Plant Soil
https://doi.org/10.1007/s11104-023-06386-9

RESEARCH ARTICLE

Effect of different *Hydrilla verticillata* harvesting intensities on *Vallisneria natans*: Implications for restoring and managing submerged macrophytes

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Received: 28 August 2023 / Accepted: 7 November 2023

Abstract
Background and aims Harvesting can regulate the overgrowth of submerged macrophytes and affect interspecific competition. However, the effects of harvesting on the growth and competition of submerged macrophytes with different growth forms, remains unclear.
Methods Simulation experiments were conducted to study the morphological and physiological indicators, competition intensity, and received light intensity of rosette-forming *Vallisneria natans* (*V.natans*) under different harvesting intensities of canopy-forming *Hydrilla verticillata* (*H.verticillata*).
Results *V. natans* had greater plant height and larger leaf area at a medium-intensity (harvest 30% and 45% of the plant height) harvesting than at other intensities. Medium-intensity harvesting was the most conducive to the accumulation of chlorophyll, whereas high-intensity (harvest 60% and 75% of the plant height) harvesting had the lowest chlorophyll content and highest malondialdehyde content in *V. natans*. Interspecific competition was observed between *H. verticillata* and *V. natans*, and the medium harvesting intensity of *H. verticillata* conferred a competitive advantage to *V. natans*. Harvesting *H. verticillata* affect the growth of *V. natans* by increasing the underwater light intensity, with a greater harvest intensity corresponding to stronger light intensity received by *V. natans*. Light conditions were the most suitable for the growth of *V. natans* under medium-intensity harvesting.
Conclusions Medium-intensity harvesting not only improved the recovery of *H. verticillata* but also increased the competitiveness of *V. natans*, thus promoting the growth of *V. natans*. Therefore, in practice, medium-intensity harvesting can be applied to the regulation of *H. verticillata* and *V. natans*.

Responsible Editor: Susan Schwinning.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s11104-023-06386-9.

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Published online: 23 November 2023

Keywords Submerged macrophytes · Harvesting · Morphological indicators · Physiological indicators · Competitive intensity

Introduction

Submerged macrophytes are important habitats for many aquatic organisms, which can promote nitrogen (N) and phosphorus (P) deposition, inhibit sediment resuspension, and absorb pollutants from water (Gao et al. 2017; Hilt et al. 2018; Liu et al. 2018). Such traits help improve water quality and maintain a clear state (Lv et al. 2018; Liu et al. 2020). Therefore, submerged macrophytes community reconstruction has become an important ecological restoration method in eutrophic lakes (Gao et al. 2020; Chao et al. 2022). However, the lack of management and regulation of submerged macrophytes communities lead to their excessive growth, and when they decay, nutrients and heavy metals will be relaesed, thereby deteriorating the water quality and further strengthening the competitive advantages of canopy-forming submerged macrophytes (Yin 2018; Wang et al. 2018; Li et al. 2023). The excessive accumulation of submerged macrophytes on the water surface also blocks the sun and affects the survival of underwater organisms (Klančnik et al. 2018), resulting in a single plant community structure and a significant decline in biodiversity (Yang et al. 2021a, b). Thus, submerged macrophytes must be effectively managed and regulated.

Submerged macrophytes can be regulated by controlling water levels, releasing herbivorous fish and herbicides, harvesting, salvaging, and other methods (Xu et al. 2014; Gao et al. 2017; Wu 2012). Harvesting is widely used because it removes plants quickly and effectively; moreover, it can effectively prevent the release of nutrients and heavy metals associated with plant decomposition into the water (Verhofstad et al. 2017; Zhang et al. 2023) by inhibiting canopy formation (Ni 1999; Zhu et al. 2022). Harvesting regulations have been implemented for Taihu Lake and Erhai Lake in China and Biwa Lake in Japan (Zhu et al. 2019; Kohzu et al. 2019; Yuan et al. 2021). However, the harvest intensity should be controlled at harvesting. A medium harvesting intensity can not only inhibit the growth and reproduction of algae, promote the attachment of new microorganisms, and inhibit the diffusion of the population to a certain extent (Wu et al. 2012; Li et al. 2014; Luo et al. 2020) but also promote the recovery of the harvested plant (Zhu et al. 2022). However, excessive harvesting intensity affects the restoration of submerged macrophytes and can even lead to the disappearance of communities (Wu et al. 2012; Hilt et al. 2018). Therefore, harvesting of submerged macrophytes with appropriate intensity is required (Xu et al. 2014; Ban et al. 2019; Ban et al. 2019) due to the effect of harvesting on interspecific competition among submerged macrophytes. According to their ecological niche, submerged macrophytes can be divided into two growth forms: canopy form and rosette form (Gopal and Goel 1993). For similar growth form plants, interspecific competition is particularly strong because of niche overlap (Suo et al. 2017; Guo et al. 2020). Various submerged macrophytes with different growth forms can grow together. However, because the large canopy formed on the surface of water occupies a large amount of growth space and shades the rosette-forming submerged macrophytes, canopy-forming submerged macrophytes often present a competitive advantage in terms of attaining living space, light, and other resources without harvesting (Zhang et al. 2019a; Hu et al. 2022). Current research has focused on how harvesting floating plants affects submerged macrophytes (Xu et al. 2014; Zhu et al. 2019) and impacts competition among submerged macrophytes with different growth forms (Mony et al. 2007; Silveira et al. 2018). However, studies on the effects of harvesting on interspecific competition are limited (Zuo et al. 2014) and need to be further explored.

Vallisneria natans (*V. natans*) and *Hydrilla verticillata* (*H. verticillata*) are common submerged macrophytes in the middle and lower reaches of the Yangtze River. Because of their fast breeding speed and strong adaptability, regeneration ability, and nutrient removal ability, they are often used for ecological restoration. Through the field investigation, in most lakes in Huangshi City, *H. verticillata* and *V. natans* are also widespread. Although both belong to Hydrocharitaceae, *H. verticillata* and *V. natans* have different growth forms and occupy surface and lower spatial niches in the water, respectively. The effects of harvesting *H. verticillata* on its growth, as well as the water quality (Wu 2012; Zhu et al. 2022) and interspecific competition between *H. verticillata* and *V. natans* (Zhang et al. 2015; Yin 2018), have been studied. However, the effect of implementing different harvesting intensities of *H. verticillata* on the growth and competition of *V. natans* remains to be further explored. Therefore, this study select two different growth forms of submerged macrophytes of Hydrocharitaceae, canopy-forming *H. verticillata* and rosette-forming *V. natans*, to explore the effects of different harvesting intensities of *H. verticillata* on the morphology, physiology, and competition with *V. natans* and provide a recommendations for the restoration in freshwater systems and management of submerged macrophytes.

Materials and methods

Experimental design

Our experimental site is located outside the Laboratory of Aquatic Ecological Restoration of Hubei Normal University (adjacent to Qingshan Lake) in Huangshi City, Hubei Province, China (Fig. 1). The region belongs to the subtropical monsoon climate, warm in winter and hot in summer. The average temperature during our experiment is 31.01 ± 3.76 °C and the average duration of sunshine is 11 h.

The experiment lasted from May 10, 2019 to July 18, 2019. Well-grown stout seedlings of *H. verticillata* and *V. natans* were collected as test samples from typical shallow lakes in the middle reaches of the Yangtze River (115.05° E, 30.24° N; 114.73° E, 30.29° N). Each plant was wrapped in a black plastic bag containing sediment and kept under reasonable humidity in a fresh-keeping box for transport to

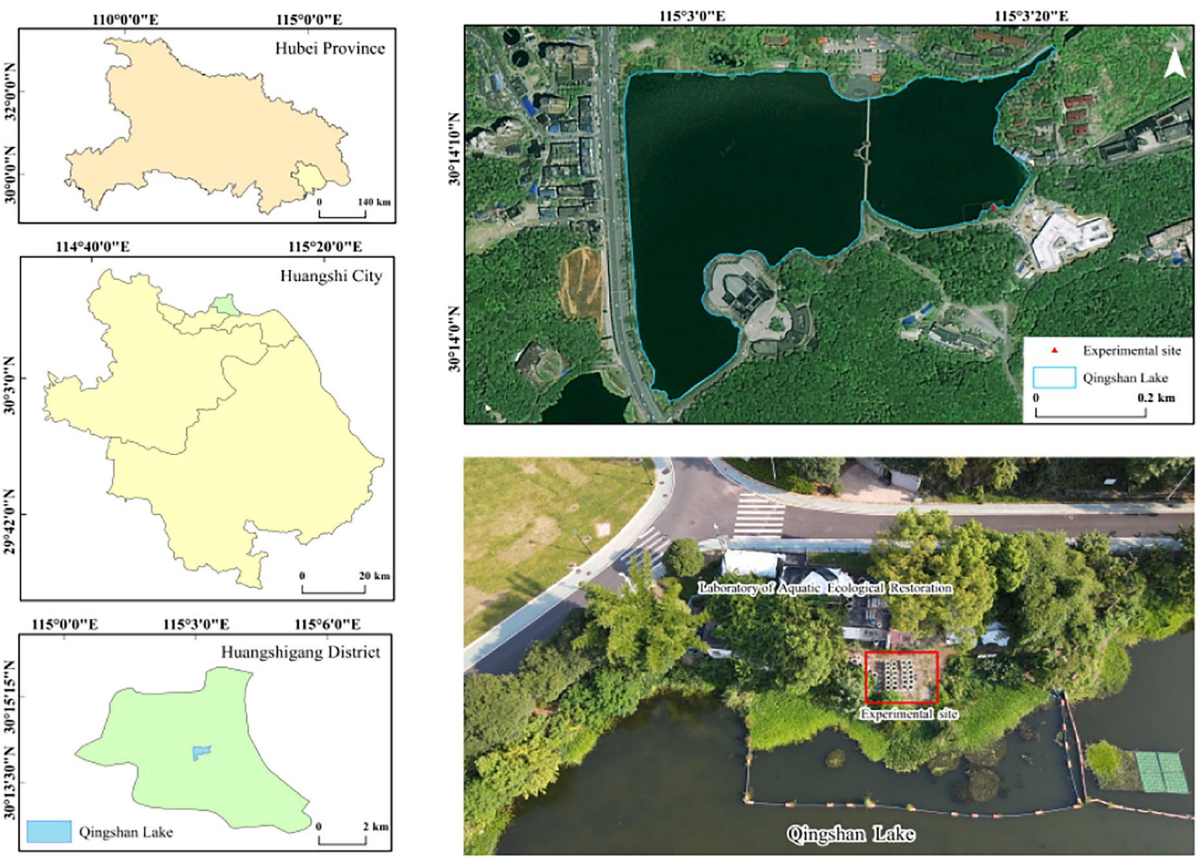


Fig. 1 Study area

our experimental site. Each sample was washed with water to clean the soil from the seedling roots and sprayed with 46% Cu $(OH)_2$ wettable powder for disinfection and to maintain freshness.

Sediment (TP: 1201.77 ± 106.85 mg/kg, TN: 620.74 ± 171.75 mg/kg, OM:71.32 ± 6.36 g/kg) samples from Qingshan Lake, which is a typical urban eutrophic lake, were added to individual barrels (height: 70 cm; upper diameter: 60 cm; lower diameter: 50 cm). Before adding sediment to the barrel, we sieved the sediment from Qingshan lake for many times, and screened out a small amount of snails, small fish and other debris. Then twenty *H. verticillata* and *V. natans* seedlings with a height of 15 cm were planted in each barrel. *H. verticillata* and *V. natans* we selected have no branched and the weight of *H. verticillata* was about 0.47 ± 0.0482 g with 20 ± 1 stem nodes, and the weight of *V. natans* is about 0.72 ± 0.0903 g with 6–7 leaves. In order to make up for the evaporation of water, water was replenished in time during the experiment to ensure that the water level was 65 cm. When most of *H. verticillata* in different treatment groups grew to the water surface, they were harvested at different intensities at the same time. The first harvest and third harvests were June 8 and July 18, 2019, respectively.

The harvest intensity was set to 15% (C15), 30% (C30), 45% (C45), 60% (C60), and 75% (C75) of the plant height. C15 was low harvest intensity, C30 and C45 were medium harvest intensity, C60 and C75 were high harvest intensity. The non-harvest group (CK), *V. natans* alone group (VK), and *H. verticillata* alone group (HK) were set up as the three control groups (Fig. 2). Each treatment group had three replicates, and a total of 24 barrels were cultured. In the first two harvests, we only harvested three replicates of *H.verticillata* in different treatment groups, and did not ended any replicate. It was not until the third harvest that we uprooted all the plants in the barrels (24 barrels). At the end of the experiment, we measured the water temperature, dissolved oxygen, turbidity, conductivity, pH, total suspended solids, redox potential (Table S1).

Measured indicators

Morphological indicators

After harvesting *H. verticillata* at different intensities, the morphological indexes of *V. natans* were measured every 7 days. Nine *H. verticillata* and *V. natans* were randomly selected from each barrel. Plant height and leaf number were recorded, and 3–4 leaves were selected to measure the leaf area of *V. natans*. When most of the *H. verticillata* grew to the surface of water again, second harvest was performed. After *H. verticillata* grew to the surface of water a third time, all plants in each bucket were uprooted and rinsed with water, the water was wiped off with absorbent paper, and the plants were weighed to obtain the fresh weight. Finally,

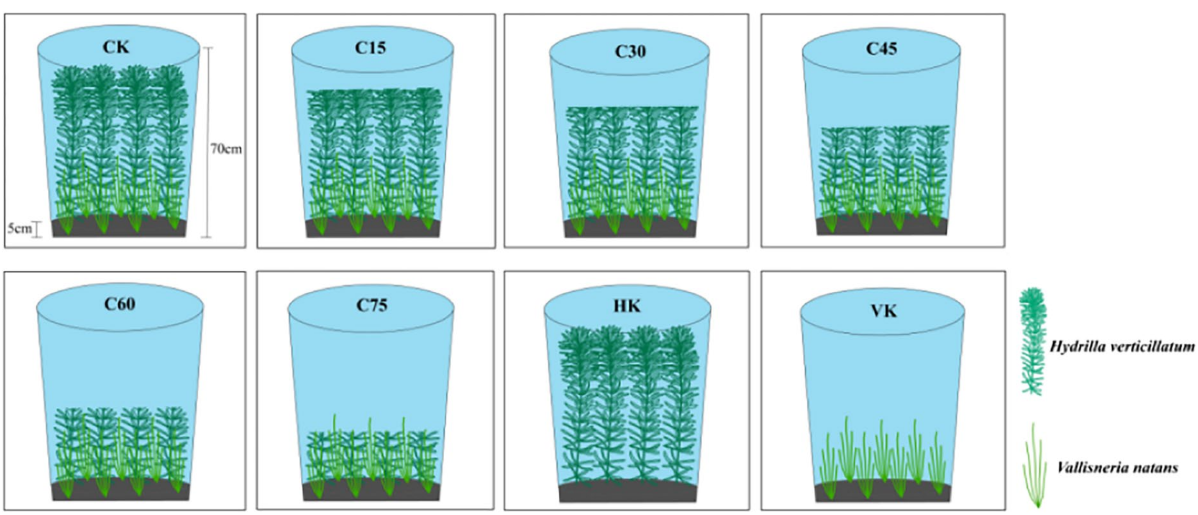


Fig. 2 Experimental design

all plants were dried in an oven at 85 °C to constant weight.

Physiological indicators

At the end of the experiment, the chlorophyll (Chl) and malondialdehyde (MDA) contents of *V. natans* were determined. According to the method in 'Plant Physiology Experiment Tutorial' (Wang 2017), the Chl in the leaves of *V. natans* was determined using 95% ethanol-spectrophotometry, and the MDA content was determined using the thiobarbituric acid method.

Competitive intensity

The relative yield (RY) is used to measure the intraspecific and interspecific competition between plants. RY < 1 indicates when a species is mixed planting with another species, its growthe is better than its single species, and the intraspecific competition is stronger than the interspecific competition. More than 1 is the opposite. The competition intensity (RCI) can measure the effect of interspecific competition on plants. When it is greater than 0, it indicates that the plant is greatly affected by the interspecific competition of other plant species. The relative crowding coefficient (RCC) is related to competitive advantage.The larger the RCC value is, the stronger the competitive advantage of species is. So RY, RCI and RCC were selected to determine the competitive ability of *V. natans* (Williams and McCarthy 2001; Weigelt and Jolliffe 2003).

The formula is as follows:

$$RY_i = \frac{Y_{ij}}{P_i Y_i} \tag{1}$$

$$RCI_i = 1 - RY_i \tag{2}$$

$$RCC_i = \frac{P_i Y_{ij}}{P_i (Y_i - Y_{ij})} \tag{3}$$

where Y represents the biomass of the species in each barrel; i and j represent the different species, in our experiment, i and j refer to *V. natans* and *H. verticillata*, respectively; Y_{ij} represents the biomass of *V. natans* in the presence of *H. verticillata*; Y_i and Y_j represents the biomass of *V. natans* and *H. verticillata* for individual plantings, respectively; P_i and P_j represent the proportion of *V. natans* and *H. verticillata* in mixed planting, respectively, $P_i + P_j = 1$. In our experiment, the proportion of *H. verticillata* and *V. natans* accounted for 50% respectively.

Light intensity

After harvesting *H. verticillata*, the light intensity of each treatment group at water depths of 10, 20, 30, 40, and 50 cm was measured using an illuminometer (ZDS-10W-1D). The measurement frequency was once per week.

Data processing

ArcGIS10.2 was used to illustrate the map of study area and experimental design. The data were processed using Microsoft Excel. In Origin 2021, a one-way analysis of variance (ANOVA) was performed to test the differences in morphological indicators, physiological indicators, competition intensity, and light intensity of the different treatment groups (the significance level was set to 0.05). All data were tested for normality and homogeneity of variance prior to the ANOVA. Post hoc multiple comparisons were performed using Tukey test.

Results

Morphological indicators

Plant height

During three harvests, the plant height in the VK group which planted *V. natans* alone and no harvest was the highest (Fig. 3). After the first harvest, the plant height of C15 was the slowest only 24.17 ± 1.84 cm, and increased rapidly in the two weeks after harvest, which was 10.92% and 15.85% higher than that at harvest, respectively (Fig. 3(a)). Therefore, at the second harvest, C15 treatment group became the highest plant height (Fig. 3(b)). After the third harvest, the plant height of C60 and C75 were only 18.29 ± 2.86 cm and 18.19 cm ± 3.22 cm, respectively (Fig. 3(c)). During the whole experiment, the plant height increased rapidly in the first week after the first harvest, whereas the growth rate was relatively slow during the second week. Compared to

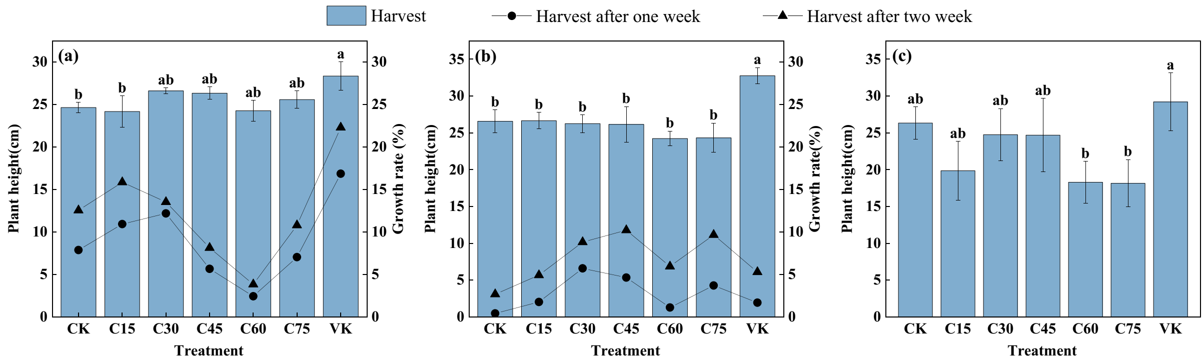


Fig. 3 Effect of harvesting *H. verticillata* on the plant height of *V. natans*. (**a**), (**b**), and (**c**) represent the first, second, and third harvests of *H. verticillata*, respectively. Different lowercase letters represent the difference between the treatment groups at a significant level of 0.05 (ANOVA). The error bar represents SD. C15, C30, C45, C60 and C75 represent the harvesting intensity, respectively, which means harvesting at 15%, 30%, 45%, 60% and 75% of the plant height. (same below). The bar graph represents the plant height of *V. natans* at harvest, and the dotted line graph represents the growth rate of plant height change of *V. natans* within two weeks after harvest

the first harvest, the growth rate of plant height of *V. natans* after the second harvest was generally lower.

Leaf number

There was no significant difference in leaf numbers of *V. natans* among the groups (ANOVA, $p > 0.05$) (Fig. 4). After the first harvest, the average leaf number in each harvest treatment group was 11.63 ± 0.27 pieces and decreased within 2 weeks after harvest. The leaf number of C15 and C30 decreased the fastest within two weeks after harvest, which decreased by 12.68% and 18.06%, respectively (Fig. 4(a)). After the second and third harvests, the leaf number of *V. natans* decreased to 8.20 ± 0.23 and 8.20 ± 0.51 pieces, respectively (Fig. 4(b, c)).

Leaf area

Different harvesting intensities of *H. verticillata* had a great effect on the leaf area of *V. natans* (Fig. 5). The leaf area of *V. natans* in the VK treatment group (*V. natans* alone) was always larger than that in the harvested groups. Among the three harvests, the leaf area of C60 and C75 was always lower, especially after the second harvest. However, the leaf area tended to increase within 2 weeks after each harvest. Especially, the leaf area of C60 treatment group increased by 27.83% within two weeks after the first harvest, and

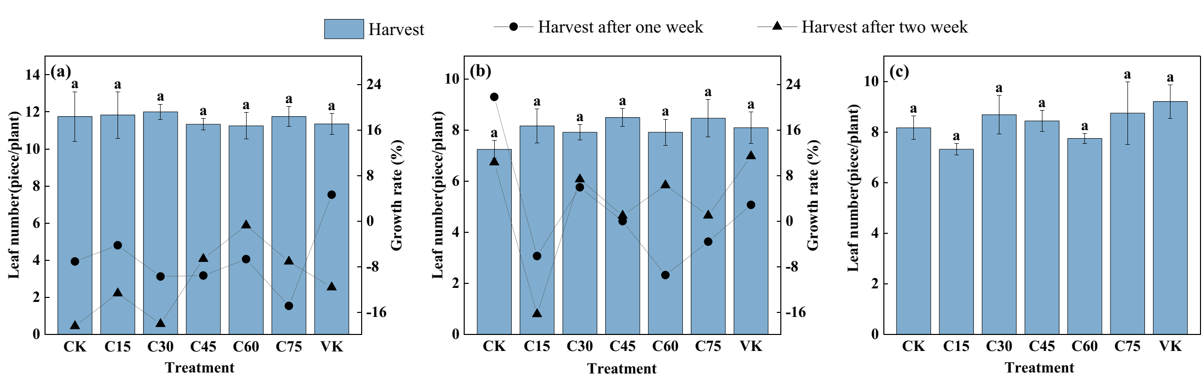


Fig. 4 Effect of harvesting *H. verticillata* on the leaf number of *V. natans*

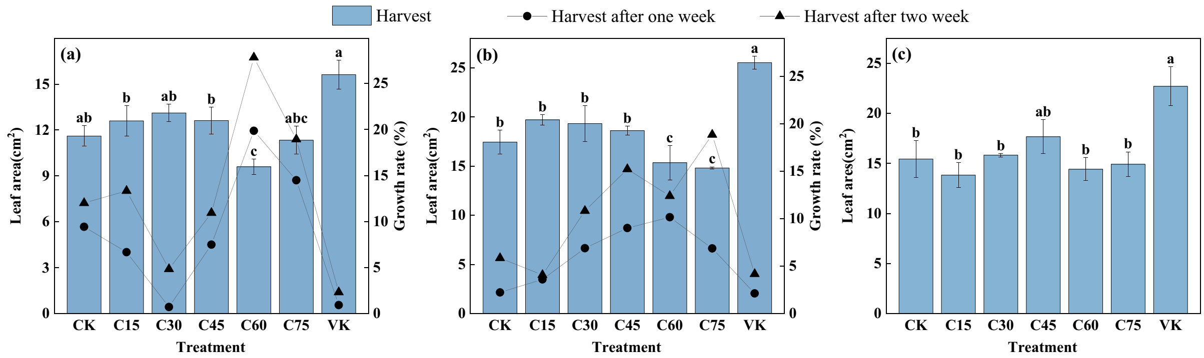


Fig. 5 Effect of harvesting *H. verticillata* on the leaf area of *V. natans*

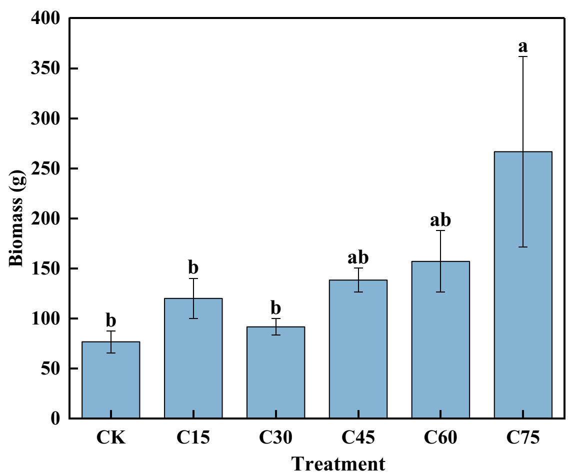


Fig. 6 Effect of harvesting *H. verticillata* on the biomass of *V. natans*

C75 treatment group increased by 18.85% after the second harvest. At the third harvest, C45 had the largest leaf area.

Biomass

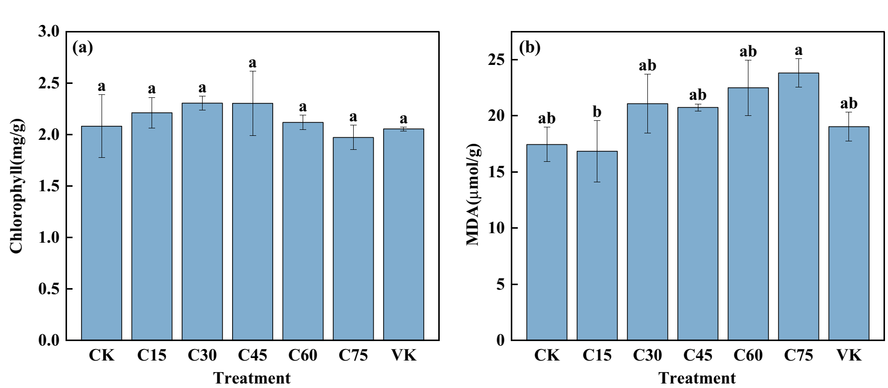
The final biomass of *V. natans* decreased first and then increased with the increase of harvesting intensity of *H. verticillata* (Fig. 6). The smallest biomass was C30, only 91.67 ± 14.43 g. The biomass of C75 was the largest in all treatment groups, which was 2.91 times that of C30.

Physiological indicators

Chlorophyll content

As the harvesting intensity of *H. verticillata* increased, the Chl content initially increased and then decreased (Fig. 7(a)); however, significant differences were not observed among the treatment

Fig. 7 Effect of harvesting *H. verticillata* on the Chlorophyll (**a**) and MDA content (**b**) of *V. natans*



groups (ANOVA, $p = 0.4851$). The Chl content in the C30 treatment group was the highest at 2.30 ± 0.07 mg/g, whereas that of the C75 treatment group was the lowest at only 1.97 ± 0.12 mg/g.

MDA content

Harvesting *H. verticillata* at different intensities affected the MDA content of *V. natans* (Fig. 7(b)). The MDA content of the C75 treatment group was the highest and reached 23.80 ± 1.27 μmol/g, which was significantly higher than that of the C15 treatment group (ANOVA, $p = 0.0357$). The higher the harvesting intensity, the higher the MDA content in *V. natans*.

Competitive intensity

Relative yield

The RY of each treatment group initially increased and then decreased with increasing harvest intensity (Fig. 8(a)). After harvesting *H. verticillata* at different intensities, the RY of *V. natans* was greater than 1, indicating that the intraspecific competition intensity of *V. natans* was greater than that of *H. verticillata*. The RY value of C30 was the largest at 2.65 ± 0.52, which was significantly higher than that of the CK (ANOVA, $p = 0.0193$), C60 (ANOVA, $p = 0.0270$) treatment groups.And the lowest RY was C75 (0.85 ± 0.47).

Relative competitive intensity

As the harvesting intensity increased, the RCI value of *V. natans* initially decreased and then increased, reaching the minimum value of -1.65 ± 0.52 in C30 (Fig. 8(b)). The RCI value of C30 was significantly lower than that of CK (ANOVA, $p = 0.0193$), C60 (ANOVA, $p = 0.0270$), indicating that the growth of *V. natans* was least affected by interspecific competition with *H. verticillata* under a 30% harvesting intensity. The RCI of C75 was greater than 0, the other treatment groups were less than 0, indicating that *V. natans* was greatly affected by interspecific competition after 75% harvest of *H. verticillata* but less affected by interspecific competition in the other groups.

Relative crowding coefficient

Except for C30, the RCC of other treatment groups were all greater than 0. (Fig. 8(c)).The RCC of C45 was the largest (up to 3.32 ± 1.02), but significant differences were not observed compared to the other treatment groups (ANOVA, $p > 0.05$). The RCC_i of C30 was -5.80 ± 2.10, which was significantly lower than that of CK (ANOVA, $p = 0.0013$), C60 (ANOVA, $p = 0.0011$), and C75 (ANOVA, $p = 0.0080$).

Light intensity

After harvesting *H. verticillata* at different harvesting intensities, the underwater light intensity of each treatment group changed in the order C75 > C60 > C45 > C30 > C15 > VK > CK. The greater the harvesting

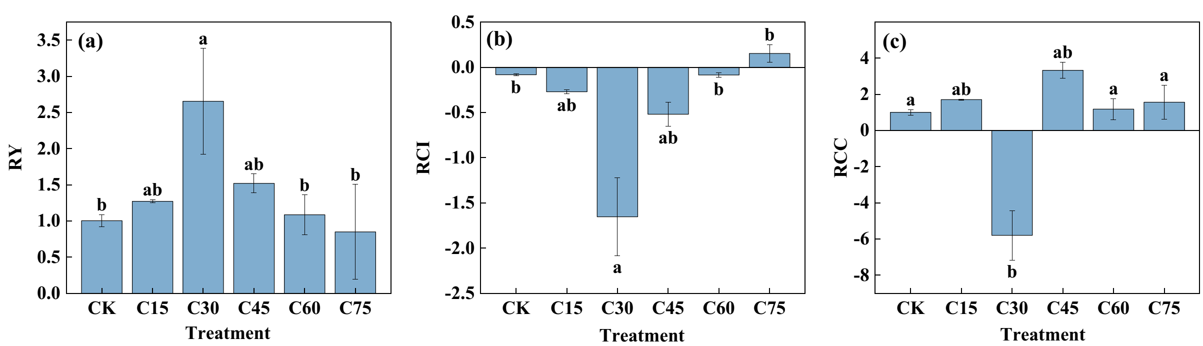


Fig. 8 Effect of harvesting *H. verticillata* on the relative yield (**a**), relative competition intensity (**b**) and relative crowding coefficient (**c**) of *V. natans*

intensity, the stronger the underwater light (Fig. S1). The light intensity in the VK treatment group was greater than that in the CK treatment group, indicating that interspecific competition affected the underwater light intensity. The light intensity at a depth of 10–30 cm changed greatly, whereas that at a depth of 30–50 cm was relatively small. After harvesting intensities of *H. verticillata*, the underwater light intensity of each treatment rapidly weakened in the first week (Fig. S1(a)). The rate of decrease in underwater light intensity in the second week was slower than that in the first week and faster than that in the third week, indicating that plant recovery was mainly concentrated in the first two weeks after harvest. While the growth of branches and leaves in the third week slowed; therefore, the rate of decrease in underwater light intensity was relatively slow.

Discussion

Effect of harvesting *H. verticillata* on the growth of *V. natans*

Harvest and competition are two factors affect the growth and development of submerged macrophytes. After three harvestes, *H. verticillata* could still recover at each harvesting intensity (Table S2). It indicated that *H. verticillata* had a strong recovery ability, which was consistent with the findings of Zhu et al. (2022). Harvesting *H. verticillata* leads to changes in environmental conditions (such as sufficient space, sunlight and nutrients), which can affect the growth of *V. natans*. A previous study showed that nutritional competition occurred between *H. verticillata* and *V. natans* (Van et al. 1999). The low-intensity harvesting enabling *H. verticillata* to recover almost completely in a short period. And when the harvesting intensity was low, *V. natans* was sheltered by *H. verticillata*, thereby inhibiting the growth of *V. natans*, so *V. natans* in the C15 treatment group (harvested 15% height of *H.verticillata*) had the lowest plant height after the first harvest. But within two weeks after the first harvest, the growth rate of C15 was the fastest, and the plant height was the highest at the second harvest. Research have showed that when light was sufficient, *V. natans* was more inclined to grow horizontally and accumulate biomass, while under lower light, it was more inclined to grow vertically and obtain more light resources by extending its leaf length (Fu et al. 2012; Yu 2022). So in the face of shading caused by *H. verticillata*, *V. natans* will actively increase plant height and leaf length to obtain more light. It was consistent with the study of Li et al. (2017) and Xiao et al. (2007). Under medium-intensity harvesting (C30 and C45), harvesting removed a certain amount of biomass of *H. verticillata* (Table S3), weakened the recovery ability of *H. verticillata* and delayed its recovery time. Therefore, the competition for nutrients, light and space likely decreased, which is conducive to the increase of plant height and leaf extension of *V. natans*. After the second and third harvests, the lowest plant height of *V. natans* was observed in C60, C75 treatment groups because high-intensity harvesting significantly inhibited the growth of *H. verticillata* and the light intensity was higher than that of the other treatment groups, which may have resulted in photoinhibition of *V. natans* under strong light (Li et al. 2020). However, sufficient space and limited nutrient competition make *V. natans* have larger biomass.Wu (2012) also found that the growth of *H. verticillata* was inhibited to a certain extent in the early stage of high-intensity harvesting and *H. verticillata* aging and withering in the later stage of the experiment. In addition, *H. verticillata* occupies space close to the water surface due to its dense canopy, which has a significant impact on algal growth. Because algal and phytoplankton mainly grow in the surface of water, and the branches and leaves of *H. verticillata* can compete for space, light and nutrients (Zhu et al. 2022; Xie et al. 2023). Thus, the growth or outbreak of phytoplankton and algae in the water also affect the growth of *V. natans* after harvesting *H. verticillata*. (Yu et al. 2017).

Effect of harvesting *H. verticillata* on the physiology of *V. natans*

Chlorophyll is the most important pigment in plant photosynthesis and represents an important indicator of plant growth status (Gadallah 1995).Under low light stress, plants accelerate the synthesis of photosynthetic pigments and increase their Chl content to obtain greater photosynthetic capacity, which is one of the manifestations of stress in submerged macrophytes (Wang et al. 2020; Wei et al. 2018; Wang 2021). However, excessive light intensity can lead to Chl decomposition (Gao 2020). In our study, the Chl content of *V. natans* was highest in the C30 and C45 treatment groups but lowest in the C75 treatment group, indicating that medium harvesting of *H. verticillata* could promote the accumulation of the Chl content in *V. natans*. However, if the harvesting intensity was too high, the lack of coverage of *H. verticillata* would lead to photoinhibition in *V. natans*; this change causes the Chl in *V. natans* to be decomposed, resulting in a decrease in Chl content. Gao (2020) also found that high light intensity reduced the Chl content and photosynthetic capacity of *H. verticillata*.

In addition to adapting to changes in the external environment, plants have an adversity regulation system to cope with the effects of adverse environments. The protective enzyme system of plant tissues can regulate enzymes in the plant to resist damage under adverse conditions. However, when damage to the cell membrane by external conditions exceeds the defense ability of plants, the activities of superoxide dismutase (SOD), peroxidase (POD), catalase (CAT), and other enzymes in the tissue cannot be maintained at high levels. Subsequently, membrane lipid peroxidation is enhanced, and the cell membrane is destroyed, resulting in higher MDA levels (Hemalatha et al. 2020). The higher the MDA content, the more serious the damage to cell functions and the more obvious the inhibition of plant growth and metabolism (Gu et al. 2022). In this experiment, the greater the harvesting intensity of *H. verticillata*, the greater the light enhancement. Such changes led to serious damage in the cell membrane of *V. natans* leaves because of oxygen free radicals. Therefore, the MDA content of *V. natans* in the C75 and C60 treatment groups was higher. Under the lower harvesting intensity of *H. verticillata*, *V. natans* be shaded by *H. verticillata*; therefore, the MDA content of C15 was lower. Wang (2021) also found that the MDA content decreased under shading conditions.

Effect of harvesting *H. verticillata* on the competitive intensity of *V. natans*

Owing to the limitations of light, nutrition, and other resources in a specific space–time environment, plants growing together often experience intraspecific and interspecific competition for resources and living spaces (Silvertown and Charlesworth 2001). Previous studies have shown that when *H. verticillata* grew together with *V. natans* without harvesting, *H. verticillata* had a strong competitive ability and would gradually become a dominant species (Yin 2018). The lowest competitive advantage of *V. natans* was observed relative to *Potamogeton maackianus*, and *Elodea nuttallii*(*E.nuttallii*), while it had a strong competitive advantage relative to *Myriophyllum spicatum* (*M. spicatum*) (Guo et al. 2023). In our experiment, after harvesting *H. verticillata*, the relative yield of each treatment group was greater than 1, indicating that different harvesting intensities could weaken the competition of *H. verticillata* to *V. natans*; therefore, the intraspecific competition intensity of *V. natans* was greater than that of *H. verticillata*. Among the treatments, the intraspecific competition of *V. natans* in the C30 treatment group was the most intense, which may be related to the limited growth space of *V. natans*. Under the harvest intensity of C45, C60, and C75, the growth space was sufficient; therefore, the competition intensity was relatively small. The environmental conditions (light, nutrition, living space, etc.) created for *V. natans* make the competitiveness of *V. natans* stronger than that of *H. verticillata*.

Effect of harvesting *H. verticillata* on the light intensity of *V. natans*

The existence of canopy causes asymmetric competition for light between species (Schwinning & Weiner 1998; Austin Åsa et al. 2023); and the resulting shading affects interspecific competition (Ellawala et al. 2020). *H. verticillata* can produce a large number of branches on the water surface and form a dense upper canopy, which can shade other plants, especially rosette-forming plants. Owing to canopy, *H. verticillata* has certain advantages in occupying the upper space of the water and obtaining sunlight. While *V. natans* occupies less upper space in the water as a typical rosette-forming submerged macrophytes. Higher canopy-forming aquatic macrophytes are at a spatial competitive advantage, which, in turn, leads to a light competitive advantage (Zhang et al. 2015). Therefore, changes in light can affect interspecific competition (Sun et al. 2022; Austin Åsa et al. 2023).

Deterioration of the underwater light environment is the main reason why submerged macrophytes cannot grow normally or even disappear (Luo et al. 2020; Feng et al. 2022; Arthaud et al. 2021). The greater the harvesting intensity of *H. verticillata*, the stronger the underwater light. Because the branches and leaves of *H. verticillata* are mainly concentrated in the upper water layer, the light intensity of the 10–30 cm water layer changed greatly after the harvest of *H. verticillata*. Although *V. natans* grows in the lower layer of water and is highly tolerant to low light (Zhu et al. 2018; Zhang et al. 2021a), light intensities that either too high or too low are not conducive to the growth of *V. natans* (Zhang et al. 2021b; Chen et al. 2022). Excessive light can weaken the stress tolerance of *V. natans* (Goss et al. 2002). Morris et al. (2004) also found that the large-scale decline in *Vallisneria americana* in urban lakes was related to low oxygen in the water and low light underwater through field and indoor simulation experiments. In this study, both high and low light limited the growth of *V. natans*. Therefore, the underwater light environment created by the medium harvesting of *H. verticillata* was most conducive to the growth of *V. natans*. Notably, if the two competing submerged macrophytes are canopy-forming plant, light is no longer a limiting factor, and the reproduction, diffusion and shade tolerance of the submerged macrophytes will play a more dominant role (Yin 2018; Gergő et al. 2022). He et al. (2018) found that pruning *E. nuttallii* under shade conditions could prevent *E. nuttallii* from growing back to the water surface for a long time. And waterfowl grazing can also reduce the vegetation canopy height.

Implications for restoration and management of submerged macrophytes

The use of aquatic macrophytes is important for restoring eutrophic waters. The combined planting of various submerged macrophytes has a more obvious effect on water purification than a single submerged macrophytes (Liu et al. 2020; Zhang et al. 2019b), but it is not the case that the more the species, the better the purification effect (Hu et al. 2022; Guo et al. 2023). The higher the species abundance, the stronger the competitive effect between species than the promotive effect, which affects the growth and role of plants (Fu et al. 2019; Guo et al. 2023). So it is worth further consideration to select appropriate plant species for planting.

A large amount of biomass of canopy-forming plant often accumulates in the upper water, which not only has little effect on water purification (Gao et al. 2020) but also has adverse effects on the growth of other plants due to the shielding effect of the canopy. In this experiment, the canopy formed by *H. verticillata* on the water surface affected the light of the lower water; therefore, although *V. natans* has a certain ability to tolerate low light, too low light still affects its growth. Thus, while planting canopy-forming plants, it is necessary to consider the planting density (Silveira and Thiébaut 2020) and harvest them reasonably. Studies have shown that harvesting plants at the end of the growing season can effectively weaken the degree of eutrophication level of water (Zhang et al. 2023). But high-intensity harvesting may decrease or eliminate the association area of the plant in the following year, which is not conducive to the stability of the aquatic ecosystem. Moreover, appropriate methods should be adopted, and artificial harvesting should be adopted as much as possible. Because the intensity of mechanical harvesting is usually high and can easily disturb the water, resulting in an increase in turbidity and a decrease in dissolved oxygen, which affect the efficiency of aquatic macrophytes in utilizing light (Tan et al. 2019; Kohzu et al. 2019; Zhang et al. 2023). In addition, many broken branches will be produced during harvesting. If these broken branches are not collected, then submerged macrophytes (such as *H. verticillata* and *M. spicatum*) that can be vegetatively propagated by the broken branches will accelerate their spread.

However, under laboratory conditions, water depth, competition, plant growth space are limited, without water flow and wave interference, which were different compared to the field environment. When submerged macrophytes grow together, the interaction between species fluctuates between competition and facilitation (Hao et al. 2013), which will also affect the competitive relationship between *H. verticillata* and *V. natans,* due to different response to increased nutrient inputs (Van et al. 1999). Therefore, it is necessary to develop explore in field practice to further the restoration and application of submerged macrophytes in lakes.

Conclusions

We explored the effects of different harvesting intensities of *H. verticillata* on the growth and competition of *V. natans*. Interspecific competition occurred between *H. verticillata* and *V. natans*. Medium-intensity harvesting of *H. verticillata* created suitable light conditions for *V. natans* with higher plant height ($p < 0.05$), more leaves ($p > 0.05$), which was conducive to the advantage of *V. natans*. Medium-intensity harvesting was the most conducive to the accumulation of Chl. While under high-intensity harvesting, the Chl content of *V. natans* was the lowest and the damage to the cell functions of *V. natans* was the most serious. These results suggested that medium-intensity harvesting of *H. verticillata* can promote the growth of *V. natans* and the recovery of *H. verticillata*. Excessive harvesting intensity is not conducive to the growth of *V. natans*. In practice, medium-intensity harvesting can be applied to the regulation of *H. verticillata* and *V. natans*.

Acknowledgements This research was funded by the Open Foundation of Hubei Key Laboratory of Pollutant Analysis & Reuse Technology (Hubei Normal University) (PA220103), the Open Foundation of Research Center for Transformation and Development of Resource depletion Cities (Hubei Normal University)(KF2023Z01), graduate innovative research project construction of Hubei Normal University (No.20220454), and the College Students' Innovative Entrepreneurial Training Plan Program (No.S202210513073, No. 202210513014).

Author contributions Xiaowen Lin analyzed the data, wrote and revised the manuscript; Xiaodong Wu and Xuguang Ge conceived the ideas, designed the methodology and review the manuscript; Daoya Liu and Liang Chen designed the methodology and planned the experiment; Shixing Song, Chenxin Zhong, Zian Xiang collected the data; Zhenni Gao analyzed the data. All authors gave final approval for publication.

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

Declarations

Competing interest All authors declare no conflicts of interest.

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