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PRIMARY RESEARCH PAPER

Density-dependent facilitation and inhibition between submerged and free-floating plants

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Abstract This study aimed at testing the hypothesis that free-floating plants may facilitate the growth of submerged plants under hypertrophic conditions and intermediate plant density. The effects of *Lemna* presence on the growth of two submerged plants (*Elodea nuttallii* and *Ceratophyllum demersum*) over a nitrogen gradient were experimentally investigated. This was complemented with analysing the presence of *C. demersum* and *E. nuttallii* in Hungary and in Germany in relation to the density of free-floating plants. Results showed a negative exponential pattern between underwater light intensity and *Lemna* cover. *Ceratophyllum* and *Elodea* relative growth rate decreased with increasing nitrogen concentrations and additional low *Lemna* density stimulated *Ceratophyllum* and suppressed *Elodea*. *Elodea* decreased linearly with *Lemna* density while *Ceratophyllum* showed a unimodal response. Total algal biomass (epiphytic and planktonic) was higher in *Ceratophyllum* than in *Elodea* treatments and decreased rapidly with increasing *Lemna* density. The field studies showed a positive relationship between *Ceratophyllum* and a negative one between *Elodea* and free-floating plant cover. This study clearly showed that free-floating plants can have either facilitating or inhibiting impact on the growth of submerged plants depending on cover density and macrophyte species. The facilitating effect on *Ceratophyllum* is most likely due to suppressing epiphytic algal growth.

Keywords Competition · Regime shift · *Ceratophyllum* · *Elodea* · *Lemna* · Algae · Shading

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Introduction

Light and nutrients are two major abiotic factors that shape abundance patterns of submerged macrophytes together. Besides depth and turbidity, underwater light conditions are also modified by several biotic factors such as shading by neighbouring submerged plants (Szabó et al., 2020), phytoplankton

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and epiphytic algae (Koleszár et al., 2022b). Also, the presence of grazing snails (Bayley et al., 2007; Yang et al., 2020) and bioturbation by benthic fauna (Adámek & Maršálek, 2013) are important influencers. It is well known that higher availability of nutrients may lead to increased growth of epiphytic algae (Song et al., 2015, 2017), and decreased growth of submerged plants (Yang et al., 2020; Koleszár et al, 2022a). Epiphytic algae not only reduce the light level, but also form a barrier between the macrophyte and the water, thus strongly reducing the availability of nutrients (Sand-Jensen 1977; Roijackers et al., 2004).

It is also known that in small lentic, wind sheltered waterbodies, high nutrient concentration leads to the dominance of free-floating plants (Peeters et al., 2013; Smith et al., 2014; Szabó et al., 2022). These dense mats create dark and anoxic underwater conditions that leave little opportunity for submerged plant to survive (Scheffer et al., 2003). Therefore, due to the reduced light levels in the water body, eutrophication strongly contributes to the decline of submerged vegetation (Phillips et al., 1978, 2016). Shade tolerance and persistence of submerged plants may be the key traits in determining when such a regime shift occurs (Lu et al., 2013). Plants with lower light compensation point or higher shade tolerance can be expected to have higher survival chance in turbid waters or in the shade of floating macrophytes (Szabó et al., 2020; Koleszár et al., 2022a). Free-floating plants reduce available light not only for submerged plants but for phytoplankton and epiphytic algae too. Beyond shading, they also reduce the available nutrients for epiphytes, resulting in their slower growth (Lu et al., 2013; Pinto & O'Farrell, 2014). Consequently, not only submerged plants can be inhibited by the shading effect of free-floating plants, but epiphytic algae as well. Therefore, it can be concluded that the shade of free-floating plants may not always be negative on the growth of submerged plants. It is already well known that intermediate shading stimulates apical elongation, chlorophyll concentration and photosynthetic efficiency of rooted submerged plants (Lu et al., 2013; Szabó et al., 2019, 2020) and decreases root formation and degree of branching (James et al., 2006; Szabó et al., 2019, 2020). However, all of the studies examining the interactions between the two plant groups reported that shading by free-floating plants have obvious negative effect on the biomass-based growth rate of submerged plants (Janes et al., 1996; Morris et al., 2004; Larson 2007).

If the negative impact by epiphytic algae is stronger than shading by free-floating plants, on the other hand, a certain level of floating plant density may in principle favour the growth of submerged macrophytes. Therefore, we hypothesized that under hypertrophic conditions combined with intermediate plant density, the presence of free-floating plants facilitated submerged plant growth due to suppressing algal growth. In the present study, we tested this assumption on two widespread submerged plant species: a rooted [*Elodea nuttallii* (Planch.) H. St. John] and a rootless one (*Ceratophyllum demersum* L.), respectively. Here, we evaluated this hypothesis by investigating how free-floating duckweed *Lemna gibba* L. changed light conditions in the water column and how this affected the growth of algae and the submerged plants *C. demersum* and *E. nuttallii*. Furthermore, monitoring data on the occurrence and abundance of *C. demersum* and *E. nuttallii* in Hungary and in Germany were studied in relation to the density of free-floating plants.

Materials and methods

Plant collection and preincubation

Fronds of *L. gibba* (subsequently termed *Lemna*) and shoots of *C. demersum* (subsequently termed *Ceratophyllum*) were collected from Igrice channel (N 47.996376°, E 21.734152°), while shoots of *E. nuttallii* (subsequently termed *Elodea*) were obtained from the Eastern Principal Channel, (N 47.860911°, E 21.382270°) NE Hungary. After their collection and before the experiment, we rinsed the plants with tap water removing the epiphytic algae and debris. The plants were preincubated for a month in 10 l plastic boxes containing a general purpose culture medium modified from Barko and Smart (1985). Nitrogen and phosphorus were supplied by adding stock solution of NH_4NO_3 and K_2HPO_4 to a final concentration of 2 mg N l^{-1} and 0.4 mg P l^{-1}, respectively. We added TROPICA supplier micronutrient solution to ensure micronutrient supply using 10,000-fold dilution. The following final concentrations were set in the medium: Fe 0.080, Mn 0.045, Zn 0.002, Cu 0.006

and Mo 0.002 mg l^{-1}, respectively. Illumination was carried out by Philips 400 W metal halogen lamps.

Effects of *Lemna* density on light attenuation

Underwater light intensities were measured under different *Lemna* biomass densities in 2 l plastic black covered aquaria (height 11.5 cm, width 11 cm, length 18 cm) containing 2 l culture medium. Initial light intensity was 280 µmol m^{-2} s^{-1} photon flux density above the water surface. Sensor of MQ-510 full spectrum quantum metre (Apogee-Instruments, Logan USA) was placed 10 cm below the water surface and photosynthetic active radiation was measured with increasing *Lemna* biomass (0, 1, 5, 10, 15, 20, 25, 30, 35 and 40 g fresh weight FW) corresponding to 0, 50, 250, 500, 750, 1000, 1250, 1500, 1750 and 2000 g FW m^{-2}. We used the mean of six measurements per biomass density. We repeated the measurement three times using the same *Lemna* densities detailed above.

Impact of *Lemna* on submerged plant with nutrient increase

Semi-static conditions were applied to mimic a situation in which nutrient release or replenishment from the sediment to the water column takes place (Szabó et al., 2022). We introduced an initial biomass of 10 ± 0.2 g (500 g m^{-2}) *Ceratophyllum* (13–15 cm length), and *Elodea* (13–15 cm length) shoots in 2 l plastic aquaria separately. The sides of the aquaria were covered with black foil to avoid light penetration from the sides. We co-cultured the plants with 0.5 ± 0.02 g FW of *Lemna* (25 g m^{-2}) resulting 5% of *Lemna* cover and without *Lemna* as control. We applied five different nitrogen concentrations to reach 0.5, 1, 2, 5 or 10 mg N l^{-1} by adding NH_4NO_3. The initial concentration of phosphorus was the same as in the preincubation. Similarly, we applied the same dilution of microelements that was 1:10,000. Three aquaria per treatment (in total 30–30 aquaria) were incubated for 20 days under 280 µmol m^{-2} s^{-1} photon flux density and a photoperiod of 16-h light/8-h dark. The aquaria were kept in a temperature-controlled (24–26°C) water bath. We renewed half of the medium (1 l) twice a week. The medium was drained by gravity and fresh medium was carefully added to the aquaria through a PVC tube placed in the corner in order to avoid any perturbation. At days 12 and 19 (between 6 AM and 4 PM), pH and dissolved oxygen in each aquarium were recorded. At the end of the experiment (day 20), plants were harvested and measured for fresh weight (FW), dried at 80°C for 2 days and then measured again for dry weight (DW). We calculated relative growth rates per day (RGRs) as $RGR = (\ln FW_t - \ln FW_0)/t$ in which FW_t and FW_0 were the fresh weights at time t (20) and time 0, respectively.

Impact of *Lemna* density on submerged plants

In a subsequent experiment, *Ceratophyllum* and *Elodea* shoots (10 ± 0.2 g) were placed separately in 2 l plastic aquaria covered with black plastic foil on their sides. We co-cultured the plants with 0.5, 5, 20, 40 g FW of *Lemna* (25, 250, 1000, 2000 g m^{-2}) and without *Lemna* as control. The applied densities resulted zero, low, intermediate, complete and dense cover (0, 5, 50, 200, 400%) on the surface. We applied two different nitrogen concentrations by adding NH_4NO_3 to reach 2 and 10 mg N l^{-1}. The initial concentration of phosphorus was the same as in the preincubation as well as the dilution factor of microelement solution was 1:10,000. Three aquaria per treatment (in total 30 aquaria) were incubated for 20 days under the same conditions detailed in previous experiment. At the end of the experiment (day 20), epiphytic algae were gently removed from the surface of *Ceratophyllum* and *Elodea* shoots and from the side of the aquaria into the media using a paintbrush. After filtration (pore diameter 5–8 µm) of the medium, total algal biomass (epiphytic + planktonic) was dried (80°C for 48 h) and the dry mass was measured. Fresh and dry weights were measured and daily yield of the plants was calculated. At day 19 (4 PM), we analysed water for pH and dissolved oxygen (DO) concentration.

Assessment of macrophyte abundances in field sites

Using the Hungarian Biotic Database of General Directorate of Water Management (OVF, www.ovf.hu/en) and MaPHYTE database (http://data.freshwaterbiodiversity.eu/metadb/bf_mdb_view.php?uid=64da4b8287450&code=22), we compiled macrophyte abundance data from Hungary (2005–2019 June–September), and from Germany (1994–2011 June–September) including the records of either (or

both) free-floating plants (FFPs) (*Azolla caroliniana* Willd., *Salvinia natans* L., *Lemna minor* L., *L. minuta* Kunth, *L. gibba* L., *Spirodela polyrhiza* L., *Hydrocharis morsus-ranae* L.) or submerged species *Ceratophyllum demersum/Elodea nuttallii* (Birk and Willby 2010). Macrophyte abundance data were converted into mean values of Braun–Blanquet's cover classes 1–5 (that is, 3%; 15%; 37.5%; 62.5%; 87.5%) using the method of Engloner (2012). To avoid interfering effects by dominance of other submerged plants if *Ceratophyllum* cover was less than 87.5%, we selected only those sites where total cover of other submerged plants did not exceed the cover of *Ceratophyllum* or where their total cover was less than 20%. The same filtering method was applied for the selection of *Elodea*. To avoid disturbance by dominance of rooted floating-leaved plants (i.e. *Potamogeton natans* L., *Nymphaea alba* L., *Nuphar lutea* (L.) Sibth. & Sm., *Trapa natans* L.) in case total free-floating plant cover was less than 87.5%, we selected only those sites where total cover of floating-leaved plants did not exceed the cover of free-floating plants or where their total cover was less than 20%. Using those data, the abundance of *Ceratophyllum* or that of *Elodea* was analysed as a function of free-floating plant abundance (Szabó et al., 2022).

Statistical analyses

For the laboratory experiments, we used Kolmogorov–Smirnov tests to check the normality of the variables. As the measured variables (RGR, yield, biomass of periphytic algae) were normally distributed ($P > 0.05$), general linear model (GLM) was used to test the significance of the effects of different factors (*Lemna* density, nitrogen concentration, submerged species) and their interactions on these variables. We checked residuals for normality, and we evaluated homogeneity of variances by Levene's test. We applied Tukey's post hoc tests to evaluate which *Lemna* density treatments differed from each other. We used pairwise comparisons (PC) to test the variables for significant differences among *Lemna* treatments, where the mean difference (MD) ± standard error was indicated.

Pearson Chi-square Tests were performed to evaluate whether there was an association between *Ceratophyllum* and free-floating plants in the Hungarian vegetation survey ($n = 992$) and between *Elodea* and free-floating plants in the German dataset ($n = 295$). All analyses were done using SPSS 16.0 software. Nonlinear models were fitted in Lemna density-dependent light attenuation studies, in density-dependent submerged plant yield, and in field survey. The weighted regression models that considered the standard errors of the means were calculated by LAB Fit curve-fitting software (Silva & Silva, 2018). We choose the best fitting curves based on the simplicity of the function, the lowest confidence intervals and the highest R^2 values.

Results

Effects of *Lemna* density on light attenuation

Underwater light intensity followed a negative exponential pattern with increasing biomass cover. Intermediate *Lemna* density (48%, 241 g m^{-2}) decreased the underwater light intensity by 50% and complete *Lemna* density (200%, 1000 g m^{-2}) by 95% (Fig. 1).

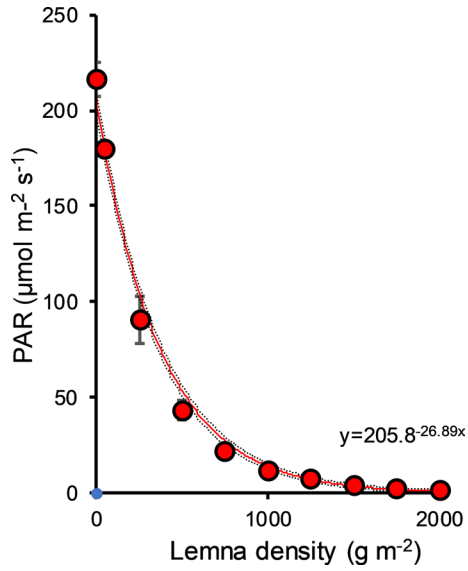

Fig. 1 Change of underwater photosynthetic active radiation (PAR) under different *Lemna* densities. Means ± SE, dotted lines are 95% confidence intervals, $n = 3$

Impact of *Lemna* on submerged plants with nutrient increase

Overall, increasing nitrogen concentration (from 0.5 to 10 mg l^{-1}) significantly decreased the growth rate of the submerged plants ($P<0.001$, MD 0.009–0.028 ± 0.002, PC) and *Elodea* showed significantly higher RGR than *Ceratophyllum* ($P<0.001$, MD 0.052 ± 0.002, PC). The relative growth rate of *Ceratophyllum* was significantly higher ($P<0.001$, MD 0.011 ± 0.002, PC) while RGR of *Elodea* was significantly lower ($P<0.001$, MD 0.017 ± 0.003, PC) with the presence of *Lemna* comparing to control cultures (Fig. 2a, b).

Impact of *Lemna* density on submerged plants

Change in plant growth

The yield (g m^{-2} day^{-1}) of *Ceratophyllum* was significantly stimulated ($P<0.001$, MD 8.34 ± 1.67, PC) under intermediate initial *Lemna* density (50%) compared to control cultures (Fig. 3a, b). Under higher nitrogen concentration (10 mg l^{-1}), the facilitation of *Ceratophyllum* yield was even higher ($P=0.005$, MD 10.57 ± 2.92, PC). However, above this *Lemna* density level of 50%, further increasing *Lemna* cover significantly reduced the yield of *Ceratophyllum* and the highest initial *Lemna* density (400%) resulted in complete decay of *Ceratophyllum* (Fig. 3b).

The yield of *Elodea* grown at 2 mg l^{-1} N was significantly decreased ($P=0.001$, MD 5.83 ± 1.18, PC) under intermediate (50%) or higher initial *Lemna* density and showed linear pattern with increasing biomass cover. At 10 mg l^{-1} N, the inhibitory impact of *Lemna* cover was even stronger where low (5%) initial *Lemna* density resulted in significantly ($P=0.001$, MD 8.03 ± 2.45, PC) reduced *Elodea* yield. Here, both complete and dense initial density resulted in complete decay of *Elodea* (Fig. 3c, d). Overall, under intermediate *Lemna* density or above, the yield of *Ceratophyllum* was significantly ($P<0.001$, MD 12.5 ± 0.87, PC) higher than that of *Elodea*.

Change in algal growth

Total algal biomass (DW) was significantly higher ($P=0.024$, MD 76 ± 31, PC) in the cultures of *Ceratophyllum* compared to *Elodea*. *Lemna* cover

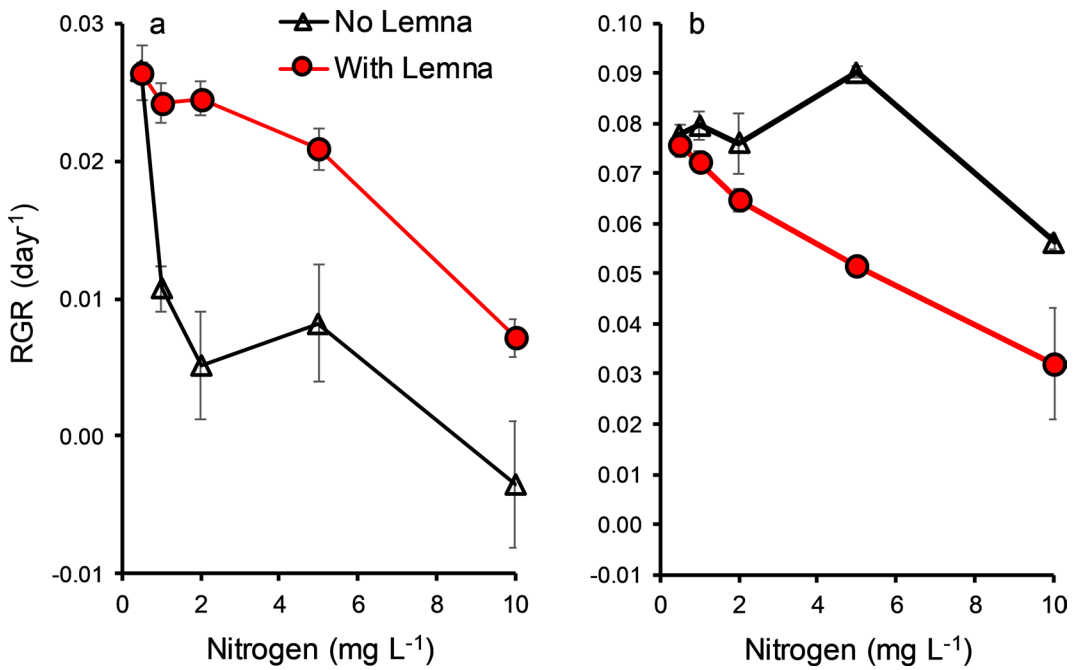

Fig. 2 The impact of the presence of *Lemna* on the growth of *Ceratophyllum* (**a**) and *Elodea* (**b**) under different nitrogen concentration. Initial *Lemna* density was 25 g FW m^{-2}. Means ± SE, n = 3

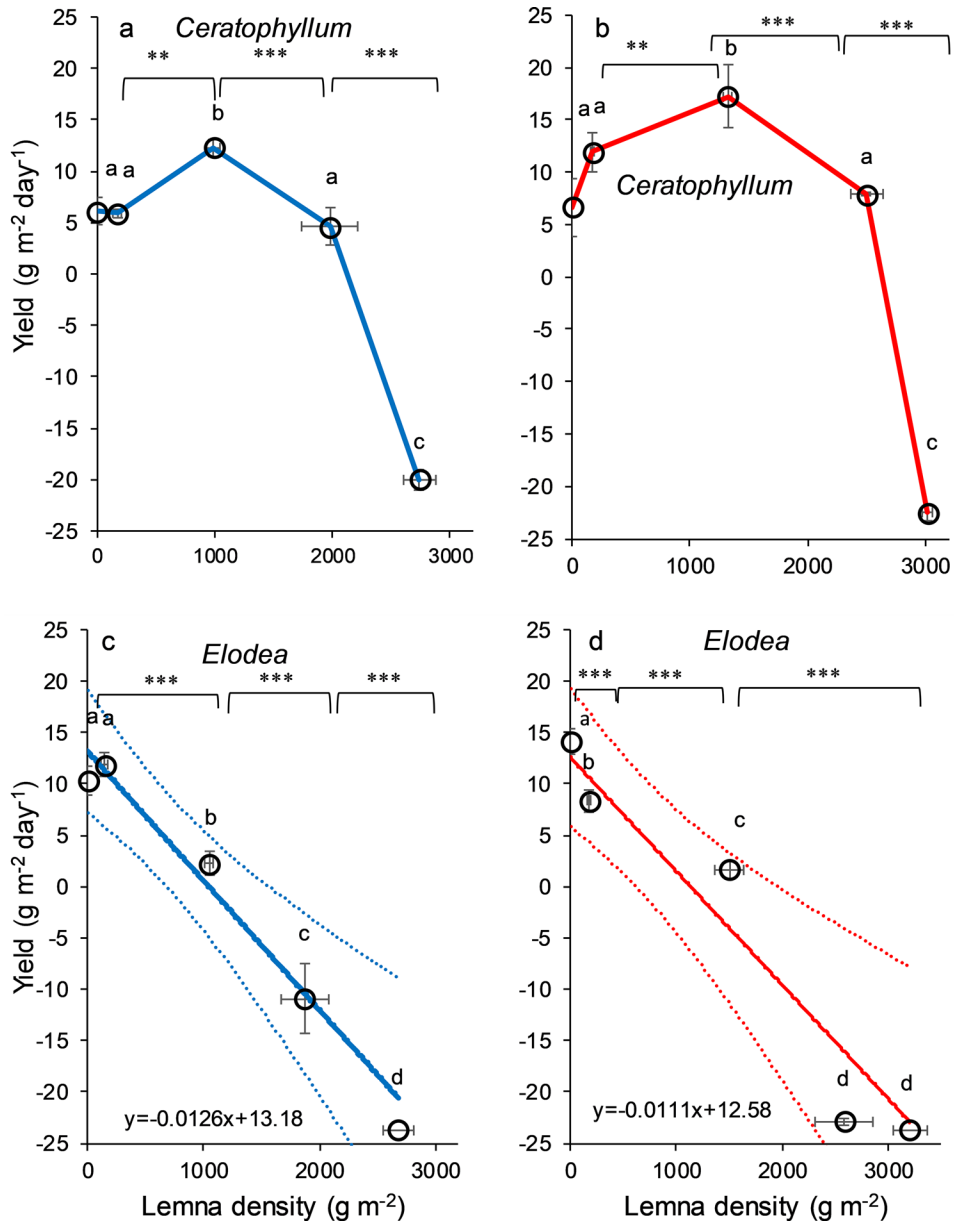

Fig. 3 The effect of *Lemna* density on yield of *Ceratophyllum* (**a**, **b**) and of *Elodea* (**c**, **d**) cultivated in 2 (**a**, **c**) and 10 mg N l^{-1} (**b**, **d**) nutrient concentration. *Lemna* density was measured at the 20th day of the experiment. Means ±SE, n = 3; dotted lines are 95% confidence intervals (**c**, **d**). Significant differences (Tukey's test, $P < 0.05$) of the yield among treatments are indicated with different lowercase letters; asters indicates significant differences of the Pairwise comparisons (**$P < 0.01$, ***$P < 0.001$)

strongly reduced algal biomass where even low initial *Lemna* density (5%) resulted in significantly reduced algal biomass compared to control cultures (*Ceratophyllum*: $P = 0.022$, MD 260 ± 96; *Elodea*: $P < 0.001$, MD 129 ± 23, PC). Algal biomass values showed negative logarithmic pattern with increasing *Lemna* biomass both in *Ceratophyllum* and in *Elodea* co-cultures (Fig. 4).

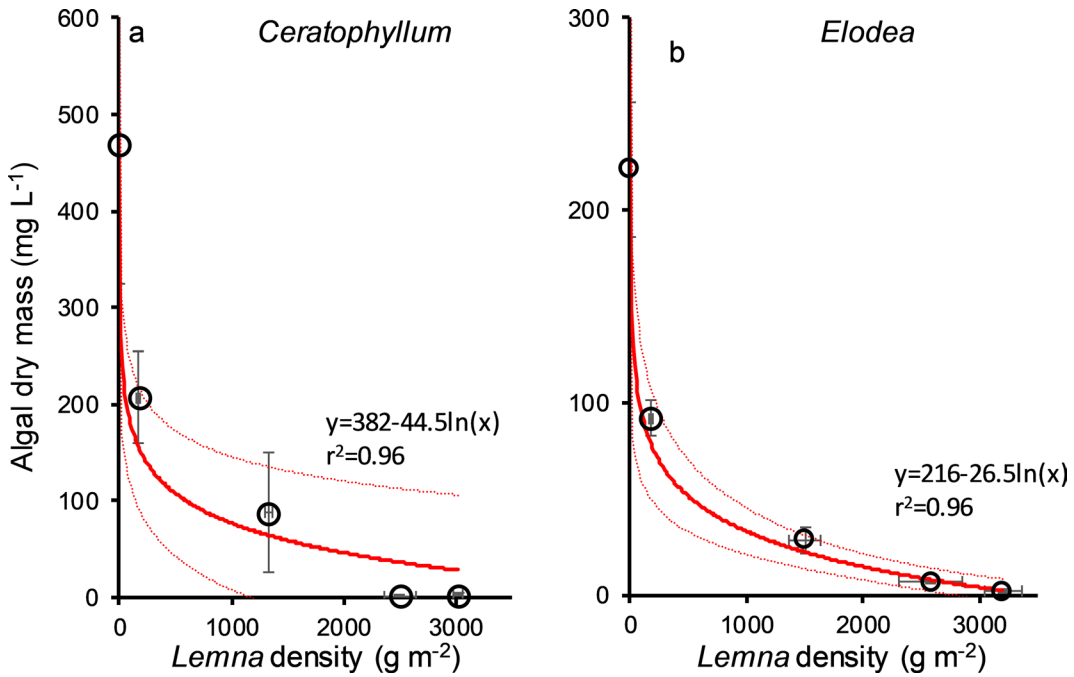

Fig. 4 The effect of *Lemna* density on algal biomass cultivated with *Ceratophyllum* (**a**) and with *Elodea* (**b**) in 10 mg N l^{-1} nutrient concentration. The indicated *Lemna* densities were measured at the 20th day of the experiment. Means ± SE, $n = 3$; dotted lines are 95% confidence intervals. *Note* There is two times difference in the scale of the two *Y*-axis in panel **a** and **b**

Change in pH and oxygen concentration

Lemna density had significant ($P < 0.000$, ANOVA) effects on the pH and on the DO of the medium. Both submerged plant species showed a similar pattern with increasing *Lemna* density (Fig. 5). Regarding to both pH and DO, there were no significant effects between the two species ($P = 0.718$, ANOVA). In *Ceratophyllum* and in *Elodea* cultures, intermediate (50%) or higher initial *Lemna* density reduced the pH from 9.73 and 9.96 to below 6 (Fig. 5a–c). Complete and dense initial *Lemna* density reduced DO of the medium below 1.5 mg l^{-1} in *Ceratophyllum* cultures and below 0.5 mg l^{-1} in *Elodea* cultures.

Field survey

In the Hungarian field survey, high *Ceratophyllum* coverage was observed significantly more often than expected under high free-floating plant (FFP) cover (> 30%) and less frequent than expected for low FFP (Fig 6a). In addition, low FFP resulted in significantly more observations of low *Ceratophyllum* abundance (Pearson Chi-Square = 41.304, $df = 1$, $P < 0.001$) and *Ceratophyllum* abundance showed positive linear pattern with increasing FFP cover (Fig 6a).

The Pearson Chi-square test applied to the German survey showed that there were significant differences between the observed and expected frequencies (Pearson Chi-Square = 5.431, $df = 1$, $P = 0.023$). The observed frequency of high *Elodea* cover (> 30% cover) under high FFP cover (> 30% cover) was significantly lower than the expected frequency and the observed frequency of high *Elodea* under low FFP was significantly higher than the expected frequency. The same analysis showed also that low *Elodea* occurred significantly more frequently under high FFP and less under low FFP.

We found a negative power function relationship between the cover of FFP and that of *Elodea* (Fig. 6b). High *Elodea* density was 4.4 times more likely in those sites where duckweed density was low (0–30% cover) comparing to sites with high duckweed density (cover > 30%).

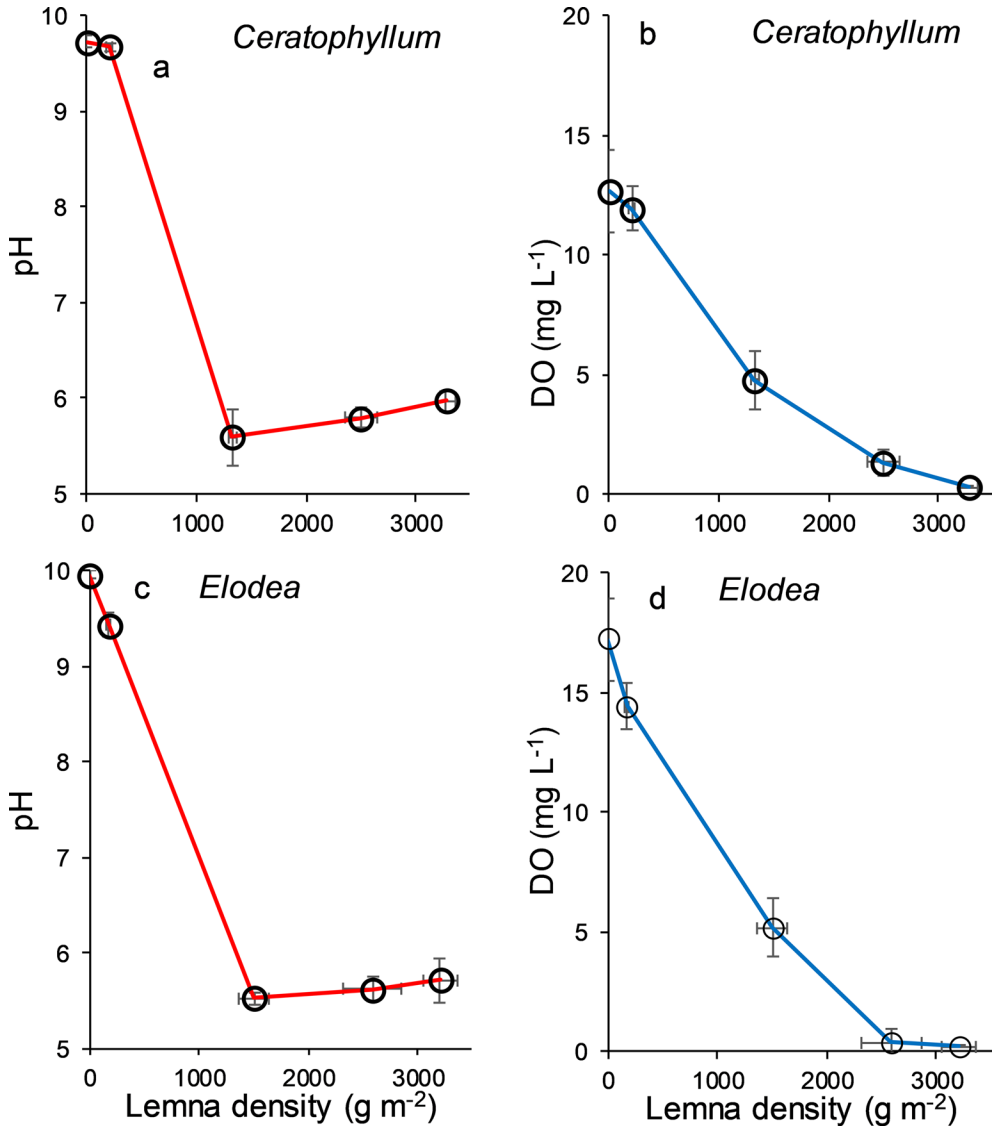

Fig. 5 The effect of *Lemna* density on the pH and dissolved oxygen concentration of the water in *Ceratophyllum* (**a**, **b**) and *Elodea* (**c**, **d**) cultures cultivated in 10 mg l^{-1} N. The indicated *Lemna* densities were measured at the 20th day of the experiment. Means ± SE, $n = 3$

Discussion

The present study clearly showed that, depending on cover density and species identity, free-floating plants can have either facilitating or inhibiting impact on the growth of submerged plants. The growth responses of the two submerged species (*Ceratophyllum*, *Elodea*) to shading by *Lemna* were completely different. The impact of dense *Lemna* cover was much more negative on the growth of *Elodea* compared to *Ceratophyllum*. Increasing nitrogen concentration also increased the biomass of *Lemna* that, in turn, reduced both the underwater light availability and algal biomass. Algal growth was strongly reduced even under low (5%) initial *Lemna* cover. There are several possible reasons for growth stimulation of *Ceratophyllum* under intermediate *Lemna* density. Since total algal biomass was nearly two times higher in the presence of *Ceratophyllum* as compared to *Elodea*, the strong drop in algal biomass under

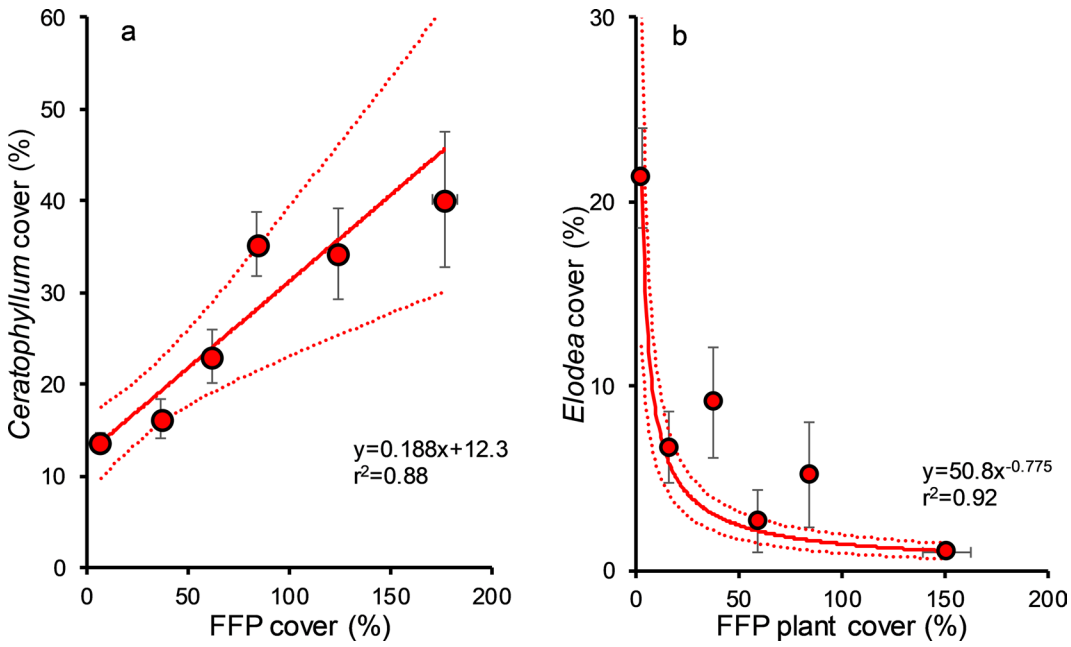

Fig. 6 Correlation of *Ceratophyllum* (**a**, $N = 992$) and *Elodea* (**b**, $N = 295$) cover with total free-floating plant (FFP) cover. Means ± SE; data were $X + 1$ transformed. Dotted lines are 95% confidence intervals

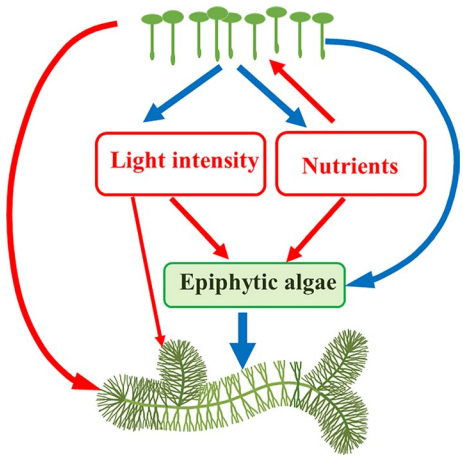

Fig. 7 Interactions among abiotic factors (underwater light intensity, nutrient concentration) epiphytic algae, *Lemna* and *Ceratophyllum* under intermediate *Lemna* density (250 g m^{-2}). The strength of a relationship is indicated by arrow colour (red positive, blue negative)

intermediate *Lemna* cover could indirectly facilitate the growth of *Ceratophyllum* (Fig. 7). On the other hand, as there were less algal biomass in the presence of *Elodea*, an intermediate *Lemna* cover did not result such a drastic drop in algal biomass. Therefore, shading by *Lemna* had only an inhibiting impact on *Elodea*. In the presence of *Elodea*, reduced algal biomass concurs with the findings that *Elodea* produces allelopathic substances reducing the growth of several epiphytic and planktonic cyanobacteria and green algal species (Erhard & Gross, 2006; Lürling et al., 2006; Vanderstukken et al., 2014).

It is already well investigated that in water bodies dominated by submerged plants, algal biomass was largely restricted to epiphytic algae, and planktonic algae constituted only a minor fraction of the total algal biomass (Koleszár et al., 2022b). It is also well known that epiphytic algae can reduce light availability for submerged plants by more than 90% (Tóth, 2013). Beyond reducing light, the layer of epiphytic algae on the plant surface limits nutrient availability for the host plants as well. Consequently, there is a possibility that free-floating plants have stimulating effect on submerged plants if the restricting effects on epiphytic algae (i.e. shading + direct contact inhibition) are larger than on free-floating plants.

Field survey of the two submerged plants supported our experimental findings where the abundance of *Ceratophyllum* correlated positively

with the total cover of free-floating plants. On the other hand, there was a strong negative correlation between total cover of free-floating plants and *Elodea* abundance. Our field survey also indicated that *Ceratophyllum* tolerated the dense cover of free-floating plants much better than *Elodea*. *Elodea* was absent at complete (100%) cover of free-floating plants, while the presence of *Ceratophyllum* was still 73% in sites with 100% of free-floating plant cover. Based on the basic literature (Szabó et al., 2020, Koleszár et al., 2022a, b), *Elodea* has considerably low light compensation point comparing to other submerged plants like *Myriophyllum spicatum*, meaning that *Elodea* well tolerated the shade. We think that beyond the shading of *Lemna*, the created anoxia has much more negative effect on *Elodea* comparing to *Ceratophyllum* (Morris et al., 2004). The strong resistance of *Ceratophyllum* to anoxia corresponds well to the field results where dense cover of free-floating vegetation resulted the extinction of all submerged species with exception of *Ceratophyllum* (Jaklič et al., 2020).

The results of the present experiment on Elodea and FFP support the view that high coverage of free-floating plants may result in a loss of plant species and frequently to complete lack of submerged plants (e.g. Scheffer et al., 2003). The presence of only Ceratophyllum under a FFP layer is a sign that the system may quickly switch to a situation without any submerged plant. Recovery from such a situation might be very difficult since high coverage with FFP may also lead to a deteriorated propagule bank in the sediment (van Zuidam et al., 2012).

Our laboratory experiments may overestimate the facilitating effects of free-floating plants on *Ceratophyllum*, as a few natural occurring buffering mechanisms were missing in the aquaria. For instance, in field conditions grazing snails consume the epiphytic algae on the surface of *Ceratophyllum* (Koleszár et al., 2022a). Through top-down control, grazing snails strongly increase the light availability for *Ceratophyllum* and thus they reduce the negative effect of epiphytic algae (Yang et al., 2020, Koleszár et al., 2022a). Consequently, the grow rate of *Lemna* free *Ceratophyllum* cultures would be higher with the presence of snails.

Conclusion

Submerged and free-floating vegetations are regarded as two alternative states that may occur under similar conditions. Here field data implied that there is mutual relationship between *Ceratophyllum* and FFP. Dense *Ceratophyllum* mats may support FFP by slowing the water movements and give chance for FFP anchoring on the surface when *Ceratophyllum* already dominates the water body. On the other hand, under hypertrophic conditions, by reducing the growth of epiphyton, intermediate FFP cover slightly stimulates the growth of *Ceratophyllum*. Comparing to *Elodea, Ceratophyllum* tolerates shade and anoxia better; thus, it is a better survivor under denser FFP plant cover. Above a certain nutrient concentration, however, FFP strongly overgrows *Ceratophyllum*. Exceeding a threshold FFP, plant density eventually causes total decay of *Ceratophyllum* resulting in the complete dominance of FFP.

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Author contributions SS and EP conceived the idea, SS, AC and GK designed and performed the experiments; SB provided field survey data; SS, SB and EP analysed the data; SS, VO and EP wrote the manuscript. All authors contributed to the article and approved the submitted version.

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Data availability The datasets analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors declare no conflict of interest.

Research involving human and animal participants No human participants and animals were involved in the research.

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