

EFFECT OF UV-B RADIATION ON MORPHOLOGICAL PLASTICITY, FORAGING RESPONSES AND TURION OF *POTAMOGETON CRISPUS*

WANG, J. Q.* – SONG, Y. Z.

*School of Applied Meteorology, Nanjing University of Information Science & Technology,
Nanjing 210044, China*

*Key Laboratory of Ecosystem Carbon Source and Sink, China Meteorological Administration,
Beijing, China*

**Corresponding author
e-mail: w_j_q2000@hotmail.com*

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Abstract. *Potamogeton crispus* is an important species in purifying water and maintaining a healthy aquatic ecosystem. To find the effect of UV-B radiation on the life history of *P. crispus*, the seeding plants of *P. crispus* were exposed to different doses of UV-B radiation for 7 h within 81 days. Plant growth status, morphological indexes, turion morphology, and germination indexes of the turion were monitored. The results showed that UV-B radiation can promote *P. crispus* to branch, *P. crispus* did not branch in the absence of UV-B radiation. *P. crispus* had the most branches when the radiation intensity was 100 $\mu\text{W}/\text{cm}^2$. UV-B radiation accelerated plant decline when the exposure dose exceeded 100 $\mu\text{W}/\text{cm}^2$. Plant height, internode length, leaf area, and dry weight per plant all decreased with increasing radiation doses. UV-B radiation could stimulate *P. crispus* to form turions and increase the number of turions but reduced the weight of turions, it also led to low germination rate and reduced the growth index of shoots sprouted from these turions, especially when the exposure dose exceeded 100 $\mu\text{W}/\text{cm}^2$. These results suggest that moderate UV-B radiation plays an important role in controlling the branches, plant height and turion formation of *P. crispus*.

Keywords: *branch, plant height, leaf morphology, dry weight, germination rate*

Introduction

Potamogeton crispus is a submerged herbaceous perennial plant (Wang et al., 2022). It grows in freshwater lakes, ponds, paddy fields, and rivers (Deng et al., 2022), and produces large quantities of biomass (Yuan et al., 2021). *P. crispus* is a native aquatic submerged plant in Europe, Asia, Africa, Australia, and North America (Wang et al., 2022). *P. crispus* is an important primary producer in freshwater ecosystems, providing food for herbivorous fish and waterfowl (Jian et al., 2003). Therefore, the presence of *P. crispus* is of important significance in maintaining the balance and health of aquatic ecosystems (Zhou et al., 2017; Hao et al., 2018). As *P. crispus* consumes large amounts of nutrients, it sometimes depletes phosphorus and nitrogen in the water column (Yan et al., 2021; Yuan et al., 2021), decreases chemical oxygen demand (COD), enhances water transparency and dissolved oxygen concentration (Leoni et al., 2016; Lv et al., 2019; Yan et al., 2021; Yuan et al., 2021), and inhibits phytoplankton growth (Yuan et al., 2021). In addition, *P. crispus* can accumulate metals such as Fe, Pb, Ni, Mn, and Cu (Nabi, 2021; Geng et al., 2022), which makes it a potential candidate for bioremediation of polluted waters (Leoni et al., 2016; Lyu et al., 2019) to remove toxic metals such as Cd, Hg, and Pb from wastewater (Yang et al., 2010; Qiao et al., 2015; Nabi, 2021; Xu et

al., 2022). So, *P. crispus* is often used in the ecological restoration of eutrophic lakes because of its strong purification ability (Cao et al., 2018; Hao et al., 2018).

The life history of *P. crispus* differs from most submerged species (Zhu et al., 2022). When the water temperature begins to rise in the spring, it rapidly increases in vegetative growth (Sastroutomo, 1981; Adamec, 2018; Wang et al., 2021a; Wang et al., 2022). It flowers and produces turions almost simultaneously when the water temperature is higher than 20 °C and the photoperiod is longer than 12 h (Sastroutomo, 1981; Adamec, 2018). The turions begin to germinate from September to October in succession (Heuschele and Gleason, 2014; Adamec, 2018), enter into the seedling growing period from December to February, live through the winter from January to February in the next year, exponentially grow from March to April (Xie et al., 2014; Zhou et al., 2019; Deng et al., 2022). However, mass mortality of *P. crispus* can occur from May to June (He et al., 2023), possibly due to high water temperature and nutrient depletion in late spring and early summer (Rogers et al., 1988). However, a recent study revealed that intense light may be the real reason for the decline of *P. crispus* in that period. In the early stage of growth, the plant usually immerses under the water, and thus the impact of light on its growth is limited. In the later growing period, while the plant arrives at the water surface after rapid growth in late spring and early summer, intense light may inhibit its growth, resulting in the decline of *P. crispus* (Su et al., 2001; Wang et al., 2021a).

P. crispus could grow normally in the glass house in our laboratory throughout the year. The height of the *P. crispus* in this laboratory was 2-3 times higher than that in the field. What causes *P. crispus* in this laboratory to grow all year round, and why is its height several times higher than that in the wild? Through long-term observation, we found that the illumination difference between the inside and outside glasshouse was small, but ultraviolet radiation (UVR) especially UV-B decreased significantly. In general, photosynthetic active radiation outside penetrates into glass greenhouse at 80%~85% rate, 60-70% of UV-A but only 2-5% of UV-B radiation. Can UV-B radiation change the life history of *P. crispus*?

Many investigations on terrestrial plants have proved that UV-B radiation can inhibit the plants growth and reproduction (Zhang et al., 2022). A multitude of studies indicate that increased UV-B exposure is detrimental and has lethal or mutation effects on aquatic organisms, including phytoplankton, zooplankton, macroalgae, seagrass, fish, and amphibian (Aksakal and Ciltas, 2018; Kumar et al., 2019; El-Sheekh et al., 2021). Although UV-B radiation makes up only a small portion of the total energy of solar radiation and attenuates rapidly in the water column (Neha et al., 2021), the high sensitivity of living organisms to UV-B radiation makes it potentially important in aquatic ecosystems (Williamson et al., 2019). The ecological effects of UV radiation present a diversity of levels from biochemistry to community (Pérez et al., 2017; Gateva et al., 2022; Li et al., 2022). Several studies have indicated that phytoplankton is more sensitive to UVR, and UVR is generally considered to cause negative effects on phytoplankton such as inhibition of growth and photosynthetic rates (Mustaffa et al., 2020; Zhang et al., 2021). Some studies showed that zooplankton is negatively affected by the high intensity of UVR (Wolinski et al., 2016; Fernández et al., 2018). The most common effects of UVR on macroalgae include direct damage to photosynthetic apparatus, DNA reproductive tissue, and reduced nutrient uptake (Zhao et al., 2021; El-Manaway and Rashedy, 2022). UV-B radiation affects the physiology and ecology of seaweed, it leads to severe changes in

the functioning of coastal ecosystems by affecting the spatial, species, and functional structure of seaweed communities (El-Manaway and Rashedy, 2022). UVR can induce cellular and molecular damage in marine invertebrates and fish; it also can impair sperm motility, reduce fertilization, cause embryo malformation, and affect recruitment and the sustainability of natural populations (Ding et al., 2019; Alves and Agustí, 2020). Moreover, in the early short-term experiment (only 28 days), we found that high-intensity UV-B radiation was harmful to the growth of adult plants and promoted the decline of *P. crispus* (Wang et al., 2020). So, how does UV-B radiation affect the whole life history of *P. crispus*?

Therefore, the objectives of this study are to investigate the growth of *P. crispus* from the seedling stage under UV-B radiation, it is helpful to understand the effect of UV-B radiation on the life history of *P. crispus* and its role in its growth.

Materials and methods

Experimental condition

The experimental site was located in a glass greenhouse of Jiangsu Key Laboratory of Environmental Change & Ecological Construction (32.11°N, 118.91°E), China. According to the observation data of ultraviolet radiation intensity of Nanjing Meteorological Station from 2005 to 2009 (Fig. 1), the UV-B intensity increased gradually from January to May in Nanjing, and reached its annual peak in May, weakened in June on account of plum rains, maintained relatively higher intensity in July and August, and then declined till January next year.

The average water temperature and average day length at the experimental site during the experiment were listed in Table 1.

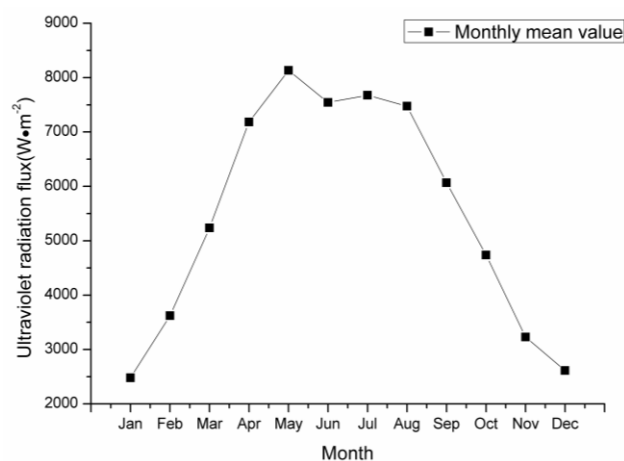


Figure 1. Monthly average value of ultraviolet radiation flux in Nanjing from 2005 to 2009

Table 1. Average water temperature and light condition of the experimental site

Item (time)	Beginning (May 8)	Growing period (May 9-May 31)	Breeding period (June 1-Jun 28)	Decline phase (June 29-July 28)
Average water temperature (°C)	23.6	21.9	24.4	27.8
Average day length (h)	13.6	13.9	14.2	14.1

Materials

The turions of *P. crispus* were collected from Xuanwu Lake of Nanjing on September 10, 2015. The newly formed turions were green or greenish brown, which was elected as the experimental materials and stored in the dark. These turions germinated completely on November 18, 2015, but the seedlings of *P. crispus* grew slowly because of the low water temperature. The seedlings entered into the growing period on March 12, 2016, and the seedlings with the same height were selected to be planted in the flowerpots. The height of the seedlings was 25 ± 2 cm. A small amount of clay and gravel was placed to fix the plant's roots in every flowerpot to reduce the effect of sediment. Each flowerpot contained 10 seedlings, and each flowerpot with 10 seedlings was placed in a 240-L plastic bucket (the height was about 105 cm), three replicates were set for each treatment, so each treatment had 30 seedlings.

The overlying water was made from tap water and nutrient solution, and the total nitrogen and total phosphorus content in overlying water were controlled by 2.0 ± 0.3 mg/L and 0.1 ± 0.02 mg/L constantly in all treatments during the experimental period, and the water depth was controlled in 80 ± 2 cm in all treatments.

Radiation dose

We selected the daily dose from April ($131.2 \mu\text{W}\cdot\text{cm}^{-2}$) to August ($239.8 \mu\text{W}\cdot\text{cm}^{-2}$) 2008 in Jiangsu Keylaboratory of Agriculture Meteorology as the reference for the experimental UV-B dose. In this study, the UVR intensity could not change gradually with the solar radiation, so we analyzed the UVR intensity of Nanjing Meteorological Station (Mao et al., 2011), and the time with the strongest radiation in a day was selected for radiation (9:00—16:00). The seedlings were exposed to UV-B radiation at different doses ($50 \mu\text{W}/\text{cm}^2$, $100 \mu\text{W}/\text{cm}^2$, $150 \mu\text{W}/\text{cm}^2$, and $200 \mu\text{W}/\text{cm}^2$) for 7 h every day. They were recorded as D50, D100, D150, and D200. The control group was only exposed to UV-A radiation and photosynthetically active radiation (PAR), and it was recorded as CK. Both PAR and UV-A radiation were set to the same condition for all groups. UV-B intensity was set through the SpectroSense2 (British SKYE company) to connect the SKU 430 UV-B sensor (280-315 nm). CK was adjusted with a polyester film layer and inclination direction, and therefore it received the same PAR as the treatment groups.

UV-B tubes were suspended in stainless steel with the height of 120 cm from the plants. The UV-B tubes were manufactured by Nanjing Huaqiang Special Light Source Factory (40 W, peak 313 nm, Fig. 2). The treatment doses were acquired by adjusting the height of the lamp. The UV-B tubes were hung in an east-west direction to reduce the impact of the tube shadows and ensure that each treatment group is exposed to the equivalent PAR.

Monitoring indexes and methods

Plant height: The lengths of 9-15 plants in the three replicates were measured from the border to the top of the main plant stem using stainless steel ruler, and the average length was calculated.

Internode length: The 10-15th internode length from the top was also measured in the three replicates in each treatment group, and the average value was calculated.

Leaf area: The first three to five fully expanded leaves from the top to the bottom of the plants were selected to measure the leaf area. The length of the main leaf veins was

measured using a ruler, and the leaf width was measured at the widest in the leaf. The leaf area of *P. crispus* was calculated according to Xie et al. (2004).

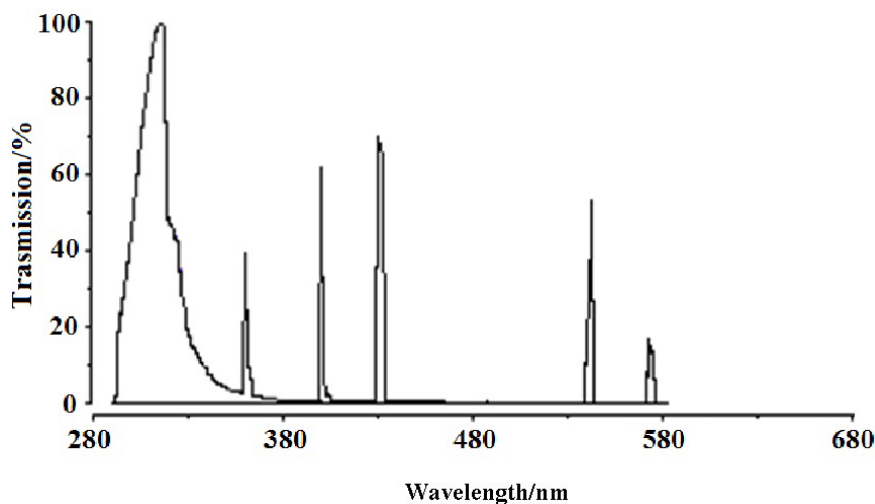


Figure 2. Spectrum distribution of the UV-B tube

Number of branches: The number of branches in the three replicates was counted and their average values were calculated.

Dry weight per plant: 9-15 plants in each group were cut from the plant root. The water was removed using absorbent paper. All samples were oven dried at 80 °C for 48 h to a constant weight to determine the dry weight. The dry weight per plant was calculated. The electronic balance (Quintix224-1CN, Sartorius, Germany) was applied to measure the dry weight, and the accuracy is one-millionth of a gram.

Weight and morphology of turion: On the last day of the experiment (at 81 d), all turions were collected. The water outside the turions was absorbed using absorbent paper, and removed attachments with a soft brush. Then the fresh weight of these turions was determined by the electronic balance described above, and the length and width of these turions were measured at the longest and widest place with a stainless steel ruler (*Fig. 3*).

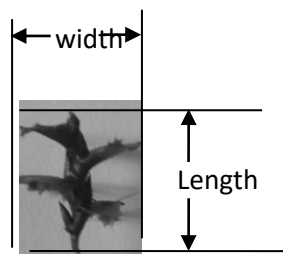


Figure 3. Determination schematic diagram of turion morphology

Turion morphology and growth condition of seedlings germinated from these turions: The turions formed and sunk to the bottom, and then were collected and preserved in distilled water to avoid the impact of water nutrients, and wrapped in a black blackout fabric to prevent inconsistent germination times. These turions were

placed in the natural light on November 31, 2016, and these turions germinated gradually, and the shoots began to grow after two weeks. The germination rate of turions was calculated on December 27, and the percentage was also calculated for turions that germinated two or more shoots. The height, leaf length, and width of the shoots were measured using a stainless steel ruler.

Ratio of two shoots: The ratio of two shoots was defined as the percentage of the turions number that can germinate two shoots or more shoots in the total number of turions.

Determination of growth duration

The growth duration was determined according to the plant growth status (*Table 1*), the growing period was from the second day to the 23rd day (May 9-May 31), the breeding period was from the 24th day to the 51st day (June 1-Jun 28), and the decline phase was the 52nd day to the 81st day (June 29-July 28).

Sampling frequency

All monitoring indexes were determined at intervals of about 7 days, and the experiment lasted for 81 days.

Statistical analysis

Statistical analyses were performed with SPSS 16.0, and statistical comparison by a two-way analysis of variance (ANOVA) was performed at a significance level of $p < 0.05$.

Results

Plant growth status

The leaves near the water surface in D50 to D200 groups began to bleach at 3d, and the leaves near the water surface at 5-10 cm in depth also appeared chlorosis and some bleaching speckles (*Fig. 4*). The bleaching speckles increased with increasing radiation dose. At 16 d, some leaves gradually returned to green. At 44 d, the plants of D200 began to decline, and the plants from the water surface to 20 cm deep turned yellow and rot. At 60 d, the plants of D150 began to decline, while some underwater dwarf branches grew normally, and D200 all declined. At 71 d, the leaves of D150 were severely damaged; partial leaves began to rot from the leaf margin to the leaf vein, and the whole bodies of a small number of plants died and rotted. At the same time, the leaves of D100 began to turn yellow only at the leaf margin, and a few of them showed necrosis symptoms. At 81 d, the leaves of D150 began to turn yellow at the leaf margin and decayed, with only the veins remaining, and the remaining plants were short. Meantime, the top of plants in D100 began to appear a little yellow and the damage degree was not significant. The top of D50 was almost uninjured and appeared a small amount of necrotic spots, the plants of CK grew well.

During the growing period, the plants of *P. crispus* started to produce turions on the top of the plants after 10 days of UV-B radiation (*Fig. 5*), but these turions were very light and soft and were significantly different from those formed in the natural environment. Within the next month, all these turions decayed and decomposed.



Figure 4. Damaged leaves of *P. crispus* under UV-B radiation



Figure 5. Turions formed at the beginning of the experiment (the place where the black finger points is the formed turions)

Number of branches

According to *Table 2*, at 16 d, the plants of CK had no branches, but the other treatment groups exhibited branches. The average number of branches appeared on D50 was 0.33. The average number of branches in D100 was 1.67, the most significant among all treatment groups ($p < 0.05$). D50 and D150 also were 0.33 and 0.67, respectively. The average number of branches in D200 significantly increased and the branch number was about 1.00. At 38 d, the average number of branches in all treatments did not increase significantly ($p > 0.05$), but D100 still showed the most significant compared with other treatment groups ($p < 0.05$), the average number of branches was 2.33, it increased by 40% compared with that at 16d. The number of branches in D150 and D200 did not increase significantly at 38 d ($p > 0.05$), compared with that at 16 d. Since then, the number of branches in each treatment has not changed.

Table 2. Number of branches affected by UV-B radiation ($n = 10$)

Time	CK	D50	D100	D150	D200
Branches number at 16d	0.00 ± 0.00Aa	0.33 ± 0.58Aa	1.67 ± 0.58Ab	0.67 ± 0.58Aa	1.00 ± 0.00Aa
Branches number at 38d	0.00 ± 0.00Aa	0.33 ± 0.58 Aa	2.33 ± 0.58 Ab	0.67 ± 0.58 Aa	1.33 ± 0.58Aa

Values represents the mean ± SD; Capital letters indicate statistical differences between different sampling date for the same treatment group, lowercase letters indicate statistical differences between different treatment groups on the same sampling day, the equal letters indicate no differences and different letters indicate significant differences

Morphological index

Plant height

The heights of all plants were about 70 cm-75 cm, and the four treatment groups (D50-D200) and CK exhibited no significant difference ($p > 0.05$) at the beginning (Fig. 6-1). During the growing period, the height of CK was significantly higher than those of the four treatment groups ($p < 0.05$). The plant height of CK increased by 16.36% compared with the beginning of the experiment, while the plant heights of D50-D200 reduced significantly by 15.44% ($p < 0.05$), 17.57% ($p < 0.05$), 25.95% ($p < 0.05$), and 18.84% ($p < 0.05$) compared with the beginning. The heights of D50-D200 were all lower than 70 cm and decreased with increasing radiation doses, and the heights of D50-D200 were significantly lower than that of CK by 29.42% ($p < 0.05$), 30.89% ($p < 0.05$), 38.65% ($p < 0.05$), and 34.97% ($p < 0.05$), respectively. During the breeding period, the heights of all groups decreased. The heights of D50-D200 were all lower than 60 cm and gradually decreased with increasing radiation doses, the height of D200 was the lowest at only 53.51 cm. The heights of D50-D200 decreased by 25.12% ($p < 0.05$), 24.95% ($p < 0.05$), 25.03% ($p < 0.05$), 25.68% ($p < 0.05$) compared with the beginning, and decreased by 28.48% ($p < 0.05$), 29.97% ($p < 0.05$), 37.83% ($p < 0.05$), and 34.10% ($p < 0.05$) compared with CK. During the decline phase, the height of CK was significantly higher than that in other treatment groups. The heights of D50-D200 decreased with increasing radiation doses, and the reduction rate increased gradually with increasing radiation doses. Compared with the beginning, the heights of D50-D200 were decreased by 18.55% ($p < 0.05$), 24.25% ($p < 0.05$), 29.19% ($p < 0.05$), and 41.90% ($p < 0.05$), respectively. The heights of D50, D100, D150, and D200 were also lower than that of CK by 16.01% ($p < 0.05$), 21.54% ($p < 0.05$), 27.52% ($p < 0.05$), and 42.48% ($p < 0.05$), respectively.

Internode length

During the growing period, the internode length of all treatment groups decreased (Fig. 6-2); CK decreased by 66.25% compared with the beginning, whereas the internode lengths of D50-D200 decreased respectively by 73.82% ($p < 0.05$), 77.02% ($p < 0.05$), 70.47% ($p < 0.05$), and 75.00% ($p < 0.05$) from the beginning. The internode lengths of D50-D200 groups decreased respectively by 27.77% ($p < 0.05$), 35.54% ($p < 0.05$), 17.86% ($p < 0.05$), and 32.15% ($p < 0.05$) compared with that of CK. During the breeding period, the internode length of CK had no significant change compared with that during the growing period ($p > 0.05$), but reduced by 66.97% ($p < 0.05$) compared with that at the beginning ($p < 0.05$). The internode lengths of D50-D200 groups were generally lower than those at the beginning by 74.62% ($p < 0.01$), 76.08%

($p < 0.01$), 76.65% ($p < 0.01$), and 80.10% ($p < 0.01$), respectively. Compared with the values in CK, their internode lengths of D50 –D200 groups were also lower by 28.46% ($p < 0.05$), 31.46% ($p < 0.05$), 33.62% ($p < 0.05$), and 44.81% ($p < 0.01$), respectively. During the decline phase, the internode lengths of D50-D200 were reduced gradually with increasing radiation doses. Compared with that of CK, their internode lengths decreased respectively by 23.20% ($p < 0.05$), 40.00% ($p < 0.05$), 49.78% ($p < 0.01$), and 99.30% ($p < 0.01$) for D50-D200 groups. The internode length of D50 had no significance from the growing period to the decline phase ($p > 0.05$), but that of D100, D150, and D200 decreased continuously. Compared with the internode lengths of the beginning period, the internode lengths of D100, D150 and D200 decreased from the beginning by 78.10% ($p < 0.01$), 81.52% ($p < 0.01$), and 82.50% ($p < 0.01$).

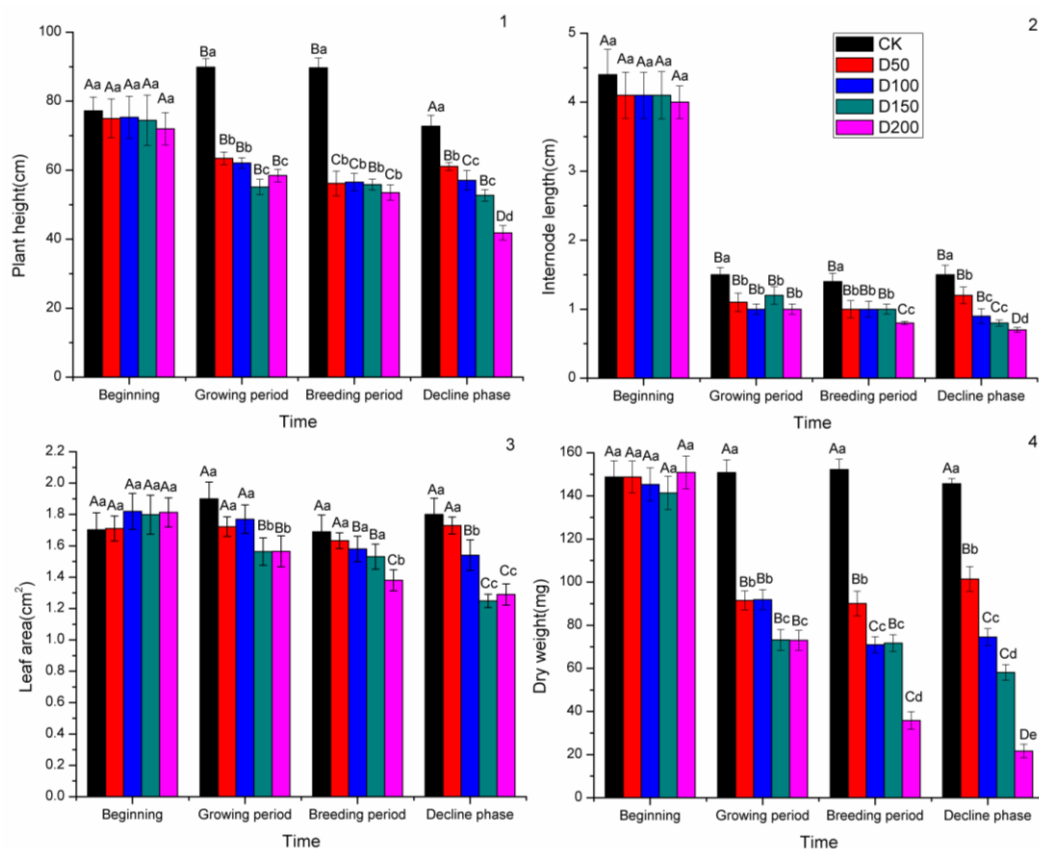


Figure 6. Morphological change of *Potamogeton crispus* affected by UV-B radiation (1. plant height; 2. internode length; 3. leaf area; 4. dry weight per plant). Capital letters indicate statistical differences between different sampling date for the same treatment group, lowercase letters indicate statistical differences between different treatment groups on the same sampling day, the equal letters indicate no differences and different letters indicate significant differences.; Error bars represent the standard deviations between the three parallels

Leaf area

There was no difference ($p > 0.05$) in leaf area among all treatment groups at the beginning (Fig. 6-3), but the leaf area decreased from CK to D200 throughout the entire experiment period. During the growing period, the leaf areas of D50-D200 were lower than CK respectively by 9.35% ($p > 0.05$), 6.84% ($p > 0.05$), 17.74% ($p < 0.05$), and

17.66% ($p < 0.05$). During the breeding period, the leaf areas of D50-D200 were lower than CK by 3.39% ($p > 0.05$), 6.51% ($p > 0.05$), 9.42% ($p > 0.05$), and 18.34% ($p < 0.05$), respectively. During the decline phase, the leaf areas of D50-D200 were lower CK respectively by 3.89% ($p > 0.05$), 14.44% ($p > 0.05$), 30.64% ($p < 0.05$), and 28.33% ($p < 0.05$). Meantime, the leaf areas of CK and D50 increased respectively by 5.75% ($p > 0.05$) and 1.17% ($p > 0.05$) compared with those of the beginning, whereas the leaf areas of D100, D150, and D200 decreased by 15.38% ($p < 0.05$), 30.61% ($p < 0.05$), and 28.87% ($p < 0.05$), respectively.

Dry weight per plant

The dry weights per plant of D50-D200 groups were reduced after UV-B radiation, whereas that of CK increased (Fig. 6-4). During the growth period, the dry weights per plant of D50-D200 were significantly lower than CK ($p < 0.05$). Compared with those at the beginning, the dry weights per plant of D50-D200 decreased respectively by 38.47% ($p < 0.05$), 36.78% ($p < 0.05$), 48.22% ($p < 0.05$), and 51.60% ($p < 0.05$), while that of CK increased by 1.37% ($p > 0.05$). During this period, the dry weights per plant of D50-D200 were lower than CK by 39.31% ($p < 0.05$), 39.08% ($p < 0.05$), 51.46% ($p < 0.05$), and 51.58% ($p < 0.05$), respectively. The dry weights per plant of D50-D200 were lower than CK by 40.83% ($p < 0.05$), 53.36% ($p < 0.05$), 52.87% ($p < 0.05$), and 76.48% ($p < 0.05$) during the breeding period. During the decline phase, the dry weights per plant still showed a gradual downward trend from CK to D200. In particular, the dry weight per plant of D200 was the lowest among all treatment groups, lower than that of CK by 85.12% ($p < 0.01$). During the whole growth period, the dry weights per plant of CK were stable, whereas D200 exhibited the greatest reduction, accounting for 85.64% ($p < 0.01$) decrease from the beginning.

Turions morphology and growth condition of shoots germinated from these turions

Turions morphology

(1) Number and single fresh weight of turion

UV-B radiation promoted the turions formation of *P. crispus* from the final number of turions (Fig. 7-1). Compared with that of CK, the number of D50-D200 increased by 164.7% ($p < 0.01$), 105.9% ($p < 0.01$), 164.7% ($p < 0.01$), and 276.5% ($p < 0.01$), respectively; D200 had the highest number. However, the single weight of turion reduced gradually with increasing the radiation doses (Fig. 7-2). Compared with that of CK, the single weight of turion of D50-D200 decreased by 17.3% ($p < 0.05$), 30.5% ($p < 0.05$), 36.4% ($p < 0.05$), and 70.1% ($p < 0.05$), respectively. The average single weight of turion of D200 was only 0.062 g, only 29.9% of that of CK.

(2) Turions morphology

The turion lengths of D50-D200 were also lower than that of CK, but the difference was not significant ($p > 0.05$) (Fig. 8). The width, however, decreased gradually from CK-D200; the width of CK was 100% greater than that of D200, and the difference was significant ($p < 0.01$). The length/width ratio also increased with increasing the radiation doses, D200 was the most significant among all treatment groups, and the length/width ratio was 75.2% ($p < 0.05$) greater than that of CK.

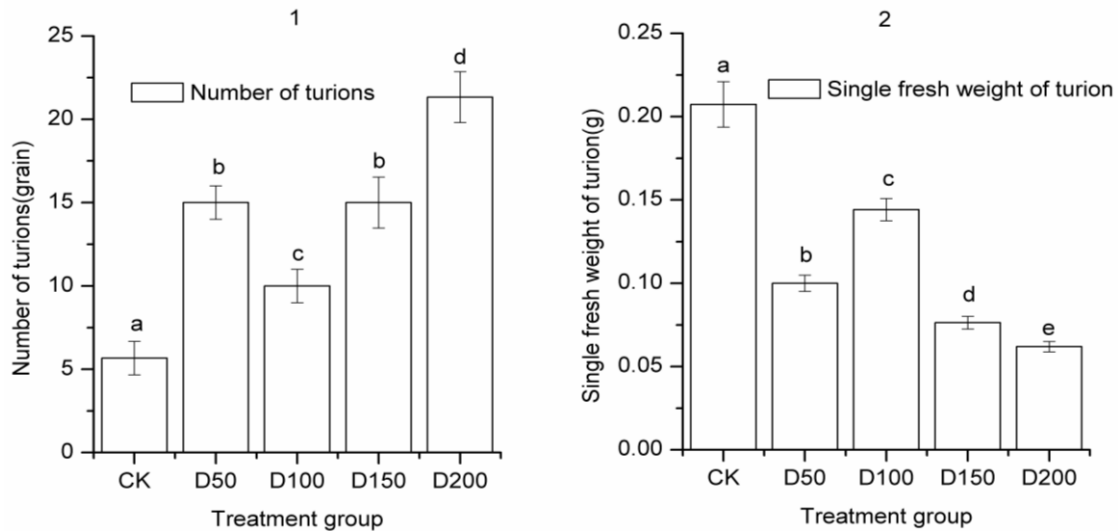


Figure 7. Quantity and weight of the turions of *P. crispus* affected by UV-B radiation (1. number; 2. single fresh weight of turion). Lowercase letters indicate statistical differences between different treatments, the equal letters indicate no differences and different letters indicate significant differences

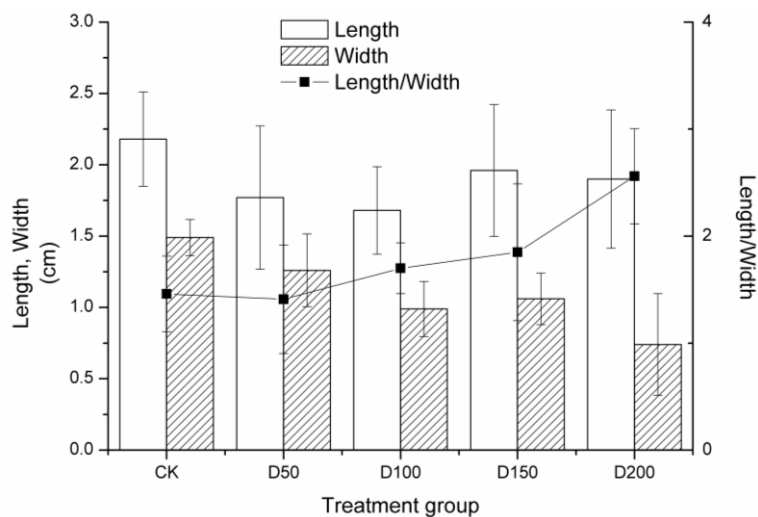


Figure 8. Morphology of the turions of *P. crispus* affected by UV-B radiation

Germination rate and growth condition of shoots germinated from turions

The germination rate of turions decreased with increasing radiation doses (Table 3). The germination rate of CK was 100%, and 50% of turions could germinate 2 or more than 2 shoots. But the turions germination rate of D200 was only 6.3%, even four turions had decomposed during the storage period. The shoot height, leaf number, leaf length, leaf width, and leaf area all decreased significantly with increasing radiation doses, and the shoot heights and leaf numbers of D50-D200 were significantly lower than those of CK ($p < 0.05$). But there was no significant difference in leaf length among CK, D50 and D100 ($p > 0.05$), the leaf lengths of D150 and D200 were significantly lower than that of CK ($p < 0.05$), the height of D200 was only 49.01% of

CK ($p < 0.05$). However, there was no significant difference in leaf area between CK and D50 ($p > 0.05$), the leaf areas of D100, D150, and D200 were significantly lower than that of CK ($p < 0.05$), and the leaf area of D200 was only 8.13% of CK.

Table 3. Germination rate and the shoots condition generated by turions

Treatment group	Germination rate/%	Rate of two shoots/%	Plant height/cm	Leaf number	Leaf length/cm	Leaf area/cm ²
CK	100.0(n = 17)	50.0(n = 17)	5.06 ± 0.95a	8.40 ± 1.35a	2.02 ± 0.37a	0.289 ± 0.14a
D50	90.9(n = 45)	15.9(n = 41)	3.16 ± 0.62b	6.20 ± 0.40b	1.66 ± 0.05a	0.209 ± 0.04a
D100	88.6(n = 35)	14.3(n = 31)	3.06 ± 0.45b	6.20 ± 0.84b	1.58 ± 0.22a	0.057 ± 0.05b
D150	82.2(n = 45)	6.7(n = 37)	2.80 ± 0.31b	6.20 ± 0.71b	1.53 ± 0.35a	0.050 ± 0.07b
D200	81.3(n = 64)	6.3(n = 52)	2.48 ± 0.31b	6.00 ± 0.89b	1.42 ± 0.19b	0.026 ± 0.05b

Values represent the mean ± SD; Lowercase letters indicate statistical differences between different treatments, the equal letters indicate no differences and different letters indicate significant differences

Discussion

Many clonal plant species consist of potentially independent units, usually referred to as ramets, which are connected by stolons or rhizomes (Batzer et al., 2018; Herben and Klimeová, 2020). *P. crispus* can reproduce a large number of ramets by underground rhizomes and stem fragments, its population is the synthesis by a number of ramets. Clonal plants can break through the limitation of resource distribution by adjusting their morphological and physiological characteristics to match the current conditions (Gao et al., 2012; Ma et al., 2022; Qin et al., 2022), so that they can expand the growth space, that is, expand the space for themselves (Zhu et al., 2020). Thus, phenotypic plasticity or morphological plasticity can be defined as the ability of one genotype to produce more than one phenotype when exposed to different environments (Manfredini et al., 2019; Ratikainen and Kokko, 2019; Yang et al., 2021). Foraging responses indicates that clonal plant species can decrease rhizome, steal internode length, and/or increase clonal branching in the favorable environments (Wang et al., 2016; Quan et al., 2021). *P. crispus* showed some foraging responses in different environments as a typical stoloniferous clonal plant. In this experiment, *P. crispus* also showed some foraging responses. Not only it decreased internode length, but it also increased clonal branches after UV-B radiation treatment. At the beginning of the experiment, each group contained 10 plants of *P. crispus*, and the height of the experimental bucket was only 72 cm so that the plants could expand their habitat and grow to the water surface quickly. After the plants' tops of D50-D200 rapidly appeared albinism in different degrees after UV-B radiation treatment, they were damaged, and therefore the plants lost the upward space to expand their habitat, *P. crispus* must increase the biomass of underwater branches to occupy the habitat. Therefore, UV-B radiation promoted plant branching. The plants of CK, however, received heat and light by expanding to the water surface, and there is no harmful light inhibiting their upward expansion. As a result, the plant height was higher than the other treatment groups.

The higher the intensity of UV-B radiation, the more likely it is that UV-B radiation can penetrate deep into the water, thus further damaging *P. crispus* in the water column. The top leaves of the plants are more severely injured because of the continuous radiation from the top. As the top plant accounts for a majority of the biomass, the injuries at the top of the plants substantially affect the physiological functions of the

plants, inhibit plant growth, and ultimately cause the death of plants. Therefore, in this study, the plants of D200 grew for only 60 days, and most of the plants of D150 only survived for 71 days, while the plants in D50 and D100 groups were alive for longer.

Clonal plants may undergo certain plasticity changes in morphology, physiology, biomass, and so on (Li et al., 2018; Rajpal et al., 2022). The ramet number, propagule number, mean spacer length, rhizome length, and biomass allocation within each patch can be measured to identify plant foraging responses (Gao et al., 2012; Liu et al., 2020; Si et al., 2020; Wang et al., 2021b). The clonal branches of *P. crispus* also have a strong adaptability and can adapt to environmental change through phenotypic plasticity (Yi et al., 2020; Dai et al., 2022). For example, the plant height, leaf area, and the formation and growth of turions of *P. crispus* are altered to adapt to environmental change under different nutrient conditions (Xie et al., 2004; Wang et al., 2013; Xu et al., 2019; Yi et al., 2020; Yan et al., 2021). UV-B radiation can significantly inhibit internode length or leaf area (Reddy et al., 2016; Moghaddam et al., 2019), therefore, inhibit plant growth and dwarf plant according to the researches of UV-B radiation on terrestrial plants (Skórska, et al., 2019; Fernández et al., 2022). In the present experiment, once *P. crispus* reached the water surface, and the harmful effect of UV-B radiation resulted in leaf fading and bleaching. This effect was more significant in the initial radiation stage. Because UV-B radiation could penetrate deeper into experimental water than in the natural water in the present experiment, as the penetration depth increased with increasing radiation doses, the harmful effect on the top of plants augmented, the plant height decreased, and internode length also reduced. When the plants were exposed to UV-B radiation, they lost the upward extension space, therefore, the plant height and internode length decreased rapidly with increasing radiation doses. However, our results also indicated that the internode lengths of CK and the other treatment groups all decreased. The decrease of internode length in CK might be because the plant height of CK exceeded the water depth, and the plants had no extension space due to the limited volume of the buckets, inhibiting the increase of plant height and reducing internode length.

Internode length and leaf morphology can also be influenced by UV-B radiation. However, during the growing period, as the penetration depth of UV-B radiation increased with increasing radiation doses, the harmful effect of UV-B radiation increased gradually from D50 to D200. Because the damage was concentrated on the top of the plants, the middle stem of plants in D50-D200 started to replace the top of plants as the new apex. Because the plant height decreased with increasing radiation doses, the leaf length and leaf width on the new tops significantly decreased with increasing radiation doses, ultimately resulting in a downward trend of leaf area from CK to D200. However, there was no significant difference in plant height and leaf area in these treatment groups (D50-D200) due to the short radiation time. During the breeding period, the adaptability of plants in D50-D200 groups to the UV-B radiation was enhanced, as the plants must enhance the leaf area to absorb more energy to form the turions. As a result, the leaf areas of D50-D200 groups did not decrease significantly with increasing radiation doses compared to those of CK or the growing period, this was also a reaction of the plant to adversity. In the decline phase, the plants of D200 had no ability to resist UV-B radiation due to the strongest radiation. The rapid reduction in leaf area severely impeded photosynthetic capacity and led to the death of the entire plant. Because the harmful effects on plant height, internode length, and leaf area increased with increasing radiation doses, which inevitably led to the reduction of dry weight per plant. Finally, the dry weight per plant from CK to D200 decreased in sequence.

P. crispus spreads primarily by turions, a plant may produce hundreds of turions, which are then dropped into the sediment to germinate the following year (Heuschele and Gleason, 2014; Xie et al., 2015). *P. crispus* depends mainly on turions for its population propagation and dispersal (Wang et al., 2012; Xie et al., 2015; Zhu et al., 2022). In particular, intense light can promote the production of turions. It is reported that May is the time for the formation of a large number of turions in southern China, and May is also the time of enhanced solar radiation, especially UV-B radiation at its annual peak in Nanjing (Mao et al., 2011). It can be inferred that UV-B radiation may be a key factor leading to the turion production of *P. crispus*. In this study, UV-B radiation promoted the formation of turions after about 10 days of radiation, so a few nutrition materials were stored in the plant stems and leaves because of the short growth time, and the turions were incomplete and subsequently decomposed. UV-B radiation could promote stem metamorphosis and the formation of turions during the breeding period, as the formation of more branches of plants, and the number of turions also increased with increasing radiation doses. Turions are always modified shoot apices and consist of modified, short leaves condensed on extremely shortened stems (Adamec, 2018), as the leaf length, leaf width, and leaf area were gradually reduced with increasing radiation doses, so the average width of the turion reduced. Meanwhile, the plants seemingly stored more nutrients by increasing the turion length because of the reduction of the turion width. Therefore, the length, the length/width ratio of the turions also increased with increasing radiation doses.

The turions are storage organs for non-structural carbohydrates and mineral substances (N, P) (Adamec et al., 2020). Theoretically, more than 54% of the total N and 70% of the total P amount in mature turions could be allocated to newly sprouting shoots (Adamec et al., 2020). High levels of primary metabolites have higher sprouting rates (Xie et al., 2015). Therefore carbohydrate reserved in the turion of *P. crispus* is important for its germination and vigor in waters (Jian et al., 2003; Adamec, 2018). Studies have shown that heavy turions have a high germination rate and more germination shoot numbers. Shen et al. (2008) showed a significant positive correlation ($p < 0.05$) between the weight of turion and the number of germination shoots. Turion germination rate and growth condition of shoots germinated from these turions can reflect the nutritional status of the turions because turions germination and the growth status of shoots depend entirely on the initial conditions of the nutrition level of turions (Xie et al., 2015). Our result also confirmed this correlation that the weight of turion gradually decreased with increasing the radiation doses. Those large and heavy turions stored more nutrients and therefore had high germination rates, and they could germinate 2 or 3 shoots. In addition, these shoots would receive more nutrition in the early growing period, and they would be in better overall growth condition. However, as the severe metamorphosis turions stored fewer nutrients, the germination rate of turion reduced, and the shoots could not get the best growth conditions, the rate of 2 shoots and the growth indexes of the shoots decreased with increasing radiation doses. Therefore, the growth indexes were generally low.

Conclusion

When the UV-B radiation exposure dose exceeded $100 \mu\text{W}/\text{cm}^2$, it could accelerate plant decline and negatively affect branch, plant height, internode length, leaf area, and the average fresh biomass. When the plants were in the growth stage, the plants could

be induced to produce turions after 7-10 days of UV-B radiation, but as fewer nutrients were stored, then all of them rotted. Although UV-B radiation could stimulate *P. crispus* to form turions and enhance the number of turions, the quality of these turions decreased with increasing radiation doses, resulting in lower germination rate and the ratio of two shoots as well as low height, leaf number, leaf length, leaf width, and leaf area of the shoots. Based on these findings, we deduced that intense surface UV-B radiation may be an important factor in promoting *P. crispus* branching and may also play an important role in turion formation. Further research is necessary to investigate whether UV-B radiation acts synergistically with other environmental factors on the decline of *P. crispus* and the role of UV-B radiation in turions formation.

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