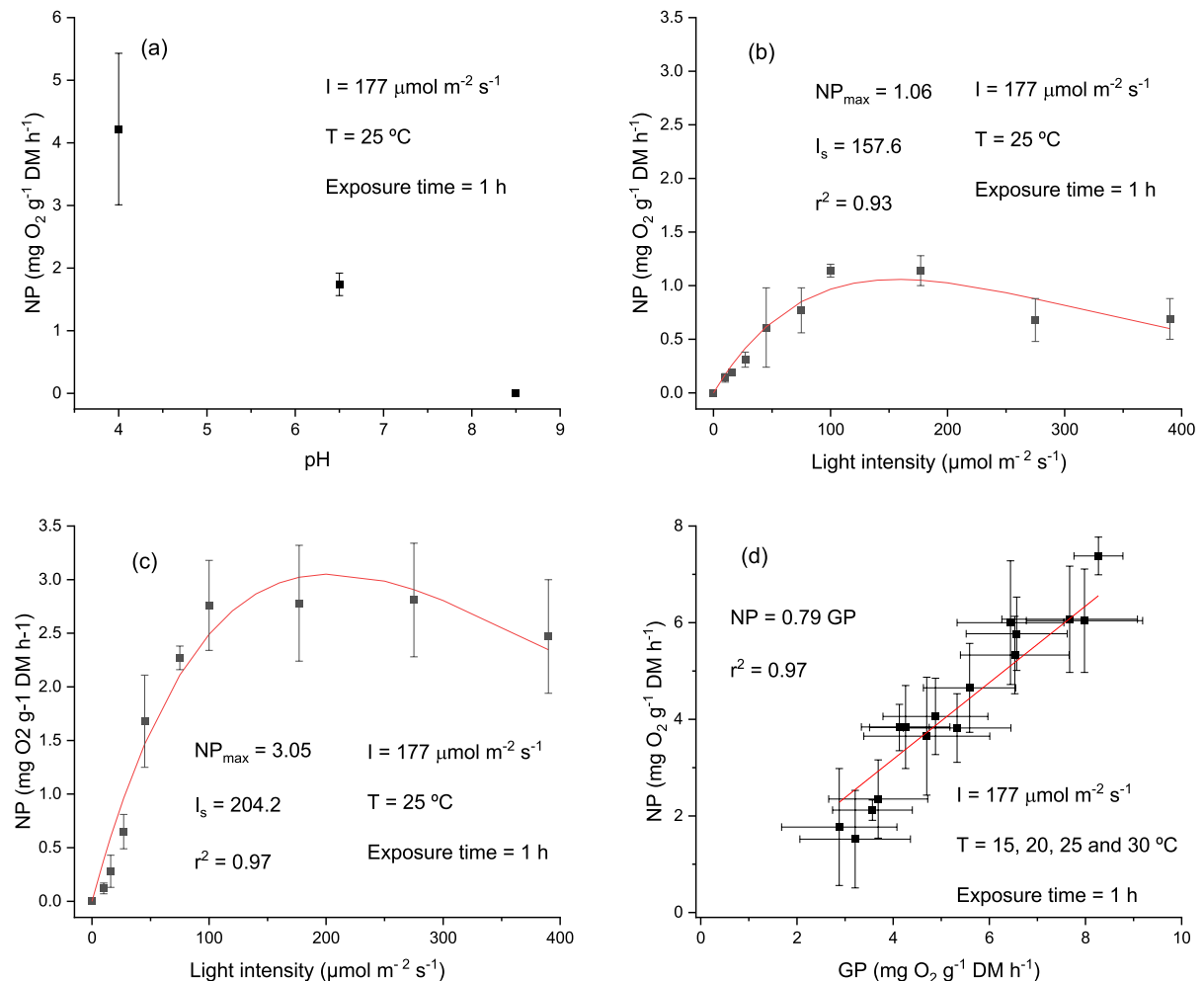
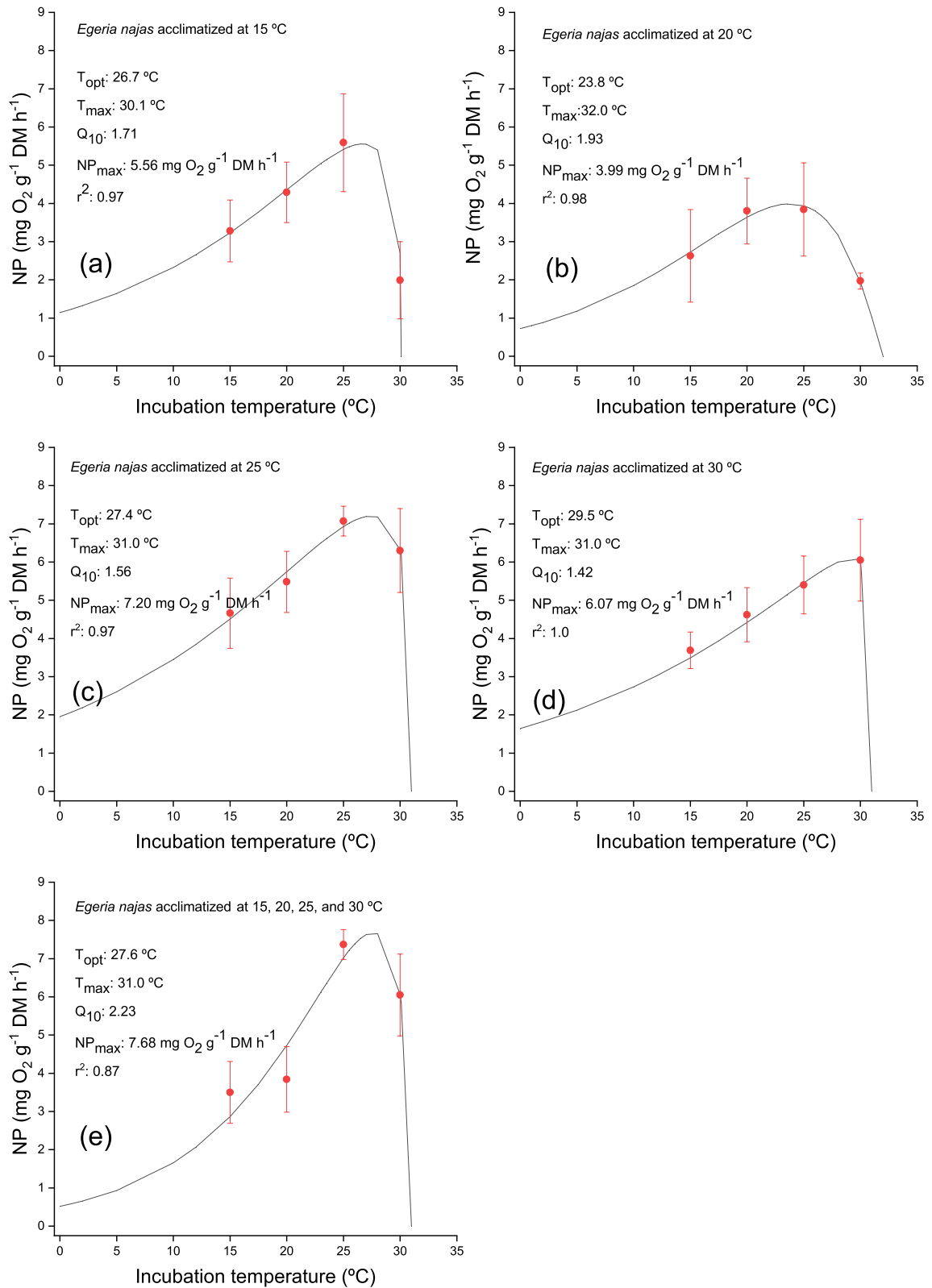


Fig. 3 Changes of the net photosynthetic rate of *Egeria najas* related with (i) medium pH (a); (ii) light intensity in sample water from Óleo Lagoon (b) (iii) light intensity in nutrient artificial medium (c); Relationship between GP and NP of *E. najas* from incubations with temperature variations (d). Dots refer to mean values and bars (\pm) to standard deviations. The

lines correspond to the values calculated from the non-linear (b, c) and linear (d) regressions. GP: gross photosynthetic rate; NP: net photosynthetic rate; NP_{max} : maximum value of NP; I : light intensity; I_s : optimum (saturating) light intensity; r^2 = determination coefficient



◀**Fig. 4** Temperature response curves for the net photosynthetic rate of *Egeria najas*. Where: (a) temperature optimum curve for plants acclimatized at 15 °C and incubated at 15, 20, 25, and 30 °C; (b) temperature optimum curve for plants acclimatized at 20 °C and incubated at 15, 20, 25, and 30 °C; (c) temperature optimum curve for plants acclimatized at 25 °C and incubated at 15, 20, 25, and 30 °C; (d) temperature optimum curve for plants acclimatized at 30 °C and incubated at 15, 20, 25, and 30 °C; (e) temperature optimum curve for plants acclimatized and incubated at 15, 20, 25, and 30 °C, respectively. Dots refer to mean values and bars (\pm) to standard deviations. The lines correspond to the values calculated from the non-linear regressions. NP: net photosynthetic rate; NP_{max} : maximum value of NP; Q_{10} : ratio of reaction rates (NP) at 10 °C temperature increments; T_{opt} : optimum temperature; T_{max} : maximum temperature (NP=zero); r^2 =determination coefficient

the differences between the light versus NP curves were essentially due to the nutrient contents of the culture medium (i.e., Óleo Lagoon water sample and Hoagland–Arnon medium).

When considering all temperature variations, the comparison of gross photosynthesis rates with net photosynthesis rates, showed that NP responds to 79% of the GP, and therefore, R is equal to 21%. These proportions were also maintained when the temperatures coincided with those of the parent cultures selected (Fig. 3d).

In general, the optimal temperature functions did not present very evident differences ($P \geq 0.05$) as a function of cultivation temperatures (Fig. 4). A significant difference ($P \leq 0.05$) was registered between the optimal temperature curves of plants grown at 20 and 25 °C (Fig. 4b, c; S1); at 20 °C the lowest NP values occurred and at 25 °C the highest. Significant differences ($P \leq 0.001$) were also noted between the curves of plants grown at 20 °C and without temperature variation (Fig. 4b, e). However, the acclimatization of the cultures interfered with the values of the parameters of the optimal temperature curve (i.e., Q_{10} , T_{opt} and T_{max}). T_{opt} values slightly increased with increasing temperature of parent cultures; thus, the culture acclimatized to 15 °C presented $T_{opt} = 26.7$ °C and the culture acclimatized to 30 °C presented $T_{opt} = 29.5$ °C, the other cultures generated intermediate and practically ascending values of T_{opt} . On the other hand, the respective Q_{10} values tended to continuously decrease; Q_{10} of the culture at 15 °C = 1.71 and that of the culture at 30 °C = 1.42. The T_{max} values (i.e., the temperature at which NP=zero) did not show apparent variation as a function of the temperature

of the parent cultures, however, it always varied little (between 30 and 32 °C).

The values of the net photosynthesis rates at the optimal temperature (NP_{max}) varied between 3.99 (ref. culture acclimatized to 20 °C; Fig. 4b) and 7.68 mg O₂ g⁻¹ DM h⁻¹ (ref. plants acclimatized and incubated at 15, 20, 25, and 30 °C, respectively; Fig. 4e); however, there was no clear trend of NP_{max} variation as a function of the parent cultures temperature. Selecting only the NPs from incubations in which the temperatures of the parent cultures were not changed (i.e., incubations at 15, 20, 25 and 30 °C from the cultures acclimatized at 15, 20, 25 and 30 °C, respectively) for the fit of the temperature curve, the highest value of Q_{10} (2.23) and NP_{max} (7.68 mg O₂ g⁻¹ DM h⁻¹) are obtained, and intermediate values for T_{max} (31.1 °C) was verified. This situation directly compares the net photosynthesis rates of acclimated cultures (e.g., *E. najas* acclimatized and incubated at 15 °C) without the imposed interferences of temperature change (e.g., *E. najas* acclimated at 15 °C and incubated at 20, 25 and 30 °C).

The values of T_{max} , T_{opt} and Q_{10} defined by GP and NP were always close and convergent. As verified for the Q_{10} calculated by the NP variations, the Q_{10} values referring to the GP also tended to decrease with the increased temperature of the acclimatized culture. On the other hand, the Q_{10} values related to respiration did not show a definite trend as a function of the temperature of the parental cultures (Table 1). According to the direct measures of GP and NP (Fig. 3d), the average value of NP_{max} was 82% of GP_{max} (Table 1).

Discussion

Different abiotic factors (e.g., inorganic carbon and nutrient availability, light intensity, photoperiod, and temperature) contribute to controlling the growth of submerged aquatic plants. Such factors are changed temporally and, consequently, alternate in the definition of photosynthesis rates (Hussner et al., 2016; Ersoy et al., 2020; Petracco et al., 2022). Information dealing with physiological variables is relevant to understanding the effects of short-term events (e.g., period: day-week) on aquatic plant growth. Such events can assist with the successful establishment, colonization or disappearance of these

Table 1 Parameters (GP_{max} , NP_{max} , T_{max} , T_{opt} , Q_{10}) calculated from gross photosynthesis (GP), respiration (R) and net photosynthesis (NP) rates variations

Growth T (°C)	GP_{max} (*)	$GP-T_{opt}$ (°C)	$GP-T_{max}$ (°C)	$GP-Q_{10}$	R- Q_{10}	NP_{max} (*)	$NP-T_{opt}$ (°C)	$NP-T_{max}$ (°C)	$NP-Q_{10}$
15	6.54	26.9	30.1	1.80	2.06	5.56	26.7	30.1	1.71
20	4.89	26.2	31.0	1.70	3.45	3.99	23.8	32.0	1.93
25	8.60	28.0	30.5	1.49	1.30	7.20	27.4	31.0	1.56
30	7.71	29.7	30.5	1.52	2.70	6.07	29.5	31.0	1.42
LT	9.45	28.4	30.5	2.25	4.62	7.68	27.6	31.0	2.23

Where: LT refers to long term: i.e., plants acclimatized and incubated at 15, 20, 25, and 30 °C, respectively

(*) $mg\ O_2\ g^{-1}\ DM\ h^{-1}$

macrophytes (Jørgensen & Fath, 2010). The changes (pH, light intensity, temperature, and nutrient availability) imposed in the experiments exemplify the rapid response of photosynthetic activity that *E. najas* exhibits to chemical and physical environmental changes, and the NP values obtained (Figs. 3 and 4) were of the same order of magnitude as those typically verified for this species and gender (Kahara & Vermaat, 2003; Pezzato & Camargo, 2004; Petracco et al., 2022).

After 1 h of exposure, *E. najas* practically already reached the maximum performance of a photosynthetic activity, which was maintained for several consecutive hours. This is within the NP:GP ratio generally found for this genus (e.g., 0.78; Yoshida et al., 2022). These characteristics and the T_{opt} values (23.8–29.5 °C) point out that *E. najas* quickly responds to short-term abiotic changes. Therefore *E. najas* has the potential to survive and grow in various aquatic environments in tropical and subtropical regions. In addition, thermal pollution and climate change could aid its establishment in new regions. However, as several abiotic factors act together in the development of submerged macrophytes, formulations that deal with net photosynthetic rates can include (e.g., pH, sediment nutrients for rooted species) or suppress elements and factors in the growth limiting function (Eq. 1), according to the aquatic plant life form and predominant features of the environment. If necessary (i.e., when using the exponential or sigmoid models), the NP and NPmax parameters (Eq. 1) can be changed to the growth rate constant (μ ; $time^{-1}$; Yoshida et al. 2022).

The available forms of inorganic carbon and elements vary according to environmental factors, such

as pH, oxidation state, degree of dissociation, and macrophytes and algae capacity to assimilate elements from different (organic or inorganic) compounds (Sand-Jensen, 1989; Hussner et al., 2016; Bottino et al., 2018). Inorganic carbon speciation is closely linked to the pH of aquatic environments; the preferred assimilation forms of C_3 plants are “free” CO_2 (i.e., CO_2 and H_2CO_3) which predominate in acidic media. Bicarbonate ion (HCO_3^-), which predominates at pH above 6.5 (Golterman et al., 1978; Langmuir, 1997), not always is the preferred or even available form for the assimilation of inorganic carbon. The experiment clearly showed the (indirect) effect of pH on the photosynthetic activity of *E. najas*. Similar decreases in photosynthetic activity as a function of pH were observed for *Egeria* (Kahara & Vermaat, 2003); however, such activity was still recorded after pH 8 (Pierini & Thomaz, 2004). The NP was null at pH 8 because the acid condition is predominant (pH 5.2 ± 0.5 ; range: 4.6–5.8) in the location where the plants were harvested (Óleo Lagoon; Petracco et al., 2022).

A comparison of the light response curves showed the effect of irradiation and nutritional availability for the *E. najas* photosynthetic activity. It was found that under the same conditions, NP irradiance was significantly lower (2.9-fold), limited by the amount of nutrients, and possibly for some high value of the assimilation half-saturation constants (Christiansen et al., 2016; Kim et al., 2018). In the case of this species, rooted individuals can attenuate nutrient shortages in properly illuminated environments (e.g., $160\text{--}200\ \mu mol\ m^{-2}\ s^{-1}$). Overall, the NP values obtained in the experiments were of the same magnitude as those verified in Óleo Lagoon. The NP of *E.*

najas in the Óleo Lagoon (0–22 mg O₂ g⁻¹ DM h⁻¹; Petracco, 2006) are mainly influenced by the flood pulse and light intensity, being generally higher in the dry period. The flood pulse defines the nutrient input, the increase in turbidity and the relative depth of the plant establishment. In the dry period (winter) there is greater light availability, and temperatures are high enough for the occurrence of high NP (Petracco et al., 2022).

The optimal temperature function describes that for *E. najas*, CO₂ fixation and reduction occur slowly at low temperatures, increasing rapidly with warming up to an optimal value (NP_{opt} range: 23.8–29.5 °C). At supraoptimal temperatures, the CO₂/O₂ ratio is modified in favor of oxygen and therefore, the carboxylation work of RUBP carboxylase/oxygenase decreases (Larcher, 2003). Extreme temperature values (in this study, NP_{max} range: 30–32 °C) interrupt entirely the absorption of CO₂ (Nievola et al., 2017); if favorable conditions occur again, the plant will only gradually recover (Larcher, 2003). Above 35 or 40 °C, denaturation of most plant enzymes rapidly occurs, and low temperatures can also denature certain enzymes (Salisbury & Ross, 1992).

According to NP_{opt} and NP_{max} ranges, the temperature amplitude in tropical aquatic environments (e.g., Óleo Lagoon: 19.1 ± 1.2 to 27.3 ± 2.1; Petracco, 2006; Pezzato, 2007) is favorable to the occurrence of this species, as corroborated by the results obtained in these photosynthesis experiments. In this sense, the thermal conditions in tropical regions favor the presence of this species throughout the year, with no defined periods of growth and senescence, decreasing the importance of temperature in the determination of NP values, increasing the influence of light (turbidity), pH and trophic state on the photosynthetic activity of this species. In this case, as *E. najas* can be fixed in sediments by roots, the effects of the trophic state (i.e., possible nutrient deficiencies) can also be attenuated, suggesting that at low lake water nutrient concentrations, *E. najas* can survive on the nutrient pools in the sediment porewater, as verified for others submerged species (Christiansen et al., 2016).

Since Q₁₀ is proportional to the activation energy (E_a), the greater its value, the greater the dependence on temperature for the metabolic process to overcome E_a. However, photosynthesis is catalyzed by enzymes that mitigate the role of temperature (i.e., increased vibration and collision of molecules) in overcoming

the E_a barrier (Jones, 2014). At low temperatures, Q₁₀ values are higher; at these temperatures, the set of enzymatic reactions is the limiting factor for the reaction rate. At high temperatures, the values of Q₁₀ are small since, in this situation, it is the physical processes that limit the rate of the reaction (e.g., the diffusion rate of solutes in water); Larcher (2003). In these experiments, the downward trend in Q₁₀ values as a function of increasing temperature was more evident for photosynthetic activities (GP and NP) than respiratory rates. In addition, there was an evident difference in the Q₁₀ values (both GP and NP and R) of plants subjected to thermal stress in relation to those of parent cultures. The Q₁₀ values of the plants maintained at ever the same temperature were always higher. Lower sensitivity to temperature variations (i.e., lower Q₁₀ values) suggests that *E. najas* may not rapidly generate biomass accumulation in response to temperature increases that begin in spring. On the other hand, they may indicate greater resistance to NP decline in decreasing temperature (autumn–winter). Considering the intensity and regime of seasonal temperature variations in aquatic environments, this attribute can constitute an adaptive advantage.

Optimal temperature curves obtained from acclimatized cultures generally mimic the effect of short-term thermal changes on the growth of *E. najas*. Comparing the Q₁₀ values obtained directly from plants kept at a constant temperature (2.23) and those that suffered thermal stress, it is verified that short-term thermal alterations do not prevent the adequate development of the species. The decreasing values of Q₁₀ can point out that, after short-term thermal stress, the NP limitation was mainly related to physical processes other than temperature. Temperature also affects reactions by changing the shape of the enzyme, which determines its ability to combine with the substrate and causes catalysis. Various enzymes differ greatly in their response to temperature. Thus, some enzymes function optimally at any given temperature while others function below ideal. The metabolism of an organism varies greatly with temperature once this force function defines the action of enzymes that control rate-limiting reactions (Burke et al., 1988). Considering the geographic distribution and occurrence of the genus *Egeria* in both hot and cold regions (Cook & Urmi-Konig, 1984), this genus has physiological, morphological and anatomical characteristics capable of tolerating and adapting

more efficiently to changes in temperature than many other submerged aquatic macrophyte species.

The parameters of the optimal temperature curve obtained from plants subjected to thermal stress ($NP-T_{opt}$; $NP-T_{max}$; Table 1) were close to those obtained from acclimatized plants; however, in parental cultures, these parameters were calculated from the growth rates, obtained from the sigmoid model fit (Pezzato et al., 2023). This result is particularly important in practice, as shows that short-term NP determinations (e.g., hours) are as effective and accurate in describing growth as long-term experiments (e.g., months). In addition, it shows the importance of this methodology (i.e., determination of NP) to update growth parameters as a function of short-term environmental changes; this aspect is extremely important for simulations or monitoring that aim to describe the growth of macrophytes as a function of short-term changes (e.g., the passage of a turbidity plume, abrupt temperature changes generated by thermal pollution, accidental effects of toxic substances releases).

Conclusion

Our results showed that *E. najas* presented quick NP responses to short-term changes for all factors considered (pH, light and temperature), which may constitute a relevant adaptive advantage of this species. In tropical and subtropical aquatic environments where low temperature and pH variations occur in relation to light intensity and trophic state, temperature and acidity may become secondary factors for the growth and maintenance of *E. najas*, as verified for cyanobacterial biomass (Bonilla et al., 2023). Thus, for individuals of submerged and rooted *E. najas*, light can become the main factor for growth and maintenance, as these plants are not affected by the trophic state since they can supply the demands for nutrients from the sediments. On the other hand, the trophic state acts directly on the NP of unrooted individuals, intensifying photosynthetic activity with increased nutrient availability.

E. najas did not require high light intensity to achieve good photosynthetic performance (i.e., high NP values). This characteristic also contributes to its spread, even more so, in aquatic environments where the intensity of incident light is normally

high throughout the year (e.g., tropical and subtropical aquatic systems). For the rooted forms, this performance can be reduced mainly by the occurrence of shading due to the intense growth of algae and other floating species [e.g., *Eichhornia crassipes* (Mart.) Solms (Pontederiaceae), *Pistia stratiotes* Linnaeus (Araceae), *Salvinia molesta* DS Mitch (Salvinaceae)]. For the unrooted individuals (that can act as propagules) the results showed that rapidly increasing light availability in a more fertile environment constituted a situation of extreme advantage for these individuals (i.e., expressive increase in NP values).

The results of the experiments carried out suggest that in tropical and subtropical aquatic environments, short-term changes in the set of variables formed by light and trophic states can overcome the effects of short-term variations in temperature and pH for the growth and maintenance of *E. najas*. Knowledge of these characteristics helps build predictive models of the dispersal and growth of this species as a function of the prevailing abiotic characteristics of the environment. Predicting the potential of colonization of *E. najas* is crucial for helping public policies and management strategies to avoid species that have a high potential for growth to spread under stressful or changing environmental conditions.

Acknowledgements The authors thank Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for the scholarships (CNPq proc. No. 140406/2003-4; 150169/2004-3; 306564/2020-0) and financing (CT-Hidro/CNPq, proc. No. 550188/2002-9; Edital MCT/CNPq 02/2006—Universal; proc. No. 470527/2006-4).

Author contributions IBJ and MBCS developed the math procedures. MMP, AFMC and MBCS participated in the design of the study, field surveys, experimental works, and data analyses, and wrote the manuscript. AFMC, MBCS and IBJ participated in the design of the study, edited the manuscript, and secured the funding. All authors read and approved the final manuscript. This paper has not been submitted elsewhere in an identical or similar form after its submission to *Hydrobiologia*. The four authors agree with the entire content (data and interpretation) of this manuscript and declare that the data are available under request.

Funding This study was supported by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) proc. No. 140406/2003-4; 150169/2004-3; 306564/2020-0; 306564/2020-0; CT-Hidro/CNPq, proc. No. 550188/2002-9; Edital MCT/CNPq 02/2006—Universal; proc. No. 470527/2006-4).

Data availability The data that support the findings of this study are available from the corresponding author (IBJ.) upon request.

Declarations

Conflict of interest The authors declare that there is no conflict of interest or competing interests.

References

- Barko, J. W. & R. M. Smart, 1981. Comparative influences of light and temperature on the growth and metabolism of selected submersed freshwater macrophytes. *Ecological Monographs* 51(2): 219–235. <https://doi.org/10.2307/2937264>.
- Berry, J. & O. Björkman, 1980. Photosynthetic response and adaptation to temperature in higher plants. *Annual Review of Plant Physiology* 31: 491–543. <https://doi.org/10.1146/annurev.pp.31.060180.002423>.
- Bianchini, I., Jr., A. L. Bitar & M. B. Cunha-Santino, 2006. Crescimento de *Egeria najas* Planchon da Lagoa do Óleo em condições laboratoriais. In Santos, J. E., J. S. R. Pires & L. E. Moschini (eds), *Estudos Integrados em Ecossistemas: Estação Ecológica de Jataí*, Vol. 4. EdUFSCar, São Carlos: 99–111.
- Bianchini, I., Jr., M. B. Cunha-Santino, J. U. Ribeiro & D. G. B. Penteado, 2014. Implication of anaerobic and aerobic decomposition of *Eichhornia azurea* (Sw.) Kunth. on the carbon cycling in a subtropical reservoir. *Brazilian Journal of Biology* 74(1): 100–110. <https://doi.org/10.1590/1519-6984.17912>.
- Bianchini, I., Jr., M. B. Cunha-Santino, J. A. M. Milan, C. J. Rodrigues & J. H. P. Dias, 2015. Model parameterization for the growth of three submerged aquatic macrophytes. *Journal of Aquatic Plant Management* 53: 64–73.
- Bonilla, S., A. Aguilera, L. Aubriot, V. Huszar, V. Almanza, S. Haakonsson, I. Izaguirre, I. O'Farrell, A. Salazar, V. Becker, B. Cremella, C. Ferragut, E. Hernandez, H. Palacio, L. C. Rodrigues, L. H. S. Silva, L. M. Santana, J. Santos, A. Somma, L. Ortega & D. Antoniadis, 2023. Nutrients and not temperature are the key drivers for cyanobacterial biomass in the Americas. *Harmful Algae* 121: 102367. <https://doi.org/10.1016/j.hal.2022.102367>.
- Bottino, F., S. Vargas, A. C. P. Miwa, M. C. Calijuri, I. Bianchini Jr. & D. G. F. Cunha, 2018. Effects of macrophyte leachate on *Anabaena* sp. and *Chlamydomonas moewusii* growth in freshwater tropical ecosystems. *Limnology* 19(2): 171–176. <https://doi.org/10.1007/s12021-017-0532-0>.
- Bowie, G. L., W. B. Mills, D. B. Porcella, C. L. Campbell, J. R. Pagenkopf, G. L. Rupp, K. M. Johnson, P. W. H. Chan, S. A. Gherini & C. E. Chamberlin, 1985. Rates, Constants, and Kinetics Formulations in Surface Water Quality Modeling, 2nd ed. U.S. Environmental Protection Agency, Athens.
- Burke, J. J., J. R. Mahan & J. A. Hatfield, 1988. Crop-specific kinetic windows in relation to wheat and cotton biomass production. *Agronomy Journal* 80: 533–556. <https://doi.org/10.2134/agronj1988.00021962008000040001x>.
- Carr, G. M., H. C. Duthie & W. D. Taylor, 1997. Models of aquatic plant productivity: a review of the factors that influence growth. *Aquatic Botany* 59: 195–215. [https://doi.org/10.1016/S0304-3770\(97\)00071-5](https://doi.org/10.1016/S0304-3770(97)00071-5).
- Casati, P., M. V. Lara & C. S. Andreo, 2000. Induction of a C₄-like mechanism of CO₂ fixation in *Egeria densa*, a submerged aquatic species. *Plant Physiology* 123(4): 1611–1622. <https://doi.org/10.1104/pp.123.4.1611>.
- Chapra, S. C. & R. P. Canale, 2010. *Numerical Methods for Engineers*, 6th ed. McGraw-Hill, New York.
- Christiansen, N. H., F. Ø. Andersen & H. S. Jensen, 2016. Phosphate uptake kinetics for four species of submerged freshwater macrophytes measured by a ³³P phosphate radioisotope technique. *Aquatic Botany* 128: 58–67. <https://doi.org/10.1016/j.aquabot.2015.10.002>.
- Cook, C. D. K. & K. Urmi-Konig, 1984. A revision of the genus *Egeria* (Hydrocharitaceae). *Aquatic Botany* 19(1–2): 73–96. [https://doi.org/10.1016/0304-3770\(84\)90009-3](https://doi.org/10.1016/0304-3770(84)90009-3).
- Cordeiro, P. F., F. F. Goulart, D. R. Macedo, M. C. S. Campos & S. R. Castro, 2020. Modeling of the potential distribution of *Eichhornia crassipes* on a global scale: risks and threats to water ecosystems. *Revista Ambiente & Água* 15(2): e2421. <https://doi.org/10.4136/ambi-agua.2421>.
- Cristoforo, S., A. Vadineanu & A. Sarbu, 2003. Long-term changes of submerged macrophytes in the Lower Danube Wetland System. *Hydrobiologia* 506: 625–634. <https://doi.org/10.1023/B:HYDR.0000008601.16757.35>.
- Dar, N. A., A. K. Pandit & B. A. Ganai, 2014. Factors affecting the distribution patterns of aquatic macrophytes. *Limnological Review* 14(2): 75–81. <https://doi.org/10.2478/limre-2014-0008>.
- Duarte, C. M., D. Planas & J. Peñuelas, 1994. Macrophytes, taking control of ancestral home. In Margalef, R. (ed), *Limnology Now: A Paradigm of Planetary Problems Elsevier*, Amsterdam: 59–79.
- Dumont, E. R., C. Larue, S. Lorber, H. Gryta, E. Billoir, E. M. Gross & A. Elger, 2019. Does intraspecific variability matter in ecological risk assessment? Investigation of genotypic variations in three macrophyte species exposed to copper. *Aquatic Toxicology* 211: 29–37. <https://doi.org/10.1016/j.aquatox.2019.03.012>.
- Ersoy, Z., U. Scharfenberger, D. L. Baho, T. Bucak, T. Feldmann, J. Hejzlar, E. E. Levi, A. Mahdy, T. Nöges, E. Papastergiadou, K. Stefanidis, M. Šorf, M. Søndergaard, C. Trigo, E. Jeppesen & M. Beklioglu, 2020. Impact of nutrients and water level changes on submerged macrophytes along a temperature gradient: a pan-European mesocosm experiment. *Global Change Biology* 26: 6831–6851. <https://doi.org/10.1111/gcb.15338>.
- Florêncio, F. M., D. C. Alves, F. M. Lansac-Tôha, M. J. Silveira & S. M. Thomaz, 2021. The success of the invasive macrophyte *Hydrilla verticillata* and its interactions with the native *Egeria najas* in response to environmental factors and plant abundance in a subtropical reservoir. *Aquatic Botany* 175: 103432. <https://doi.org/10.1016/j.aquabot.2021.103432>.
- Fylstra, D., L. Lasdon, S. J. Watson & A. Waren, 1998. Design and use of the Microsoft Excel solver. *Interfaces* 28: 29–55. <https://doi.org/10.1287/inte.28.5.29>.

- García-López, X. A., J. R. Ortiz-Zayas, R. Díaz, A. Castro-Jiménez & C. F. Wahl, 2023. Limnological response of Las Curiás Reservoir, San Juan, Puerto Rico: successful management of the invasive aquatic fern, *Salvinia molesta*. *Water* 15(22): 3966. <https://doi.org/10.3390/w15223966>.
- Gillard, M. B., J.-P. Caudal, C. Deleu & G. Thiébaud, 2021. Heterogeneous impact of water warming on exotic and native submerged and emergent plants in outdoor mesocosms. *Plants* 10(7): 1324. <https://doi.org/10.3390/plant10071324>.
- Gimenes, L. L. S., G. P. G. Freschi, I. Bianchini Jr. & M. B. Cunha-Santino, 2020. Growth of the aquatic macrophyte *Ricciocarpos natans* (L.) Corda in different temperatures and in distinct concentrations of aluminum and manganese. *Aquatic Toxicology* 224: 105484. <https://doi.org/10.1016/j.aquatox.2020.105484>.
- Golterman, H. L., R. S. Clymo & M. A. M. Ohmstad, 1978. *Methods for Physical and Chemical Analysis of Freshwaters*. IBP Handbook No 8, 2nd ed. Blackwell, Oxford.
- Hall, R. O., Jr., C. B. Yackulic, T. A. Kennedy, M. D. Yard, E. J. Rosi-Marshall, N. Voichick & K. E. Behn, 2015. Turbidity, light, temperature, and hydropeaking control primary productivity in the Colorado River, Grand Canyon. *Limnology and Oceanography* 60(2): 512–526. <https://doi.org/10.1002/lno.10031>.
- He, Y., N. Song & H.-L. Jiang, 2018. Effects of dissolved organic matter leaching from macrophyte litter on black water events in shallow lakes. *Environmental Science and Pollution Research* 25: 9928–9939. <https://doi.org/10.1007/s11356-018-1267-0>.
- Hoagland, D. R. & D. I. Arnon, 1950. The water culture method of growing plants without soil. *California Agricultural Experimental Station Circular* 374. University of California, Berkeley.
- Hussner, A., C. Meyer & J. Busch, 2008. The influence of water level and nutrient availability on growth and root system development of *Myriophyllum aquaticum*. *Weed Research* 49(1): 73–80. <https://doi.org/10.1111/j.1365-3180.2008.00667.x>.
- Hussner, A., T. Mettler-Altmann, A. P. M. Weber & K. Sand-Jensen, 2016. Carbon stimulation of photosynthesis and growth of ten submerged freshwater plants. *Freshwater Biology* 61(10): 1720–1732. <https://doi.org/10.1111/fwb.12812>.
- Janssen, A. B. G., S. Hilt, S. Kosten, J. J. M. Klein, H. W. Paerl & D. B. Van de Waal, 2021. Shifting states, shifting services: linking regime shifts to changes in ecosystem services of shallow lakes. *Freshwater Biology* 66(1): 1–12. <https://doi.org/10.1111/fwb.13582>.
- Jetter, K. M., J. Madsen, D. Bubenheim & J. Dong, 2021. Bioeconomic modeling of floating aquatic weeds in the Sacramento-San Joaquin River Delta. *Journal of Aquatic Plant Management* 59s: 98–106.
- Jones, H. G., 2014. *Plants and Microclimate: A Quantitative Approach to Environmental Plant Physiology*, 3rd ed. Cambridge University Press, Cambridge.
- Jørgensen, S. E. & B. D. Fath, 2010. *Fundamentals of Ecological Modelling* (4th ed): Application in Environmental Management and Research, Elsevier, Amsterdam.
- Kahara, S. N. & J. E. Vermaat, 2003. The effect of alkalinity on photosynthesis–light curves and inorganic carbon extraction capacity of freshwater macrophytes. *Aquatic Botany* 75(3): 217–227. [https://doi.org/10.1016/S0304-3770\(02\)00179-1](https://doi.org/10.1016/S0304-3770(02)00179-1).
- Kim, D.-K., A. Javed, C. Yang & G. B. Arhonditsis, 2018. Development of a mechanistic eutrophication model for wetland management: sensitivity analysis of the interplay among phytoplankton, macrophytes, and sediment nutrient release. *Ecological Informatics* 48: 198–214. <https://doi.org/10.1016/j.ecoinf.2018.09.010>.
- Kuar, M., M. Kumar, S. Sachdeva & S. K. Puri, 2018. Aquatic weeds as the next generation feedstock for sustainable bioenergy production. *Bioresource Technology* 251: 390–402. <https://doi.org/10.1016/j.biortech.2017.11.082>.
- Langmuir, D., 1997. *Aqueous Environmental Geochemistry*, Prentice Hall, Upper Saddle River.
- Lara, M. V., P. Casati & C. S. Andreo, 2002. CO₂-concentration mechanisms in *Egeria densa*, a submerged aquatic plant. *Physiologia Plantarum* 115(4): 487–495. <https://doi.org/10.1034/j.1399-3054.2002.1150402.x>.
- Larcher, W., 2003. *Physiological Plant Ecology*, Springer, Berlin.
- Li, W., J. Zhou, H. Ding, H. Fu, J. Liu, Y. Chen, T. Dai, Q. Lou, X. Zhong, H. Fan & J. Zhong, 2020. Low-dose biochar added to sediment improves water quality and promotes the growth of submerged macrophytes. *Science of the Total Environment* 742: 140602. <https://doi.org/10.1016/j.scitotenv.2020.140602>.
- Littler, M. M. & K. E. Arnold, 1985. Electrodes and chemicals. In Littler, M. M. & D. S. Littler (eds), *Handbook of Physiological Methods. Ecological Field Methods: Macroalgae* Cambridge University Press, Cambridge: 349–375.
- Machado, R., I. Bianchini Jr. & M. B. Cunha-Santino, 2020. Temperature and turbidity as drive forces to the growth of *Egeria densa* (Planchon) under to controlled conditions. *Aquatic Botany* 164: 103234. <https://doi.org/10.1016/j.aquabot.2020.103234>.
- Madsen, T. V. & K. Sand-Jensen, 1991. Photosynthetic carbon assimilation in aquatic macrophytes. *Aquatic Botany* 41(1–3): 5–40. [https://doi.org/10.1016/0304-3770\(91\)90037-6](https://doi.org/10.1016/0304-3770(91)90037-6).
- Mahujcharyawong, J. & S. Ikeda, 2001. Modelling of environmental phytoremediation in eutrophic river: the case of water hyacinth harvest in Tha-chin River, Thailand. *Ecological Modelling* 142: 121–134. [https://doi.org/10.1016/S0304-3800\(01\)00283-6](https://doi.org/10.1016/S0304-3800(01)00283-6).
- Majewski, W. & D. C. Miller, 1979. Predicting Effects of Power Plant Once-Through Cooling on Aquatic Systems; A State-of-Art Report of IHP Working Group 6.2 on the Effects of Thermal Discharges, UNESCO, Paris.
- Mackay, A. J., E. J. Muturi, M. P. Ward & B. Allan, 2016. Cascade of ecological consequences for West Nile virus transmission when aquatic macrophytes invade stormwater habitats. *Ecological Applications* 26(1): 219–232. <https://doi.org/10.1890/15-0050>.
- Martins, D., L. R. Cardoso, E. E. Mori & R. H. Tanaka, 2003. Caracterização genética de acessos de *Egeria* (*Egeria* spp.) coletados no estado de São Paulo utilizando RAPD. *Planta Daninha* 21(spe): 1–6. <https://doi.org/10.1590/S0100-83582003000400001>.

- Menendez, M. & A. Sanchez, 1998. Seasonal variations in P-I responses of *Chara hispida* L. and *Potamogeton pectinatus* L. from stream Mediterranean ponds. *Aquatic Botany* 61(1): 1–15. [https://doi.org/10.1016/S0304-3770\(98\)00061-8](https://doi.org/10.1016/S0304-3770(98)00061-8).
- Morgan, V. H., E. Baker, C. Stottlemeyer & J. Li, 2023. *Egeria densa* Planch. NOAA Great Lakes Aquatic Nonindigenous Species Information System. Available at: https://nas.er.usgs.gov/queries/greatlakes/FactSheet.aspx?Species_ID=1107&Potential=Y&Type=2&, Revision Date: 8/2/2018, Access Date: 3/10/2023
- Nievola, C. C., C. P. Carvalho, V. Carvalho & E. Rodrigues, 2017. Rapid responses of plants to temperature changes. *Temperature* 4(4): 371–405. <https://doi.org/10.1080/23328940.2017.1377812>.
- Padial, A. A. & S. M. Thomaz, 2008. Prediction of the light attenuation coefficient through the Secchi disk depth: empirical modeling in two large Neotropical ecosystems. *Limnology* 9: 143–151. <https://doi.org/10.1007/s10201-008-0246-4>.
- Petracco, P., 2006. Efeito das variáveis abióticas na produção primária de *Egeria najas* e *Utricularia breviscapa* da lagoa do Óleo (Estação Ecológica de Jataí, Luiz Antônio-SP). Tese, Universidade Federal de São Carlos, São Carlos. <https://repositorio.ufscar.br/handle/ufscar/1564>
- Petracco, P., M. M. Pezzato & M. B. I. Cunha-SantinoBianchini Jr., 2022. Net photosynthetic rates of *Egeria najas* and *Utricularia breviscapa* changes directed by seasonal hydrological variations. *Brazilian Journal of Botany* 45(3): 1129–1138. <https://doi.org/10.1007/s40415-022-00828-x>.
- Pezzato, M. M. & A. F. M. Camargo, 2004. Photosynthetic rate of the aquatic macrophyte *Egeria densa* Planch. (Hydrocharitaceae) in two rivers from the Itanhaém River Basin in São Paulo State, Brazil. *Brazilian Archives of Biology and Technology* 47(1): 153–162. <https://doi.org/10.1590/S1516-89132004000100021>.
- Pezzato, M. M., 2007. Macrófitas aquáticas submersas: fotossíntese, crescimento e variáveis abióticas da água. Tese, Universidade Federal de São Carlos, São Carlos. <https://repositorio.ufscar.br/handle/ufscar/1603>
- Pezzato, M. M., P. Petracco, M. B. Cunha-Santino & I. Bianchini Jr., 2023. Assessment of cardinal temperatures of *Egeria najas* Planchon and its potential growth in a tropical foodplain lagoon. *Hydrobiologia* 850: 2127–2138. <https://doi.org/10.1007/s10750-023-05224-4>.
- Pierini, S. A. & S. M. Thomaz, 2004. Effects of inorganic carbon source on photosynthetic rates of *Egeria najas* Planchon and *Egeria densa* Planchon (Hydrocharitaceae). *Aquatic Botany* 78(2): 135–146. <https://doi.org/10.1016/j.aquabot.2003.09.007>.
- Reitsema, R. E., P. Meire & J. Schoelynck, 2018. The future of freshwater macrophytes in a changing world: dissolved organic carbon quantity and quality and its interactions with macrophytes. *Frontiers in Plant Science* 9: 629. <https://doi.org/10.3389/fpls.2018.00629>.
- Riis, T., B. Olesen, J. S. Clayton, C. Lambertini, H. Brix & B. K. Sorrell, 2012. Growth and morphology in relation to temperature and light availability during the establishment of three invasive aquatic plant species. *Aquatic Botany* 102: 56–64. <https://doi.org/10.1016/j.aquabot.2012.05.002>.
- Salgado, J., M. I. Vélez, L. C. Caceres-Torres, J. A. Villegas-Ibagon, L. C. Bernal-Gonzalez, L. Lopera-Congote, N. M. Martinez-Medina & C. González-Arango, 2019. Long-term habitat degradation drives Neotropical macrophyte species loss while assisting the spread of invasive plant species. *Frontiers in Ecology and Evolution* 7: 140. <https://doi.org/10.3389/fevo.2019.00140>.
- Salisbury, F. B. & C. W. Ross, 1992. *Plant Physiology*, 4th ed. Wadsworth, Belmont.
- Sand-Jensen, K., 1989. Environmental variables and their effect on photosynthesis of aquatic plant communities. *Aquatic Botany* 34(1–3): 5–25. [https://doi.org/10.1016/0304-3770\(89\)90048-X](https://doi.org/10.1016/0304-3770(89)90048-X).
- Shugart, H. H., R. A. Goldstein, R. V. O'Neill & J. B. Mankin, 1974. TEEM: a terrestrial ecosystem energy model for forests. *Oecologia Plantarum* 9(3): 231–264.
- Sierra, C. A., 2012. Temperature sensitivity of organic matter decomposition in the Arrhenius equation: some theoretical considerations. *Biogeochemistry* 108: 1–15. <https://doi.org/10.1007/s10533-011-9596-9>.
- Silveira, M. J. & G. Thiébaud, 2017. Impact of climate warming on plant growth varied according to the season. *Limnologia* 65: 4–9. <https://doi.org/10.1016/j.limno.2017.05.003>.
- Song, Y.-B., M.-Y. Zhou, Y.-L. Qin, J. H. C. Cornelissen & M. Dong, 2021. Nutrient effects on aquatic litter decomposition of free-floating plants are species dependent. *Global Ecology and Conservation* 30: e01748. <https://doi.org/10.1016/j.gecco.2021.e01748>.
- Steele, J. H., 1965. Notes on some theoretical problems in production ecology. In Goldman, C. R. (ed), *Primary Production in Aquatic Environments* University of California Press, Berkeley: 393–398. <https://doi.org/10.1525/9780520318182-028>.
- Steinberg, C. E. W., T. Meinelt, M. A. Timofeyev, M. Bittner & R. Menzel, 2008. Humic substances. Part 2: Interactions with organisms. *Environmental Science and Pollution Research* 15: 128–135. <https://doi.org/10.1065/espr2007.07.434>.
- Strange, E. F., P. Landi, J. M. Hill & J. A. Coetzee, 2019. Modeling top-down and bottom-up drivers of a regime shift in invasive aquatic plant stable states. *Frontiers in Plant Science* 10: 889. <https://doi.org/10.3389/fpls.2019.00889>.
- Tavecchio, W. L. G. & S. M. Thomaz, 2003. Effects of light on the growth and photosynthesis of *Egeria najas* Planchon. *Brazilian Archives of Biology and Technology* 46(2): 203–209. <https://doi.org/10.1590/S1516-89132003000200011>.
- Taveira, R., 2022. Crescimento e distribuição de duas espécies de macrófitas aquáticas submersas em diferentes condições ambientais. Dissertação. Universidade Estadual Paulista. Rio Claro. <http://hdl.handle.net/11449/217173>
- Thomaz, S. M., P. A. Chambers, S. A. Pierini & G. Pereira, 2007. Effects of phosphorus and nitrogen amendments on the growth of *Egeria najas*. *Aquatic Botany* 86(2): 191–196. <https://doi.org/10.1016/j.aquabot.2006.10.004>.
- Thomaz, S. M., 2023. Ecosystem services provided by freshwater macrophytes. *Hydrobiologia* 850: 2757–2777. <https://doi.org/10.1007/s10750-021-04739-y>.
- Verhofstad, M. J. J. M. & E. S. Bakker, 2019. Classifying nuisance submerged vegetation depending on ecosystem

- services. *Limnology* 20: 55–68. <https://doi.org/10.1007/s10201-017-0525-z>.
- Vollenweider, R. A., 1971. A Manual on Methods for Measuring Primary Production in Aquatic Environments. IBP Handbook No 12, 2nd ed. Blackwell, Oxford:
- Weber, M. A., L. A. Wainger, N. E. Harms & G. M. Nesslage, 2021. The economic value of research in managing invasive hydrilla in Florida public lakes. *Lake and Reservoir Management* 37(1): 63–76. <https://doi.org/10.1080/10402381.2020.1824047>.
- Yarrow, M., V. H. Marín, M. Finlayson, A. Tironi, L. E. Delgado & F. Fischer, 2009. The ecology of *Egeria densa* Planchon (Liliopsida: Alismatales): a wetland ecosystem engineer? *Revista Chilena De Historia Natural* 82: 299–313. <https://doi.org/10.4067/S0716-078X2009000200010>.
- Yoshida, L. L., L. S. A. Valletta, M. B. Cunha-Santino & I. Bianchini Jr., 2022. A proposal for the equivalence between the rates of net photosynthesis and growth rate constants for submerged aquatic plants. *Hydrobiologia* 849: 77–88. <https://doi.org/10.1007/s10750-021-04711-w>.

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Springer Nature or its licensor (e.g. a society or other partner) holds exclusive rights to this article under a publishing agreement with the author(s) or other rightsholder(s); author self-archiving of the accepted manuscript version of this article is solely governed by the terms of such publishing agreement and applicable law.