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Research Article

Effects of water temperature on growth of invasive *Myriophyllum aquaticum* species

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Abstract

This study sought to investigate the invasive mechanism of *Myriophyllum aquaticum* by subjecting it to simulation experiments in varying water temperatures ranging from 0 °C to 30 °C. The results showed that water temperature considerably affected both the growth and reproduction of *M. aquaticum*. The optimal temperature range for the growth of *M. aquaticum* was 25–30 °C. Although the growth of *M. aquaticum* was inhibited at temperatures between 0–5 °C, this did not result in mortality. The stem nodes, branches, and diameter reached maximum values over a temperature range of 20–25 °C. High-temperature stress at 30 °C led to a gradual decrease or disappearance of branches. Compared to the 0 °C, 5 °C, and 30 °C treatment groups, a temperature of 20 °C led to biomass accumulation and significantly higher values. *M. aquaticum*'s physiological activities were affected by temperature. Except for 10 °C and 15 °C, the catalase activity varied among different water temperatures. *M. aquaticum* catalase activity was maximal at 5 °C and minimal at 25 °C. Conversely, the synthesis of photosynthetic pigments was highest at 10 °C and 15 °C. The plant's optimal temperature for growth was between 20 °C and 25 °C. When the temperature was <10 °C, *M. aquaticum* adapted to the water temperature's potential damage. This plant has a notable ability to tolerate various temperatures.

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Key words: Temperature gradient, submerged macrophytes, high- and low-temperature stress, invasion mechanisms

Introduction

Myriophyllum aquaticum (*M. aquaticum*) is a perennial herbaceous plant that grows as both submerged and emergent plants. This plant is native to the Amazon basin in South America and has become widely distributed in Australia, Africa, North America, Europe, and Southeast Asia (Guillarmod 1979; Cook 1985).

M. aquaticum has successfully established robust populations in 14 provinces, autonomous regions, and municipalities throughout China. *M. aquaticum* primarily achieves its growth and reproduction through vegetative propagation from stem cuttings and stolons, and quickly spreads through asexual reproduction. This species has a potential competitive advantage over native plants (Orchard 1981; Sytsma and Anderson 1993a; Xiong et al. 2021). Because of its decorative properties and sewage purification abilities, *M. aquaticum* has been cultivated in China for sewage treatment and as an ornamental plant (Sytsma and Anderson 1993b; Polomski et al. 2009). Unfortunately, most introduced *M. aquaticum* species have become invasive and threaten ecosystems, including rice paddy fields and shallow lakes in southern China (Wang et al. 2013; Liu et al. 2017).

Temperature is a crucial abiotic factor that affects plant growth, reproduction, and geographic distribution, and plays a key role in determining the distribution and productivity of plants (Santamaría and van Vierssen 1997; Descamps et al. 2018). Invasive plant species adapt to local temperatures when colonizing new areas. *Mimulus guttatus* may have invaded regions through broad temperature tolerance rather than through rapid evolution during its introduction. *Ipomoea cairica* has developed a thermal-adaptation mechanism that enhances photosynthetic growth compared with native plants. This mechanism involves an increase in soluble sugar levels and antioxidant enzyme activity, along with a decrease in malondialdehyde and oxide formation (Querns et al. 2022; Chen et al. 2023).

High or low water temperatures can significantly affect the growth, development, physiology, and biochemical processes of submerged plants (Jumrani and Bhatia 2014; Wang et al. 2016; Yang et al. 2016). Climatic conditions are a major contributing factor to fluctuations in water temperature (Wang and Niu 2020; Bai et al. 2022). The lake surface temperature refers to the temperature of lake water between 0 and 1 m in depth (Yang et al. 2017). Several studies have reported that an increase in near-surface air temperature leads to an increase in lake surface water temperature (Pan et al. 2022). *M. aquaticum* thrives at water depths of 0–77 cm, but poorly at depths of 97–137 cm (Wersal and Madsen 2011). Thus, the near-surface air temperature affects the water temperature of the *M. aquaticum* environment.

Water temperature can affect the germination of seeds as well as photosynthetic and reproductive strategies of submerged plants (Su et al. 2001; Xiao et al. 2010; Souza et al. 2016). Water temperature has regulatory effects on seed germination, and as the water temperature rises, plant metabolism increases. Water temperature has regulatory effects on seed germination, and as the water temperature rises, plant metabolism increases. This accelerates germination speed, although at the cost of increased metabolic energy consumption. Therefore, at decrease in the energy required for growth can result in a lower germination rate of seed. At low-water temperatures, energy consumption decreases, leading to comparatively lower germination rates at extremely low-water temperatures (You and Song 1995). The optimal water temperature for photosynthesis varies among submerged plants. The highest photosynthetic oxygen production in the top branches of *Potamogeton crispus* (*P. crispus*) occurs at 15−25 °C, that is the optimal temperature for its growth (Su et al. 2001). *Hydrilla verticillata* (*H. verticillata*) and *Egeria densa* photosynthesize more effectively over a temperature range of 28–37 °C (Su and Li 2005), indicating the relationship between water temperature and photosynthesis via oxygen production and the light compensation point. The light compensation points of *V. natans*, *P. crispus*, *Ceratophyllum demersum* (*C. demersum*), *Caulerpa taxifolia*, and *Najas marina* increase as the water temperature rises between 4 °C and 30 °C (Ren et al. 1996).

M. aquaticum is a globally invasive species that has been extensively studied for its distribution (Guillarmod 1979), reproductive characteristics (Orchard 1981), water purification capacity (Jamil et al. 2019), and invasion prevention and control measures (Moreira et al. 1999; Gray et al. 2007; Wersal et al. 2010). Numerous factors impact the growth of *M. aquaticum*. The growth of *M. aquaticum* has been extensively studied with respect to factors such as harvesting (Yu et al. 2022), carbon dioxide availability (Malheiro et al. 2013), light intensity (Wersal and Madsen 2013), and nutrient levels (Tan et al. 2018), among others. However, there is a lack of information regarding the environmental adaptability of this species and the effects of various temperatures on its growth and reproductive processes. This study aimed to investigate how *M. aquaticum* responds to varied water temperatures through simulation experiments to determine the impact of temperature on this invasive plant.

Materials and methods

Materials

Branches of *M. aquaticum* were harvested in January, 2019, at Baoan Lake, Hubei Province (30°15'51.92"N, 114°43'12.33"E). Subsequently, they were submerged in an aquarium filled with water for pre-cultivation. Two days later, healthy uniformly sized shoots of *M. aquaticum* were selected for transplantation.

Experimental design

This study was conducted in January, 2019, in a greenhouse at the Hubei Normal University Aquatic Environment and Ecology Restoration Laboratory. Four hundred and eighty *M. aquaticum* plants, pre-cultivated and uniformly grown, were chosen and weighed to determine their initial weight. Each plant's average fresh weight was 2.47 ± 0.05 g, with an average height of 25.39 ± 0.62 cm. Sixty plants were air-dried to measure their initial dry weight, which was used to calculate moisture content. The remaining 420 plants were planted in experimental buckets, each containing 20 plants. The buckets had a height of 56 cm, an upper diameter of 52 cm, a lower diameter of 38 cm, and a volume of 90 L. Next, a 12 cm layer of sediment was applied to the pots, which originated from the eutrophic Qingshan Lake. The sediment contained 1,201.77 mg/kg of total phosphorus (TP), 620.74 mg/kg of total nitrogen (TN), and 71.32 mg/kg of organic matter (OM).

TN concentrations in the lake substrates were analyzed using the semi-micro Kjeldahl method following digestion with H_2SO_4 and $HClO_4$, as indicated by Wang et al. (2017). TP concentrations were determined using the ascorbic acid method, as suggested by Varol and Sen (2012). OM concentrations were determined using the potassium dichromate-sulfuric acid method, as described by Zhang et al. (2015).

The water level in each container was continuously maintained as the *M. aquaticum* plants were inundated. The water used was extracted from the Qingshan Lake (TN: 3.23 mg/L, TP: 0.32 mg/L). Seven water temperatures (0 °C, 5 °C, 10 °C, 15 °C, 20 °C, 25 °C, and 30 °C) were selected for the experiment, with three duplicates for each temperature. A thermometer recorded the lake water temperature at 5 °C. Ice cubes were added to the buckets of the 0 °C treatment group to maintain the experimental temperature. A heating rod, equipped with four probes, was inserted into the water in the middle of all treatment groups except those kept at 10 °C to provide heat. On April 1, 2019, the experimental plants were harvested after a 72-day experimental period.

Determination of indicators

Growth indicators

The height, number of stems diameter, and number of stem nodes were measured every 3–7 d, whereas the length, diameter, and number of branches of each stem were measured using Vernier calipers and a tape-measure every 10–12 d. Nine *M. aquaticum* plants were randomly selected from each temperature treatment bucket to determine their average values. The biomass of *M. aquaticum* was weighed at the end of the experiment at each temperature to obtain the total weight.

Physiological indicators

After harvesting, three–five young and undamaged leaves were selected from the top of the main stem. To determine chlorophyll content, 0.2 g of fresh leaves was weighed and subjected to the 80% acetone extraction method (wavelength: 665, 649, and 470 nm) under light-avoidance conditions by placing the samples in the dark (Wang 2006).

Fresh leaves (0.5 g) were weighed to determine activity levels of catalase (CAT), an antioxidant enzyme that is widely found in organisms (Hu et al. 2016). CAT activity was assessed spectrophotometrically by monitoring the reduction in hydrogen peroxide (H_2O_2) absorbance at 240 nm based on the method established by Beers and Sizer (1952). Data were recorded at 1-min intervals for 4 min. The magnitude of CAT activity was denoted as the amount of H_2O_2 decomposed over a specific timescale, as explained by Saxena et al. (2016) and Wang et al. (2017). The initial minutes of the reaction exhibited a stronger response, which gradually subsided as the enzyme was depleted. CAT contributes to the development of heat-induced cold tolerance and its activity is positively correlated with increased cold resilience (Sala and Lafuente 1999).

For the test conducted to grow *M. aquaticum*, water indicators were determined using the following method: TN concentrations in the experimental water were determined using the alkaline potassium persulfate oxidation-UV photometric method (wavelengths: 220 and 275 nm), whereas TP was determined using the potassium persulfate digestion method (wavelength: 700 nm) (Zhu et al. 2022).

Data analysis and statistics

Microsoft Excel 2003 (Microsoft Inc., Redmond, WA, USA) was used for data processing, and correlation and analysis of variance were performed using SPSS 27.0.1 software (SPSS Inc., Chicago, IL, USA). To examine differences in biomass, leaf pigment content, and CAT activity at different temperatures, one-way analysis of variance (ANOVA) was performed. Data were assessed for normality and homogeneity ($P > 0.05$) using the Shapiro–Wilk and Levene methods, respectively. Transformations were performed on data that did not meet the assumptions of normality or variance homogeneity, followed by post hoc testing using the Waller-Duncan method. Growth index analysis of *M. aquaticum* was conducted using Origin 8.5 software (Origin Labs Inc., Northampton, MA, USA).

Results and analysis

Growth of *M. aquaticum* at different temperatures

Over time, *M. aquaticum* grew rapidly during the first 20 days, but slowed from days 20 to 50 and continued to grow from days 50 to 75 (Figure 1). Temperature

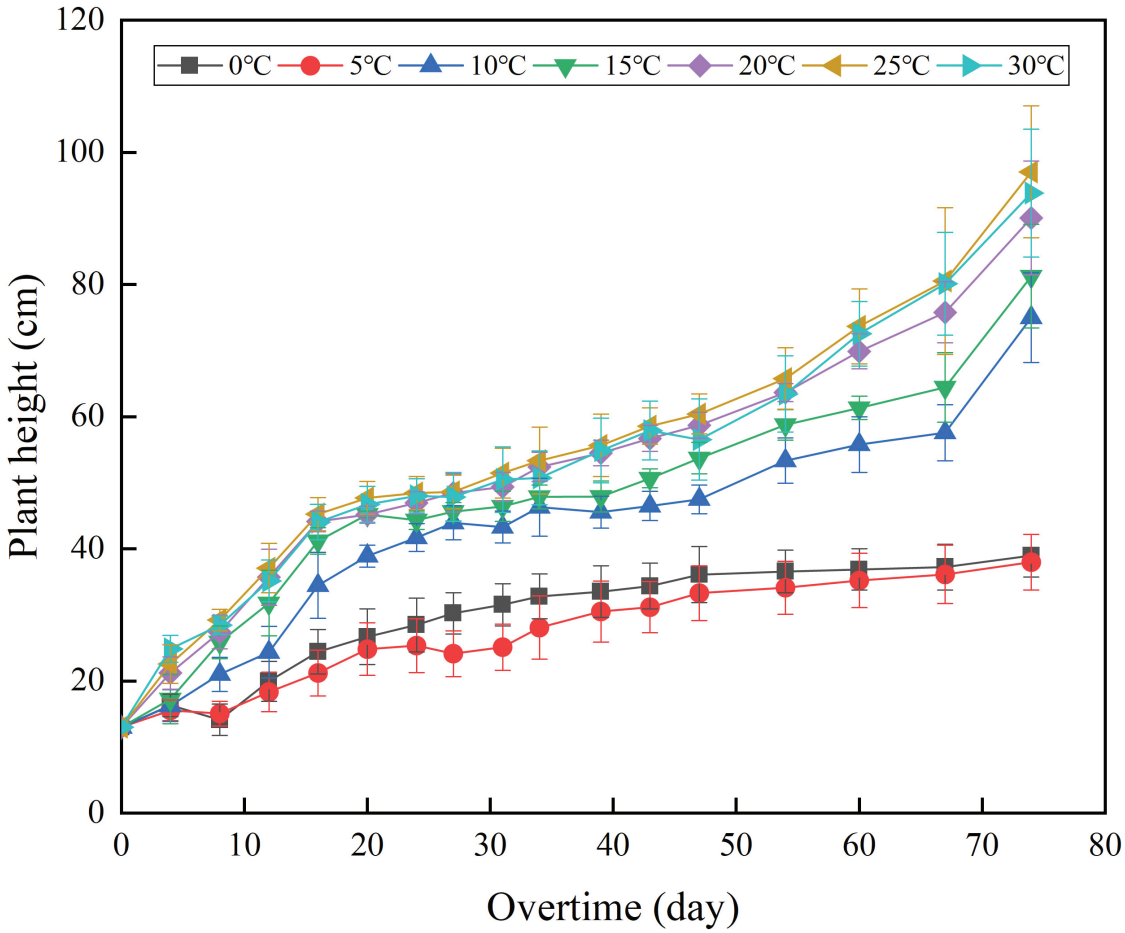

Figure 1. Height of *Myriophyllum aquaticum* at different water temperatures.

had a noticeable influence on plant height. In all the treatment groups, an increase in water temperature resulted in an increase in plant height. The tallest plants, measuring 93 cm, were observed on day 72 at 25 °C. The plant height increased gradually under treatments of 0 °C and 5 °C, registering the highest values of 38.97 cm and 37.98 cm, respectively, on day 72.

Water temperature affected stem diameter, as shown in Figure 2. Stem diameters were greater in treatment groups at 5 °C, 25 °C, and 30 °C. Between days 0 and 67, stem diameter peaked under the 5 °C treatment. On day 39, stem diameter grew more rapidly in the 25 °C and 30 °C treatment groups, surpassing those at 5 °C that reached a peak of 1.35 cm on day 67. By day 72, stem diameter was maximized at 1.67 cm under the 25 °C treatment.

Differences in the number of stem nodes in *M. aquaticum* were observed at different water temperatures (Figure 3). Initially, each plant contained an average of 10 ± 1 stem nodes, but noticeable variation emerged after 15 days. After day 15, the maximum quantity of stem nodes, reaching 25 ± 3 per plant, was observed at both 25 °C and 30 °C, whereas at 0 °C and 5 °C, only 13 stem nodes were observed per plant. By day 72, the group subjected to a 25 °C treatment had the highest number of stem nodes, with 51 per plant. The amount of stem nodes in the groups treated at 0 °C and 5 °C remained relatively stable from day 20 onwards, accounting for 30% of the stem node number of the 25 °C group.

Except for 30 °C, the number of branches increased progressively with growth of the plants at different water temperatures. The numbers of branches at 0 °C, 5 °C, and 10 °C were lower than that at the other water temperatures (Figure 4).

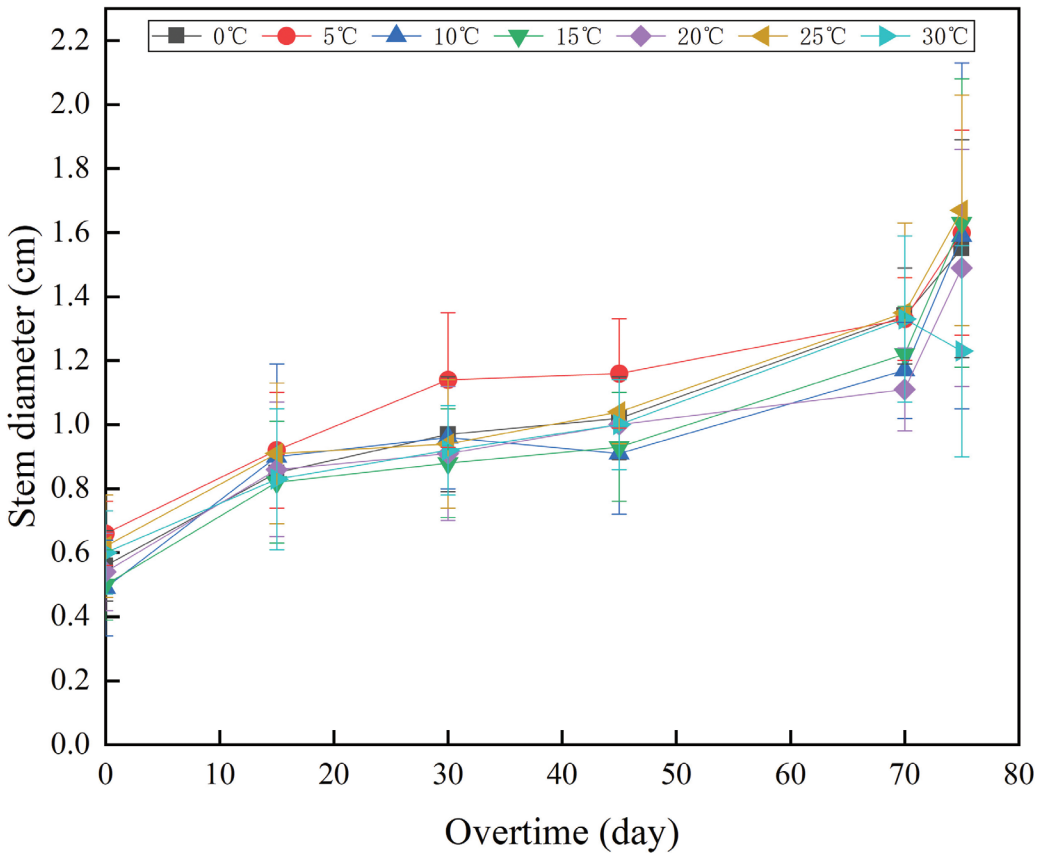

Figure 2. The stem diameter of *Myriophyllum aquaticum* at different water temperatures.

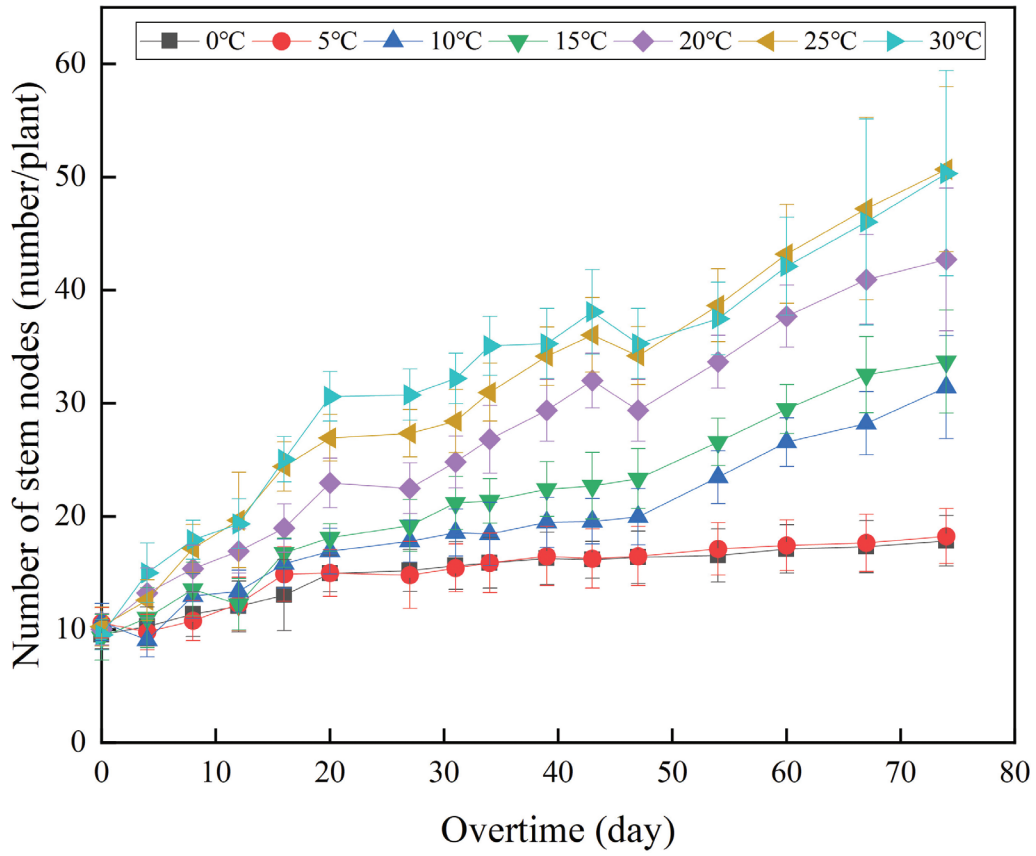

Figure 3. Number of stem nodes of *Myriophyllum aquaticum* at different water temperatures.

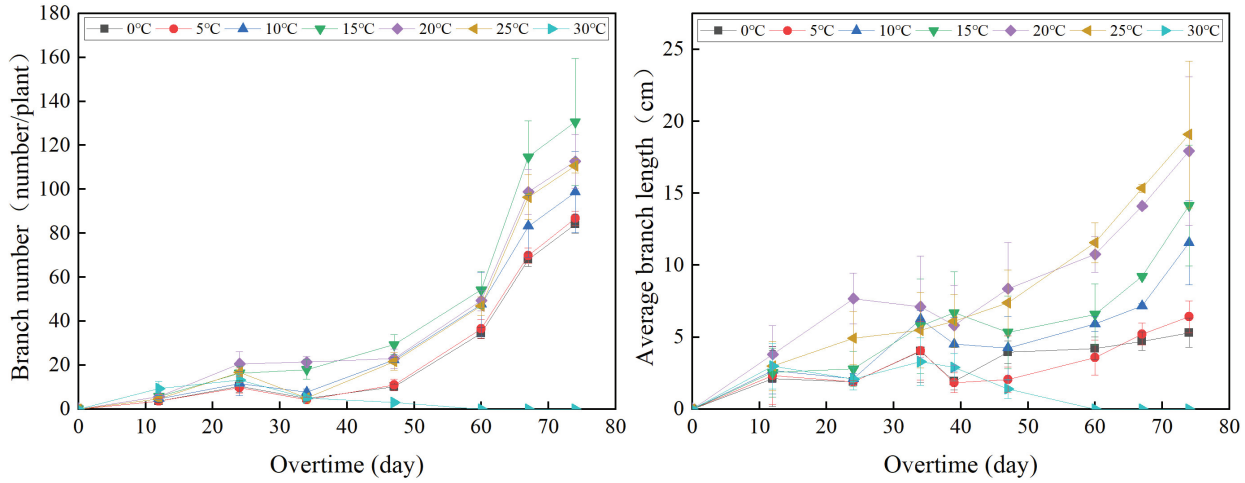

Figure 4. Number of branches and average branch length of *Myriophyllum aquaticum* at different water temperatures.

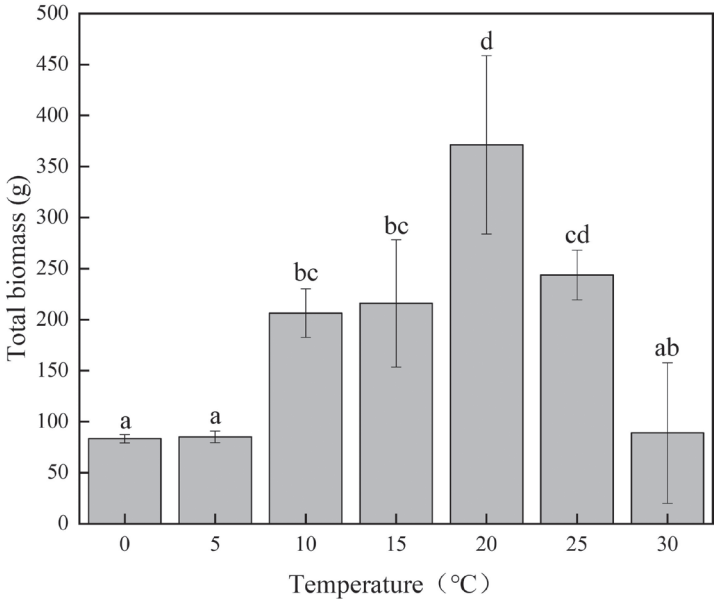

Figure 5. Total biomass of *Myriophyllum aquaticum* under different water temperatures.

Differences in the number of branches were observed starting on day 24. Subsequently, by day 34, the number of branches had declined at 30 °C, gradually leading to their disappearance. At the termination of the experiment, the greatest amount of branches, 134 per plant, was noted at 15 °C.

Total biomass initially increased and subsequently decreased with rising water temperatures, with observed differences in biomass among the various water temperature treatments (Figure 5). Significantly higher biomass was found in the 20 °C treatment group compared to the 0 °C, 5 °C ($P < 0.01$) and 30 °C ($P < 0.05$) treatment groups.

Physiological characteristics of *M. aquaticum* under different temperatures

Effects of temperature on pigment content of *M. aquaticum*

The levels of carotenoid (Car), chlorophyll a (Chl-a), chlorophyll b (Chl-b), and total chlorophyll (total Chl) were the lowest at 20 °C. The Car, Chl-a, and total Chl contents were highest at 10 °C, whereas the Chl-b content was highest at

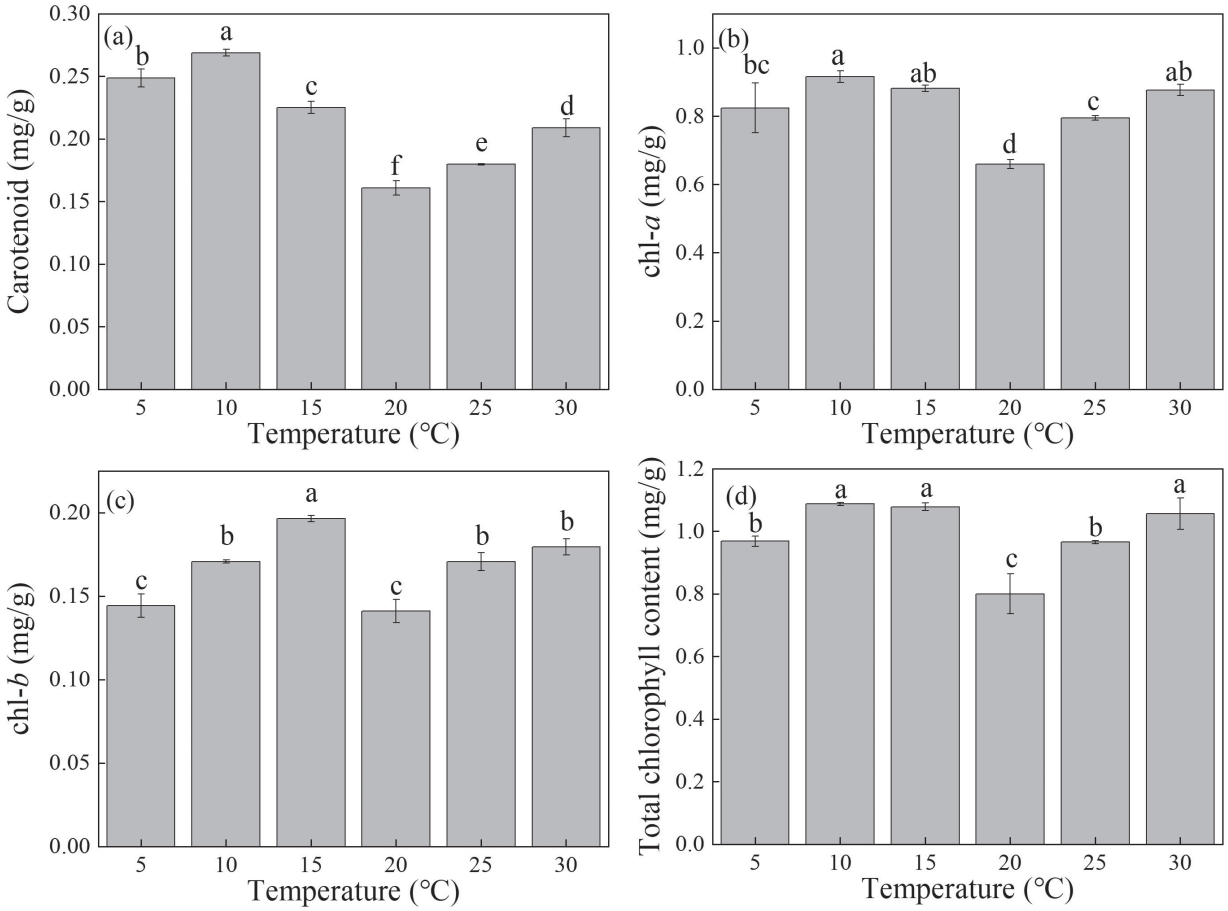

Figure 6. Pigment content in the leaves of *Myriophyllum aquaticum* at different water temperatures.

15 °C, as shown in Figure 6. However, the fluctuations in Chl-*a*, Chl-*b*, and total Chl contents were less prominent than those of Car at different temperatures. Considering all temperatures, Chl-a and Chl-b ranged from 0.66–0.92 and 0.14–0.20 mg/g, respectively, throughout the experiment. Moreover, Car and total Chl content were 0.16 to 0.27 and 0.80 to 1.09 mg/g, respectively.

Effect of temperature on CAT activity in *M. aquaticum*

Reaction time and CAT activity were directly proportional to the amount of CAT in equal-quality leaf fractions. When the amount of CAT was high, the H_2O_2 decomposition rate was higher than that when the amount of CAT was low. In the first minute of the reaction, CAT activity was highest at 5 °C (51.56 g/min), followed by 20 °C (29.38 g/min), and lowest at 15 °C (17.50 g/min). CAT activity in the second minute of the reaction was similar. During the final two minutes of the reaction, the activity of CAT was highest at 5 °C, closely followed by 30 °C. Treatment at 5 °C had the most significant effect on the activity of *M. aquaticum* CAT (Figure 7).

Discussion

Effect of temperature on growth of *M. aquaticum*

This study showed that *M. aquaticum* growth and development were significantly affected by different water temperatures. Height, biomass, and growth rates were higher at 10–25 °C. Conversely, high water temperatures (30 °C) inhibited the

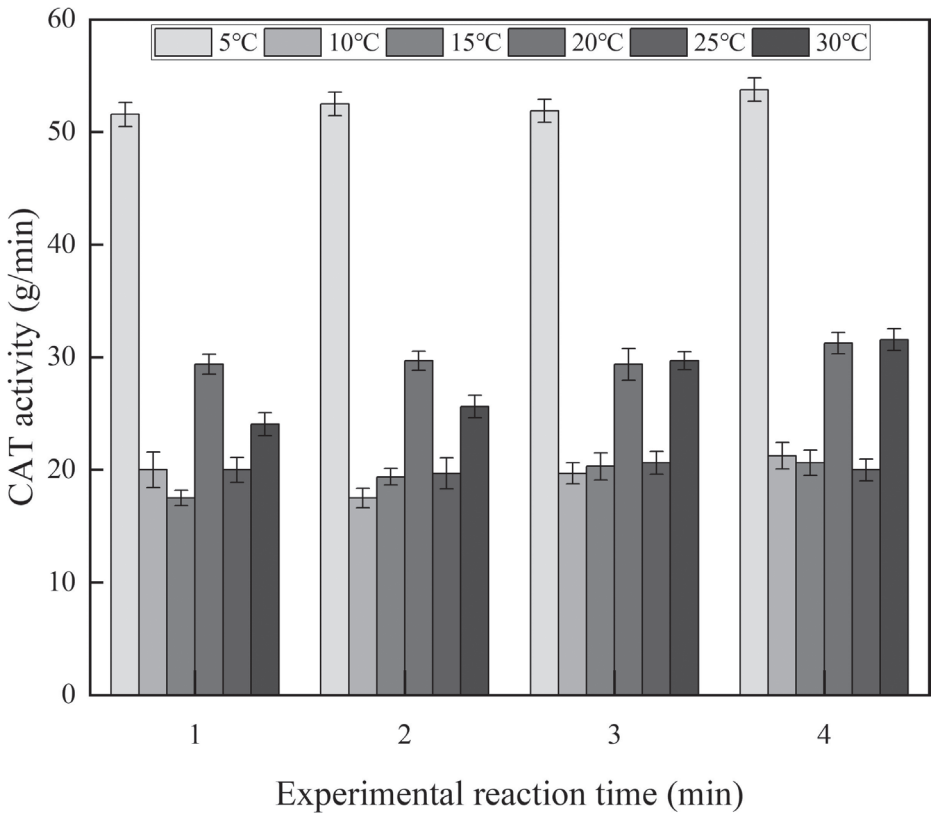

Figure 7. Catalase activity of *Myriophyllum aquaticum* under different water temperatures.

plant, resulting in lower height and number of stem nodes. On day 34, the number of stem nodes was significantly decreased at 30 °C, whereas it increased at 0–25 °C. The overall biomass of *M. aquaticum* at 30 °C was lower than that at 10–25 °C, as the plants had fewer and shorter branches. High water temperatures led plants to expend more energy for metabolism, thereby reducing the number of branches (Wang et al. 2008). Therefore, 10–25 °C had a positive effect on the growth of *M. aquaticum*, whereas high water temperatures (30 °C) were not suitable.

In our study, low-water temperatures (0–5 °C) hindered the growth of *M. aquaticum* (excluding stem diameter). Cold stress induces several physiological and biochemical changes in plants in response to the damage caused by low temperatures through self-regulation (Quan et al. 2023). Thus, *M. aquaticum* responds to low-temperature stress by decreasing plant height and increasing stem diameter. Specifically, at 5 °C, *M. aquaticum* exhibited the shortest plant height but the greatest stem diameter compared to the other temperatures throughout the experiment until day 67. The advantages of dwarf plants, such as maintaining optimal temperatures and increasing heat absorption while reducing heat loss, have been previously demonstrated (Jiang et al. 2020).

The adaptation of *M. aquaticum* to low-temperature stress was demonstrated by the observed changes in CAT activity. CAT activity increased with decreasing temperature, indicating that low temperatures can induce an increase in CAT activity to mitigate damage (Wang et al. 2019). However, with increasing stress, the antioxidant defense system can be damaged and enzyme activity diminished. Wang et al. (2019) provided further information concerning this topic. In this study, it was found that *M. aquaticum* exhibited higher CAT activity when subjected to 5 °C low-temperature treatment as compared to the 10–30 °C treatment ($P < 0.01$). This suggests that *M. aquaticum* responds to low-temperature stress by increasing its CAT activity, a phenomenon also reported by Zhang et al. (2013). Therefore, we

can infer a direct correlation between elevated cold tolerance and CAT activity. One explanation for the reduced CAT activity at 30 °C is the insensitivity of *M. aquaticum* CAT towards high temperatures. High-temperature stress in *M. aquaticum* can produce significant amounts of reactive oxygen species (ROS) that trigger lipid peroxidation of membranes, inhibit enzyme expression, disrupt enzyme-active centers, or change enzyme structures, resulting in decreased CAT activity (Zhou et al. 2010). CAT increases photosynthetic pigment content in plants (Nan and Fan 2008). In this experiment, CAT content was highest at 5 °C. However, the photosynthetic pigments content did not reach their maximum. This discrepancy could potentially be attributed to prolonged exposure to low temperatures causing detrimental effects to the chloroplast structure and subsequently impairing both the functionality and efficiency of photosynthetic organs within the chloroplasts (Fang et al. 2023).

Exploring the invasiveness of *M. aquaticum* from a temperature perspective

M. aquaticum, a tropical species native to South America, thrives in warm, humid, and sunny climates, and is widely distributed in tropical and subtropical regions (Liu et al. 2017). Heat and water temperature are the leading environmental factors that influence the growth and reproduction of *M. aquaticum*.

In Huangshi City, the average daily maximum temperatures during 2018 were 22 °C in spring, 32 °C in summer, 23 °C in fall, and 10 °C in winter (China Weather 2018). In our study, the temperature treatments were set to simulate the different seasons: 10–25 °C during spring and fall, 30 °C in the summer, and 0–10 °C in the winter. At both 20 °C and 25 °C, *M. aquaticum* survived and produced the highest number of new shoots. This suggests that the temperature for the growth of this species is between 20 °C and 25 °C (Ditomaso and Healy 2003). Especially, at 10–25 °C, *M. aquaticum* experienced an increase in biomass and leaf photosynthetic capacity. The increased capacity for leaf photosynthesis was evident from the increase in Chl content.

During winter (0–10 °C), the dormancy of *M. aquaticum* contributes to its competitiveness in various environments. *M. aquaticum* undergoes partial winter dormancy, with only the upper aerial portion decaying. During this time, the plant overwinters with its roots submerged in the mud. As the water temperature increases in spring, the upper stems regenerate. There were no instances of disease or death throughout the growth period, suggesting a robust capacity for adaptation to the environment or regeneration (Ditomaso and Healy 2003; Liu et al. 2017).

In the Northern hemisphere, macrophytes rouse from winter and re-start producing biomass during spring with an increase in both air and water temperatures, as well as longer day length (Silveira and Thiebaut 2017). Common submerged plants in China, such as *Vallisneria natans* (*V. natans*), *H. verticillata*, *Potamogeton maackianus* (*P. maackianus*) and *P. crispus*, differ in their life histories from *M. aquaticum*. *V. natans* and *H. verticillata* overwinter with winter buds, then seeds and sprouts in the spring. However, germination from seed or winter buds must to meet certain conditions (nutrients, temperature, etc.) (Nielsen et al. 2003; Xiao et al. 2010) and time, and the survival rate is easily affected by environmental factors during seedling growth. Although *P. maackianus* and *P. crispus* begin sprouting in early April, they reach their maximum biomass in July and then gradually wilt and die (Wang et al. 2015). However, *M. aquaticum* begins to grow in spring but does not die-off in summer and fall. During fall, *M. aquaticum* peaked. *M. aquaticum* can also grow during the over winter. In winter, we observed that even when *M. aquaticum* was frozen, it did not die and could still grow even

after the ice had melted. In our experiments, even if the temperature was only 0–5 °C, the *M. aquaticum* could still grow. Although its growth was relatively slow, until the end of the experiment, *M. aquaticum* did not die under conditions of 0–5 °C. This is attributed to its reliance on roots for winter survival (Liu et al. 2017). In addition to seed reproduction, submerged plants can also reproduce asexually using stolons, rhizomes, bulbs, tubers and fragments (Titus and Hoover 1991; Riis and Sand-Jensen 2006). After asexual reproduction, a certain amount of time is required to establish roots and then colonize and grow after successful rooting. Moreover, such plants are equally susceptible to environmental conditions such as seed germination. In spring, because *M. aquaticum* retains its original roots and stems before dormancy, it can continue growing. Compared to other plants, *M. aquaticum* does not need to spend time on seed germination or root formation. This allows *M. aquaticum* to occupy its ecological niches relatively quickly.

Based on the growth and physiological indicators of *M. aquaticum* at various temperatures, the ideal water temperature range for its growth is between 20 °C and 25 °C. However, *M. aquaticum* can regulate itself under high and low-temperature stress to survive and thrive at temperatures ranging from at least 0 °C to 30 °C. This adaptation is advantageous for *M. aquaticum* when invading subtropical and temperate regions, where temperature variations occur throughout the four seasons.

Conclusions

In this study, we examined the effects of various temperatures *M. aquaticum*. Our results confirmed the significant impact of different water temperatures on the growth of *M. aquaticum*. As water temperature increased, the growth rate of *M. aquaticum* decreased. The research revealed that growth was inhibited at 0 °C and 5 °C. The number of stem nodes, branches, and stem diameter were highest at temperatures ranging from 20 °C to 25 °C. The number of branches progressively decreased or branches vanished under high-temperature stress at 30 °C. In contrast, 20 °C contributed significantly to a higher accumulation of biomass compared to the 0 °C, 5 °C and 30 °C treatment groups. *M. aquaticum*'s physiological activities were also influenced by temperature. CAT activity varied significantly at different water temperatures, except for 10 °C and 15 °C. The highest CAT activity was measured in the 5 °C treatment group and the lowest in the 25 °C group. Temperatures of 10 °C and 15 °C facilitated photosynthetic pigment synthesis by *M. aquaticum*. The optimal temperature range for *M. aquaticum* growth was between 20 °C and 25 °C. However, at low temperatures (<10 °C), the plants were able to adjust to mitigate damage caused by water temperature. These plants exhibit robust adaptability toward various temperatures.

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Authors' contribution

XW conceived the idea and designed the methodology. CL, LC and CH conducted the experiment. NW and SZ explored the software and prepared the figures.

CL and LC collated the data. NW wrote the manuscript. XL made the revisions and translation. XW and XG significantly contributed to the manuscript writing and critical review.

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