

Turion production and nutrient reserves in *Potamogeton crispus* are influenced by sediment nutrient level

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ABSTRACT: The influence of sediment nutrient content on asexual propagule production in plants is poorly understood, especially in submersed macrophytes. To improve the understanding of turion (an aboveground asexual propagule) production, *Potamogeton crispus* L. was planted in 2 experimental conditions that differed in their levels of sediment nutrients. After 10 wk of growth, sediment nutrient level had significantly impacted the plants' vegetative and reproductive traits. Most vegetative trait measures of *P. crispus* (e.g. leaf mass fraction and stem mass fraction) were higher when plants were grown in nutrient-rich sediment compared with plants grown in nutrient-poor sediment. Reproductive trait measures (e.g. turion mass fraction and individual turion biomass) were higher in plants grown in nutrient-poor sediment compared with plants grown in nutrient-rich sediment. Plants grown in nutrient-rich sediment produced a larger number of small turions (<50 mg), in which more nutrients (total nitrogen and total phosphorus) were stored; plants grown in nutrient-poor sediment produced more large turions (>100 mg) and stored more total nonstructural carbohydrate (the major proportion of which was starch) in them. Path analysis revealed that total plant biomass (strong positive effect), leaf and stem biomass (weak negative effects) had direct effects on total turion biomass, which consequently affected turion size and number. Moreover, ramet number and mean shoot height also had weak but direct effects (both negative effects) on turion size and number. These results demonstrate that sediment nutrient content mediates plant vegetative traits and can subsequently affect turion production and reserves in *P. crispus*.

KEY WORDS: Asexual reproduction · *Potamogeton crispus* · Reserves · Sediment nutrients · Turion

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INTRODUCTION

Many environmental factors affect reproductive output in plants (e.g. Hartnett 1990, Schmid et al. 1994, Worley & Harder 1996, Stoll et al. 1998, Jongejans et al. 2006). Nutrients in sediment are among the factors that have been most widely studied. Indeed, even small variations in nutrient availability can create large differences in plant growth and reproductive output (Sugiyama & Bazzaz 1998, Bonser & Aarssen 2003). Plant size, biomass allocation, plant

structure, and total rhizome length all vary substantially according to sediment nutrients (Stoll et al. 1998, Müller et al. 2000, Vojtíšková et al. 2004, Maire et al. 2009). These traits may determine both the ongoing fitness of plants and the performance of future propagules.

Under varying nutrient conditions, plants presumably allocate an optimal level of resources to propagules. For instance, larger tubers are more likely to survive in nutrient-poor substrates, whereas abundant smaller tubers are common in nutrient-rich sub-

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strates (Hangelbroek et al. 2003). However, much of the research dedicated to understanding the relationship between sediment nutrients and reproductive output has focused on sexual reproduction. Although the influence of sediment nutrients on clonal plants has begun to receive attention, we do not have a thorough understanding of asexual propagation, particularly for plants in aquatic habitats (Slade & Hutchings 1987, Dong et al. 1997, Hangelbroek et al. 2003, Xiao et al. 2006). Asexual reproduction is generally assumed to be more common in aquatic habitats than in terrestrial habitats because of unfavorable ecological conditions for sexual reproduction, e.g. decreased pollination success and low reproductive success (for a review, see Santamaría 2002). Indeed, many asexual propagules of aquatic macrophytes can self-initiate abscission—examples include auto-fragments of *Myriophyllum spicatum* L. (Smith et al. 2002) and turions of *M. verticillatum* L. (Weber & Noodén 2005). Therefore, aquatic plants are very suitable for examining the relationship between sediment nutrients and successful asexual reproduction.

For a given amount of resources that a plant can allocate to propagation, there is a compromise between propagule size and number (i.e. the size-number trade-off, Smith & Fretwell 1974). Previous studies have suggested that this trade-off also exists in submersed macrophytes. For example, *Potamogeton pectinatus* L. balances size and number in its production of tubers (below-ground asexual propagules) (Santamaría & Rodríguez-Gironés 2002). Interestingly, the size-number trade-off in *P. pectinatus* tubers differs significantly among field sites (Santamaría & Rodríguez-Gironés 2002), which suggests that site-specific conditions (e.g. sediment type, nutrient conditions and light levels) may contribute to the way in which resources are partitioned into propagule size and number.

Potamogeton crispus L. is a perennial aquatic macrophyte native to Europe and Asia that is dominant in lakes, rivers and ponds throughout China (Xie et al. 2003). Unlike other aquatic macrophytes, *P. crispus* simultaneously flowers and produces above-ground turions almost continuously from late May to late October (Sastroutomo 1981, Wu et al. 2009). Turions are resistant plant buds found on certain aquatic plants that allow the plants to survive winter in a vegetative state without setting seeds (Rogers & Breen 1980, Kunii 1982). Large nutrient reserves may be stored in turions, which allow the turions to serve multiple functions for the plant including storage, propagation and dispersal (Jian et al. 2003, Woolf &

Madsen 2003, Adamec 2010). Although *P. crispus* produces seeds, the viability and germination of these seeds is reportedly very low (0.001%; Rogers & Breen 1980), which supports the hypothesis that the primary means of propagation for this species is the dispersal of turions (Jian et al. 2003, Woolf & Madsen 2003). Field studies have indicated that turion production is high in *P. crispus*. For example, densities of 1000 to 1500 turions m^{-2} have been documented in South Africa (Rogers & Breen 1980). In addition, densities ranging from 200 to 1700 turions m^{-2} have been reported in Japan (Kunii 1982), and densities ranging from 726 to 2713 turions m^{-2} have been documented in ponds in the USA (Woolf & Madsen 2003). Successful propagation from turions (up to 60% of turions germinate, Rogers & Breen 1980) results in the formation of monospecific stands of *P. crispus*, a degradation of water quality (the aboveground portions of *P. crispus* decompose in summer) and a reduction in the relative abundance and richness of other local species (Bolduan et al. 1994).

In this study, we examined how vegetative growth and turion production in *Potamogeton crispus* were affected when the plants were grown in 2 types of sediment that had different nutrient content. The following questions were addressed: (1) Does *P. crispus* adjust its vegetative traits (e.g. overall plant biomass) and biomass partitioning in response to different levels of sediment nutrients? (2) Does *P. crispus* adjust its turion production (e.g. turion number and size) and storage matter in response to different levels of sediment nutrients?

MATERIALS AND METHODS

Sample site and collection

This study was conducted at The National Field Station of Freshwater Ecosystem of Liangzi Lake, China (30° 5′–30° 18′ N, 114° 21′–114° 39′ E). In March 2008, 100 apical shoots of *Potamogeton crispus* (approximately 10 cm long with 6 to 7 leaves) were collected from randomly selected plants in Liangzi Lake. The collection sites were covered by monospecific stands of *P. crispus* during March. The water depth at the collection site was 0.6 to 1.2 m and the site contained both muddy substratum, with a total nitrogen (TN) content of 2.86 $mg\ g^{-1}$ and a total phosphorus (TP) content of 0.13 $mg\ g^{-1}$, and sandy substratum, with a TN content of 0.04 $mg\ g^{-1}$ and a TP content of 0.001 $mg\ g^{-1}$. The apical shoots were

transplanted into containers filled with sand and water to a depth of 20 cm. Containers were stored in a greenhouse (water temperature $25.62 \pm 2.17^\circ\text{C}$; light intensity $1923 \pm 37.45 \mu\text{mol photons m}^{-2} \text{s}^{-1}$, mean \pm SE) for approximately 2 wk until the plants had well-developed root systems.

Experimental design

The experiment was conducted from April 9, 2008 to June 18, 2008. During the experimental period, individual plants were grown in either of 2 test sediments and each treatment was replicated 24 times for a total of 48 individual plants. Two different sediment nutrient levels were tested: a nutrient-poor sediment, which consisted of 25% muddy substratum mixed with 75% sand substratum and had a TN and a TP content of 0.74 mg g^{-1} and 0.03 mg g^{-1} , respectively; the nutrient-rich sediment consisted of 75% muddy substratum mixed with 25% sand substratum and had a TN and a TP content of 2.20 mg g^{-1} and 0.09 mg g^{-1} , respectively. Both substrata were obtained from the collection site in Liangzi Lake. Each plant was individually placed as an apical shoot into a plastic pot (diameter 25 cm, height 20 cm) along with 4 kg (dry weight) of substratum. Each pot was placed in a fiberglass tank (diameter 100 cm, height 100 cm) and the tanks were filled with ambient lake water to a depth of 100 cm (TN 0.71 mg l^{-1} , TP 0.04 mg l^{-1}). All tanks (48 tanks in total) were placed outdoors in a block design with 6 replicated blocks (four tanks from each treatment were randomly placed in one block). At the beginning of the experiment, the plants had a fresh weight of $0.48 \pm 0.02 \text{ g}$ (mean \pm SE) and a total height of $24.8 \pm 0.5 \text{ cm}$ (mean \pm SE). Water temperatures and light intensities in the experimental tanks were recorded at noon every 3 d (the water temperature was $26.40 \pm 3.61^\circ\text{C}$ and the light intensity was $2132 \pm 38.23 \mu\text{mol photons m}^{-2} \text{s}^{-1}$, mean \pm SE, $n = 24$). To reduce the influence of algae on plant growth, the water in the tanks was changed weekly.

Plant harvest

After 10 wk of growth, plants from each nutrient treatment were carefully uprooted and rinsed to remove sediment from the roots. Fresh weights and stem lengths were recorded for harvested plants before separating each plant into roots, stems, leaves, turions and rhizomes. Plant tissue samples were

dried at 80°C for 72 h before weighing. All vegetative trait measures (root, stem, rhizome and turion mass fractions) were calculated as dry weight (DW) percentages of the total plant biomass, and individual turion biomass was calculated as the average DW of individual turions.

Chemical analysis

Upon collection, water, sediment and turion samples were digested with H_2SO_4 and analyzed for TN and TP content. The TN and TP content were reported on a %DW basis. Total nonstructural carbohydrate (TNC) content was measured using the perchloric acid/anthrone method (Morris 1948) by combining the soluble sugar and starch fractions. The soluble sugar and starch contents were reported as mg g^{-1} DW. For further details on sample preparation and analytical methods, see Xie & Yu (2011). TN, TP and TNC measurements were collected in triplicate.

Statistical analysis

All data were $\log(x)$ transformed to ensure homoscedasticity and normality of residuals. The differences among blocks were treated as random effects, and there were no significant effects ($p > 0.05$). Thus, the statistical differences between nutrient levels were analyzed using t -tests ($\alpha = 0.05$). In addition, we performed a path analysis of partial correlation coefficients obtained from a hierarchical set of multiple regressions, which allowed us to evaluate the effects of vegetative traits (e.g. total plant biomass, leaf and stem biomass) on total turion production and its allocation into turion size and number (Santamaría & Rodríguez-Gironés 2002, Hangelbroek & Santamaría 2004). All data were analyzed using SPSS 13.0 software (SPSS, Chicago).

RESULTS

After 10 wk of growth, we observed significant differences in total plant biomass between the rich and poor nutrient conditions (Table 1). Specifically, *Potamogeton crispus* grown in nutrient-rich sediment had higher stem and leaf mass fractions, and lower root mass fractions compared with plants grown in nutrient-poor sediment. Rhizome mass fraction, however,

Table 1. *Potamogeton crispus*. Traits of the macrophyte grown in nutrient-poor and nutrient-rich sediments from Liangzi Lake, China. Absolute values (mean \pm SE) are shown with *t*-values and *p*-values from *t*-test. All data were transformed using a log(*x*) function. Significant *p*-values (*p* < 0.05) are indicated in **bold**

Trait	Nutrient-poor sediment	Nutrient-rich Sediment	n	<i>t</i>	<i>p</i>
Vegetative traits					
Total plant biomass (g)	4.50 \pm 0.4	6.67 \pm 0.6	48	2.817	0.007
Root mass fraction (%)	5.49 \pm 0.6	3.89 \pm 0.3	48	-2.261	0.029
Stem mass fraction (%)	15.05 \pm 0.7	25.50 \pm 1.3	48	7.629	<0.001
Leaf mass fraction (%)	20.34 \pm 1.2	38.52 \pm 2.1	48	7.160	<0.001
Rhizome stem mass fraction (%)	1.90 \pm 0.1	1.53 \pm 0.1	48	-1.866	0.068
Root:shoot ratio (%)	5.91 \pm 0.7	4.07 \pm 0.3	48	-2.275	0.028
Ramet number	10.96 \pm 0.6	14.67 \pm 0.9	48	3.255	0.002
Rhizome stem length (cm)	78.33 \pm 5.2	87.03 \pm 6.7	48	0.644	0.523
Rhizome internode length (cm)	7.38 \pm 0.3	6.30 \pm 0.3	48	-2.754	0.008
Mean shoot height (cm)	60.37 \pm 2.3	80.19 \pm 3.1	48	4.647	<0.001
Turion traits					
Turion mass fraction (%)	57.22 \pm 2.2	30.55 \pm 2.9	48	-6.363	<0.001
Individual turion biomass (mg)	85.2 \pm 6.0	56.4 \pm 5.1	48	-3.777	<0.001
Turion number	31.21 \pm 2.8	36.79 \pm 3.8	48	0.710	0.487
(Stem+leaf):turion ratio (%)	69.00 \pm 8.1	290.44 \pm 39.8	48	11.332	<0.001

was similar regardless of nutrient condition. Thus, plants grown in nutrient-poor sediment had significantly higher root:shoot ratios than plants grown in nutrient-rich sediment. Plants grown in nutrient-rich sediment had shorter rhizome internode lengths, which led to an increased number of ramets. There was no difference in total rhizome length between the 2 sediment treatments. Plants grown in nutrient-rich sediment were taller than those grown in nutrient-poor sediment (Table 1).

Although the total number of turions was similar between the 2 nutrient conditions, plants grown in nutrient-poor sediment had significantly greater turion mass fractions and (stem+leaf):turion ratios (Table 1). The biomass of individual turions was greater in nutrient-poor sediment compared with nutrient-rich sediment (Table 1). Furthermore, the size of turions was significantly different between the 2 nutrient treatments. Plants grown in nutrient-rich sediment tended to produce more small turions (<50 mg), whereas plants grown in nutrient-poor sediment tended to produce more large turions (>100 mg) (Fig. 1).

The path analysis revealed that total plant biomass, leaf and stem biomass had direct effects on turion production and that these effects together explained 94.6% of the variation in turion production. Among these traits, the positive effect of total plant biomass on turion production was stronger than the negative

effects of leaf and stem biomass. However, these 3 vegetative traits did not directly affect turion number or size (Fig. 2). Total turion biomass had a strong positive effect on both turion number and size, which were negatively correlated (Fig. 2). Ramet number had a direct negative effect on turion number, and mean shoot height had a direct negative effect on both turion number and size; however, the negative effects of shoot height were weaker than the effect of turion production on turion number and size (Fig. 2). Root biomass, rhizome stem biomass, rhizome stem length and

rhizome internode length did not have significant effects on any trait.

Starch content was higher in turions produced in nutrient-poor sediment compared with turions produced in nutrient-rich sediment, but soluble sugar content was similar (Fig. 3). Furthermore, the majority of TNC in turions was starch (70 to 99% and 75 to 99% in turions produced in nutrient-poor and nutrient-rich sediment, respectively). Plants grown in nutrient-rich sediment produced turions with higher TN and TP content than equivalent plants grown in nutrient-poor sediment (Fig. 3).

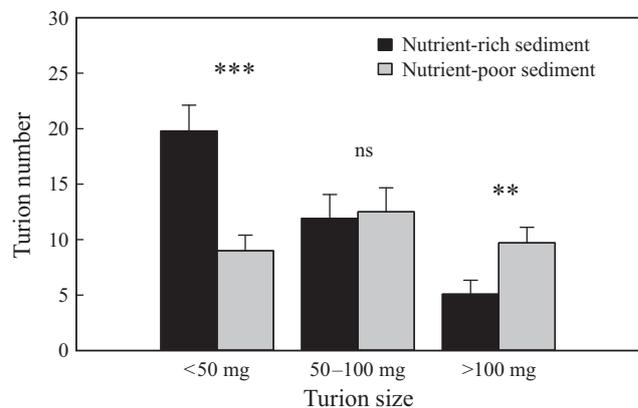


Fig. 1. *Potamogeton crispus*. Turion number (mean \pm SE, *n* = 24) in relation to turion size categories (dry mass) under nutrient-poor and nutrient-rich sediment regimes. The results were analyzed with a *t*-test. ****p* < 0.001, ***p* < 0.01, ns *p* > 0.05

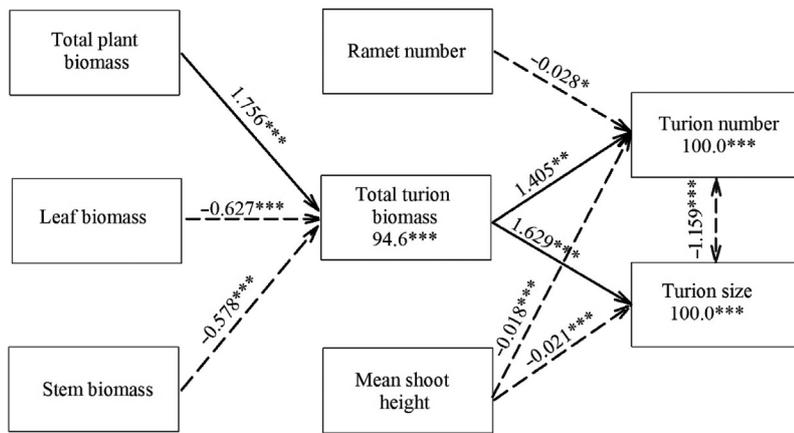


Fig. 2. Results of the path analysis for the effects of traits on turion size and number in *Potamogeton crispus*. All possible pathways were tested, but only the significant relationships are shown here. Solid arrows indicate positive correlations, and dashed arrows show negative correlations. Partial correlation coefficients and their significance levels are indicated on the arrows, and the percentages of explained variation (adjusted R^2), and the significance level of the multiple regression analysis are indicated within boxes: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$

DISCUSSION

The present study shows that the elevated nutrient levels in the sediment of Liangzi Lake support greater total biomass in *Potamogeton crispus* plants. These findings are consistent with our previous studies on other plant species (Xie et al. 2010, Xie &

Yu 2011). In nutrient-rich sediment, the significant increase in total plant biomass and decrease in root:shoot ratio were caused by significant increases in leaf and stem biomass. These findings are similar to those of several previous studies in both terrestrial and aquatic clonal plants (Müller et al. 2000, Vojtíšková et al. 2004). Although we found that rhizome stem length was similar between treatments, rhizome internode length was shorter and ramet number was significantly greater in plants grown in nutrient-rich sediment compared with plants grown in nutrient-poor sediment; these findings are also consistent with previous studies of clonal plants (Slade & Hutchings 1987, Stoll et al. 1998, Xiao et al. 2006, Wang & Yu 2007). These vegetative responses (i.e. changes in leaf mass fraction, stem mass fraction, root:shoot ratio and

rhizome internode growth) resulted from exposure to different nutrient conditions and indicate the plasticity of *P. crispus*.

Our results confirm that total plant biomass has a strong direct positive effect on turion production, which is consistent with previous field observations in *Potamogeton crispus* (Kunii 1982). Kunii (1982) also observed that tall-growing plants tended to produce small ramets through rhizomes. Both ramet number and mean shoot height had weak negative effects on turion number and mean shoot height also had a weak negative effect on turion size in our experiment. This may be due to the innate reproductive strategy of perennial clonal plants. Indeed, perennial clonal plants grown in nutrient-rich sediment increase their clonal growth to enhance their competitive abilities and nutrient influxes and they decrease their production of asexual propagules (Takada & Nakajima 1996, Jongejans et al. 2006).

Turions produced by *Potamogeton crispus* can act as storage organs to buffer against unfavorable ecological conditions (Adamec 2010). Although the total number of turions for plants grown in nutrient-rich versus nutrient-poor sediments was similar, individual turion biomass was higher in plants grown in nutrient-poor sediment. These results may be explained by the finding that nutrient limitation causes resources to be re-allocated to carbohydrate reserves instead of being utilized for vegetative growth processes (Hangelbroek et al. 2003). For instance, plants in stressful habitats allocate more

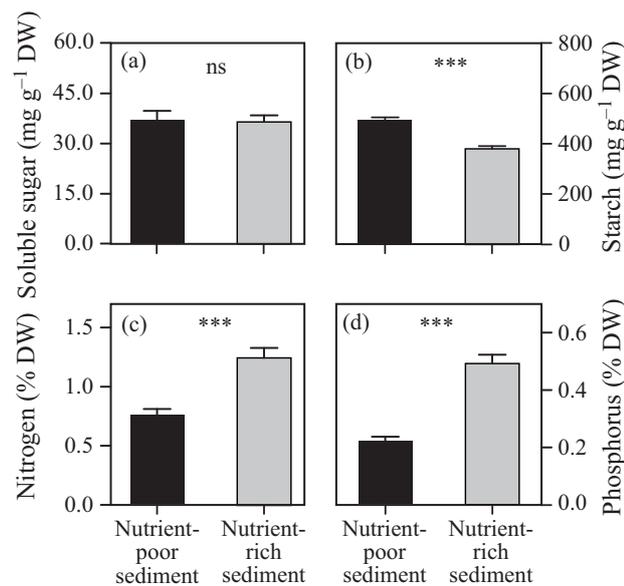


Fig. 3. *Potamogeton crispus*. Differences in (a) soluble sugar, (b) starch, (c) nitrogen and (d) phosphorus content of turions between the sediment nutrient treatments. Data are means \pm SE ($n = 72$). The results were analyzed with a t -test: *** $p < 0.001$, ns $p > 0.05$

dry mass to the development of storage organs than plants in favorable habitats (Puijalón et al. 2008). The plasticity of *P. crispus* was demonstrated by its ability to re-allocate resources to carbohydrate reserves (turions in this case) when faced with nutrient-poor conditions.

Turion size and number were negatively related in our study, and this trade-off differed significantly between plants grown in nutrient-rich sediment and those grown in nutrient-poor sediment. Plants grown in nutrient-poor sediment produced larger propagules, whereas plants grown in nutrient-rich sediment produced smaller propagules. These findings are consistent with a previous study of *Potamogeton pectinatus* (Hangelsbroek et al. 2003). This pattern can be explained in several ways. Firstly, plants may decrease their investment in leaf and stem biomass, which can result in a decreased supply of carbohydrate to newly growing propagules and allow plants to store carbohydrate in previously formed turions under conditions of nutrient-poor sediment (Hangelsbroek et al. 2003). Secondly, differences in the timing of turion formation may explain why plants grown in nutrient-rich sediment produced smaller turions. Because we harvested all plants after 10 wk of growth, we did not fully account for differences in the length of the turion formation period. For plants grown in nutrient-poor sediment, turion formation probably began earlier, whereas plants grown in nutrient-rich sediment allocated more carbohydrate to vegetative growth.

Carbohydrate reserves play an important role in propagule performance (e.g. survival, sprouting and spread) (Spencer & Ksander 1996, Suzuki & Stuefer 1999, Werger & Huber 2006), and in determining whether the propagules of aquatic plants sink or float. Studies have shown that turions of *Potamogeton crispus* contain high TNC, particularly starch (Woolf & Madsen 2003). This starch is relatively dense (1.44 g cm^{-3}) and may alter the density of aquatic plant propagules; however, other factors, such as lacunal volume, are also important (Weber & Noodén 2005). In fact, an increase in starch content can increase propagule density enough to cause sinking—for example, stems of *Elodea nuttallii* (Planch) St. John (Kunii 1984) and turions of *Myriophyllum verticillatum* (Weber & Noodén 2005). In our experiment, the starch content in turions from nutrient-poor sediment was higher compared with turions from nutrient-rich sediment. Large amounts of starch stored in turions from plants grown in nutrient-poor sediment would probably enable turions to rapidly sink. Interestingly, TN and TP content were higher in

turions from nutrient-rich sediment. This result is consistent with previous studies, which show that plants grown in infertile environments accumulate more carbohydrates but store fewer nutrients in propagules (Bloom et al. 1985). In addition, other studies have suggested that propagule production is limited by nutrient shortages (Hangelsbroek et al. 2003, Xie et al. 2010, Xie & Yu 2011). Moreover, the predominant function of nutrient reserves in turions may be to promote plant survival during dormancy (e.g. to support the growth of new roots or shoots for mineral uptake from water or sediment, Adamec 2010). Therefore, it is possible that higher nutrient levels in turions from nutrient-rich sediment facilitate survival and establishment during the dispersal process.

Although previous studies have shown that the seedling growth and plant distribution of *Potamogeton* species can tolerate a wide range of sediment grain sizes (Nicholson et al. 1975, Ailstock et al. 2010), our study was limited by mixing different types of substrata to create 2 different nutrient levels. We did not perform a comprehensive examination of how other abiotic factors (e.g. drainage rate, nutrient adsorption, biological availability or oxygen circulation) may interact with sediment nutrients to determine turion production. For instance, the growth of submerged species is negatively correlated with mean dissolved organic carbon content in the interstitial waters of the sediment (Barko & Smart 1983). Therefore, in further studies regarding the impact of sediment nutrient on asexual reproduction, the possible roles of other abiotic conditions should be considered.

CONCLUSIONS

This study revealed that, under experimental conditions, total plant biomass has a strong direct positive effect on turion production in *Potamogeton crispus*. The influence of sediment nutrient level on vegetative and reproductive growth was examined, and we found that the vegetative trait measures (e.g. total plant biomass, leaf and stem mass fractions) of plants grown in nutrient-rich sediment significantly increased whereas reproductive trait measures (e.g. turion mass fraction and turion size) significantly decreased. Our findings also suggest that increases in some vegetative traits (e.g. leaf and stem biomass and ramet number) of plants grown in nutrient-rich sediment have weak negative effects on turion traits. Although nutrient reserves were significantly lower

in turions from nutrient-poor sediment, the amount of carbohydrate stored in these turions was significantly higher, which suggests that nutrient shortages may result in decreased turion production. Furthermore, there are various factors that may influence turion production, ranging from sediment nutrients to abiotic environmental aspects of the sediment. Thus, additional studies on these topics should be performed.

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