

EFFECTS OF DIFFERENT SHADED CONDITIONS AND WATER DEPTHS ON THE GROWTH AND REPRODUCTIVE STRATEGY OF *VALLISNERIA SPINULOSA*

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Abstract

The occurrence and growth of submerged macrophytes mainly depends on a suitable light environment. Nowadays, however, lake eutrophication increasing phytoplankton and epiphyton overgrowth has caused shading habitats. This change influences light quantity and quality under lake water. The decrease of light availability will play a spectacular and unusual role on the establishment, growth and survival of submerged macrophytes. So the effects of four shaded treatments and three water depth treatments on the growth and reproductive strategy of *Vallisneria spinulosa* were carried out to investigate how light availability imposed an adverse influences on the growth and reproduction of submerged macrophytes. This study confirmed that both light quality and quantity affected by shaded treatments and water depth treatments had negative impacts on growth, reproduction and the associated morphological traits of *V. spinulosa*. Compared to shaded treatments, the effect of water-depth gradient on sexual reproduction was less significantly different. The treatments of sunshades associated light attenuation played a determinant role in the growth and reproductive strategy of macrophyte *V. spinulosa*, while the depth gradients had a scaling effect. In addition, length of the total stolons, number of inflorescences, stolon biomass, seed biomass, total biomass, and resource allocation ratios of seeds and ratios between above-ground biomass and below-ground biomass per plant were relatively insensitive to light quantity and quality affected by water depth treatments. Resource allocation ratios of tubers was less changeable to light quantity and quality affected by shaded treatments. So the effects of irradiance decrease has been suggested to be the main reason for the disappearance of submerged macrophytes from eutrophic waters owing to shaded effects.

Introduction

Light is one of the most important environmental factors for plants because it provides energy for photosynthesis and controls their establishment, growth and survival. Developmental responses of plants to fluctuating light conditions are numerous, including specific adjustments in all aspects of their phenotype-morphology, anatomy and physiology (Valladares & Pearcy, 1998; Poorter, 2001). A decrease in light availability has been the primary cause of the worldwide decline in submerged macrophytes (Orth & Moore, 1983; Short & Wyllie-Echeverria, 1996). Decreases in water clarity restrict submerged macrophytes to grow in shallow water (Stevenson & Confer, 1978; Orth & Moore, 1983; Dennison & Alberte, 1985). Light reduction not only results in a decrease in submerged macrophytes' area coverage, but also reduces submerged macrophytes productivity (Dunton & Tomasko, 1994).

Shading by phytoplankton and water depth are 2 important factors for light availability. Recent studies have addressed morphological plasticity of submerged macrophytes in response to light availability. Some species of submerged angiosperms can show morphological adaptations to available light, such that they produce longer, wider and thinner leaves at low light conditions, leading to an increase in light absorption per unit biomass (Barko *et al.*, 1982; Bintz & Nixon, 2001). In addition, adaptations of aquatic plants to available light include shoot elongation in low light (Barko & Smart, 1981). Plants modify their morphology and physiology and eventually their growth and reproduction, once one of these components of light changes. However, studies focusing on the effects of light quantity and quality on biomass allocation between vegetative propagation and sexual

reproduction of submerged macrophytes are relatively scarce.

The occurrence of submerged macrophytes depends on a suitable light climate among other environmental parameters (Campbell, 1997). Under water light climate is highly variable because of sun position, weather conditions, water colour, turbidity, depth and wave form (Rorslett *et al.*, 1997; Pott & Remy, 2000; Schubert *et al.*, 2001). Adaptations to available light conditions therefore play a fundamental role in plant survival. Eutrophication causes nutrient levels to increase in aquatic systems. Under these conditions, macrophytes are subject to epiphytic overgrowth or shading by phytoplankton. To compensate for the reduced light, submerged macrophytes exhibit structural growth or physiological strategies that include: an increase in chlorophyll concentration during turbid conditions (Goldsborough & Kemp, 1988; Twilley & Barko, 1990); increased numbers of chloroplasts in the leaves (Wetzel, 1983); high surface area-to-volume ratio (Goldsborough & Kemp, 1988); apical growth and canopy formation and morphological plasticity and physiological flexibility with reduced light levels (Barko & Smart, 1981; Dennison & Alberte, 1986; Goldsborough & Kemp, 1988).

Vallisneria spinulosa. Yan has been the dominant member of the submerged plant community of shallow lake in the middle and lower reaches of the Yangtze (Changjiang) River since the middle 20th century. *Vallisneria spinulosa* not only provides important food resource for waterfowl and fish, but also has a strong influence on water quality. However, under certain lake conditions the distribution and abundance of *Vallisneria* have been limited (e.g., high water due to dam in the early 1960s and shading effects by phytoplankton and epiphyton because of lake eutrophication in the 1980s). Declines in submerged aquatic vegetation (SAV), including

Vallisneria spinulosa, have been widely reported since the 1980s, especially in the middle and lower reaches of the Yangtze (Changjiang) River (Li, *et al.*, 2002). These losses in SAV have prompted considerable research to identify causal conditions and to develop effective restoration methods. Reasons for the declines remain uncertain, but most appear to be linked to serious natural and/or anthropogenic disturbances, e.g., eutrophication, drought, flooding, herbicides, navigation and herbivory. Developing effective restoration strategies for SAV requires thorough knowledge of species biological traits and propagule production, early stages of growth and establishment in response to key environmental factors.

The present study is to investigate influence of light quantity and quality on the biomass allocation between vegetative propagation and sexual reproduction of submerged macrophyte *V. spinulosa*. Yan with two modes of reproduction (tuber and seed production) under different shading conditions and water depth. It is necessary to study plant growth response under variable resource conditions in order to understand survival strategies of plants and the maintenance of the population. The aim of the particular study was to: (1) examine how the submerged macrophyte *V. spinulosa*. Yan alter the biomass allocation between vegetative propagation and sexual reproduction to adapt different shading conditions and water depth. (2) determine whether the mode of the influence of shading was as same as that of the influence of water depth on the growth and reproductive strategy of submerged macrophyte *V. spinulosa*.

Material and Methods

Tubers of *V. spinulosa* were collected from Poyang Lake (28°25'-29°45'N, 115°48'-116°44'E), one of the largest Chinese lakes in the Jiangxi Province, China, on 7th March, 2005. About 200 tubers (fresh weight 0.6196 ± 0.1075 g, length 2.32 ± 0.15 cm) were brought to the Wuhan Botanical Garden, and then were placed to two plastic bins (50cm × 40cm × 20cm) covered with 10cm water depth in a greenhouse, where the temperature was controlled at 20 ± 2 °C in the day and 15 ± 2 °C at night and light was kept in the natural conditions. The water in the bins was changed every two days. The tubers sprouted out new buds after two weeks.

The experiment started on 28th March, 2005 at the Aquatic Plant experimental station of Wuhan Botanical Garden. A total of 70 tubers with fresh cotyledons (2-3 leaves, 10cm length) were picked out and transplanted into 70 small plastic trays (27cm in diameter, 14cm in height), which had been filled with 10cm fertilized sediment. A tuber with fresh cotyledons was planted in each plastic tray. The trays were then placed into several large pools (200cm × 200cm × 200cm).

The effects of 4 shading treatments and three water depth treatments on the growth and reproductive strategy of submerged macrophyte *V. spinulosa* were carried out. Four shading treatments were designed: CP (plant in full natural daylight, 100% photosynthetic photon flux density, $1800-2300 \mu\text{mol m}^{-2} \text{s}^{-1}$ at midday during the experiment), SH1 (plant in 50% full sunlight intensity with one layer of neutral shading net), SH2 (plant in 20% full

sunlight intensity with two layers of neutral shading net), SH3 (plant in 10% full sunlight intensity with Three layers of neutral shading net). The light gradient was made using different numbers of layers of a neutral shading net fixed above the pools. The pools were filled with lake water to a depth of 100cm. Three water depth treatments were 50cm water depths (WD1), 100cm water depths (WD2) and 150cm water depths (WD3). The water treatments were selected to represent water-level gradient found in *V. spinulosa* population in the shallow lake of the Yangtze (Changjiang) River. Each treatment was replicated 10 times.

Plants were harvested after 4 months growth. Before harvest, the number of ramets and inflorescences was counted for each part of the whole plants in different treatments. Then we measured total stolon length, total leaf areas, the number of tubers and the length of the longest leaf in each container. After collection, all plants were divided into roots, stolons, tubers, seeds and leaves, then oven dried to constant mass at 80°C for 48 hours and the dry weight was recorded.

The experimental design was a single factorial set-up to research the effects of four shading treatments and three water depth treatments. Data were analysed by analysis of variance (one-way ANOVA or Kruskal-Wallis test) with the software Statistical Package for the Social Science (SPSS) version 11.0. Multiple comparison was performed using the least significant difference (LSD) procedure at the 0.05 significance level. The number of the tubers, flowers and ramets was analysed by Nonparametric tests.

Results and Discussion

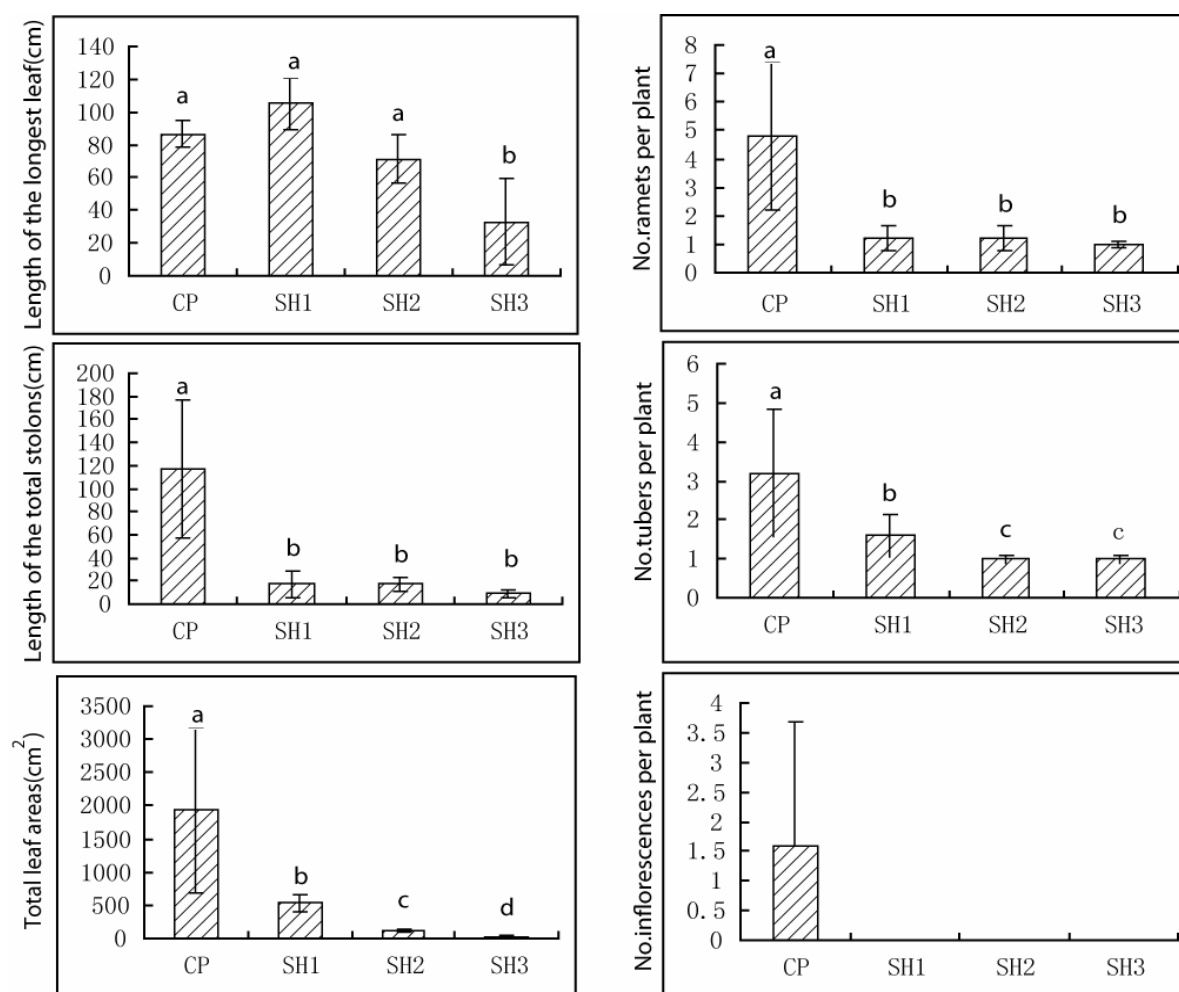
The length of the longest leaf, length of the total stolons and total leaf areas of *V. spinulosa* were significantly different under the four kind of light environments (Table 1). The length of the longest leaf increased significantly under appropriate shaded conditions (SH1), while it was significantly restricted by other shaded conditions (SH2 or SH3) (Fig. 1). The length of the total stolons and total leaf areas significantly decreased under shaded environments.

The effect of water depth treatments on morphological traits of *V. spinulosa* was different from that of shaded treatments. The length of the longest leaf and total leaf areas were significantly affected by water depth treatments, while the length of stolons was less affected (Table 1). Among the three water-depth treatment, the total leaf areas of *V. spinulosa* in one meters water depth were significantly the largest (Fig. 2).

V. spinulosa grown in natural light condition (CP) had more total biomass than plants in shaded conditions (Table 2), which was also reflected in biomass of roots, stolons, leaves, seeds and tubers. Percent biomass allocation among treatments differed significantly in tubers, seed, the ratios between above-ground and below-ground biomass (Fig. 3). In the shaded treatments, the less light was, the more biomass was allocated to the below-ground parts, and the less ratios between above-ground and below-ground biomass were.

Table 1. Results of one-way Anova or kruskal-wallis testing the effects of shading levels and water depths on the performances of *Vallisneria spinulosa*. At harvest.

Traits	Shading level		Water depth	
	$F_{3,36}$ or X^2	P	$F_{2,27}$ or X^2	P
Morphological traits				
Length of the longest leaf (cm)	10.221	<0.001	16.567	<0.001
Length of the total stolons (cm)	12.638	<0.001	0.594	0.568
Total leaf area (cm ²)	73.753	<0.001	6.837	<0.001
No. tubers per plant	11.185	<0.05	6.564	<0.05
No. ramets per plant	10.122	<0.05	6.094	<0.05
No. inflorescences per plant	9.981	<0.05	0.482	0.786
Dry biomass (g)				
Root biomass per plant	37.091	<0.001	12.022	<0.001
Leaf biomass per plant	58.896	<0.001	4.265	<0.05
Stolon biomass per plant	12.119	<0.001	2.17	0.157
Tuber biomass per plant	39.481	<0.001	4.209	<0.05
Seed biomass per plant	4.99	<0.05	0.419	0.667
Total biomass per plant	35.152	<0.001	2.811	0.1
Ratios				
Resource allocation ratios of tubers	5.994	<0.112	5.558	<0.05
Resource allocation ratios of seeds	9.981	<0.05	0.419	0.667
Ratios between above-ground biomass and below-ground biomass	32.85	<0.001	2.768	<0.103

Fig. 1. Phenotypic means (and standard errors) for morphological traits observed in individual plant raised in four shading treatments. Different letters indicate significant differences in means ($p < 0.05$, LSD or Kruskal-Wallis test).

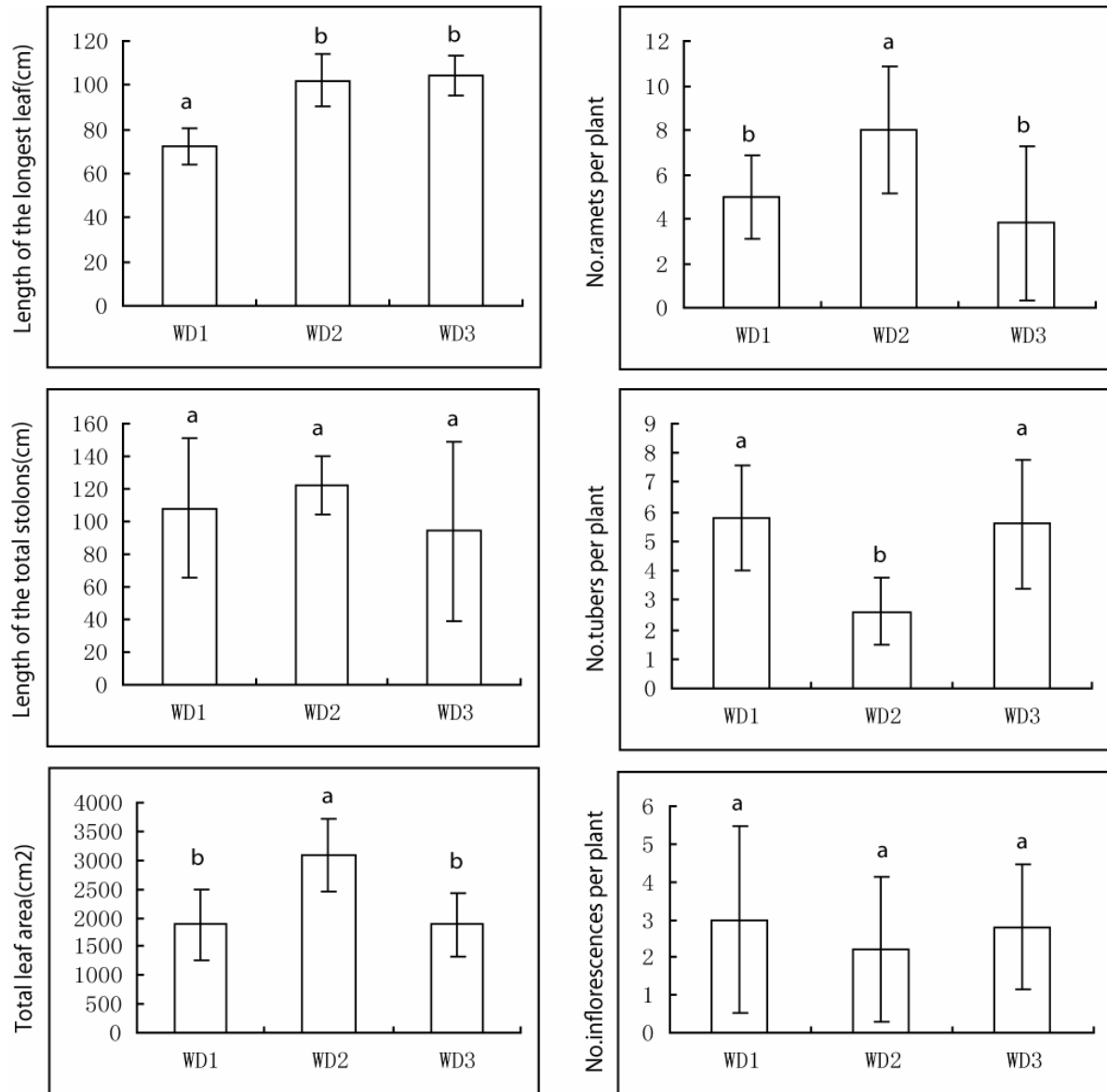


Fig. 2. Phenotypic means (and standard errors) for morphological traits observed in individual plant raised in three water depth treatments. Different letters indicate significant differences in means ($p < 0.05$, *LSD* or *Kruskal-Wallis* test).

Table 2. Growth and reproductive organ biomass of *Vallisneria spinulosa* cultivated under different shading conditions.

Variables	CP	SH1	SH2	SH3
Total biomass per plant (g)	3.601 ± 1.161a	1.135 ± 0.366b	0.282 ± 0.048c	0.086 ± 0.029c
Root biomass per plant (g)	0.215 ± 0.073a	0.0514 ± .022b	0.018 ± 0.007b	0.010 ± 0.007c
Leaf biomass per plant (g)	2.346 ± 0.926a	0.801 ± 0.270b	0.169 ± 0.032c	0.033 ± 0.022c
Stolon biomass per plant (g)	0.331 ± 0.201a	0.061 ± 0.047b	0.028 ± 0.009b	0.009 ± 0.006b
Tuber biomass per plant (g)	0.699 ± 0.237a	0.222 ± 0.067b	0.067 ± 0.036c	0.034 ± 0.018c
Seed biomass per plant (g)	0.011 ± .0107a	ob	ob	Ob

The effect of water depth treatments on biomass allocation followed another pattern. Total biomass among different treatments was the same. Tuber biomass, leaf biomass and root biomass were significantly different among treatments while stolon and seed biomass were the same (Table 3). Percent of biomass allocation among treatments differed significantly in tubers, but not in

seeds, ratios between above-ground and below-ground biomass (Fig. 3). Light had a positive effect on reproductive strategy of *V. spinulosa*. The number of ramets, tubers and inflorescences decreased significantly in response to shaded treatments (Fig. 1). Sex reproduction of *V. spinulosa* was restricted by shading.

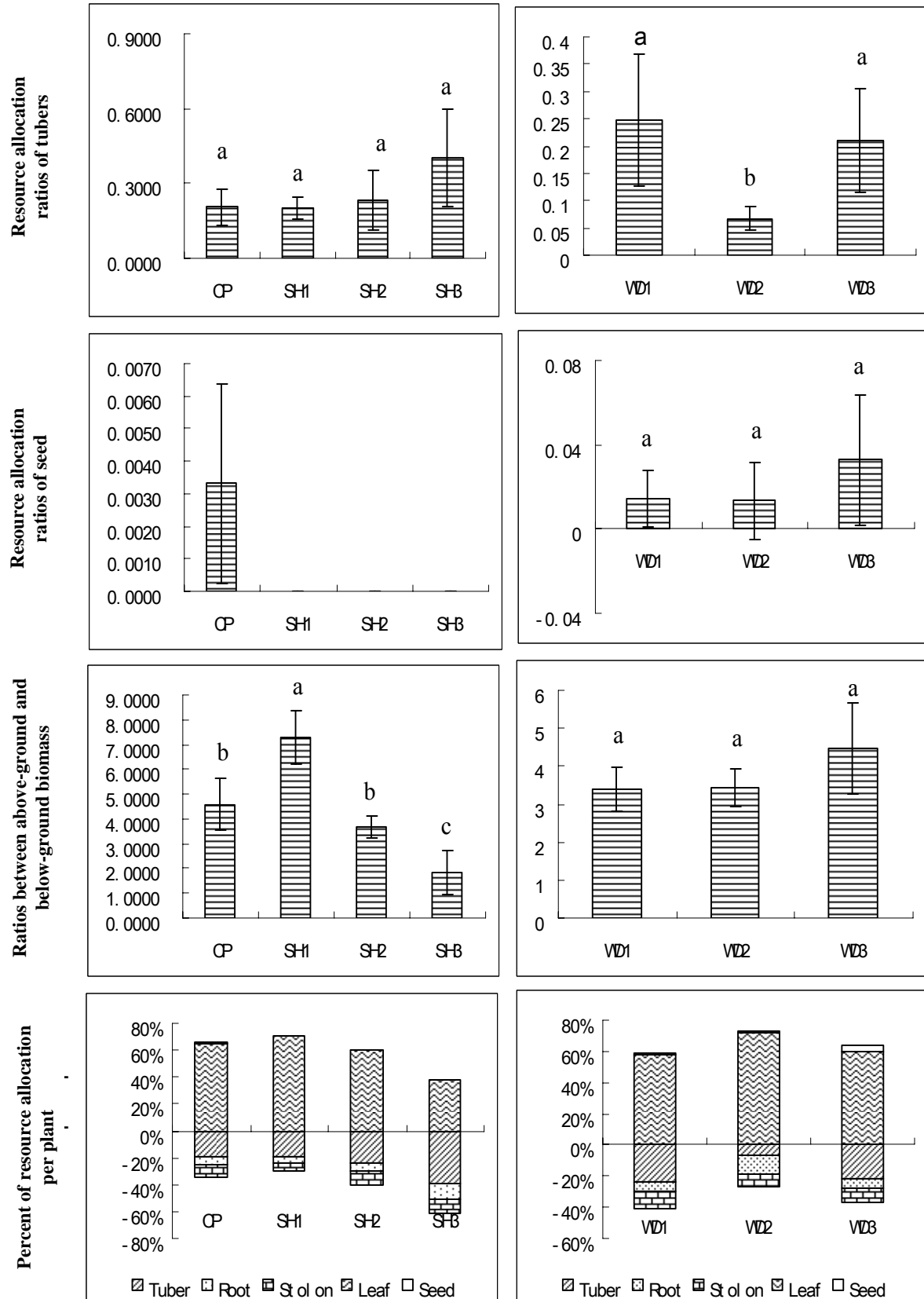


Fig. 3. Means (and standard errors) for resource allocation ratios observed in individual plant raised in four shading conditions and three water depth treatments. Different letters indicate significant differences in means ($p \leq 0.05$, *LSD* or *Kruskal-Wallis* test).

Table 3. Growth and reproductive organ biomass of *Vallisneria spinulosa* cultivated under different water depths.

Variables	WD1	WD2	WD3
Total biomass per plant (g)	4.512± 0.758a	5.384 ± 1.915a	3.250 ± 1.377a
Root biomass per plant (g)	0.267 ± 0.070b	0.650 ± 0.181a	0.191 ± 0.195b
Leaf biomass per plant (g)	2.594 ± 0.845ab	3.846 ± 1.467a	1.940 ± 0.659b
Stolon biomass per plant (g)	0.502 ± 0.153a	0.457 ± 0.181a	0.302± 0.142a
Tuber biomass per plant (g)	1.084 ± 0.522a	0.348 ± 0.136b	0.698 ± 0.399a
Seed biomass per plant (g)	0.065 ± 0.063a	0.082 ± 0.106a	0.120 ± 0.114a

Water depth had an indirect effect on vegetative strategy of *V. spinulosa*, but not that of sex reproduction. The number of tubers and ramets differed significantly among the water depth treatments. The number of ramets was maximized and the number of tubers was minimized in the one meters water-depth treatment (Fig. 2).

Both light quality and quantity affected by shaded treatments and water depth treatments had profound influences on growth, reproduction and the associated morphological traits of *V. spinulosa*. As observed in many other studies (Barko & Smart, 1981; Dennison & Alberte, 1986; Goldsborough & Kemp, 1988; Stuefer & Huber, 1998), the changes in both light quantity and quality had more profound effects on the morphology, growth and reproduction of plants than changes in light quantity alone. However, not all the traits examined in the study were sensitive to reduced light quantity and quality. For instance, Length of the total stolons, number of inflorescences per plant, stolon biomass per plant, seed biomass per plant, total biomass per plant, resource allocation ratios of seeds and ratios between above-ground biomass and below-ground biomass were relatively insensitive to light quantity and quality affected by water depth treatments, as well as resource allocation ratios of tubers was less changeable to light quantity and quality affected by shaded treatments. This study confirms that the treatments of shading associated light attenuation play a determinant role in the growth and reproductive strategy of macrophyte *V. spinulosa*, while the water-depth gradient has a scaling effect.

V. spinulosa employed a variety of morphological responses both apparently to shading treatments and to water depth gradients. Phenotypic plasticity is meant the ability of an individual organism to alter its morphology in response to environmental conditions (Schlichting, 1986). This study confirms that the length of the total stolons and total leaf areas significantly decreased under shaded environments as well as by water depth treatments. Similar morphological responses in plant height and branch length to increased water depth have previously been reported (Barko & Smart, 1981; Chambers & Kalff, 1985), although these studies did not consider the effect of plant size. Switching energy and biomass allocation to produce longer branches and taller plants, which was associated with decreased investment in branch number and below-ground biomass, is thought to be a relevant strategy for plants under poor light conditions, in both aquatic (Barko & Smart 1981; Barko *et al.*, 1991; Maberly, 1993) and terrestrial environments (Assmann, 1992; Pigliucci & Schlichting, 1995; Dudley

& Schmitt, 1996). Field study and the glasshouse experiment suggested that the primary responses to the lower light levels at increased depth were to increase vertical growth and decrease branch number, with a switch from below to above-ground allocation only when conditions are further constrained.

The availability of irradiance may be the ultimate limiting factor for growth of submersed aquatic plants (Spence, 1982). Research studies on submerged macrophytes suggested that the depth at which intensity of irradiance approximates 1% of the surface irradiance (Z) represented the limit of the biological photic zone (the compensation depth at which photosynthesis and plant respiration are equivalent) (Davis & Brinson, 1980; Barko *et al.*, 1986). In the Potomac River, the depth of 1% Z varied between 1.0 and 2.05 m and no plants were found growing deeper than 2.05 m. Plant growth under conditions of high turbidity and low irradiance penetration was therefore confined to shallow water. This could explain the lack of submerged macrophytes at sheltered sites in shallow eutrophic lakes. This study confirmed that the number of ramets was maximized and the number of tubers was minimized in one- meters water depth. This depth should provide for adequate light energy for successful growth and reproduction and enough potential habitat area for aquatic plants's good distribution and diversity. If management plans attempt to exceed conditions for *Vallisneria*, then other submersed plant species should flourish. Certainly, Factors who may affect the performance of plants at permanently inundated locations negatively are wave exposure, low redox conditions in the sediment due to a high organic matter content (Brock *et al.*, 1987; Van den Brink *et al.*, 1994; Li *et al.*, 2008., Wu *et al.*, 2011), and low internal oxygen availability (Yamasaki & Tange, 1981) if plants grow in deeper water.

Our study had shown complex responses to shading treatments and increasing water depth. There were similarities and differences in the biomass allocation responses of *V. spinulosa* to two different treatments. Not only shading treatments but also water depth limited the vegetative ability of *V. spinulosa*. Maybe water depth and shading treatments were important factors affecting rhizome survival and initial growth. The submerged macrophyte *V. spinulosa* allocated more biomass to the leaves, but not tubers. Hence *V. spinulosa* produced less tubers in those unfavourable conditions. (Warwick *et al.*, 2003) also showed that wetland reproductive dynamics was strongly influenced by depth, duration and season of

inundation. On the other hand, the response of *V. spinulosa* to two factors showed different modes. The more degree shaded treatments were, the more biomass was allocated to the below-ground parts, the less ratios between above-ground and below-ground biomass. Nevertheless, ratios between above-ground and below-ground biomass were less significantly different among water depth treatments. One of the important reasons was that the effect of water depth on the growth of *V. spinulosa* was indirect process to light and those effects could be counteracted by allocating more biomass to leaves of *V. spinulosa*. Optimal partitioning models and theories suggested that plants responded to variation in the environment by partitioning biomass among various plant organs to optimize the capture of nutrients, light, water, and carbon dioxide in a manner that maximizes plant growth rate (Thornley, 1969, 1972; Bloom *et al.*, 1985; Robinson, 1986; Dewar, 1993). But optimal partitioning models and theories would not adapt to the change of *V. spinulosa* while the normal growth of *V. spinulosa* was severely limited by environmental factors.

Submerged macrophytes *V. spinulosa* has two modes of reproduction: (i) vegetative propagation through tuber production; and (ii) sexual reproduction through seed production. Reduced light quantity and quality may decrease the proportion of flowering ramets and the fraction of biomass allocated to flowers and fruits. Changes in fruit (seed) number and quality directly influence plant fitness. The functional differentiation of the two reproductive types, together with environmental selective forces, leads to some modifications in the reproductive strategy of clonal species, which differs from unitary plants (Harper, 1977; Silvertown & Doust, 1993). Following the allocation principle, a standard explanation is that a large investment into clonal propagation necessarily implies a low sexual reproductive effort. In the past years, clonal propagation was viewed as a mechanism for plants to persist when sexual reproduction was hindered for some reason (Gustafsson, 1947). Shading can alter the plant's architecture as a result of effects on meristem initiation and fate as well as organ size and structure. Then submerged macrophytes *V. spinulosa* has reproduced less of ramets and tubers under shaded conditions versus natural conditions. Our result suggests that irradiance may indeed limit the distribution and abundance of *V. spinulosa* by reducing the number and size of winter buds.

Our results demonstrated that not only the morphological character in submerged macrophytes *V. spinulosa* was plastic and sensitive to changing availability of light by shaded treatments and water depth treatments, but that the regulating mechanism of biomass allocation and reproductive strategy was also environmentally sensitive. We found, like other studies (Xie *et al.*, 2003, 2004), that structure of phenotypic correlation matrices was sensitive to environmental conditions. It is not single traits but rather a particular combination of character correlations that appear to evolve under environmentally-specific selection, thereby providing the basis for local adaptation. The present paper demonstrates significant phenotypic plasticity in many vegetative and reproductive traits that are important ecologically and can facilitate successful recovery of *V.*

spinulosa population. The results also suggest that the effects of irradiance decrease is the main reason for the disappearance of submerged macrophytes from eutrophic waters and such information can be crucial for developing vegetation recovery strategies and predictive models of its spread.

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