

Research Article

Can invasive aquatic plants thrive in cold water or low light conditions? Implications for control – an experimental study

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Abstract

Light and temperature are critical factors for the growth of all plants, including invasive macrophytes. The high invasiveness of these species is often linked to their ability to outcompete native plants through greater shade tolerance and rapid growth at elevated temperatures. In our experimental study, we tested two hypotheses: (1) the high competitiveness of invasive alien macrophytes stems from their exceptional shade tolerance, and (2) although thermophilic invasive aquatic plants thrive in warm water, they retain the capacity to survive in colder conditions. To test these hypotheses, three invasive aquatic plant species: *Elodea nuttallii*, *Cabomba caroliniana*, and *Vallisneria spiralis* - were cultivated in two separate experiments: one testing low light conditions under constant temperature, and the other testing low temperature conditions under constant light. Each cultivation lasted seven weeks. Following this period, key morphological traits, including shoot length, number of offshoots, dry mass, and chlorophyll *a* content, were measured for each species. Our results show that all tested species were able to temporarily survive at 7 °C, although their growth was generally inhibited. *E. nuttallii* was the exception, exhibiting growth even at this low temperature. Moreover, *V. spiralis* and *C. caroliniana* demonstrated broad tolerance to varying light levels, while *E. nuttallii* thrived under low light conditions but exhibited reduced growth at higher intensities. Additionally, low temperature and light levels inhibited daughter ramet production in *V. spiralis*, while extremely low light induced partial necrosis in the lower parts of *E. nuttallii* shoots, possibly as a strategy to escape unfavorable light conditions. Overall, our research underscores the critical role of temperature in the development of invasive aquatic plants and confirms their high shade tolerance, a key factor in their competitiveness.



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Key words: *Cabomba caroliniana*, control methods, *Elodea nuttallii*, invasive aquatic plant species, light, temperature, *Vallisneria spiralis*

Introduction

Despite the growing impact of climate change on the environment, the spread of invasive species continues to be a leading threat to ecosystems worldwide (Brook et al. 2008; Cafaro 2015). In many cases, these environmental changes actually accelerate the spread of alien species (Lodge 1993; Sage 2020). Rising temperatures and increasingly frequent catastrophic events disrupt natural ecosystems, making them more susceptible to invasion by thermophilic and highly competitive species (Rahel and Olden 2008; Robinson et al. 2020). Unfortunately, freshwater ecosystems, which are recognised as distinctive biodiversity hotspots (Dudgeon 2019), remain particularly vulnerable to invasion by alien aquatic species (Ricciardi and Rasmussen 1999; Dudgeon et al. 2006). Aquatic invasive plants are particularly problematic within this group of species due to their ability to alter the physico-chemical water conditions of a water body, once their biomass reaches a certain threshold. While the presence of a strong plant community within a water body usually tends to have a strong beneficial effect on the state of the ecosystem, massive development of alien macrophytes can also have a detrimental effect on the water quality (Nino et al. 2005; Stiers et al. 2011; Ribaudo et al. 2018; Pinero-Rodríguez et al. 2021). Consequently, their rapid spread has the potential to endanger the structure of entire habitats, usually leading to a severe damage to local biodiversity (Tasker et al. 2022). Unfortunately, halting the expansion of alien aquatic plants despite decades of experience remains an extremely difficult and expensive task (Hussner et al. 2017). Moreover, field experience has shown that in many cases, once well established, a population of alien aquatic plants is almost impossible to remove without also inflicting significant damage to the environment itself (Zehnsdorf et al. 2015; Simberloff 2021). For this reason, it is preferable to act while the invasion is still in its early stages, while the plant is still adapting to the local environment and covers only a small area of the water body. There is a general consensus that a thorough understanding of the biology and ecology of invasive species is crucial for any serious attempt to stop their expansion (Hussner et al. 2017). Such specialized knowledge is also essential for an early identification of aquatic ecosystems most susceptible to biological invasions and for accurate selection and application of the most suitable control methods.

Among the most important species traits that are in need of study, if we want to have a glimpse into an invasive plant's biology and ecology, are their thermal and light preferences (Bornette and Puijalon 2011). While the issue of light limitation is crucial for all plants, the ability to cope with low light levels is especially valuable underwater, where light availability decreases dramatically with water depth (Best et al. 2001). Furthermore, the intensity of light reaching the bottom of the freshwater ecosystem may be subject to a rapid and possibly long-term decline due to phytoplankton blooms events (Sharma et al. 2010) - a harmful phenomenon increasingly observed in aquatic ecosystems worldwide - which usually has negative impact for highly light dependent submerged macrophytes. It is thus unsurprising that in such environments, competition for light is usually fierce, and the high tolerance to low light levels displayed by an alien competitor may be what determines its total domination over native macrophytes (Szabó et al. 2019; Koleszár et al. 2022).

Tolerance to a wide range of temperatures is another factor that is extremely important for the evaluation of competitiveness of invasive aquatic plants and the range of habitats that they may inhabit (Kelley 2014). While there is a great variety of invasive aquatic plant species, many of the most problematic originate from tropical regions of the world (Hussner 2012). Although these species

usually excel at vegetative reproduction, growth rate and/or biomass accumulation (Havel et al. 2015), because of their place of origin they typically lack overwintering strategies and are thus susceptible to low temperatures (Hussner et al. 2017). Thus, these species usually lose their invasive character or are outright absent in countries that experience freezing temperatures throughout the winter. The importance of temperature as a key factor in aquatic invasions is likely reflected by the uneven distribution of alien aquatic plants in Europe, which are predominantly widespread in the warmer southwestern regions or in countries with a high number of thermally altered water bodies (Hussner 2012; Lukács et al. 2016). However, steadily rising mean air and water temperatures (O'Reilly et al. 2015), resulting from ongoing global warming events, may soon alter the current situation and likely promote their further spread into previously unsuitable regions of the world (Draga et al. 2024). Thus, determining the range of thermal optima for different invasive aquatic species - especially the low-temperature threshold for their growth - is crucial for both understanding range limits of these invaders and for predicting their further spread.

While some information usually exists about the environmental preferences of alien species, it often refers to their preferences within their natural range. Unfortunately, a number of studies show that in a great number of cases the behavior of invasive species differs greatly between its original and introduced range (Grigulis et al. 2001; Jakobs et al. 2004; Hejda et al. 2015; Hejda et al. 2019). While the mechanism behind this phenomenon is probably complex in its nature (Mitchell and Power 2003; Parker et al. 2013), its role should not be underestimated, and thus researchers interested in the ecology and biology of invasive species should study the behavior of local and already established introduced populations. This is particularly important since many invasive aquatic plant species reproduce exclusively through vegetative means in their introduced range (Hussner et al. 2017). As a result, the individuals found in the field are often genetic clones of one or a few original plants (Ren and Zhang 2007; Zhang et al. 2010; McCracken et al. 2013) that, after a period of acclimatization, successfully established themselves in the new environment (Mounger et al. 2021). It should be expected that such populations may differ greatly in their abilities and environmental preferences from the native and more genetically diverse populations of the same species. Although a number of papers have investigated in laboratory conditions the behavior of invasive aquatic plants, it is important to note that only the most widespread species have been so far thoroughly studied. Additionally, a portion of studies addressing the topic of environmental preferences of invasive aquatic plants focus typically on rather elevated light and temperature values (Zhao et al. 2013; Mounger et al. 2021; Koleszár et al. 2022). While the tolerance of invasive species to high insolation and overheating is undoubtedly important - in temperate climates, it is their tolerance to low light levels and/or cold water that likely contributes the most to their success and competitiveness (Draga et al. 2024). As in the foreseeable future, global warming and eutrophication will only result in warmer winters (Wallace et al. 2014) and higher occurrence of algae blooms (Hou et al. 2022), the importance of these attributes may only increase.

Given these considerations, we aimed to investigate the response of three problematic invasive plant species in Central Europe to varying light and temperature conditions, with a particular focus on their tolerance to low light and low temperature conditions. To this end, we tested two hypotheses: [1] the high competitiveness of invasive alien macrophytes stems from their exceptional shade tolerance; and [2] although thermophilic invasive aquatic plants thrive in warm water, they retain the capacity to survive in colder conditions.

Material and methods

Species description

Three perennial, submerged, and invasive aquatic plant species threatening Central Europe were selected to assess their growth responses to low light and low temperature conditions: *Cabomba caroliniana* A. Gray (carolina fanwort), *Elodea nuttallii* (Planch.) H. St. John (Nuttall's waterweed), and *Vallisneria spiralis* L. (eelweed). *E. nuttallii* is native to North America, while *C. caroliniana* occurs naturally in both Americas. *V. spiralis* originates from the Mediterranean region, with native habitats in Northern Africa, Western Asia, and Southern Europe. *C. caroliniana* and *V. spiralis* are considered thermophilic, whereas *E. nuttallii* is adapted to temperate climates. Since their introduction to Europe and parts of Asia, these species have shown high vegetative growth, strong competitiveness, and the ability to form dense monospecific stands, making them difficult to eradicate. As a result, they are classified as invasive. *C. caroliniana* and *E. nuttallii* are included on the EU List of Invasive Alien Species of Union Concern (Commission Implementing Regulation (EU) 2016/1141), requiring member states to eradicate them. These two species are commonly found in both natural and anthropogenically altered, nutrient-rich water bodies, while *V. spiralis* typically proliferates in thermally polluted waters, often associated with mining or power plants.

Experimental design

For the purpose of this study, several hundred individuals of each species were collected and transported to Adam Mickiewicz University in Poznań. *E. nuttallii* specimens were gathered from Lake Skoki (Kujawsko-Pomorskie, Poland; 52°36'18"N, 19°23'32"E), *C. caroliniana* from a fish pond in Krążek (Małopolska, Poland; 50°17'25"N, 19°27'08"E), and *V. spiralis* ramets from a thermally altered water canal near Lake Licheńskie (Greater Poland, Poland; 52°18'31"N, 18°20'31"E), part of the thermally polluted Konin Lakes. These species were collected from separate locations, as they do not co-occur naturally in Poland. Although no genetic analyses were conducted, it is likely that all specimens were clonal, considering the absence of viable seed production and the tendency of non-native aquatic plants to reproduce mainly vegetatively in their introduced ranges (McCracken et al. 2013).

Laboratory cultivation was conducted in summer using identical methods and conditions. Due to structural differences, preparation and morphometric measurements varied. *E. nuttallii* and *C. caroliniana* shoots were trimmed to 11 cm and 13 cm, respectively and included a top shoot. *V. spiralis* leaves were trimmed to a 15 cm length from shoot base. After one-week acclimation, 190 healthy and morphologically similar individuals per species were selected and randomly divided into three groups: 80 for the light experiment, 80 for the temperature experiment, and 30 as controls.

The initial morphometric parameters were recorded. For *E. nuttallii* and *C. caroliniana*, these included length of the main shoot, number of offshoots, length of individual offshoots and total plant length (sum of the length of main shoot and its offshoots). For *V. spiralis*, number of leaves, as well as their length and width, were measured. Dry weight (whole plants) was determined from control specimens. Experimental plants were randomly assigned to one of ten treatment groups (five treatments for the temperature experiment and five treatments for the light experiment). In the temperature experiment, plants were cultivated at 7, 10, 14, 17, and 21 °C under constant low light ($46 \mu\text{mol m}^{-2}\text{s}^{-1}$). In the light experiment, plants were kept at 21 °C and exposed to 3, 10, 25, 50, or 100% of maximum light (2.9, 9.7, 22.0, 46.4 and 91.1 $\mu\text{mol m}^{-2}\text{s}^{-1}$). A 12-hour day-night cycle

was applied. Light intensities matched conditions in eutrophic lakes at 1.5–5 m depth (Sobczyński et al. 2012; Rybak et al. 2024), while the tested temperature range reflects conditions commonly observed in Central European lakes during the vegetative season (Zhu et al. 2023; Ptak et al. 2024).

Each treatment group contained 16 plants divided into four replications. Four plants from each replication were placed within 2-liter glass tank (water column height: 19 cm), filled with filtered site water (0.45 µm GF/C filters) and were planted in neutral substrate (stream quartz gravel, 2–5 mm) in plastic pots. Four tanks from the same treatment were placed in the same water bath consisted of a 32 L aquarium, half-filled with distilled water, and enclosed in polystyrene containers with lids (Suppl. material 1), to stabilize temperature and light conditions. In total, 10 polystyrene containers with water baths were used for each species (five for the temperature experiment and five for the light experiment), one for each treatment group. For *V. spiralis*, pots with plants were individually numbered due to higher variability among individuals, allowing for the tracking of each specimen's fate.

Light within polystyrene containers was provided by adjustable LED lights (1.7–91.1 µmol m⁻²s⁻¹ PAR), mounted on the underside of the container lids. Light intensity was verified using a LI-1400 meter with LI-193SA spherical sensor. Water temperatures were controlled using thermostated aquarium heaters placed within the water baths and monitored by DIVER-type submersible data loggers. Plants cultivated at 21 °C were kept in the cultivation room (maintained at a constant temperature of 20 °C), while those grown at lower temperatures were placed in a cold room maintained at 5 °C. In the latter case, aquarium heaters were used to raise the water bath temperature to the desired level. Plants were cultivated under these conditions for seven weeks. Afterward, they were remeasured, including chlorophyll *a* content via CCM-300 Chlorophyll Content Meter. For *V. spiralis*, newly formed daughter ramets were also measured as well as their number. Finally, all plants were dried, and their final dry weight was recorded.

Statistics

Most statistical analyses were conducted in R (R Core Team 2023) using the RStudio environment (Posit Team 2023). To assess differences in species responses to treatments, one-way ANOVA followed by Tukey's post hoc test was used. Prior to ANOVA, assumptions of normality and homogeneity of variances were tested using the Shapiro-Wilk and Levene's tests, respectively. When variances were unequal, Welch's ANOVA was applied; in cases of strong non-normality, the Kruskal-Wallis test was used. Species response curves to temperature and light gradients were modeled using Generalized Additive Models (GAM; Hastie and Trevor 1992), with Poisson distribution and smoothing complexity determined by the Akaike Information Criterion (AIC; Lepš and Šmilauer 2003; (Suppl. material 2). Data visualization was performed with the ggplot2 package (Wickham 2016), and dplyr (Hadley et al. 2023) was used for data wrangling. ChatGPT was occasionally used to improve text grammar and fluency.

Results

Species-specific responses to different water temperatures

Tested temperature levels significantly influenced elongation (total length of the main shoot and offshoots, main shoot length) and mean chlorophyll *a* content of *Cabomba caroliniana* (Fig. 1a–d, Suppl. material 3), elongation (total

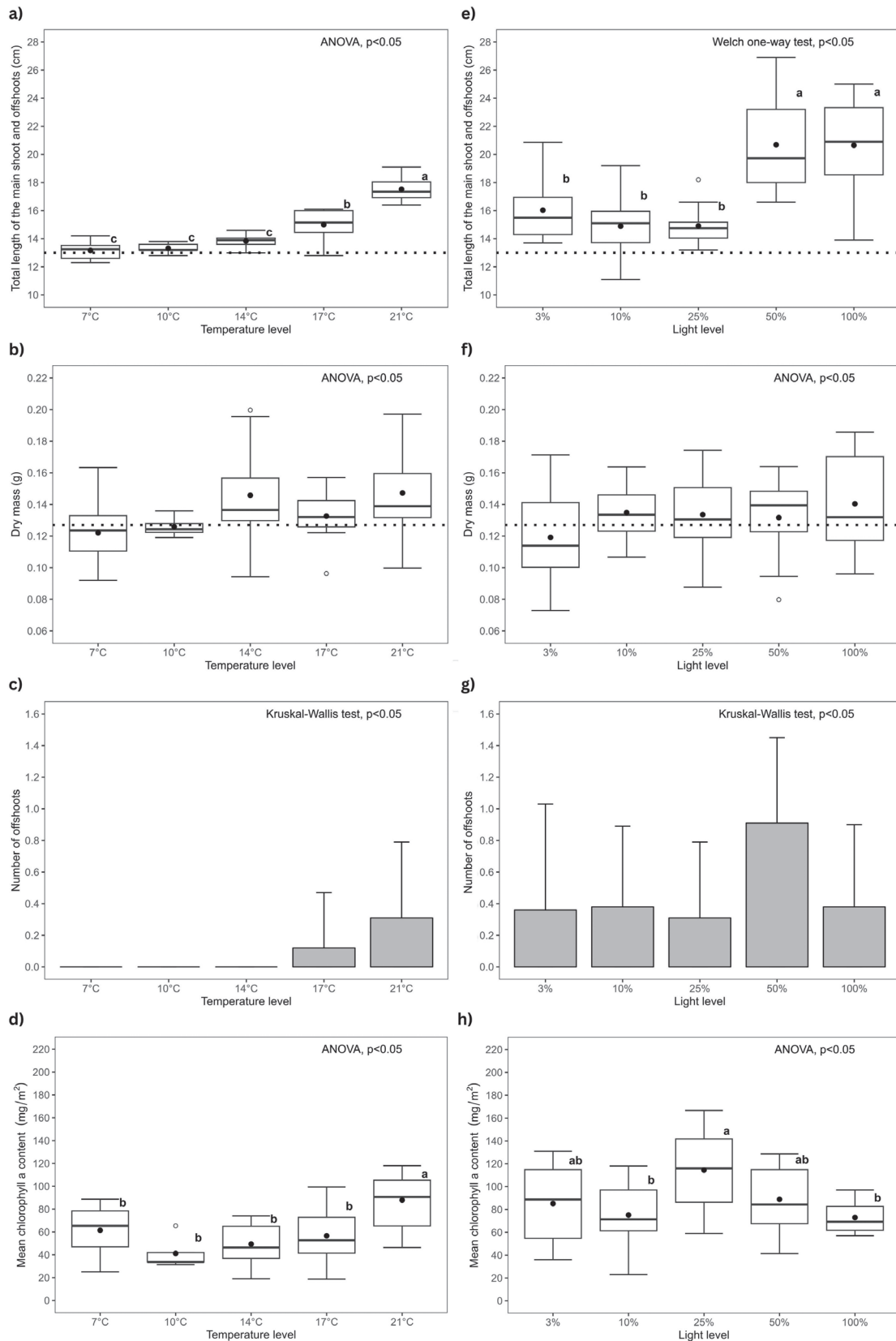


Figure 1. Trait comparison of *Cabomba caroliniana* cultivated under different water temperatures (a–d) and light levels (e–h). The name of the performed statistical test is provided on each plot. Total length was calculated as the combined length of the main shoot and its offshoots. Black dots on the boxplots represent mean values, empty dots represent outliers, while dashed lines indicate the initial parameter values of the control group.

length of the main shoot and offshoots, main shoot length) of *Elodea nuttallii* (Fig. 2a–d, Suppl. material 3) and all the tested attributes for *Vallisneria spiralis* (Fig. 3a–d, Suppl. material 3) (Table 1, Suppl. material 4). The parameters of *C. caroliniana* decreased with decreasing temperature, with the lowest dry mass recorded in treatments with the coldest water. Temperature of 14 °C or colder almost completely inhibited the plants elongation in case of this species ($p < 0.0001$ for both total and main shoot length). No offshoots were present in the treatments with water temperature of 14 °C or colder ($p = 0.0601$). Chlorophyll *a* content was highest in the individuals kept in 21 °C ($p = 0.0002$). The elongation of *E. nuttallii* decreased alongside the drop of temperature gradient with the shortest specimens found in the water temperature of 7 to 14 °C ($p < 0.0001$ for both total and main shoot length). However, even under the coldest treatments, the plants exhibited, on average, growth compared to their initial values. In general, all the parameters of *V. spiralis* decreased alongside with the decrease in the temperature gradient, including total leaf length and the mean length of the three longest leaves ($p < 0.0001$ for both parameters). Leaf elongation of the plants kept at 7 or 10 °C was minimal. Dry mass growth was observed across all treatments, with the lowest values recorded in plants grown at temperatures of 10 °C or lower ($p = 0.0026$). Plants cultivated at the temperature of 7 or 10 °C on average produced almost no leaves ($p < 0.0001$), had the lowest chlorophyll *a* content ($p < 0.0001$) and did not produce any daughter ramets ($p = 0.0001$).

Table 1. Results of one-way ANOVA on the morphological parameters of *Cabomba caroliniana*, *Elodea nuttallii* and *Vallisneria spiralis* cultivated under different water temperatures. Bold text indicates parameters with statistically significant difference at $p < 0.05$. If the assumptions of ANOVA were not met, appropriate alternative test was performed: A – one-way ANOVA, W – Welch’s one way test, KW – Kruskal-Wallis test.

Variable	Temperature variant		
	F	P	Type of test
<i>Cabomba caroliniana</i>			
Total length of the main shoot and offshoots [cm]	58.62	< 0.0001	A
Main shoot length [cm]	58.72	< 0.0001	A
Dry mass [g]	2.30	0.0737	A
Mean chlorophyll a content [mg/m ²]	6.97	0.0002	A
Number of offshoots	–	0.0601	KW
<i>Elodea nuttallii</i>			
Total length of the main shoot and offshoots [cm]	25.97	< 0.0001	W
Main shoot length [cm]	6.50	0.0007	W
Dry mass [g]	1.60	0.184	A
Mean chlorophyll a content [mg/m ²]	0.81	0.5263	W
Number of offshoots	1.91	0.118	A
<i>Vallisneria spiralis</i>			
Change in the total length of leaves [cm]	26.40	< 0.0001	A
Change in mean length of the three longest leaves [cm]	15.44	< 0.0001	W
Change in the total number of leaves	21.67	< 0.0001	W
Dry mass [g]	4.49	0.0026	A
Mean chlorophyll a content [mg/m ²]	53.97	< 0.0001	A
Number of daughter ramets	–	0.0001	KW

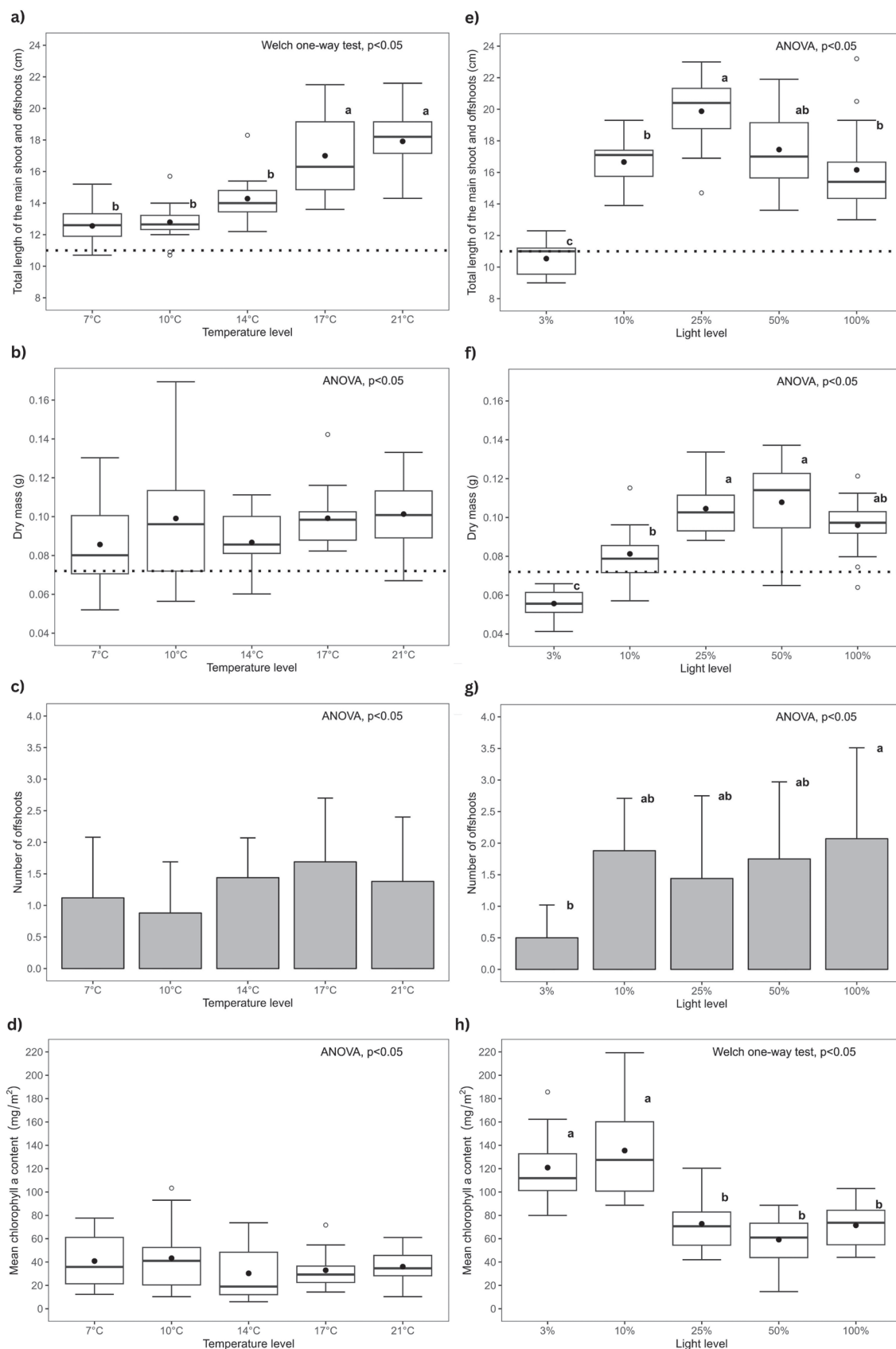


Figure 2. Trait comparison of *Elodea nuttallii* cultivated under different water temperatures (a–d) and light levels (e–h). The name of the performed statistical test is provided on each plot. Total length was calculated as the combined length of the main shoot and its offshoots. Black dots on the boxplots represent mean values, empty dots represent outliers, while dashed lines indicate the initial parameter values of the control group.

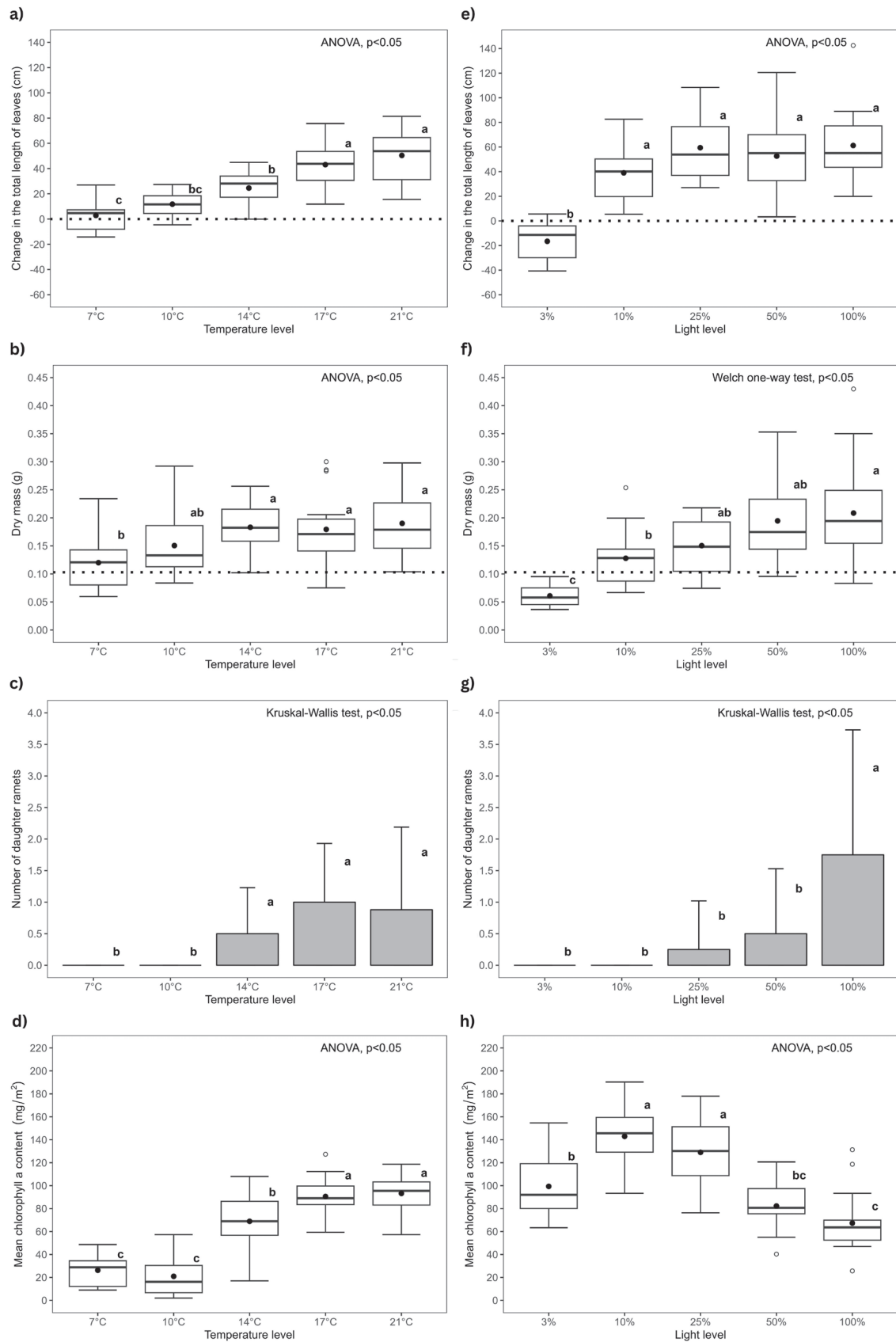


Figure 3. Trait comparison of *Vallisneria spiralis* cultivated under different water temperatures (a–d) and light levels (e–h). Change in total length was calculated as the difference in the sum of leaf lengths from the main shoot and its ramets before and after the experiment. Black dots on the boxplots represent mean values, empty dots represent outliers, while dashed lines indicate the initial parameter values of the control group.

Species-specific responses to different light intensities

Significant differences between light intensity treatments were observed across all species. In *C. caroliniana*, elongation (total and main shoot length) and mean chlorophyll *a* content varied between groups (Fig. 1e–h, Suppl. material 3). For *E. nuttallii* (Fig. 2e–h, Suppl. material 3) and *V. spiralis* (Fig. 3e–h, Suppl. material 3), all measured parameters differed significantly (Table 2, Suppl. material 4). In *C. caroliniana*, elongation was strongly reduced at 25% light intensity or lower ($p < 0.0001$ for both total and main shoot length). The highest chlorophyll *a* content occurred at 25% light ($p = 0.0112$), with lower values at both ends of the light spectrum. In *E. nuttallii*, both extreme light levels (3%, 10% and 100%) resulted in reduced values for most parameters. The highest shoot length ($p < 0.0001$) and dry mass ($p < 0.0001$) were observed at 25% and 50% light. At 3% light, elongation ceased and dry mass declined. Additionally, necrosis was observed in 7 of the 16 specimens under the 3% light treatment, affecting up to 1.5 cm (0.86 cm on average) of the basal part of the shoot. Before measurements were taken, these parts were removed, and only the green portions of the plants were analyzed. Offshoots developed in all treatments, but their number declined under the lowest light ($p = 0.0138$). Mean chlorophyll *a* content increased with decreasing light ($p < 0.0001$). For *V. spiralis*, reduced light negatively affected all growth parameters. The lowest dry mass and smallest increase in leaf number were recorded at the lowest light level ($p < 0.0001$ for both), with values falling below initial levels at 3% intensity. Daughter ramet formation was completely inhibited at 3% and 10% ($p < 0.0001$).

Table 2. Results of one-way ANOVA on the morphological parameters of *Cabomba caroliniana*, *Elodea nuttallii* and *Vallisneria spiralis* cultivated under different light intensities. Bold text indicates parameters with statistically significant difference at $p < 0.05$. If the assumptions of ANOVA were not met, appropriate alternative test was performed: A – one-way ANOVA, W – Welch’s one way test, KW – Kruskal-Wallis test.

Variable	Light variant		
	F	P	Type of test
<i>Cabomba caroliniana</i>			
Total length of the main shoot and offshoots [cm]	8.84	0.0002	W
Main shoot length [cm]	11.13	< 0.0001	A
Dry mass [g]	0.86	0.4920	A
Mean chlorophyll <i>a</i> content [mg/m ²]	3.63	0.0112	A
Number of offshoots	–	0.0676	KW
<i>Elodea nuttallii</i>			
Total length of the main shoot and offshoots [cm]	29.16	< 0.0001	A
Main shoot length [cm]	7.70	< 0.0001	A
Dry mass [g]	21.41	< 0.0001	A
Mean chlorophyll <i>a</i> content [mg/m ²]	11.66	< 0.0001	W
Number of offshoots	7.88	0.0003	W
<i>Vallisneria spiralis</i>			
Change in the total length of leaves [cm]	17.28	< 0.0001	A
Change in mean length of the three longest leaves [cm]	8.72	< 0.0001	W
Change in the total number of leaves	–	0.0001	KW
Dry mass [g]	28.11	< 0.0001	W
Mean chlorophyll <i>a</i> content [mg/m ²]	21.28	< 0.0001	A
Number of daughter ramets	–	< 0.0001	KW

Total leaf length and mean length of the three longest leaves differed significantly across treatments, with plants at 3% showing marked reductions ($p < 0.0001$ for both). Although mean chlorophyll *a* generally increased as light decreased ($p < 0.0001$), values at 3% were significantly lower than at 10% and 25%.

Response curves (GAMs)

Our findings show that three of the studied species exhibit unique responses to thermal and light conditions, occupying distinct ecological niches. Using Generalized Additive Models (GAM), we analyzed the response of key morphological traits to light and temperature (Figs 4–6, Suppl. material 5). All species exhibited negative growth responses to decreasing water temperatures. For *C. caroliniana*, a pronounced decline in total length of the main shoot and offshoots as well as in the number of offshoots occurred between approximately 14 and 21 °C, while a stable decrease in main shoot length and dry mass was observed along the entire temperature gradient (Fig. 4, Suppl. material 5). For this species, a strong negative growth response to low light intensities was also observed, notably a decrease in the total length, as well as in main shoot length. In the case of *E. nuttallii*, an especially strong decline in main shoot and total length was recorded between 14 and 21 °C, while the reduction in dry mass remained stable along the temperature gradient (Fig. 5, Suppl. material 5). In contrast, the response of *E. nuttallii* to decreasing light levels differed from that to temperature, as the species exhibited a largely unimodal pattern with an optimum around 50–55 $\mu\text{mol m}^{-2} \text{s}^{-1}$, where most parameters such as main shoot length, total length, and dry mass peaked, followed by a significant decline at higher and lower light intensities. In turn, the number of offshoots decreased steadily with decreasing light, with the rate of loss accelerating along the gradient. For *V. spiralis*, both elongation and new leaf formation decreased stably as temperature decreased, while dry mass loss accelerated at temperatures between 7 and 14 °C (Fig. 6, Suppl. material 5). For this species, a strong negative response to low light intensities was also observed, specifically an accelerating decrease in total length of the leaves and dry mass.

Discussion

Overall conclusions on the impact of low light and temperature conditions on the growth of the tested invasive species

Our results show that the studied aquatic macrophytes tolerate a broad range of water temperatures and persist under extremely low light conditions. *C. caroliniana* is often described as light-demanding (Ørgaard 1991; Hiscock 2003), with optimal growth reported at $\geq 300 \text{ light } \mu\text{mol m}^{-2} \text{s}^{-1}$ (Koleszár et al. 2022; Huang et al. 2023). However, in our experiment, where maximum light intensity was 91.1 $\text{light } \mu\text{mol m}^{-2} \text{s}^{-1}$, it still elongated and accumulated biomass in all but the darkest treatment (2.9 $\text{light } \mu\text{mol m}^{-2} \text{s}^{-1}$). These results align with recent findings suggesting *C. caroliniana* can tolerate moderate shade and outcompete other macrophytes at $\leq 150 \text{ light } \mu\text{mol m}^{-2} \text{s}^{-1}$ (Koleszár et al. 2022; Huang et al., 2023). Though considered thermophilic, *C. caroliniana* has been documented in diverse habitats, including near-freezing conditions (Ørgaard 1991). Our results support this ecological plasticity: the species survived at 7–10 °C but showed minimal growth below 14 °C. Vegetative reproduction was completely suppressed below 17 °C, suggesting that although survival in colder water is possible, growth and spread are constrained until temperatures exceed this threshold.

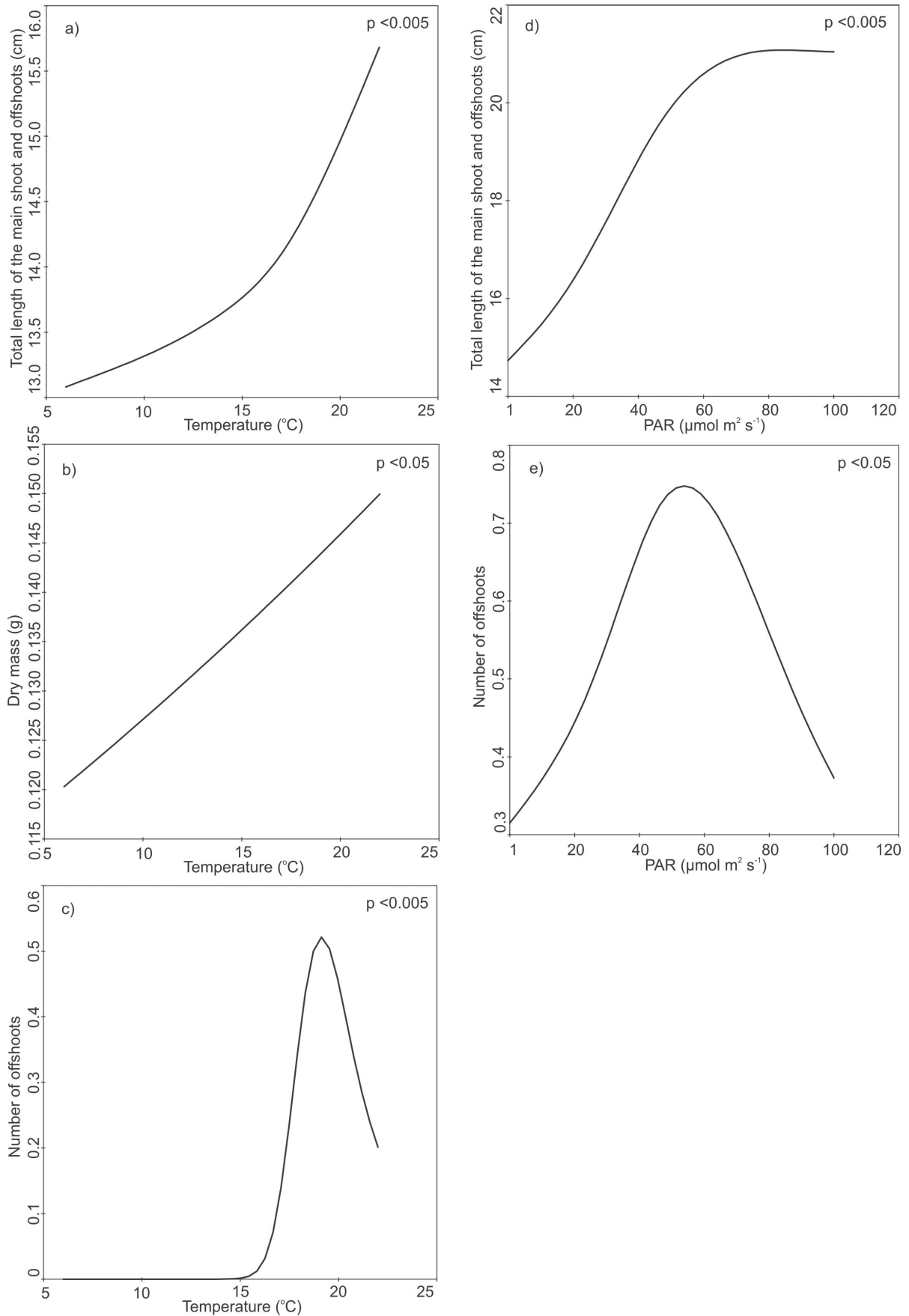


Figure 4. Generalized Additive Models (GAMs) illustrating the responses of selected, statistically significant growth traits of *Cabomba caroliniana* to varying water temperature (a–c) and light intensity (d, e).

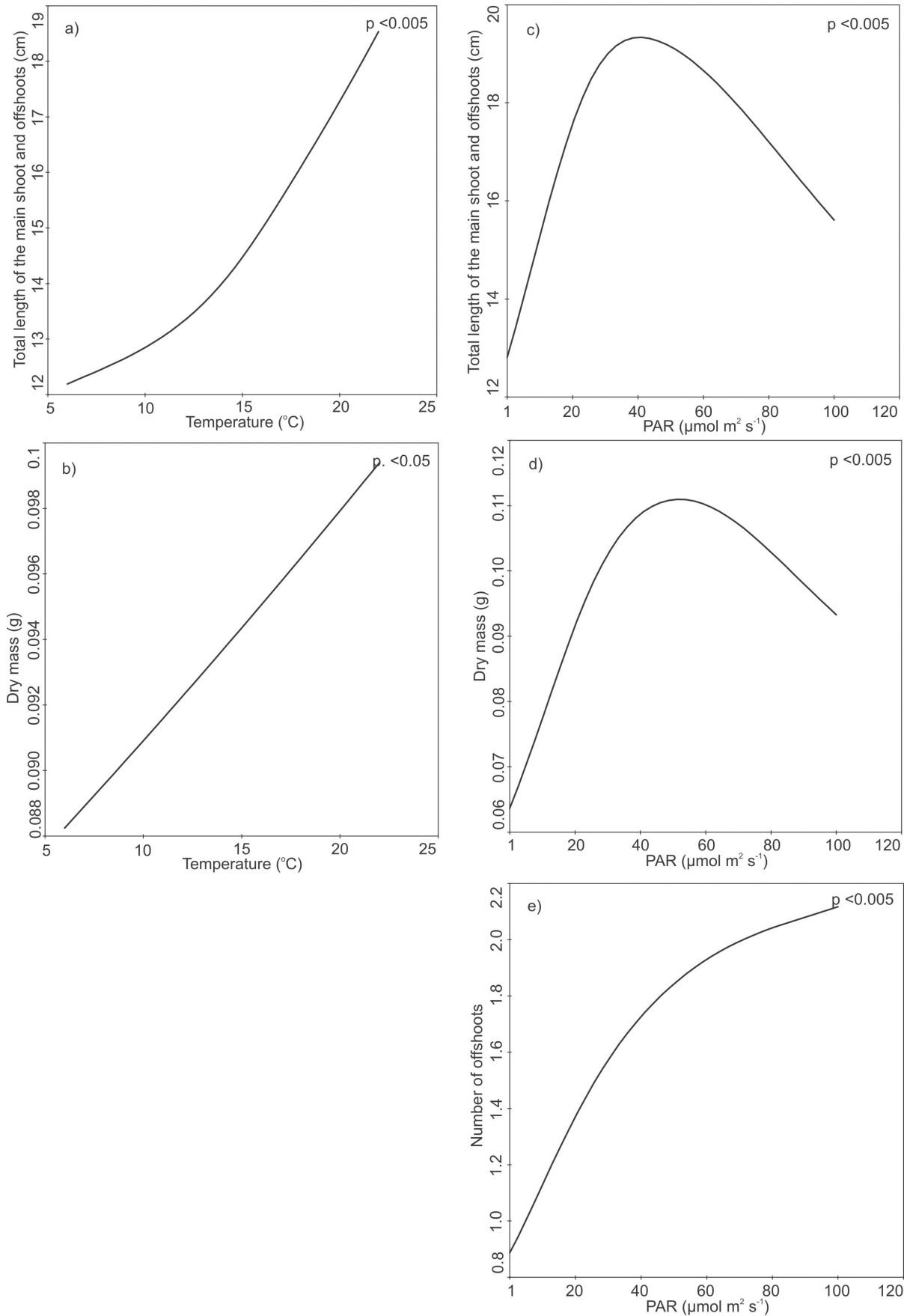


Figure 5. Generalized Additive Models (GAMs) illustrating the responses of selected, statistically significant growth traits of *Elodea nuttallii* to varying water temperature (**a, b**) and light intensity (**c–e**).

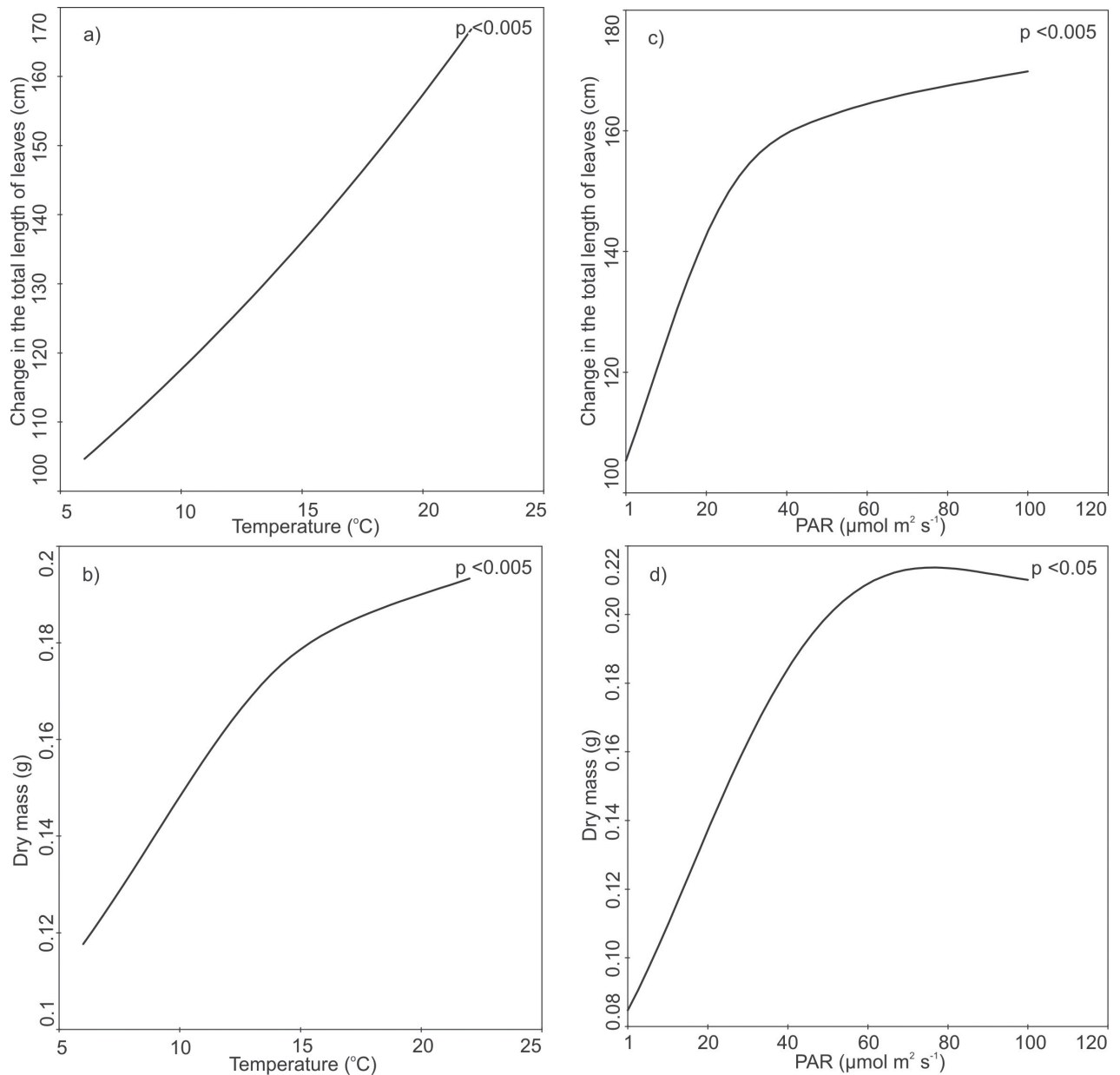


Figure 6. Generalized Additive Models (GAMs) illustrating the responses of selected, statistically significant growth traits of *Vallisneria spiralis* to varying water temperature (**a**, **b**) and light intensity (**c**, **d**).

E. nuttallii was the only species that exhibited increased growth under lower light. Its low-light preference is well-documented (Angelstein and Schubert 2009), and our results reinforce its adaptation to such environments. Optimal growth occurred between 22.0 and 46.4 light $\mu\text{mol m}^{-2}\text{s}^{-1}$ - slightly lower but consistent with prior reports: 40–48 (Barrat-Segretain 2004), 28–80 (Szabó et al. 2019), 51–94 (Angelstein and Schubert 2009), and even 80–180 in a short-term (12-day) study (Szabó et al. 2020). While direct comparisons are complicated by differing methodologies, the species consistently shows strong shade tolerance. This may provide it with a competitive advantage in early spring, facilitating its dominance in plant communities at the start of the growing season. Notably, basal shoot necrosis under low light may indicate a detachment strategy, enabling shoots to float toward better-lit zones (Kunii 1984). In nature, these detached fragments may form floating mats (Zehnsdorf et al. 2015), especially in autumn, reducing

light penetration and oxygen levels in water. Native to temperate North America, *E. nuttallii* was expected to exhibit the highest cold tolerance, which was confirmed by our findings. While shoot elongation decreased at lower temperatures, individuals grown at 7–10 °C still elongated, increased in biomass, and produced offshoots, unlike the other species. This observation aligns with findings by Kunii (1981), who observed winter growth in water as cold as 4 °C. Although growth occurred in all treatments, elongation was significantly reduced at the lowest temperatures. A three-year long field study in Slovenia (Grudnik et al. 2014) showed rapid expansion once winter/spring temperatures exceeded 10 °C. Our results, in agreement with these studies, underscore *E. nuttallii*'s broad thermal tolerance and the critical role of temperature in its growth and invasive success.

Data on *V. spiralis*' light and temperature preferences are limited. A greenhouse study (Zhao et al. 2013) showed growth across a light range of 90–500 light $\mu\text{mol m}^{-2}\text{s}^{-1}$. Similarly, in our experiment, the species grew and produced biomass even under 9.7 light $\mu\text{mol m}^{-2}\text{s}^{-1}$, though ramet formation occurred only above 22.0. Our findings suggest that *V. spiralis* is more temperature- than light-limited. Growth and vegetative reproduction were strongly inhibited below 14 °C, with optimal performance at higher temperatures. This aligns with its distribution in northern Europe, where it mainly occurs in naturally or artificially heated waters exceeding 10 °C in winter (Hussner and Lösch 2005; Hutorowicz 2006; Wasowicz et al. 2014). Field observations by Hutorowicz (2006) reported population dominance at water temperatures above 20 °C and a decline below 15 °C, consistent with our findings and highlighting the strong impact of low temperatures on the development of this species.

In summary, although the tested invasive macrophytes can survive suboptimal conditions, temperature clearly emerges as the dominant environmental factor shaping their growth dynamics and potential for spread under future climate scenarios. This confirms that temperature remains a key limiting factor for the expansion of the tested invasive macrophytes, especially for *C. caroliniana* and *V. spiralis*, whose vegetative reproduction is seriously hindered in lower temperatures. From this perspective, the broad temperature tolerance of *E. nuttallii* presented in this study is alarming, as this species may already find the optimal growth conditions in central Europe (Draga et al. 2024) therefore, further climate-induced warming of water bodies may only enhance its competitiveness and expansion potential.

Implications for control

It is widely acknowledged that the most effective control methods rely on a deep understanding of a species' ecology and behavior (Hussner 2017), and this is equally true for managing invasive aquatic plants. Notably, many of these species in their introduced ranges - such as *C. caroliniana*, *E. nuttallii*, and *V. spiralis* - do not produce viable seeds and instead depend entirely on their highly efficient vegetative reproduction. Therefore, particular attention should be paid to their process of elongation and propagule production. Our studies demonstrate a strong relationship between water temperature and the production of offshoots and ramets in species such as *C. caroliniana* and *V. spiralis*. Consequently, for these species, it is recommended to apply control methods in early spring, before water temperatures rise to levels that promote the formation of new offshoots and ramets. At the same time, the high shade tolerance observed in the tested species suggests that they may easily dominate local plant populations at the beginning of the growing season, when both the length of the day and the sun's zenith angle limits underwater light availability. Reducing populations of

these invasive species during this time of year would undoubtedly allow native, light-sensitive plants to develop undisturbed. Additionally, since species like *C. caroliniana* and *E. nuttallii* appear capable of surviving in cold water for extended periods, a second control treatment in autumn may prevent them from overwintering in dense patches. Such dense patches likely increase chances of their survival through the winter as well as accelerate the colonization process (Hoffmann et al. 2015). Furthermore, our studies indicate that although all the tested species can be considered shade-tolerant, light levels as low as 2.9 light $\mu\text{mol m}^{-2}\text{s}^{-1}$ significantly inhibited their growth, resulting in biomass levels falling below control levels early in the experiment. This biomass decline was especially evident in the case of *E. nuttallii* and *V. spiralis* suggesting that control methods based on full shading may be particularly effective for these species. Interestingly, while *C. caroliniana* and *E. nuttallii* were still able to produce a limited number of offshoots under the lowest light conditions, *V. spiralis* failed to produce any daughter ramets when exposed to light levels of 9.7 light $\mu\text{mol m}^{-2}\text{s}^{-1}$ or lower. If such inhibition of propagule production by shading can be replicated under field conditions, it would suggest that shading could be an extremely effective control strategy for *V. spiralis*.

In conclusion, both the high shade tolerance of the tested species and their resistance under low water temperatures suggest that the threat posed by these species is likely to only intensify in the future. Projections indicate that eutrophication levels in freshwater ecosystems will continue to rise (Jeppesen et al. 2009), leading to further reductions in water transparency and, consequently, limiting the availability of light for submerged macrophytes. This anticipated decline in light penetration, combined with rising water temperatures, is expected to create favorable conditions for shade-tolerant species characterized by broad thermal tolerance, such as those examined in this study. As a result, both the invasiveness and geographical range of these species are likely to expand in the coming years.

Conclusions

This study investigated the responses of three invasive aquatic plant species: *Cabomba caroliniana*, *Elodea nuttallii*, and *Vallisneria spiralis* to a range of water temperatures (7–21 °C) and light intensities (2.9–91.1 $\mu\text{mol m}^{-2}\text{s}^{-1}$). All species exhibited broad tolerance to both factors, likely contributing to their invasive potential. While elongation and offshoot production declined at lower temperatures, survival - and even growth in the case of *E. nuttallii* - persisted at 7 °C. Although *C. caroliniana* and *V. spiralis* are generally regarded as light-demanding, both were able to tolerate low light levels in our experiment. *E. nuttallii* preferred medium to low light conditions and exhibited a potential dispersal mechanism under extreme shading, based on detachment from the sediment. Overall, low temperature appears to be a stronger limiting factor than light availability, suggesting that ongoing climate warming may facilitate further spread of these species. The results also support the potential of shading as a management strategy, capable of reducing both growth and vegetative propagation of invasive macrophytes.

Author contribution

Mateusz Draga: conceptualization, methodology, formal analysis, data curation, writing - original draft, visualization. Maciej Gąbka: conceptualization, methodology, formal analysis, visualization, writing - review and editing.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary material.

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Supplementary material 1

Experimental setup

Authors: Mateusz Draga, Maciej Gąbka

Data type: docx

Explanation note: Photographs of the experimental setup, which was identical for all species. (a) Polystyrene containers in the cultivation room, each containing water tanks with plants (the image shows six out of ten containers used for each species). b) View inside a polystyrene container. Each polystyrene container contained an aquarium which, once filled with water, functioned as a water bath. Inside each aquarium, there were four water tanks, each holding four plant shoots. The photo shows the setup before placing the plants into the water tanks and before filling the aquarium with distilled water.

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Link: <https://doi.org/10.3391/ai.2026.21.2.187217.suppl1>

Supplementary material 2

Akaike Information Criterion (AIC) results

Authors: Mateusz Draga, Maciej Gąbka

Data type: xlsx

Explanation note: The AIC results obtained during GAM model development. Only results for the significant parameters are presented.

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Link: <https://doi.org/10.3391/ai.2026.21.2.187217.suppl2>

Supplementary material 3

Species responses to various temperature and light levels - remaining parameters

Authors: Mateusz Draga, Maciej Gąbka

Data type: docx

Explanation note: Plots of species responses to remaining growth parameters (not presented in the main body of the text) across different light and temperature levels.

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Link: <https://doi.org/10.3391/ai.2026.21.2.187217.suppl3>

Supplementary material 4

Supplementary data

Authors: Mateusz Draga, Maciej Gąbka

Data type: xlsx

Explanation note: Table presenting the basic statistics (mean, median, standard deviation, minimum and maximum) of the results obtained during this research.

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Link: <https://doi.org/10.3391/ai.2026.21.2.187217.suppl4>

Supplementary material 5

Generalized Additive Models (GAMs) - remaining parameters

Authors: Mateusz Draga, Maciej Gąbka

Data type: docx

Explanation note: Remaining significant (not presented in the main body of the text) GAM models of species responses for all measured growth parameters across varying light and temperature levels.

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Link: <https://doi.org/10.3391/ai.2026.21.2.187217.suppl5>