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Structural and photosynthetic improvement of *Myriophyllum aquaticum* plant traits through artificial adjustments

Daomin Cheng [a,b,c], Peili Fu [d], Qingqing Wang [a,b,c], Wei Li [e,f,g], Longyi Yuan [a,*], Yang Liu [b,c,h,**], Yu Cao [b,c]

[a] College of Horticulture and Gardening, Yangtze University, Jingzhou, Hubei 434025, China
[b] Research Center of Aquatic Plant, Wuhan Botanical Garden, Chinese Academy of Sciences, Wuhan 430074, China
[c] Hubei Key Laboratory of Wetland Evolution & Ecological Restoration, Wuhan Botanical Garden, Chinese Academy of Sciences, Wuhan 430074, China
[d] CAS Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Menglun, Mengla, Yunnan 666303, China
[e] School of Ecology and Environment, Tibet University, Lhasa 850000, China
[f] Key Laboratory of Biodiversity and Environment on the Qinghai-Tibetan Plateau, Ministry of Education, Tibet University, Lhasa 850000, China
[g] Yani Wetland Ecosystem Positioning Observation and Research Station, Tibet, Lhasa 850000, China
[h] Department of Biology, McGill University, Montréal, QC H3A 1B1, Canada

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ABSTRACT

Plant height is a key quantitative trait in plant ecology, linked with leaf area and stem diameter, affecting photosynthesis and water transport. Taller plants typically access lighte and resources, enhancing their competitive ability. However, the invasive aquatic plant *Myriophyllum aquaticum* usually reaches around 20 cm above the water surface. Despite its shorter stature, this species demonstrates rapid growth and efficient resource utilization, which contributes to its competitive success in various aquatic environments. This study aims to explore how altering its height impacts photosynthesis and water transport, providing insights into its growth adaptation mechanisms. We conducted an experiment with *M. aquaticum*, adjusting its height artificially (H) and comparing it to naturally maintained height (CK). We measured plant traits related to photosynthesis and water transport, including stem diameter, root pressure, and photosynthetic pigments (chlorophyll-a, chlorophyll-b, and carotenoids). Observations of guttation were also recorded. Under height-adjusted treatments, *M. aquaticum* exhibited positive significant growth responses with increased stem diameter and root pressure compared to the CK. Photosynthetic pigments were significantly higher in H than in CK. Notably, guttation was observed in CK but absent in H. Artificially increasing the height of *M. aquaticum* enhances its photosynthetic and hydraulic traits. However, this adjustment may lead to water deficiency issues, particularly during sunny conditions. This study contributes to understanding the ecological significance of plant height in aquatic species, highlighting the complex interplay between growth adaptations and environmental conditions.

1. Introduction

Plant height is the core morphological indicator of plants, serving as a critical trait of plant ecological strategies and a comprehensive metric for adapting to environmental pressures (Westoby, 1998). Moreover, as the longest pathway for internal water transport and photosynthate distribution within the plant body, plant height is closely associated with other functional traits (Ryan and Yoder, 1997; Marks et al., 2016; Savage et al., 2017). Taller plants typically exhibit thicker stem diameters and wider wood vessel diameters, enhancing their water transport capacity (Zhong et al., 2020). Furthermore, taller plants intercept more light, thereby promoting their own photosynthetic activity, and can overshadow neighboring individuals, thereby enhancing their competitive ability (Westoby et al., 2002). Aquatic plants are important primary producers in lake and river ecosystems, playing a crucial role in maintaining ecological balance and supporting biodiversity (Jeppesen et al., 1998). Similar to terrestrial plants, plant height of aquatic plants is an important indicator reflecting their competitive strength, growth conditions, and overall health status (Verhofstad et al., 2017).

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* Corresponding author.
** Corresponding author at: Research Center of Aquatic Plant, Wuhan Botanical Garden, Chinese Academy of Sciences, Wuhan 430074, China.
E-mail addresses: yzq29@sina.com (L. Yuan), liuyang1025future@163.com (Y. Liu).

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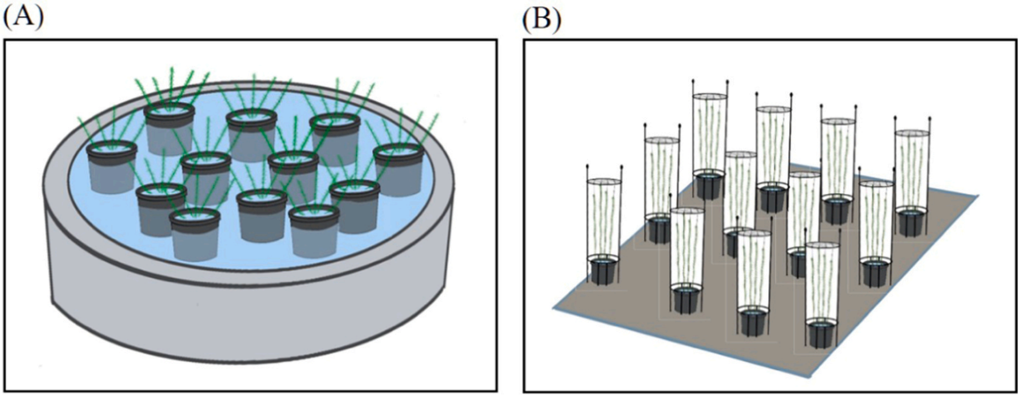

Fig. 1. Diagram of the experiment including the control (CK, A) and the artificially height supported treatment (H treatment, B).

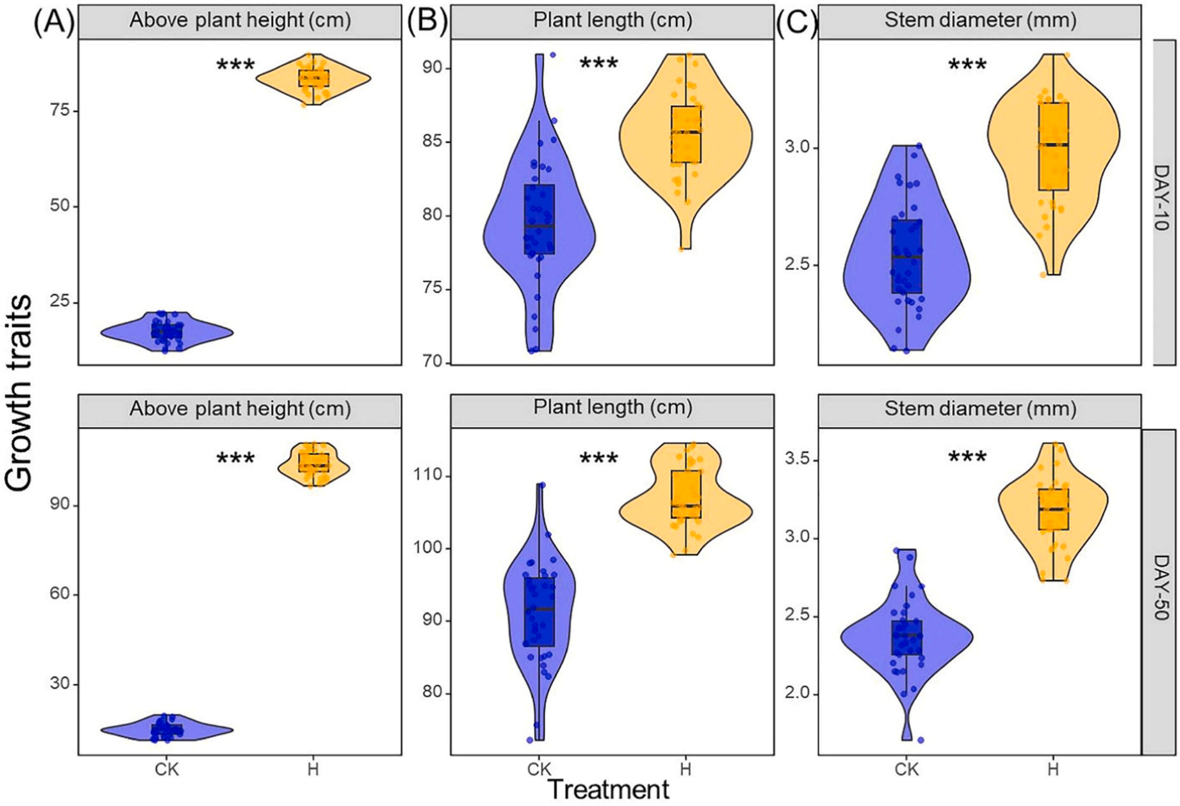

Fig. 2. Growth traits of *M. aquaticum* on Day 10 and Day 50 between two treatments ($n = 6$). (A) Above-water height, (B) absolute length and (C) stem diameter. Violin and box plots illustrate the distribution of these parameters across various time points. The violin plots display the kernel density of the data, showing its distribution shape, while the box plots represent the interquartile range (IQR), marking the middle 50 % of the data. The line inside each box denotes the median, and whiskers extend to the smallest and largest values within 1.5 times the IQR. Individual points indicate raw data, highlighting distribution and potential outliers. Significance levels: *** refers to $P < 0.001$.

In terrestrial ecosystems, as taller trees grow, hydraulic stress increases due to gravity and the elongation of water transport pathways, the density and size of stomata must be adjusted to ensure effective water transport and transpiration (O'Keefe et al., 2023). This may ultimately limit leaf expansion and photosynthesis, thereby limiting further height growth (Koch et al., 2004). In contrast, the stem xylem of aquatic plants is typically degraded, resulting in higher resistance to water transport (Pittermann, 2010; Brodersen and McElrone, 2013; Ding et al., 2018). Consequently, an increase in the height of aquatic plants may lead to an inadequate water supply to the shoot tip. Taller aquatic plants typically possess more developed root systems and leaves, allowing them to more effectively absorb nutrients, heavy metals, and organic pollutants from the water, thereby improving water quality (Gao et al., 2020, Clément et al., 2022). In our previous study, we found that shorter emergent plants, despite having a lower height above the water surface, exhibit higher root pressure (unpublished data). However, the underlying reasons for the elevated root pressure still require further investigation.

The root pressure model, first proposed by Crafts and Broyer (1938), posited that root pressure was generated by the woody tissues of the root system. The Casparian bands serve as barriers for the radial transport of water and ions in plant roots and play a crucial role in the generation of root pressure through active water absorption (Enstone et al., 2002). Studies have shown that root pressure is closely related to plant

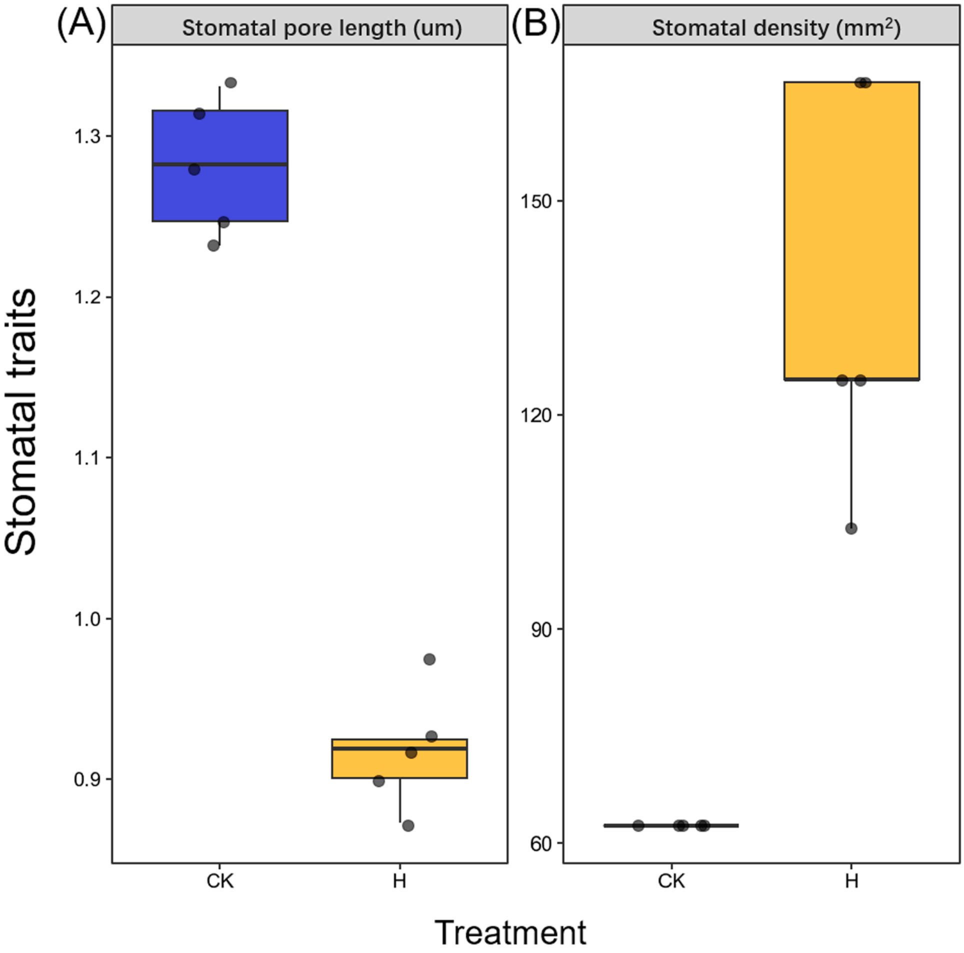

Fig. 3. Differences in stomatal traits of *M. aquaticum* in two treatments ($n = 6$). (A) stomatal size (um). (B) stomatal density (mm^2). ** refers to $P < 0.01$, *** refers to $P < 0.001$.

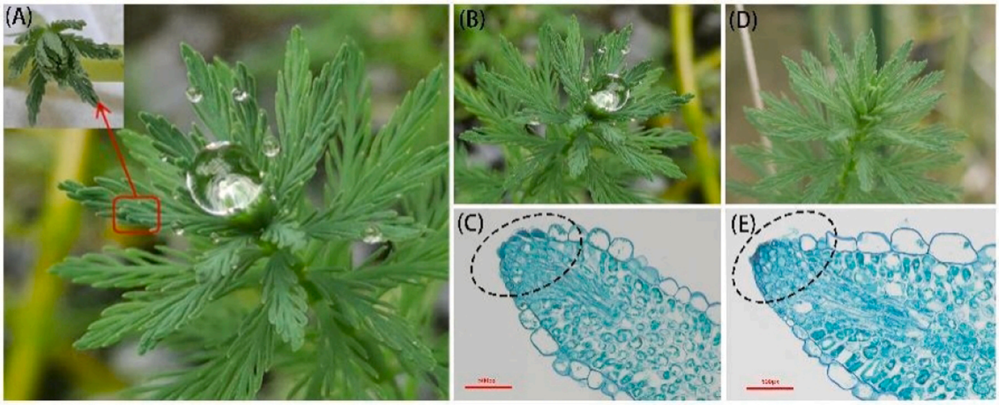

Fig. 4. The tip of a young leaf of *M. aquaticum.* (A) Guttation at the leaf tip. (B) and (C) show leaf tip and its longitudinal section in CK, while (D) and (E) show the leaf tip and its longitudinal section in H treatment. The circled areas in (C) and (E) refer to the distribution of hydathodes.

adaptation to arid or water-deficient habitats (Cao et al., 2012; Yang et al., 2012; Gleason et al., 2017; Holmlund et al., 2020). The maximum plant height of the tallest terrestrial grass, bamboo, is positively correlated with the maximum root pressure, which can repair embolisms caused by rapid daytime transpiration (Cao et al., 2012). However, aquatic plants typically have sufficient water supply, and whether root pressure still affects the maximum height of aquatic plants remains unexplored.

Myriophyllum aquaticum (Vell.) Verdc., a heterophyllous and herbaceous perennial aquatic plant, exhibits distinct submerged and emergent life forms, making it a highly competitive invasive species resilient to extreme water disturbances (Zou et al., 2024; Wersal and Madsen, 2011). In deeper water, the plant can achieve heights of up to 200 cm in its submerged form, taking advantage of increased buoyancy and light availability at greater depths. Conversely, in shallower water, *M. aquaticum* predominantly exhibits its emergent form, where the

Table 1

Comparison of anatomical traits in *M. aquaticum* leaves between CK and H treatments. Data were showed as mean ± standard deviation. Different letters and bold font indicate significant difference ($P < 0.05$) between CK and H treatments as determined by *t*-test ($n = 4$).

Parameters	6th whorl leaves		12th whorl leaves	
	CK	H	CK	H
Total cross-section area (μm^2)	13 409 ± 1 475a	13 914 ± 1 745a	17 034 ± 3 370a	13 104 ± 9 940a
Vascular bundle area (μm^2)	**5 241 ± 6 310b**	**6 937 ± 6 310a**	5 752 ± 1 889a	6 314 ± 1 889a
Lacuna (μm^2)	23 551 ± 4 002a	26 929 ± 2 079a	18 413 ± 4 784a	22 339 ± 1 528a
Leaf porosity	0.17 ± 0.02a	0.19 ± 0.01a	**0.11 ± 0.01b**	**0.17 ± 0.01a**

vertical height above the water surface remains short. Furthermore, emergent *M. aquaticum* exhibits unique growth patterns, including periodic upright and prostrate growth, as well as large vertical climbs growth under certain conditions. Initially, the plant grows upright out of the water to a height of about 20–30 cm. Subsequently, the upper portion of the plant collapses, generating stolons and potential branching before resuming upright growth. This cycle repeats as the plant reaches approximately 20–30 cm in height again and experiences another slumping phase. Interestingly, we noted that a few individuals were able to climb approximately 100 cm by attaching to nearby tall plants or broken tree branches during our field observations. Thus, the plant height of emergent *M. aquaticum*, which includes collapsed parts, significantly differs from the standard definition of plant height, which refers to the vertical height of a plant from the ground to its top. Given these variations in growth forms and heights, this study aims to investigate whether the changes in plant height of emergent *M. aquaticum* in its natural habitat, from shorter height to greater height when climbing, influence the plant's physiological and structural traits, thereby affecting its photosynthesis and water transport processes.

By supporting the plant height artificially, we analyzed the differences of plant traits between photosynthetic and water transport processes in *M. aquaticum* in summer-autumn under natural height and heightened treatment. We hypothesized that *M. aquaticum* possessed the capacity to adapt to increased water transport resistance through morphological and anatomical adjustments for its stems and leaves, as well as through smaller leaf areas and higher root pressure, facilitated by artificial height modifications. Studying the effects of plant height on the photosynthetic and hydraulic characteristics of aquatic plants helps elucidate their ecological roles and adaptive strategies within aquatic ecosystems. This research enhances our understanding of aquatic plant physiology and ecology, emphasizing the ecological importance of plant height, particularly in aquatic species.

2. Materials and methods

2.1. Experimental design and materials

Myriophyllum aquaticum was selected as a suitable experimental species due to its strong competitiveness, rapid growth in response to water level fluctuations, and ability to maintain consistent above-water height based on our previous experiment (see Supporting Information Appendix 1).

This study was conducted in a greenhouse at Wuhan Botanical Garden, Wuhan, China (114°43′E, 30°55′N), from July to October in 2023. A total of 288 healthy shoot tips of *M. aquaticum* were collected from the garden's ponds, and the tips were harvested at the length of 40 cm. Twenty-four buckets were utilized in the study, each with a top diameter of 27 cm, a bottom diameter of 22 cm, and a height of 14 cm. Each bucket contained 12 plants. These buckets were filled with approximately 8 cm of nearby pond sediment and 5 cm of tap water. The experimental design was divided into two groups: twelve buckets simulating a natural height (serving as the control, CK, Fig. 1A); and the other twelve buckets for the artificially height supported treatment, aiming for larger vertical plant height (the treatment, H, Fig. 1B). For H, a string and the plastic structure were set up to ensure a larger plant height (Fig. 1B). Plant materials were pre-cultivated for 50 days from 12 July to 31 August, 2023. The experiment was conducted during the next 10–50 days. To maintain a stable water depth of 5 cm, these plants were watered twice daily. In this experiment, sampling time points were selected on Day 10 (9 Sep.) and Day 50 (20 Oct.). Day 10 was identified as a critical time point in the experiment, during which wilting was observed at the shoot tips of the H plants between 11:00 a.m. and 13:00 p.m. in daytime. Additionally, guttation was observed in the CK during the early morning hours, while no such phenomenon was found in the H. Observations were continued due to sufficient experimental materials. On Day 50 (40 days after initial observations), it was noted that the plants in the H no longer showed wilting. The CK continued to exhibit early morning guttation, while the treatment group (H) remained unaffected.

2.2. Growth traits

Plant growth traits, including above-water height, absolute length and stem diameter, were measured on Day 10 (under warm conditions with temperatures ranging from 28 °C to 35 °C) and Day 50 (under cooling conditions with temperatures ranging from 15 °C to 24 °C). Above-water height refers to the vertical distance between the shoot tips

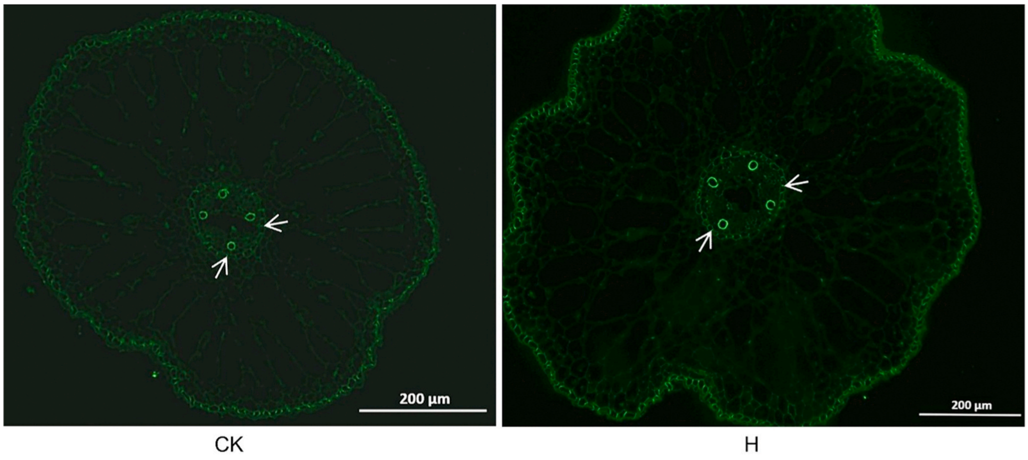

Fig. 5. Casparian bands on the roots of *M. aquaticum* in the two treatments. Arrowheads: Casparian bands on endodermis.

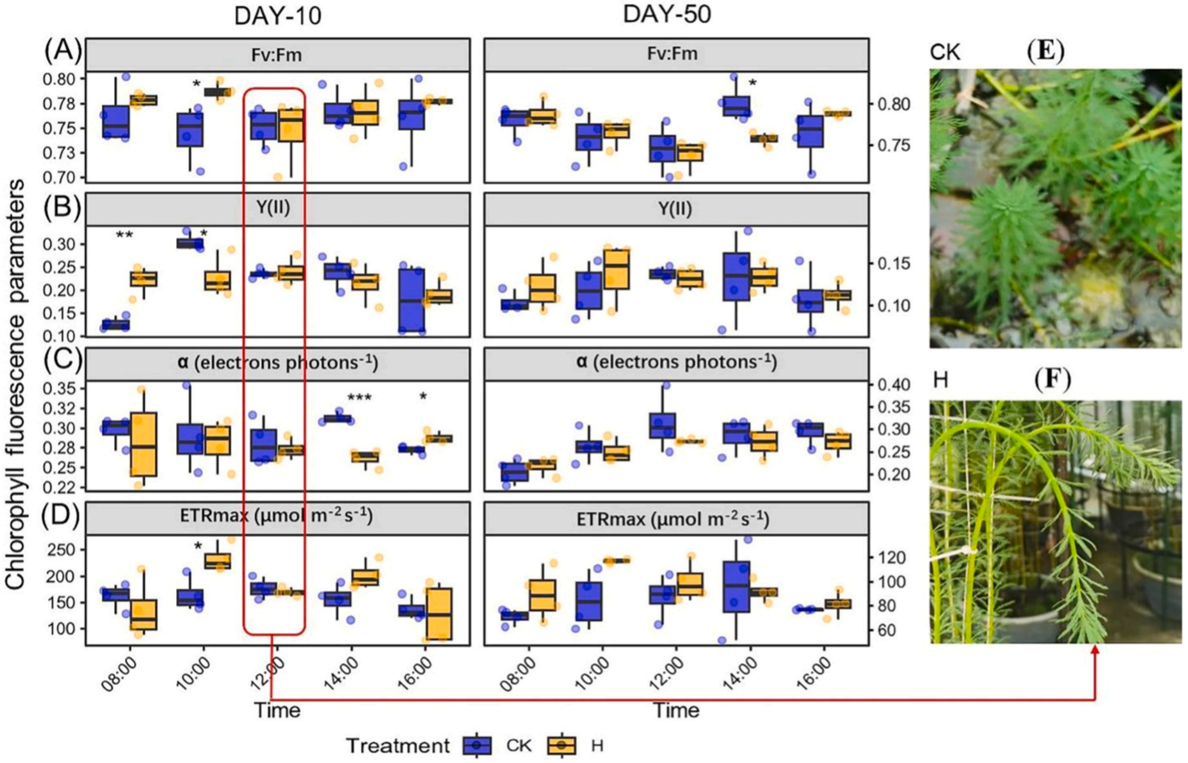

Fig. 6. Changes in (A) chlorophyll fluorescence parameters (Fv:Fm: the maximum quantum yield of PSII; (B) Y(II): the actual quantum yield of PSII; (C) α: the initial slope; (D) ETRmax: maximal electron transport rate under different treatments (CK and H) at Day 10 and Day 50 ($n = 6$). *$P < 0.1$, **$P < 0.01$, ***$P < 0.001$.

and the water surface, and absolute length refers to the total plant stem length from the shoot tips to the root, and stem diameter refers to the diameter of stem at the position of ca. 15 cm below the shoot tip. Six replicate individuals were randomly selected from the treatment, with each individual from an independent bucket. The above-water height and the absolute length were measured by using a tape. The stem diameter was measured by using an electronic digital caliper.

2.3. *Leaf, stem and root anatomical structures*

The 6th and 12th leaf whorls were selected for anatomical analysis. Preliminary observations indicated that the 6th leaf whorl had the longest leaves among the young whorls, suggesting unique physiological characteristics. The 12th leaf whorl was chosen specifically due to its stabilized leaf length at this developmental stage (see Supporting Information Appendix 2 Fig. S1). On Day 50, measurements of leaf stomatal area, stem vascular area, and Casparian strip, along with other parameters of leaves, stems, and roots, were taken for both treatments. For leaves, one leaf from the 6th and 12th whorls (the first fully expanded leaf is considered as the first whorl of the leaves, the 6th and 12th whorls leaf were selected in our study) were taken for leaf transverse section, the 6th whorl leaves for stomatal traits, and the newly-grown leaves at the stem tip for the hydathode by longitudinal section (Fig. 4A). Stem samples were taken at 12–15 cm from the stem tip, while the root samples were taken at 6 cm from the root tip (Fleck et al., 2015). Except for the determination of leaf stomata, these samples were first fixed in the formaldehyde-acetic acid-ethanol (FAA) solution, then paraffin sections were made as described in Farnese et al. (2017), and the leaf samples were initially collected and fixed in 2.5 % glutaraldehyde, followed by post-fixation in 1 % OsO_4. After standard dehydration using an ethanol series, the samples underwent critical point drying (K850, Quorum, UK), were treated for electrical conductivity, and subsequently examined using a scanning electron microscope (SU8010, Hitachi, Japan) to observe morphological characteristics on the leaf surfaces. The stomatal number was counted for each of five randomly selected views (each with an area of 0.048 mm^2 at 500x magnification) on each segment. Stomatal size was determined by randomly selecting five stomata at 500x magnification, measuring the maximum length between two guard cells, and calculating the average value. Stomatal density was calculated by dividing the stomatal number for each view by 0.048 mm^2.

For leaf and stem samples, the procedure begins with collection and fixation in the experimental site. Subsequently, the samples undergo dehydration, infiltration with paraffin wax, embedding, sectioning, deparaffinization, staining, mounting, and finally observation and photography under a microscope. The leaf transects were used for measuring traits such as the total cross-section area, lacuna, vascular bundle area of the leaves. The porosity was calculated as the ratio of air cavity area to total cross-section area, and each index of the leaves was measured at 15x magnification. Leaf longitudinal sections were used for the observation of hydathode (Hostrup and Wiegleb, 1991). For stem samples, the area and diameter of xylem conduits, thickness of cortex, number of aerenchyma, diameter and area of vascular bundles of the stems were measured under 15x magnification. For root samples, root slices were firstly treated with xylene and ethanol and then stained with berberine hydrochloride (1 h) and aniline blue solution (30 min) separately after rinsing and air-drying, and thereafter these slices were mounted and observed using a fluorescence microscope to visualize the Casparian strip (Wang et al., 2022).

2.4. *Photosynthetic physiological indicators*

On Day 10 and Day 50, the chlorophyll fluorescence parameters of PSII were measured at shoot tips using a PAM-2500 (Cao et al., 2019). Measurements were taken every two hours from 8:00 a.m. to 4:00 p.m. We measured the maximum quantum yield of PSII (Fv:Fm), the actual quantum yield of PSII (YII), maximal electron transport rate (ETRmax) simulated by using photosynthetically active radiation (PAR) and ETR,

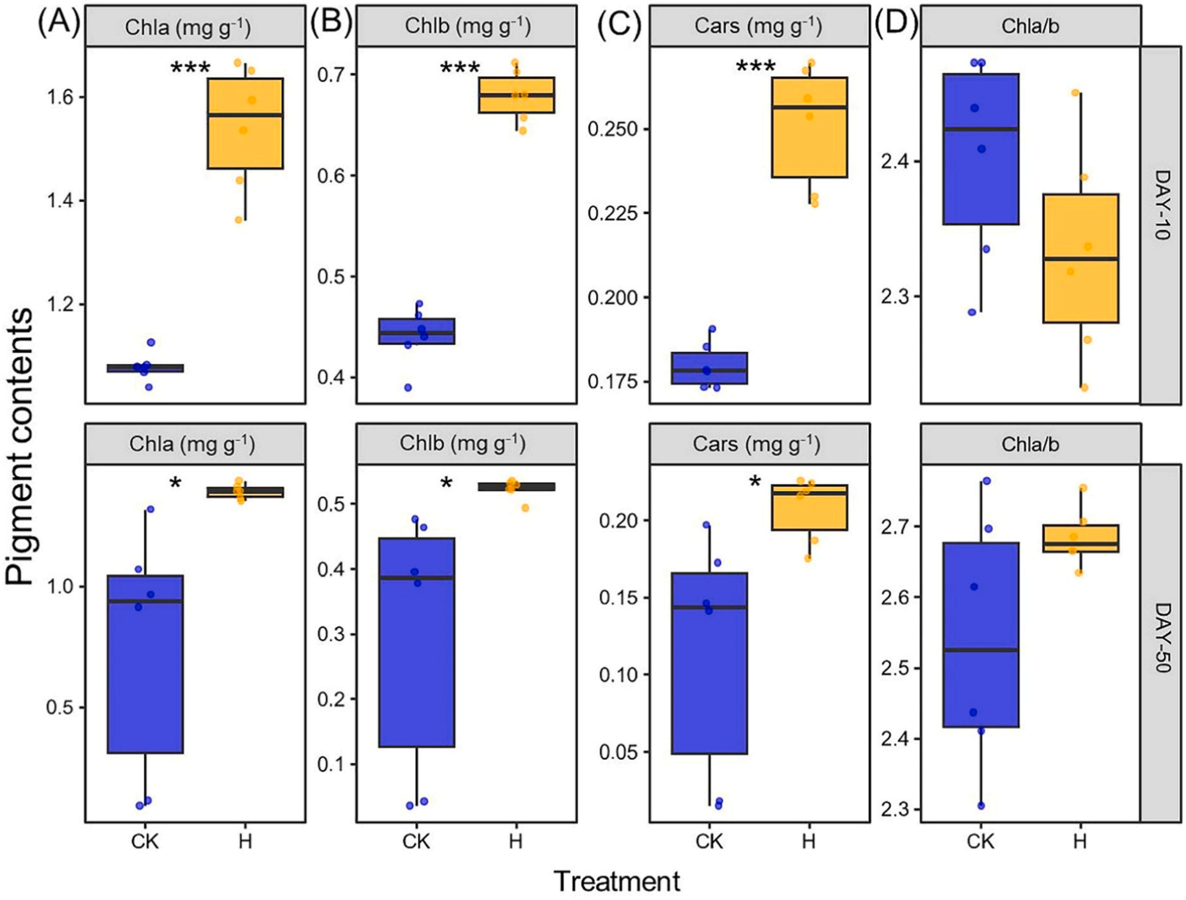

Fig. 7. Photosynthetic pigment content in *M. aquaticum* under various treatments ($n = 6$). (A) chlorophyll-a, (B) chlorophyll-b, (C) carotenoid (cars), (D) Chla/b. $^{*}P < 0.01$, $^{***}P < 0.001$.

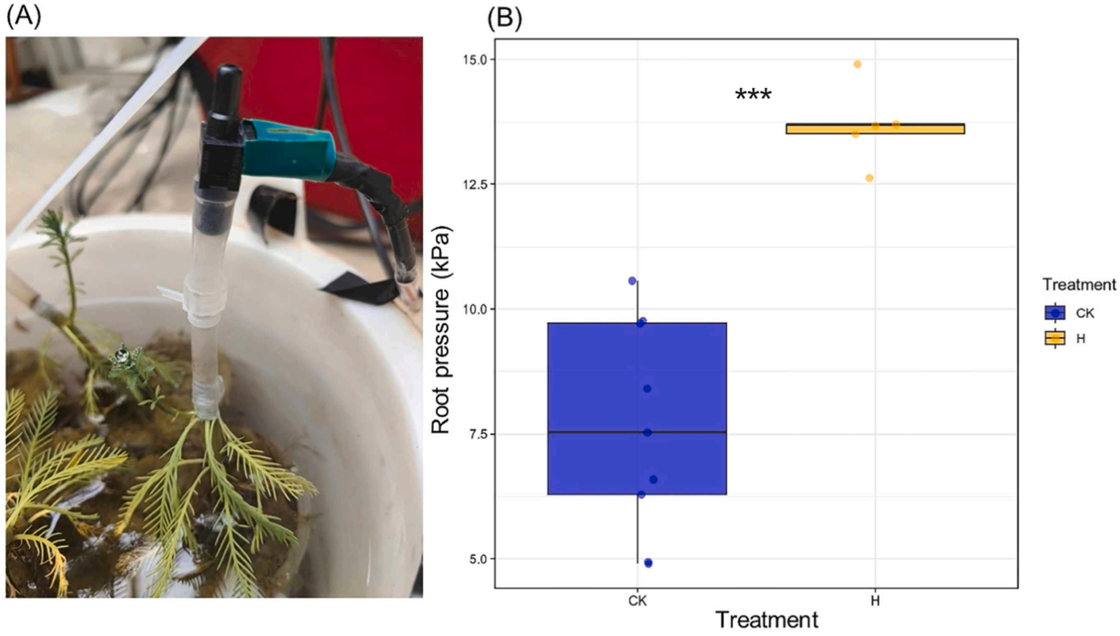

Fig. 8. (A) Root pressure determination and (B) actual maximum root pressure of *M. aquaticum* in two treatments ($n = 4$). $^{*}P < 0.05$.

and the initial slope α (Chen et al., 2020). The PAR values are set as follows: 0, 4, 13, 140, 221, 308, 433, 593, 795, 1038, 1355, 1719 (μ mol m^{-2} s^{-1}). These parameters were observed to understand the daily dynamics of fluorescence. The Fv:Fm refers to the maximal photochemical efficiency of PSII after 15 min dark adaptation, and the YII refers to the actual photosynthetic efficiency of PSII, indicating the actual primary light energy capture efficiency of the PSII reaction center under partial closure (Li et al., 2023). ETRmax is commonly used to assess the maximum rate of the electron transport chain of a plant at light saturation; and the initial slope α responds to the efficiency of light energy utilization by photosynthetic organs (Millar et al., 1978).

After this, the leaves of the 6th whorl were harvested according to Pedersen (1994), rinsed three times with distilled water, blotted with paper and weighed as fresh weight. Subsequently, the pigment contents of chlorophyll-a (Chla), chlorophyll-b (Chlb), and carotenoid (Cars) were measured using a spectrophotometer (TU–1810PC, Purkinje General, China) at the absorbance of 470, 665 and 649 nm after extraction in 5 mL 95 % ethanol at 4 °C for 24 hours (Shao et al., 2017). All the photosynthesis-related traits were determined with six replicates.

2.5. *Root pressure*

Root pressure was measured according to Cao et al. (2012). Continuous monitoring of root pressure was conducted from 6:00 p.m. to 12:00 a.m. the following day. A digital pressure sensor (PX26–015DV, Omega, USA) was connected to the cut of the stem (usually 5 cm above the water surface), and a data logger (CR1000, Campbell Scientific, Logan, UT, USA) was used with pressure data recorded every 5 minutes (Fig. 8A). Each treatment has four replicates. In addition, the pressure sensor was calibrated before connecting it to the plant by adjusting the pressure change with varying the height of the water column. The actual root pressure equals the sum of the measured root pressure and the root pressure from the water surface to the sensor.

2.6. *Statistical analysis*

We used Student's t-tests in R (R-4.1.3) to compare the differences of the plant traits between CK and H treatments.

3. Results

3.1. *Growth traits*

All growth traits of *Myriophyllum aquaticum* showed significant differences between CK and H (Fig. 2), with larger growth observed in individuals with artificial support structures on both Day 10 and Day 50. The above-water height in H treatment was significantly higher than that in the CK ($t = -100.16$, $P < 0.001$), with approximately 90 cm in H treatment and 20 cm in CK. The absolute length in H treatment (ca. 107 cm) was significantly longer than that in CK (ca. 91 cm) ($t = -7.01$, $P < 0.001$). Additionally, the stem diameter was greater in H treatment (ca. 3.17 mm) compared to the CK (ca. 2.36 mm) ($t = -8.53$, $P < 0.001$).

3.2. *Anatomical traits of leaves, stems and roots*

The stomatal length was significantly smaller in H treatment than in CK ($t = 14.29$, $P < 0.001$, Fig. 3A). In contrast, the stomatal density in H treatment was significantly greater, being twice as high as that in CK ($t = -6.00$, $P < 0.01$, Fig. 3B). No difference in anatomical traits of hydathode were found between CK and H treatments in the longitudinal section of *M. aquaticum* (Fig. 4C, E). However, guttation at the leaf tips was observed only in CK in the early morning, while no guttation was found in H treatment (Fig. 4B, D). The total cross-section area, lacuna, and leaf porosity did not differ between the CK and H treatments for the 6th whorl of leaves (all $t < -1.29$, $P > 0.05$, Table 1). However, the leaf vascular bundle area was significantly larger in H treatment than in CK ($t = -3.60$, $P < 0.05$). For the 12th whorl of leaves, only the leaf porosity showed statistical difference between the two treatments, with a notably higher value in H treatment ($t = -7.26$, $P < 0.01$).

For stem traits, there were no significant differences between CK and H treatment in aerenchyma, vascular bundle area, vascular bundle diameter, conduit area and conduit diameter ($t < -0.98$, $P > 0.05$), but cortical thickness in H treatment was significantly larger in H treatment than that in CK ($t = -2.87$, $P < 0.05$, see Supporting Information Appendix 2, Table S1). Casparian bands are visible in the radial walls of the exodermis and endodermis in stem cross section, and there was no difference in the morphology of Casparian bands in CK and H treatment (Fig. 5).

3.3. *Leaf chlorophyll fluorescence parameters and pigment contents*

No significant differences were found in Fv:Fm, Y(II), α and ETRmax between CK and H for most sampling times on Day 10 and Day 50 ($t < 1.55$, $P > 0.05$, Fig. 6). We found that ETRmax in H treatment exhibited a distinct pattern. On the sunny day (Day 10), ETRmax in H treatment showed a bimodal curve, decreasing from 233 ± 2 at 10:00–169 ± 6 at 12:00 (μmol m^{-2} s^{-1}), while CK remained relatively stable. However, on the cooler day (Day 50), ETRmax in both treatments ranged from approximately 60 to 134 (μmol m^{-2} s^{-1}), with no daily variation (Fig. 6D).

The contents of Chl a, Chl b, and Cars in H treatment were all significantly higher than those in CK ($t < -2.43$, $P < 0.05$), while no difference for chla/b ($t < -1.54$, $P > 0.05$, Fig. 7).

3.4. *Root pressure*

The actual root pressure in H treatment was significantly higher than that in CK treatment ($t = -2.74$, $P < 0.05$, Fig. 8B), with values of 17.01 ± 7.48 kPa in the H treatment and 7.64 ± 2.11 kPa in the CK treatment.

4. Discussion

Consistent with our hypothesis, many indicators related to physiological, morphological, and anatomical traits in *Myriophyllum aquaticum* showed enhanced growth under artificial support. However, it is important to note that under certain conditions, such as sunny noon, this species may experience water deficiency due to the artificially increased height. This finding suggests potential trade-offs between the benefits of artificial support and the risks of water stress, particularly in high-light environments. Our study provides valuable insights into the complex interactions between environmental conditions and the growth and physiological properties of aquatic plants.

4.1. *Adaptation to environmental variability*

Plant adaptation to varying environmental conditions can be manifested at different levels, these include morphology, physiology and structure (Gratani, 2014; Sharma et al., 2020). In our study, the Fv:Fm value ranged between 0.75 and 0.80, indicating that the photosynthetic organs of *M. aquaticum* were in a non-stressed state (Jiang et al., 2018; Wang et al., 2021). Furthermore, both the photosynthetic pigments (related to light absorption and transformation) and ETRmax were marginally higher in the artificially supported treatment. These results suggest that the artificial support might enhance light absorption and energy conversion efficiency, potentially leading to increased photosynthetic productivity. This is in line with findings from other studies on terrestrial plants, where different trellis systems affect photosynthetic characteristics, such as chlorophyll content (Guseynov and Mayborodin, 2021). The moderate growth and favorable light conditions provided by the L-shaped trellis system are suggested as the primary reasons for the observed improvements in leaf development, which significantly increased chlorophyll content compared to the fan-shaped trellis system (Guseynov and Mayborodin, 2021).

4.2. *Morphological and anatomical adjustments*

Beyond photosynthetic enhancement, we observed significant morphological changes, including an increase in leaf stomatal density and cortical thickness of the stem, following artificial support. These changes are indicative of improved photosynthetic capacity (Bertolino et al., 2019; Flexas and Carriquí, 2020; Huang et al., 2024) and enhanced mechanical support and protective function of the stem (Speck and Burgert, 2011; Shah et al., 2017). The increased cortical thickness suggests a strategic adjustment by the plant to mitigate water deficiency by enhancing energy storage capacity, thus supporting continued growth under suboptimal water conditions (Zhan et al., 2017).

4.3. Water transport challenges

While the artificial support improved overall plant growth, it had a complex impact on water transport within *M. aquaticum*. Despite no significant differences in the Casparian strip structure of the root between treatments, root pressure was significantly higher under artificial support. This increased root pressure suggests that *M. aquaticum* has the potential to grow taller or support greater height than its current stature. The high root pressure observed in our study, relative to the actual support height, is similar to that of the terrestrial resurrection plant *Paraboea rufescens*, which uses this pressure to facilitate plant recovery when rewetted (Fu et al., 2022). However, the lack of guttation observed in artificially supported plants compared to naturally-grown individuals (Fig. 4D), especially at dawn, implies increased resistance in the water transport pathway at greater heights. This phenomenon is reminiscent of the challenges faced by aquatic plants with degraded xylem structures, leading to water transport inefficiencies (Barbosa et al., 2019). The contrasting phenomena implied that aquatic plants with a more degraded xylem structure may experience greater resistance in the water transport pathway, resulting in the lack of guttation at the shoot tips when the plants were artificially supported to an extreme height (Richards and Sculthorpe, 1968; Barbosa et al., 2019). The xylem conduits of stem in *M. aquaticum* are 2.76 mm, which is significantly smaller than those in lianas (15.80 cm) (Rosell and Olson, 2014).

4.4. Midday water stress

The midday depression of photosynthesis and leaf wilting observed in *M. aquaticum* during summer, particularly under intense sunlight, could be attributed to water transport limitations rather than photoinhibition, as suggested by the stable Fv:Fm values. The chlorophyll a/b ratio of 2.3, similar to that of terrestrial shade-adapted plants, indicates a sensitivity to high temperatures and intense light (Huang et al., 2021). The midday wilting is likely due to inadequate water supply to the upper parts of the plant, leading to loss of cell turgor and subsequent leaf wilting, a phenomenon also observed in taller terrestrial plants under water stress (Petit et al., 2010; Blackman, 2018). Previous studies have shown that the photosynthetic activity of herbs fluctuates throughout the day, suggesting a potential decrease in efficiency from morning to noon (Koyama and Takemoto, 2014; Rosell and Olson, 2014; Liu et al., 2022). Moreover, water stress has been demonstrated to adversely affect both photosynthesis and water-use efficiency of *Phragmites australis*, leading to a reduction in net photosynthetic rate during midday under mild to moderate drought conditions. Additionally, wilting phenomena have been observed at the upper parts of woody plants (Pittermann, 2010; Blackman, 2018). Although artificially supported plants exhibited better water-regulating capacity, as indicated by stomatal density and vascular bundle characteristics, these adaptations were insufficient to offset the water deficit at the shoot apex caused by the artificially increased height (Krähmer and Kováč, 2016; Chen et al., 2022).

5. Conclusion

In summary, the present study provides valuable insights into how changes in plant height can influence eco-physiological traits in aquatic plants, with a specific focus on the invasive *M. aquaticum*. Although the relationship between height and physiological processes is well-studied in trees, the unique patterns observed in *M. aquaticum* reveal significant distinctions between terrestrial and aquatic plant responses. Unlike trees, which have evolved complex mechanisms to cope with height-related challenges, aquatic plants like *M. aquaticum* may exhibit distinct responses due to their unique structural and physiological adaptations to waterlogged environments. Increasing plant height alters the water transport efficiency of *M. aquaticum*, impacting its competitiveness for light and resources. As a sustainable and actionable management tool, adjusting plant height offers a novel approach to invasive species control. While current research focuses on *Myriophyllum aquaticum*, the strategy holds potential for broader applications. Future studies across diverse aquatic species will help assess the effectiveness of height manipulation as a universal management tool in various aquatic ecosystems.

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CRediT authorship contribution statement

Liu Yang: Writing – review & editing, Writing – original draft, Visualization, Supervision, Conceptualization. **Cao Yu:** Writing – review & editing, Writing – original draft, Funding acquisition, Conceptualization. **Fu Peili:** Writing – review & editing. **Wang Qingqing:** Writing – review & editing, Investigation. **Li Wei:** Writing – review & editing. **Yuan Longyi:** Writing – review & editing, Supervision, Conceptualization. **Cheng Daomin:** Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.aquabot.2025.103896.

Data availability

Data will be made available on request.

References

Barbosa, I.C.R., Rojas-Murcia, N., Geldner, N., 2019. The Casparian strip—one ring to bring cell biology to lignification? Curr. Opin. Biotech. 56, 121–129. https://doi.org/10.1016/j.copbio.2018.10.004.

Bertolino, L.T., Caine, R.S., Gray, J.E., 2019. Impact of stomatal density and morphology on water-use efficiency in a changing world. Front. Plant Sci. 10, 225. https://doi.org/10.3389/fpls.2019.00225.

Blackman, C.J., 2018. Leaf turgor loss as a predictor of plant drought response strategies. Tree Physiol. 38 (5), 655–657. https://doi.org/10.1093/treephys/tpy047.

Brodersen, C.R., McElrone, A.J., 2013. Maintenance of xylem network transport capacity: a review of embolism repair in vascular plants. Front. Plant Sci. 4, 108. https://doi.org/10.3389/fpls.2013.00108.

Cao, K., Yang, S., Zhang, Y., Brodribb, T.J., 2012. The maximum height of grasses is determined by roots. Ecol. Lett. 15, 666–672. https://doi.org/10.1111/j.1461-0248.2012.01783.x.

Cao, Y., Liu, Y., Ndirangu, L., Li, W., Xian, L., Jiang, H.S., 2019. The analysis of leaf traits of eight *Ottelia* populations and their potential ecosystem functions in karst freshwaters in China. Front. Plant Sci. 9, 1938. https://doi.org/10.3389/fpls.2018.01938.

Chen, T., Jiang, H.S., Wang, Y., Wang, S., Yin, L., Cao, Y., 2020. Responses of five submerged macrophytes to NaCl salinity in a tropical mesocosm study. CABI Agr. Biosci. 4, 359–370. https://doi.org/10.1127/fal/2020/1303.

Chen, Z., Li, S., Wan, X., Liu, S., 2022. Strategies of tree species to adapt to drought from leaf stomatal regulation and stem embolism resistance to root properties. Front. Plant Sci. 13, 926535. https://doi.org/10.3389/fpls.2022.926535.

Clément, C., Schneider, H.M., Dresbøll, D.B., Lynch, J.P., Thorup-Kristensen, K., 2022. Root and xylem anatomy varies with root length, root order, soil depth and environment in intermediate wheatgrass (Kernza®) and alfalfa. Ann. Bot. 130, 367–382. https://doi.org/10.1093/aob/mcac058.

Crafts, A.S., Broyer, T.C., 1938. Migration of salts and water into xylem of the roots of higher plants. Am. J. Bot. 25, 529–535. https://doi.org/10.2307/2436683.

Ding, L., Lu, Z., Gao, L., Guo, S., Shen, Q., 2018. Is nitrogen a key determinant of water transport and photosynthesis in higher plants upon drought stress? Front. Plant Sci. 9, 1143. https://doi.org/10.3389/fpls.2018.01143.

Enstone, D.E., Peterson, C.A., Ma, F., 2002. Root endodermis and exodermis: structure, function, and responses to the environment. J. Plant Growth Regul. 21, 335–351. https://doi.org/10.1007/s00344-003-0002-2.

Farnese, F.S., Oliveira, J.A., Paiva, E.A.S., Menezes-Silva, P.E., da Silva, A.A., Campos, F. V., Ribeiro, C., 2017. The involvement of nitric oxide in integration of plant physiological and ultrastructural adjustments in response to arsenic. Front. Plant Sci. 8, 516. https://doi.org/10.3389/fpls.2017.00516.

Fleck, A.T., Schulze, S., Hinrichs, M., Specht, A., Waßmann, F., Schreiber, L., Schenk, M. K., 2015. Silicon promotes exodermal Casparian band formation in si-accumulating and si-excluding species by forming phenol complexes. Plos One 10, e0138555. https://doi.org/10.1371/journal.pone.0138555.

Flexas, J., Carriquí, M., 2020. Photosynthesis and photosynthetic efficiencies along the terrestrial plant's phylogeny: lessons for improving crop photosynthesis. Plant J. 101, 964–978. https://doi.org/10.1111/tpj.14651.

Fu, P.L., Zhang, Y., Zhang, Y.J., Finnegan, P.M., Yang, S.J., Fan, Z.X., 2022. Leaf gas exchange and water relations of the woody desiccation-tolerant *Paraboea rufescens* during dehydration and rehydration. AoB Plants 14, plac033. https://doi.org/10.1093/aobpla/plac033.

Gao, J., Liu, L., Ma, N., Yang, J., Dong, Z., Zhang, J.S., Zhang, J.L., Cai, M., 2020. Effect of ammonia stress on carbon metabolism in tolerant aquatic plant—*Myriophyllum aquaticum*. Environ. Pollut. 263, 114412. https://doi.org/10.1016/j.envpol.2020.114412.

Gleason, S.M., Wiggans, D.R., Bliss, C.A., Young, J.S., Cooper, M., Willi, K.R., Comas, L. H., 2017. Embolized stems recover overnight in *Zea mays*: The role of soil water, root pressure, and nighttime transpiration. Front. Plant Sci. 8, 662. https://doi.org/10.3389/fpls.2017.00662.

Gratani, L., 2014. Plant phenotypic plasticity in response to environmental factors. Adv. Bot. 2014, 1–17. https://doi.org/10.1155/2014/208747.

Guseynov, S.N., Mayborodin, S.V., 2021. Photosynthesis productivity and architectonics of the Crystal grape variety canopy with different techniques of training and forming grape bushes. IOP Conf. Ser.: Earth Environ. Sci. 624, 012055. https://doi.org/10.1088/1755-1315/624/1/012055.

Holmlund, H.I., Davis, S.D., Ewers, F.W., Aguirre, N.M., Sapes, G., Sala, A., Pittermann, J., 2020. Positive root pressure is critical for whole-plant desiccation recovery in two species of terrestrial resurrection ferns. J. Exp. Bot. 71, 1139–1150. https://doi.org/10.1093/jxb/erz472.

Hostrup, O., Wiegleb, G., 1991. Anatomy of leaves of submerged and emergent forms of *Littorella uniflora* (L.) Ascherson. Aquat. Bot. 39, 195–209. https://doi.org/10.1016/0304-3770(91)90032-Z.

Huang, M.Y., Wong, S.L., Weng, J.H., 2021. Rapid light-response curve of chlorophyll fluorescence in terrestrial plants: Relationship to CO_2 exchange among five woody and four fern species adapted to different light and water regimes. Plants 10 (3), 445. https://doi.org/10.3390/plants10030445.

Huang, R., Oduor, A.M.O., Yan, Y., Yu, W., Chao, C., Dong, L., Jin, S., Li, F., 2024. Nutrient enrichment, propagule pressure, and herbivory interactively influence the competitive ability of an invasive alien macrophyte *Myriophyllum aquaticum*. Front. Plant Sci. 15, 1411767. https://doi.org/10.3389/fpls.2024.1411767.

Jeppesen, E., Lauridsen, T.L., Kairesalo, T., Perrow, M.R., 1998. Impact of submerged macrophytes on fish-zooplankton interactions in lakes. In: Jeppesen, E., Søndergaard, M., Søndergaard, M., Christoffersen, K. (Eds.), The structuring role of submerged macrophytes in lakes, ecological studies. Springer, New York, NY, pp. 91–114. https://doi.org/10.1007/978-1-4612-0695-8_5.

Jiang, H.S., Zhang, Y., Yin, L., Li, W., Jin, Q., Fu, W., Zhang, T., Huang, W., 2018. Diurnal changes in photosynthesis by six submerged macrophytes measured using fluorescence. Aquat. Bot. 149, 33–39. https://doi.org/10.1016/j.aquabot.2018.05.003.

Koch, G.W., Sillett, S.C., Jennings, G.M., Davis, S.D., 2004. The limits to tree height. Nature 428, 851–854. ⟨https://www.nature.com/articles/nature02417⟩ (accessed 11.25.23).

Koyama, K., Takemoto, S., 2014. Morning reduction of photosynthetic capacity before midday depression. Sci. Rep. 4, 4389. https://doi.org/10.1038/srep04389.

Krähmer, D., Kováč, E., 2016. Optimal sequential delegation. J. Econ. Theory 163, 849–888. https://doi.org/10.1016/j.jet.2016.03.009.

Li, Z., Ji, W., Hong, E., Fan, Z., Lin, B., Xia, X., Zhu, X., 2023. Study on heat resistance of peony using photosynthetic indexes and rapid fluorescence kinetics. Horticulturae 9, 100. https://doi.org/10.3390/horticulturae9010100.

Liu, J., Zhao, Y., Sial, T.A., Liu, H., Wang, Y., Zhang, J., 2022. Photosynthetic responses of two woody halophyte species to saline groundwater irrigation in the taklimakan desert. Water 14, 1385. https://doi.org/10.3390/w14091385.

Marks, C.O., Muller-Landau, H.C., Tilman, D., 2016. Tree diversity, tree height and environmental harshness in eastern and western North America. Ecol. Lett. 19, 743–751. https://doi.org/10.1111/ele.12608.

Millar, B.C., Fielden, E.M., Millar, J.L., 1978. Interpretation of survival-curve data for chinese hamster cells, line v-79 using the multi-target, multi-target with initial slope, and α, β equations. international journal of radiation biology and related studies in physics. Chem. Med. 33, 599–603. https://doi.org/10.1080/09553007814550521.

O'Keefe, K., Smith, D.D., McCulloh, K.A., 2023. Linking stem rehydration kinetics to hydraulic traits using a novel method and mechanistic model. Ann. Bot. 131, 1121–1131. https://doi.org/10.1111/tpj.14651.

Pedersen, O., 1994. Acropetal water transport in submerged plants. Botanica acta 107 (2), 61–65. https://doi.org/10.1111/j.1438-8677.1994.tb00409.x.

Petit, G., Pfautsch, S., Anfodillo, T., Adams, M.A., 2010. The challenge of tree height in *Eucalyptus regnans*: when xylem tapering overcomes hydraulic resistance. N. Phytol. 187, 1146–1153. https://doi.org/10.1111/j.1469-8137.2010.03304.x.

Pittermann, J., 2010. The evolution of water transport in plants: an integrated approach. Geobiology 8, 112–139. https://doi.org/10.1111/j.1472-4669.2010.00232.x.

Richards, P.W., Sculthorpe, C.D., 1968. The biology of aquatic vascular plants. J. Ecol. 56, 915. https://doi.org/10.2307/2258117.

Rosell, J.A., Olson, M.E., 2014. Do lianas really have wide vessels? Vessel diameter–stem length scaling in non-self-supporting plants. Perspect. Plant Ecol. 16, 288–295. https://doi.org/10.1016/j.ppees.2014.08.001.

Ryan, M.G., Yoder, B.J., 1997. Hydraulic limits to tree height and tree growth. Bioscience 47, 235–242. https://doi.org/10.2307/1313077.

Savage, J.A., Beecher, S.D., Clerx, L., Gersony, J.T., Knoblauch, J., Losada, J.M., Jensen, K.H., Knoblauch, M., Holbrook, N.M., 2017. Maintenance of carbohydrate transport in tall trees. Nat. Plants 3, 965–972. https://doi.org/10.1038/s41477-017-0064-y.

Shah, D.U., Reynolds, T.P., Ramage, M.H., 2017. The strength of plants: Theory and experimental methods to measure the mechanical properties of stems. J. Exp. Bot. 68, 4497–4516. https://doi.org/10.1093/jxb/erx245.

Shao, H., Gontero, B., Maberly, S.C., Jiang, H.S., Cao, Y., Li, W., Huang, W.M., 2017. Responses of *Ottelia alismoides*, an aquatic plant with three CCMs, to variable CO_2 and light. J. Exp. Bot. 68, 3985–3995. https://doi.org/10.1093/jxb/erx064.

Sharma, A., Kumar, V., Shahzad, B., Ramakrishnan, M., Singh Sidhu, G.P., Bali, A.S., Handa, N., Kapoor, D., Yadav, P., Khanna, K., Bakshi, P., Rehman, A., Kohli, S.K., Khan, E.A., Parihar, R.D., Yuan, H., Thukral, A.K., Bhardwaj, R., Zheng, B., 2020. Photosynthetic response of plants under different abiotic stresses: a review. J. Plant Growth Regul. 39, 509–531. https://doi.org/10.1007/s00344-019-10018-x.

Speck, T., Burgert, I., 2011. Plant stems: Functional design and mechanics. Annu. Rev. Mater. Res. 41, 169–193. https://doi.org/10.1146/annurev-matsci-062910-100425.

Verhofstad, M.J.J.M., Alirangues Núñez, M.M., Reichman, E.P., Van Donk, E., Lamers, L. P.M., Bakker, E.S., 2017. Mass development of monospecific submerged macrophyte vegetation after the restoration of shallow lakes: Roles of light, sediment nutrient levels, and propagule density. Aquat. Bot. 141, 29–38. https://doi.org/10.1016/j.aquabot.2017.04.004.

Wang, L., Gao, Y., Wang, X., Qin, Z., Liu, B., Zhang, X., Wang, G., 2021. Warming enhances the cadmium toxicity on macrophyte *Myriophyllum aquaticum* (Vell.) Verd. seedlings. Environ. Sci. Pollut. Res. 268, 115912. https://doi.org/10.1016/j.envpol.2020.115912.

Wang, Z., Zhang, B., Chen, Z., Wu, M., Chao, D., Wei, Q., Xin, Y., Li, L., Ming, Z., Xia, J., 2022. Three OsMYB36 members redundantly regulate Casparian strip formation at the root endodermis. Plant Cell 34 (8), 2948–2968. https://doi.org/10.1093/plcell/koac140.

Wersal, R.M., Madsen, J.D., 2011. Comparative effects of water level variations on growth characteristics of *Myriophyllum aquaticum*. Weed Research 51 (4), 386–393. https://doi.org/10.1111/j.1365-3180.2011.00854.x.

Westoby, M., 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. Plant Soil 199, 213–227. https://doi.org/10.1023/A:1004327224729.

Westoby, M., Falster, D.S., Moles, A.T., Vesk, P.A., Wright, I.J., 2002. Plant ecological strategies: Some leading dimensions of variation between species. Annu. Rev. Ecol. Syst. 33, 125–159. https://doi.org/10.1146/annurev.ecolsys.33.010802.150452.

Yang, S.J., Zhang, Y.J., Sun, M., Goldstein, G., Cao, K.F., 2012. Recovery of diurnal depression of leaf hydraulic conductance in a subtropical woody bamboo species: Embolism refilling by nocturnal root pressure. Tree Physiol. 32, 414–422. https://doi.org/10.1093/treephys/tps028.

Zhong, M., Cerabolini, B.E.L., Castro-Díez, P., Puyravaud, J.P., Cornelissen, J.H.C., 2020. Allometric co-variation of xylem and stomata across diverse woody seedlings. Plant Cell Environ. 43, 2301–2310. https://doi.org/10.1111/pce.13826.

Zou, M., Lin, X.W., Wu, X.D., Qin, Y., Ge, X.G., Hou, J.J., Peng, S., 2024. Regeneration and colonization abilities of submerged macrophytes under different fragment types and lengths: Comparison of the invasive species *Myriophyllum aquaticum* and the native species *Myriophyllum spicatum*. J. Plant Ecol. 17 (6), rtae085. https://doi.org/10.1093/jpe/rtae085.

Zhan A, Ni P, Xiong W, et al. **2017**. Zhan, A., Ni, P., Xiong, W., Chen, Y., Lin, Y., Huang, X., Gao, Y. 2017. Biological invasions in aquatic ecosystems in China. *Biological Invasions and Its Management in China: Volume 1*, 67-96.doi.org/10.1007/978-94-024-0948-2_4.