Effects of drawdown on growth and reproduction of submerged macrophyte *Vallisneria spinulosa*

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**ABSTRACT**

Water regime plays a determinant role in plant community development and patterns of plant zonation in wetlands. The waters located in the middle reach of the Yangtze River (China) have experienced a large decrease in wetland area from human activities for a long time, especially after the hydrological drought events in recent years. This outdoor study was conducted to clarify the morphological responses and reproductive strategy of *Vallisneria spinulosa* to water depth gradients (0.6 m, 1.0 m, 1.5 m) and to drawdown (down to 0.3 m). In static water, water depth of 1.0 m was the best condition for *V. spinulosa* to grow, manifested as high biomass of vegetative parts, tubers and sexual structures. However, *V. spinulosa* growing in water depth of 1.5 m was able to adapt to the decline in water depth in autumn, expressed as increased ramet number, stolon weight and belowground biomass. The low water depth of 0.6 m produced small plants with slight vegetative biomass and drawdown produced more tuber biomass. The drawdown caused a decline in vegetative ratio of *V. spinulosa*. Moreover, it caused an increase in clonal ratio at water levels of 1.5 m and 0.6 m, and a decline in sexual ratio at water levels of 1.5 m and 1.0 m. The results show that under the condition of relatively large fluctuations in water level, *V. spinulosa* will reduce the allocation of sexual biomass and increase the allocation of clonal biomass in order to cope with environmental changes so that it can proliferate better. Thus, water level changes have a great influence on the growth and reproduction of *V. spinulosa*.

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1. Introduction

The Intergovernmental Panel on Climate Change (IPCC) has predicted that the frequency of extreme climate events (heavy rainfall, droughts and heat waves) will increase in the future (Field et al. 2014), which may have significant effects on the structure and function of ecosystems, including lakes. For example, the flood or drought would affect the...
distribution patterns and growth of submerged macrophytes (Zhang et al. 2015). The
waters located in the middle reach of the Yangtze River (China) have a large decrease in
wetland area with drought because of human activities for a long time. Poyang, the largest
freshwater lake in China, is located in the middle reach of the Yangtze River (China),
within the range 28°24′–29°46′N and 115°49′–116°46′E. Poyang Lake receives inflow
from five main tributaries, including Ganjiang River, Fuhe River, Xinjiang River, Raohe River
and Xiushui River. It regulates and stores water by diverting some of this incoming water
into the Yangtze River through an estuary. The lake, its catchment and the Yangtze River
form a natural lake-catchment-river system. The complex system comprises important
ecological functions, such as serving as an important international wetland which is listed
on the Ramsar Convention on Wetlands in 1992 (Zhao et al. 2007). Due to environmental
changes, Lake Poyang has experienced frequent hydrological drought events in past deca-
des. The lowest water level is becoming lower, the dry season is coming earlier, and the
drought period is lasting longer (Hu et al. 2015). Frequent hydrological drought events
resulted in a sharp decrease of the biodiversity in Poyang Lake Wetland. The hydrological
drought events of Poyang Lake lead to the earlier and longer period of low water level to
submerged macrophytes in Poyang Lake Basin (Li et al. 2019). In the past, the water level
of Xingzi station was below 10 m and 9 m in December, but after 2006, it was advanced
to September or October (Hu et al. 2010). Thus, we intend to investigate the plant
response to early water level drop through simulation experiments.

Water depth is a major environmental factor influencing the distribution and growth
of submerged macrophytes (Xu et al. 2016), thus many researches focus on the effects of
water depths on macrophytes. Morphological characteristics, such as plant length, ramet
number, leaf width, may react to water depth (Reckendorfer et al. 2013). In order to cap-
ture more light, macrophytes allocate their biomass to aboveground parts, thus increasing
leaf area and stem in order to reach the water surface to achieve photosynthesis
(Thouvenot et al. 2013). The lower C/N metabolic level and higher carbohydrate storage
in V. natans would have contributed to its higher tolerance to deep water depths (Yuan
et al. 2016). When exposed to wave, the biomass of V. natans in water at 200 cm depth
rapidly declined because they experienced low light stress in deep water (Xu et al. 2016).
Such adaptations are favored by differential photosynthetic efficiency at low light inten-
sities (Eusebio Malheiro et al. 2013). V. spinulosa frequently distributed at depths of
20–180 cm in shallow lakes along the middle-lower reaches of the Yangtze River (Li et al.
2018). Through the data results, we try to analyze the distribution of the V. spinulosa to
the sexual biomass and clonal biomass under different water depths. The purpose of this
experiment was to (1) examine the changes in morphological characteristics to drawdown
under different growing depths; (2) determine the changes in biomass allocation to draw-
down under different growing depths.

2. Materials and methods

2.1. Materials

The sediment was collected from the shore of Lake Poyang in Xingzi City, China. Prior
to the experiment, the sediment was dried, sieved (mesh size of 5.0 mm), and mixed to
ensure homogeneity. The sediment contains 2.41 mg/g TN, 0.75 mg/g TP, 5.82% organic
matter content. V. spinulosa, a perennial submerged macrophyte with sexual and clonal reproduction,
as well as a dominant species in the Poyang Lake, was studied in this experiment. This
species frequently distributed at depths of 20–180 cm in shallow lakes along the middle-lower reaches of the Yangtze River (Li et al. 2018).

### 2.2. Experimental design

The experiment was carried out at Laboratory of Poyang Lake and Wetland Ecosystem Research, Chinese Academy of Sciences (116°03’E, 29°26’N), located at the northwestern part of Poyang Lake Basin from March 24 to September 24, 2018. Four outdoor mesocosms (2 m in length × 2 m in wide × 1.5 m in depth) of the experimental platform were used. Each even *V. spinulosa* tuber was planted in a plastic pot (diameter 26 cm, height 25 cm) containing 25 cm sediment collected from the Lake Poyang and 1 cm sand on March 24. A total of 24 pots were hung in one mesocosm. There were a total of 96 pots. The pots were hung from three iron frames above the mesocosms to the water depth of 30 cm, with eight pots per iron frame. One month later, seedlings of even size (23.0 ± 1.1 cm) were selected for further treatment on April 24, with 1 shoot per pot for *V. spinulosa*. There are four duplicate mesocosms. The tap water (DTN, 2.00 mg·L⁻¹; DTP, 0.076 mg·L⁻¹) was supplemented to mesocosms for *V. spinulosa* living. For each mesocosm, there were 3 water depths (150 cm, 100 cm and 60 cm), with eight pots per iron frame for a water depth. Throughout the study, phytoplankton visible on the water surface was removed using a filter net (pore size: 0.03 mm). Additional water was added to each mesocosm two or three times every week to maintain a consistent water level and promote water circulation. On September 1, half of the pots for each water level were adjusted to 30 cm, another half kept the water level constant respectively. The plants were harvested on September 24. The water temperature and nutrient concentrations (DTN, DTP, NO₃⁻-N, NH₄⁺-N, PO₄³⁻-P) of the water were measured every month from April 24. Light intensity in the water column (60, 100 and 150 cm deep) was recorded in each mesocosm using a Hydrolab DS5X Multi-parameter sonde with PAR sensor (Hach Company, Loveland, Colorado, USA). Light intensities at 60, 100 and 150 cm under water were 455.6, 251.7 and 115.3 μmol·m⁻²·s⁻¹, respectively, at noon on 29 August 2018.

### 2.3. Sampling procedures

Treatments were maintained 5 months. We did not use male individuals, due to the problem of quantifying reproductive biomass and sexual ratio for males that release minute flowers to the water surface at maturation. When the fruits were fully mature, all pots with healthy and ungrazed plants were removed from the mesocosms. Some pots were damaged by unidentified aquatic insects during the experiment and were excluded from analyses. Ultimately, there were six replication plants (pots) for each treatment. We began counting the number of reproductive and vegetative (mature but no flower) ramet number in each pot (each ramet was defined as a single shoot with roots). All fruits per genet were harvested and counted. Then, all pots were emptied, and tubers were carefully harvested from each genet and counted. Roots and tubers were hand-washed. The mother plant was selected, and its leaves and roots were measured by a meter ruler to determine the plant height. Finally, every genet was partitioned into vegetative (including leaves, stolons, and roots), sexual (including peduncles and fruits), and clonal (tubers) structures, separately dried at 70 °C in paper bags for 72h, and weighed immediately after drying. Vegetative biomass was the sum of leaf, stolon, and root biomasses. The vegetative biomass was partitioned into aboveground and belowground biomass. The aboveground biomass referred to leaf weight, the belowground biomass included the stolon and root.
2.4. Analysis of data

Two-way analysis of variance (ANOVA) was used to determine whether water depth and drawdown had joint effects on growth and reproduction of *V. spinulosa* using the SPSS software. Differences were considered significant at \( p < 0.05 \). Transformations were used to meet ANOVA assumptions regarding homoscedasticity and normality. The data of stolon weight, plant height and leaf number were \( 1/x^2 \) transformed. The data of ramet number, sexual biomass and belowground biomass were \( x^2 \) transformed.

3. Results

3.1. Water quality

The DTN concentration ranged from 1.13 mg L\(^{-1}\) to 1.55 mg L\(^{-1}\), the DPN content ranged from 0.06 mg L\(^{-1}\) to 0.1 mg L\(^{-1}\) (Table 1). The highest concentration of NH\(_4^+\)-N was 0.29 mg L\(^{-1}\) during the experiment. The concentration of NO\(_3^-\)-N and PO\(_4^{3-}\)-P was relatively stable during the experiment (Table 1). The nutrient content was not a factor affecting *V. spinulosa* in this experiment.

| Indicators | May     | June    | July   | August  | September |
|------------|---------|---------|--------|---------|-----------|
| T (°C)     | 21.7    | 25.7    | 28.5   | 28.8    | 26.8      |
| DTN (mg L\(^{-1}\)) | 1.46 ± 0.18 | 1.14 ± 0.22 | 1.22 ± 0.10 | 1.09 ± 0.06 | 1.29 ± 0.16 |
| DTP (mg L\(^{-1}\))  | 0.10 ± 0.01 | 0.10 ± 0.02 | 0.06 ± 0.004 | 0.07 ± 0.01 | 0.08 ± 0.007 |
| NO\(_3^-\)-N (mg L\(^{-1}\)) | 0.43 ± 0.13 | 0.41 ± 0.12 | 0.14 ± 0.06 | 0.90 ± 0.01 | 0.13 ± 0.03 |
| NH\(_4^+\)-N (mg L\(^{-1}\))  | 0.26 ± 0.02 | 0.22 ± 0.03 | 0.16 ± 0.01 | 0.16 ± 0.01 | 0.17 ± 0.03 |
| PO\(_4^{3-}\)-P (mg L\(^{-1}\)) | 0.01 ± 0.004 | 0.01 ± 0.003 | 0.01 ± 0.007 | 0.02 ± 0.06 | 0.02 ± 0.03 |

3.2. Morphological characteristics

The plant height increased with the water depth, the decline in water depth caused significant decreases in the plant height (Figure 1a). There was significant interaction between water depth and its decline on plant height (Table 2). *V. spinulosa* growing at a water depth of 1 m showed the least decrease in plant height with 31.66%. *V. spinulosa* growing at a water depth of 1.5 m had the least numbers of ramets. There was significant interaction between water depth and its decline on ramet number (Table 2). For water level of 150 cm, drawdown caused an increase in stolon number. The stolon number in *V. spinulosa* at 150 cm was obvious less than those with water levels of 100 cm and 60 cm (Figure 1d). Ramet number increased after the water depth decreased from 1.5 m to 30 cm. The ramet number declined when the water depth dropped from 1 m to 30 cm. There was no change in ramet number when the water depth decreased from 60 cm to 30 cm (Figure 1c). *V. spinulosa* growing at a water depth of 100 cm had the most number of reproductive ramet. The drawdown badly influenced the number of reproductive ramet (Figure 1d).

3.3. Biomass of *V. spinulosa*

The stolon weight in *V. spinulosa* at 60 cm was obvious less than those with water levels of 1.5 m and 100 cm (Figure 2a). The decline in water depth caused no significant influence on stolon biomass. There was significant interaction between water depth and its decline on stolon biomass (Table 2). The root biomass of *V. spinulosa* at a water level of 1 m was higher than that at a water level of 1.5 m (Figure 2b). No change in root biomass...
occurred when the water depth of 1.0 m and 0.6 m declined. For water depth of 1.5 m, the sharp decrease to 30 cm caused an increase in root biomass (Figure 2b). The tuber biomass was obviously maximum at a water depth of 1.0 m. For the shallow and medium water depth, the decline to 30 cm in water depth aroused an increase in tuber biomass.

Table 2. Results of a two-way ANOVA of plant morphology and biomass of V. spinulosa grown under different water depth and drawdown.

| Parameter                  | Water depth (W) | Drawdown (D) | W × D |
|----------------------------|-----------------|--------------|-------|
|                            | \( F \)         | \( p \)      | \( F \) | \( p \) | \( F \) | \( p \) |
| Plant height (cm)          | 89.24           | <0.0001      | 38.11  | <0.0001 | 8.25   | <0.0001 |
| Ramet number (plant\(^{-1}\)) | 24.83           | <0.0001      | 6.13   | 0.004   | 6.81   | <0.0001 |
| No. of reproductive ramet   | 7.1             | 0.002        | 26.74  | <0.0001 | 7.78   | <0.0001 |
| Stolon number (plant\(^{-1}\)) | 5.015           | 0.011        | 0.716  | 0.494   | 1.477  | 0.225   |
| Root biomass (g)           | 2.223           | 0.120        | 4.036  | 0.024   | 10.976 | <0.0001 |
| Stolon biomass (g)         | 6.49            | 0.003        | 0.65   | 0.529   | 6.0    | 0.001   |
| Aboveground biomass (g)    | 41.38           | <0.0001      | 6.09   | 0.005   | 3.23   | 0.021   |
| Belowground biomass (g)    | 4.36            | 0.019        | 5.15   | 0.1     | 14.384 | <0.0001 |
| Tuber biomass (g)          | 37.29           | <0.0001      | 12.31  | <0.0001 | 5.78   | 0.001   |
| Sexual biomass (g)         | 22.84           | <0.0001      | 39.38  | <0.0001 | 11.65  | <0.0001 |

Notes: Significant correlations are shown (\( p < 0.05 \)) in bold.
Both of water depth and drawdown had significant influence on tuber weight. There was significant interaction between water depth and its decline on tuber biomass (Table 2). For the water depth of 1 m, the drawdown caused no obvious change in tuber biomass (Figure 2c). The sexual biomass of the plant growing at a water depth of 1.0 m was the largest. The drawdown seriously affected the sexual biomass of plant with deep and intermediate water (Figure 2d).

**3.4. Biomass allocation**

Both aboveground and belowground biomass was greatest at 1.0 m water depth compared to deep and shallow water. (Figure 3). There was significant interaction between water depth and its decline on aboveground or belowground biomass (Table 2). For a water depth of 1.0 m, the decline in water depth resulted in a decline in aboveground biomass and belowground biomass (Figure 3). No change in aboveground biomass occurred when water depths of 1.5 m and 0.6 m decreased to 30 cm. The decline in water depth of 1 m resulted in a decline in belowground biomass. However, the sharp decrease in water depth from 1.5 m to 30 cm caused an increase in aboveground biomass (Figure 3). The static water level caused no change in vegetative ratio of *V. spinulosa*. The drawdown caused a
decline in vegetative ratio of *V. spinulosa* (Figure 4). For water depth of 1.5 m, the sharp decrease to 30 cm caused an increase in clonal ratio, and decline in vegetative and sexual rations of *V. spinulosa*. For water depth of 1.0 m, the sharp decrease to 30 cm caused a decline in vegetative and sexual rations of *V. spinulosa*. For water depth of 0.6 m, the sharp decrease to 30 cm caused an increase in clonal ratio, and decline in vegetative ration of *V. spinulosa* (Figure 4).

4. Discussion

The results indicate that the water depth and drawdown impacted the growth and production of *V. spinulosa*. Water regime is a major determinant of plant community development and patterns of plant zonation in wetlands (Arthaud et al. 2012). *V. spinulosa* employed a variety of morphological responses both apparently to water depth gradients and to drawdown. Water depth of 1.0 m is the best condition for *V. spinulosa* to grow and reproduce expressed by high biomass of vegetative structure, tuber and sexual structure. The plant height increased with water depth in this study because with increasing water depth, less light penetrates the submerged macrophytes to switch energy and biomass allocations to produce taller plants to maximally utilize light energy for
photosynthesis. This strategy reduces investment in branch number and belowground biomass, which is verified by Xu et al. (2014) and Xu et al. (2016), and is consistent to our results. According to the same strategy, *V. spinulosa* with 1.5 m water depth allocated less belowground biomass, tuber biomass and sexual biomass than plant at water level of 1.0 m. It was confirmed that switching energy and biomass allocation to produce longer branches and taller plants, which was associated with decreased investment in branch number and belowground biomass, is a relevant strategy for plants under poor light conditions in aquatic environments in some researches (Barko et al. 1991; Maberly 1993). However, the stolon biomass, aboveground biomass, sexual biomass and tuber biomass of plant with 0.6 m was much less than that of *V. spinulosa* with deep water, respectively. In our research, the shallow water of 0.6 m greatly affected the growth and reproduction expressed by low biomass of vegetative structure, tuber and sexual structures, but more ramet and stolon number mostly possibly because smaller life forms can be the outcome of physiological adaptation to high light (shallow water). Søndergaard et al. (2013) also found low water depths greatly inhibit growth of submerged macrophytes if they exceed the plants’ physiological limits. Thus, *V. spinulosa* could show certain morphological responses to water depth gradient for its best growth and production. *V. spinulosa* breed offspring mainly through asexual reproduction and sexual reproduction. As stated in the life history theory, the change of plant reproduction is conducive to maintaining a stable viability in a constantly changing environment (Warwick and Brock 2003). Some researchers found that submerged macrophytes have their adaptability for water depth, flood time and flood frequency through adjusting their life history period (Brock and Rogers 1998). The results of this experiment show that under the condition of stable water level, the water level of 1.0 m produced large plants with more tuber and sexual biomass. However, Li et al. (2018) found that water level of 1.0 m produced large plants with less tuber biomass and more sexual biomass, which do not completely agree with ours results. Maybe there is size effect of pots on the growth of *V. spinulosa* or because the experiment was conducted at different periods. In the study of Li et al. (2018), the pot is smaller than ours, which increased the size effects of pots on the growth, and the experimental period is longer than ours.

This study confirms that the drawdown also play a determinant role in the growth and reproduction of macrophyte *V. spinulosa*. The drawdown shorten the plant height because *V. spinulosa* is a kind of submerged macrophyte which could only survive under the water surface. However, when the water depth of 150 cm draw downed to 30 cm, the aboveground biomass did not change significantly because of more ramet number resulted from the decrease in water depth. *V. spinulosa* growing with water depth of 1.5 m adapted to drawdown by increasing the belowground biomass, ramet number and stolon weight for better growth. However, the plant with shallow water of 0.6 m had poor adaptability to drawdown. The drawdown caused a decline in vegetative ratio of *V. spinulosa*, and induced an increase in clonal ratio or a decrease in sexual ratio. The results indicated that the decrease in water depth caused certain influences to asexual reproduction and sexual reproduction of *V. spinulosa*. The water level decline in September gave *V. spinulosa* time to accumulate more energy and nutrition in asexual diaspores for breeding (Warwick and Brock 2003), which is reflected by an increase in tubers weight. It is more beneficial for *V. spinulosa* putting limited energy into propagules than keeping the growth of green tissues after the leaves start to wither (Hangelbroek and Santamaria 2004). The sexual production of *V. spinulosa* was badly affected by drawdown reflected by low sexual biomass and low sexual ratio. *V. spinulosa* breed offspring mainly through asexual reproduction and sexual reproduction. Compared with the *V. spinulosa* under the stable water level, *V.
*V. spinulosa* under the condition of fluctuating water level significantly reduced the vegetative ratio and sexual biomass, but increased the clonal biomass. It can be seen that the *V. spinulosa* changed the balance between the two reproductive methods to adapt to the drawdown. The allocation of resources between sexual reproduction and clonal reproduction has proved the trade-off of aquatic species. The trade-off of resource allocation between sexual reproduction and clonal reproduction of aquatic species has been demonstrated (Thompson and Eckert 2004; Reusch 2006; Van Drunen and Dorken 2012). Different populations living in different habitats can use different reproduction strategies. As the dominant species in Poyang Lake, the trade-off between sexual reproduction and clonal reproduction with water depth gradient is particularly important for success in the new environment (Li et al. 2018). In the case of water level fluctuations, the amount of vegetative biomass added to the clonal biomass is increased to adapt to changes in the environment to achieve better viability. It is because the clonal propagule has a relatively large size and the ability to store resources and colonization space, and may have a higher viability than seeds (Grace James 1993; Johansson and Nilsson 1993). *V. spinulosa* can achieve a relatively high level of viability through this variation in reproductive strategy in a changing environment.

Water depth and drawdown had extremely significant joint influences \((p < 0.05)\) on plant growth and reproduction. For static water environment, the water depth of 1.0 m is the best condition for plant to growth and reproduction. However, in deep water, *V. spinulosa* had good adaptability to the decline in water depth expressed as increased ramet number, stolon weight and belowground biomass. Researchers found that environmental changes led to some modifications in the reproductive strategy of some submerged macrophyte that has two modes of reproduction: (i) vegetative propagation through tuber production; and (ii) sexual reproduction through seed production, which differs from unitary plants (Silvertown and Doust 1995; Yuan et al. 2012). This allocation principle was verified by our results expressed as decreased reproductive ramet number, sexual structures biomass, and increased tuber biomass, which is clear from a standard explanation that a large investment into clonal propagation necessarily implies a low sexual reproductive effort. The adapted ability of plant growing under intermediate and low water was lower than the plant which was growing in the deep water. Although the plant growing under the low water depth of 0.6 m could adapt to the drawdown expressed as increased tuber biomass and decreased reproductive ramet number, the low water produced small plant and drawdown produced relative less tuber biomass, which limited the adaptability of *V. spinulosa*. In shallow lakes and estuaries, submerged plants play a key role in controlling ecosystem dynamics. As known, the drought period of Poyang Lake has been becoming longer and earlier. Due to environmental changes, drought in Lake Poyang in winter became more frequent from 2003 to 2013 than that from 1960 to 2003 (Zhang et al. 2017). The drought was considered as one of the most important factors to lead to the degeneration of the Poyang Lake Wetland (Hu et al. 2010). The changes in water regime in Poyang Lake could cause great bad influences to growth and reproduction of *V. spinulosa*, which explained the decay of wetland in Poyang Lake in recent years. The asexual reproduction adaptation of *V. spinulosa* is important features which explain its high tolerance to adverse environments. Therefore, the restoration of submerged macrophytes has been proposed as an important ecological measure for the rehabilitation of degraded lake ecosystem and improvement of water quality of shallow eutrophic lakes. The water-level management was proposed by many scholars to maintain suitable water level according to recent water regime in Poyang Lake (Ge et al. 2010). According to our results, the
low water level and the drawdown in autumn greatly influenced the growth and reproduction of aquatic macrophytes like *V. spinulosa* in Poyang Lake.

**5. Conclusion**

Water depth gradient and drawdown impacted the growth and production of *V. spinulosa*, and had extremely significant joint influences (*p* < 0.05) on plant. Under the condition of relatively large water level fluctuations, *V. spinulosa* will reduce the distribution of sexual biomass and increase the distribution of clonal biomass in order to be able to proliferate better. It can be seen that the change of water depth will also have a certain impact on the reproductive strategy of *V. spinulosa*. *V. spinulosa* would adapt to the decline in water level in autumn by putting a large investment into clonal propagation. However, this adapting ability of *V. spinulosa* became weak when the water depth for plant growing was lower than 1.0 m. Thus, the water level change greatly influenced the growth and reproduction of aquatic macrophytes like *V. spinulosa* in Poyang Lake.

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**Data availability statement**

The data presented in this study are available on request from the corresponding author.

**Disclosure statement**

The authors have no conflicts of interest to declare.

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