Compensatory growth of a submerged macrophyte (*Vallisneria spiralis*) in response to partial leaf removal: effects of sediment nutrient levels

Kuanyi Li · Zhengwen Liu · Binhe Gu

Abstract Many plants mitigate damage due to loss of tissues through compensatory growth, yet their compensatory abilities vary depending on physical and environmental conditions. We conducted an outdoor experiment using a 2×2 factorial experimental design (leaf damage and nutrient level), in order to evaluate the compensatory growth response of *Vallisneria spiralis* (a submerged macrophyte widely distributed in China) to partial leaf removal in two nutrient regimes. Our results reveal that under both high- and low-nutrient conditions, *V. spiralis* exhibited substantial compensatory growth response to partial leaf removal via accelerated growth rates, with significantly greater compensatory abilities observed in the high-nutrient sediments. These observations suggest that *V. spiralis* has a strong compensatory ability to partial leaf removal, providing arguably one of the major mechanisms for the coexistence of this plant with herbivores, in particular, in eutrophic freshwater ecosystems (e.g. Lake Taihu).

Keywords Compensatory growth · *Vallisneria spiralis* · Partial leaf removal · Sediment nutrient level

K. Li · Z. Liu (✉)
State Key Laboratory of Lake Science and Environment, Nanjing Institute of Geography and Limnology, Chinese Academy of Sciences, 210008 Nanjing, China
e-mail: zliu@niglas.ac.cn

K. Li
Graduate School of Chinese Academy of Sciences, 100049 Beijing, China
e-mail: kyli@niglas.ac.cn

Z. Liu
Institute of Hydrobiology, Jinan University, 510630 Guangzhou, China

B. Gu
Southwest Research and Education Center, University of Florida, Immokalee, FL 34142, USA

Introduction

For most plants, the loss of tissue (especially leaf) due to herbivory or mechanic damage is common and often leads to a reduction in plant fitness (Belsky 1986; Painter and Belsky 1993; Van Staalduinen and Anten 2005). In some situations, however, many plants are able to compensate for the lost tissue through accelerated growth (McNaughton 1983; Lennartsson et al. 1998). Compensatory growth, a positive response of plants to injury, has been used to describe such responses ranging from a partial replacement of lost tissue to a net gain of biomass (Belsky 1986). Compensation for the tissue loss can occur through a number of mechanisms, such as increases in the photosynthetic rate (Meyer 1998) or growth rates (Oba et al. 2000; Vergés et al. 2008), and branching or tillering following the release from

apical dominance (Valentine et al. 1997; Lortie and Aarssen 2000).

The capacity for a plant to compensate for tissue loss depends on the plant species, amount of damaged tissue, pattern of damage, and environmental conditions such as soil nutrient availability (Verkaar et al. 1986; Ferraro and Oesterheld 2002). Soil nutrients facilitate the compensation of the plant tissues. Therefore, plants growing in nutrient-rich habitats potentially have an adequate supply of nutrients for the replacement of the lost tissues (Zhao et al. 2008). By contrast, some plants growing in nutrient-limited soils are unable to acquire a sufficient amount of nutrients necessary to replenish a large loss of biomass (Chapin and McNaughton 1989; Zhao et al. 2008).

Vallisneria spiralis is a perennial submerged plant with a wide distribution in China. Its leaves can be consumed by both aquatic vertebrate, such as grass carp (*Ctenopharyngodon idella*) (Jin 1995), and aquatic invertebrate, such as snails (Li et al. 2006). Interestingly, *V. spiralis* is a dominant species in lakes such as East Bay of Lake Taihu, where herbivory is intense (Gu et al. 2005). In this paper, we describe an experiment on the compensatory response of *V. spiralis* to partial leaf removal. This study was designed to answer two questions: (1) Is there a compensatory growth response for *V. spiralis*? (2) Is the plant better able to compensate for leaf loss in high sediment nutrient level? This study will contribute to our understanding of the coexistence mechanism of submerged macrophytes and herbivorous aquatic animals in freshwater ecosystems.

Materials and methods

Experimental materials

The experimental plant, *V. spiralis,* is a perennial submerged macrophyte producing rosettes of strap-like leaves. It is commonly found in Lake Taihu (31°30′N, 120°30′E), a large, shallow, eutrophic lake in China. The plants were collected from the lake and cultivated in tanks for a month before the experiment was initiated.

Two types of sediments were collected from Lake Taihu. The concentrations of nutrients in the high-nutrient sediments were about twice those in the low-nutrient sediments (Table 1). Prior to the experiment,

Table 1 Content (mg g^{-1}, mean $\pm$ SE) of total nitrogen (TN), total phosphorus (TP), and organic matter (OM) in two sediment types

Sediment type	TN	TP	OM
High-nutrient sediments	1.49 ± 0.04	0.67 ± 0.03	25.99 ± 0.60
Low-nutrient sediments	0.72 ± 0.06	0.24 ± 0.03	12.42 ± 1.09

Each parameter contained 4 repeats

the sediments were dried, sieved (mesh size of 1.0 mm), and mixed to ensure homogeneity. The water collected from the lake initially contained 3.76 mg l^{-1} of total nitrogen (TN) and 132 μg l^{-1} of total phosphorus (TP); it was then filtered before use (mesh size of 15 μm).

Experimental design

In order to test the compensatory response of *V. spiralis* to partial leaf removal, an experiment was set up using a 2 × 2 factorial experimental design (leaf damage, nutrient level) at Lake Taihu Experimental Station located at the shoreline of Lake Taihu from August 27 to September 24, 2006. The experimental period (4 weeks) was determined following Jin (1995), who indicated that the recovery of *Vallisneria* from similar leaf damage intensity took about 1 month. The experimental mesocosm consisted of 12 outdoor polyethylene buckets (height 70 cm, top diameter 50 cm, bottom diameter 45 cm), each of which held 50 l of water and 10 cm of sediments. All treatments were run in triplicate. Young plants (each 5–7 leaves, 28.0 ± 2.0 cm high) were transplanted into 12 buckets, with 10 plants (total wet weight 35.0 ± 1.5 g) in each bucket. For leaf damage treatments, the top portion of the leaves was clipped using scissors and removed before the plants were transplanted, and the mass of the leaves removed was 28–30% of total plant biomass (Jin 1995). To maintain constant nutrient levels in the water column of all buckets (5.0 mg l^{-1} for TN and 0.20 mg l^{-1} for TP), we supplemented nutrients to the buckets by adding nitrogen as NaNO$_3$ and phosphorus as NaH$_2$PO$_4$.2H$_2$O twice a week over the 4-week experimental period. These nutrient concentrations were similar to those of Lake Taihu surface waters (mean concentrations in 2005, TN = 4.78 mg l^{-1}, TP = 0.18 mg l^{-1}; Li et al. unpublished data). Prior to each nutrient addition, the TN and TP concentrations

in each bucket were analyzed to calculate the amount of each nutrient to be added. A pre-weighed amount of inorganic nutrients was diluted in 100 ml deionized water on site, and poured evenly onto the water surface in each bucket. During the experimental period, water temperatures were maintained between 25 and 32°C, and temperature differences among buckets no more than 2°C. Secchi depth ranged from 40 to 45 cm, and the differences were not more than 2 cm among buckets.

At the end of the experiment, all the plants were removed from each bucket. The numbers of leaves and roots and the maximum leaf width per plant were determined. The plants were oven-dried at 60°C for 48 h, then the dry weight of the whole plant and the roots per plant were measured. The content of nitrogen and phosphorus in leaves, water columns, and sediments was analyzed according to standard methods (Huang et al. 1999). Cumulative biomass and relative growth rate were calculated, respectively. The cumulative biomass is the increased biomass for control plants and the increased biomass plus removed tissue biomass for the damaged plants (Belsky 1986). Relative growth rate (Li et al. 2005; Henry-Silva et al. 2008) was calculated as $(\ln W_f - \ln W_i)/days$, where W_f (g) and W_i (g) were final and initial total dry weights of plants in each bucket, respectively.

Statistical analyses

All statistical procedures were performed using SPSS software (Version 17.0). T-test was used to assess the difference and similarity of nutrient content in the two types of sediments. MANOVA was used to analyze to the compensatory growth response of V. spiralis to leaf damage with sediment type and leaf damage as fixed factors. The level of significance was set at 0.05 for all analyses.

Results

Cumulative biomass

Compared to the control plants, the damaged plants were able to regain up to 108% of the cumulative biomass in the low-nutrient sediments and 179% in the high-nutrient sediments within 4 weeks (Table 2), suggesting that adequate compensation response occurred in two nutrient regimes. There was a significant interaction between sediment type and partial leaf removal (MANOVA, $P = 0.044$), and the effect of leaf damage on cumulative biomass depended on sediment nutrient conditions (Tables 2, 3).

Relative growth rate

Partial leaf removal resulted in a significant increase in the relative growth rates (RGR) of V. spiralis (MANOVA, $P = 0.002$) (Table 3; Fig. 1). Compared to the control plants, the RGRs of the damaged plants increased by 64.1% in the high-nutrient sediments and by 17.9% in the low-nutrient sediments. In addition, nutrient levels of sediments significantly affected the growth of the plants (MANOVA, $P = 0.009$). Compared to the plants in high-nutrient sediments, the RGRs in the low-nutrient sediments increased by 53.3% for control plants and by 10.1% for the damaged plants, respectively. No significant interaction existed between nutrient levels and partial leaf removal (MANOVA, $P > 0.05$).

Leaf number and maximum leaf width

Leaf number of the damaged plants was significantly higher than that of the control plants (MANOVA, $P = 0.015$) (Table 3; Fig. 2). Leaf removal had no effect on maximum leaf width (MANOVA,

Table 2 Initial, final, and cumulative biomasses (g, dry weight) of V. spiralis in four treatments ($n = 3$, mean $\pm$ SE)

| Treatment	Initial biomass	Loss of biomass	Final biomass	Cumulative biomass
HNS	3.6 ± 0.2	0	7.0 ± 0.4	3.4 ± 0.6
HNS + damaged	2.4 ± 0.2	1.1 ± 0.2	7.4 ± 0.5	6.1 ± 0.6
LNS	3.6 ± 0.1	0	10.1 ± 0.4	6.5 ± 0.4
LNS + damaged	2.4 ± 0.1	1.1 ± 0.2	8.3 ± 0.8	7.0 ± 1.2

HNS and LNS are high-nutrient sediments and low-nutrient sediments, respectively

Table 3 Results of MANOVA for cumulative biomass, relative growth rate, leaf number, maximum leaf width, root number and weight, and leaf nutrient contents of *V. spiralis* at the end of the experiment
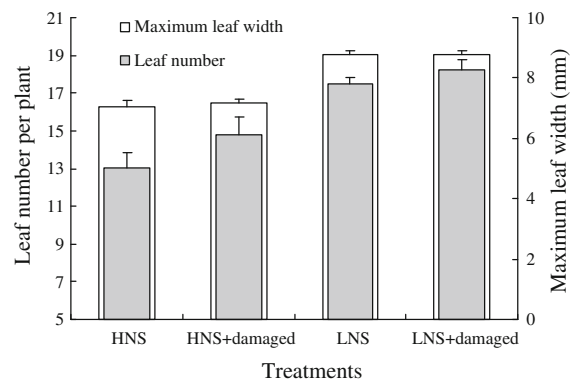
|		Cumulative biomass				Relative growth rate				Leaf number				Maximum leaf width		
	df	MS	F	P	df	MS	F	P	df	MS	F	P	df	MS	F	P
Sediment type	1	11.741	18.094	**0.003**	1	243.901	11.687	**0.009**	1	46.413	92.365	**<0.001**	1	0.083	294.12	**<0.001**
Leaf damage	1	7.192	11.083	**0.01**	1	414.187	19.847	**0.002**	1	4.813	9.579	**0.015**	1	0	0.471	0.512
Sediment type × Leaf damage	1	3.685	5.679	**0.044**	1	70.567	3.381	0.103	1	0.75	1.493	0.057	1	0	0.471	0.512
Error	8	0.649			8	20.869			8	0.503			8	0		
		Root number				Root weight				Leaf N content				Leaf P content		
	df	MS	F	P	df	MS	F	P	df	MS	F	P	df	MS	F	P
Sediment type	1	2,914.083	114.65	**<0.001**	1	0.083	37.29	**<0.001**	1	4.839	6.4	**0.035**	1	3.462	65.538	**<0.001**
Leaf damage	1	18.75	0.738	0.415	1	0.003	1.369	0.276	1	0.5	0.662	0.44	1	0.166	3.141	0.114
Sediment type × Leaf damage	1	60.75	2.39	0.161	1	0.001	0.318	0.588	1	3.23	4.272	0.073	1	0.04	0.753	0.411
Error	8	25.417			8	0.002			8	0.756			8	0.053		

P values < 0.05 are in bold
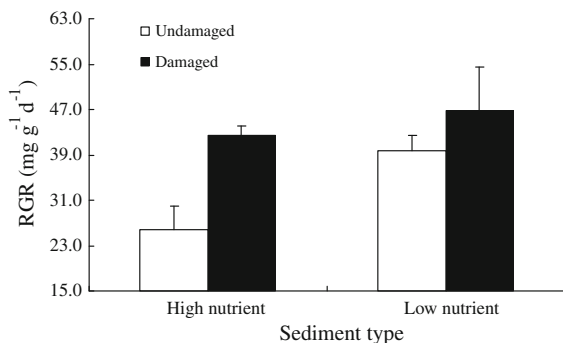
Fig. 1 Relative growth rates (*RGR*) of damaged and undamaged plant *Vallisneria spiralis* grown in high and low-nutrient sediments (*n* = 3, mean ± SE)

Fig. 2 Leaf number and maximum leaf width of damaged and undamaged plant *Vallisneria spiralis* grown in different treatments (*n* = 3, mean ± SE). HNS and LNS are high-nutrient sediments and low-nutrient sediments, respectively

$P > 0.05$), but nutrient levels of sediments significantly affected leaf number and maximum leaf width (MANOVA, $P < 0.001$). Leaf number (17–19 leaves per plant) in low-nutrient sediments was significantly more than that (12–15 leaves per plant) in high-nutrient sediments (MANOVA, $P < 0.001$), and the maximum leaf width (8.6–8.9 mm) in low-nutrient sediments was significantly larger than that (6.8–7.3 mm) in high-nutrient sediments (MANOVA, $P < 0.001$). There was no significant interaction between nutrient levels and partial leaf removal (MANOVA, $P > 0.05$).

Root number and weight

Partial leaf removal had no significant effect on root number or root weight per plant (MANOVA, $P > 0.05$) (Table 3; Fig. 3). Root number and dry weight were strongly affected by nutrient levels of sediments, significantly higher in the low-nutrient sediments than in the high-nutrient sediments (MANOVA, $P < 0.001$).
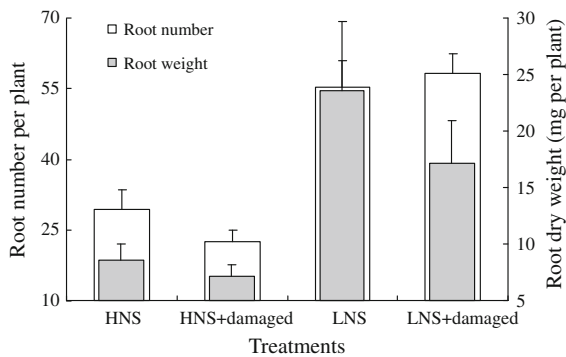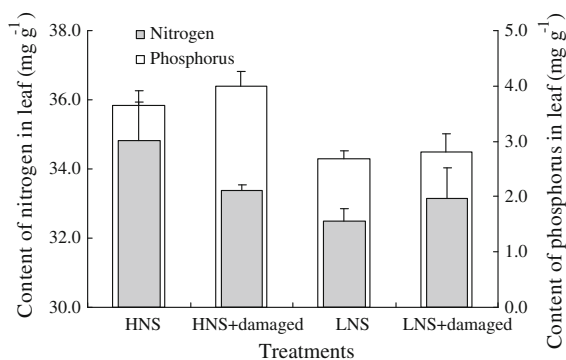
Fig. 3 Root number and root weight of damaged and undamaged plant *Vallisneria spiralis* grown in different treatments ($n = 3$, mean $\pm$ SE). HNS and LNS are high-nutrient sediments and low-nutrient sediments, respectively

The interaction of nutrient levels with partial leaf removal was not significant (MANOVA, $P > 0.05$).

Leaf nutrient contents

Leaf removal had no significant effect on the concentrations of nitrogen and phosphorus in leaf tissues (MANOVA, $P > 0.05$) (Table 3; Fig. 4). Nutrient levels of sediments, however, significantly affected the nutrient content of leaves, and the plants from the high-nutrient sediments had higher nutrient content than those from the low-nutrient sediments (MANOVA, $P = 0.035$ for nitrogen; $P < 0.001$ for phosphorus). There was no significant interaction between nutrient levels and partial leaf removal (MANOVA, $P > 0.05$).

Fig. 4 Content of nitrogen and phosphorus in leaf tissue of damaged and undamaged plant *Vallisneria spiralis* grown in different treatments ($n = 3$, mean $\pm$ SE). HNS and LNS are high-nutrient sediments and low-nutrient sediments, respectively

Discussion

Previous studies have focused on the compensatory response of aquatic plants to belowground tissue damages in freshwater ecosystems (LaMontagne et al. 2003; Nolet 2004; Sponberg and Lodge 2005). For example, LaMontagne et al. (2003) found that migrating trumpeter swans (*Cygnus buccinator*) significantly reduced the biomass of tubers and rhizomes of *Potamogeton pectinatus* in their study ponds in spring by 24% but had no significant impact on overall shoot density and biomass in the summer following herbivory, suggesting the existence of compensatory growth responses of *Potamogeton* to foraging. Our results demonstrated that the sub-mersed plant *V. spiralis* had significant compensatory growth to leaf damage, and the damaged plants were able to compensate the biomass loss over a 4-week experimental period. At least two of the mechanisms for compensatory growth in damaged terrestrial plants may apply to the aquatic plant *Vallisneria* as well. First, the damaged plants had a significantly greater relative growth rate than the control plants, and such an increase in growth rate as a result of partial leaf removal induces a compensatory response (Ferraro and Oesterheld 2002). Second, leaf damage resulted in an increase in leaf number, thus the photosynthetic capacity of the whole plant would increase (Nowak and Coldwell 1984; Meyer 1998). Unfortunately, we did not measure the photosynthetic rate during the experimental period.

The compensatory ability of plants depends on environmental conditions such as substrate nutrient availability. It is often assumed that terrestrial plants are better able to compensate for the damage at higher soil nutrient levels (Coley et al. 1985; Meyer 2000; Diemonta et al. 2006). Our experimental results supported this view. The compensation growth occurred in two nutrient levels of sediments, but the damaged plants in the high-nutrient sediments showed significantly greater compensatory abilities than ones in the low-nutrient sediments. However, the cumulative biomass and growth rate of *Vallisneria* were higher in low-nutrient sediments than those in high-nutrient sediments. Moreover, the number of leaves and roots was greater in plants from the low-nutrient sediments than that in the high-nutrient sediments. High organic matter content in the high-nutrient sediments might be the limiting factor for

plant growth. Some studies indicate that there is an apparent association between increasing sediment organic matter and the decline of rooted submersed aquatic vegetation (Carpenter 1981; Barko and Smart 1986; Sand-Jensen et al. 2008). For example, low density sediments, always accompanied with high organic matter content, could limit the growth of aquatic macrophytes. Barko and Smart (1986) found that the growth in *Hydrilla verticillata* and *Myriophyllum spicatum* declined with increasing sediment organic matter, but differential centrifugation of organic sediment facilitated an increase in sediment density with no change in organic matter content and stimulated *Hydrilla* growth. They suggested that sediment density regulated plant growth. In our study, the two types of sediments from Lake Taihu might have had high organic sediments with low sediment density which, however, was not measured. Thus, we speculated that the low sediment density in the present experiment limited the plant growth. In addition, fertile sediments always contain a number of reduced chemical substances and various byproducts of anaerobic microbial metabolism, some of which may be phytotoxic and inhibit plant growth under anaerobic conditions (Sanderson and Armstrong 1980; Barko and Smart 1983). Though submersed macrophytes are reportedly capable of adapting anaerobic conditions to certain extent by transporting photosynthetically originated oxygen to their roots (Lorenzena et al. 2001), this mechanism seems to be ineffective in fertile sediments (Carpenter et al. 1983; Chen and Barko 1988). Therefore, the high organic matter content in the high-nutrient sediment treatment might produce phytotoxins to limit the growth of *Vallisneria*. However, the sediment-related mechanisms of growth limitation in submersed macrophytes are very complex and need further investigation.

The compensatory ability of plants varies with damage intensity (McNaughton 1979; Huhta et al. 2000). Huhta et al. (2000) showed that high levels of herbivory (75% biomass removed) on *Gentianella campestris* are associated with a decrease in compensation to intermediate levels (50%). Similarly, Zhao et al. (2008) demonstrated a detrimental effect of intense clipping (80% aerial mass removed) on growth of *Leymus chinensis*. The decisive effects of damage intensity on compensatory growth of plants could be related to the amount of damaged

meristems, which are important in the ability of a plant to recover from damage and in the length of time it takes to recover (Gold and Caldwell 1989). There was no meristem damage in our experiment with the top portion of leaves clipped, as the meristem of submersed plant *Vallisneria* lies in the basal area of leaves (Jin 1995). Moreover, Li et al. (unpublished data) found that, compared with 30% leaf biomass removal treatment, *Vallisneria* exhibited a similar high growth rate after 60% leaf biomass removed. This indicates that the submersed plant *Vallisneria* can tolerate more intensive leaf damage. Therefore, the strong compensatory growth ability of *Vallisneria* may be one of mechanisms through which the plant coexists with herbivores.

In conclusion, the submersed plant *V. spiralis* exhibited evidently compensatory growth responses to partial leaf removal through mechanisms such as an increased growth rate. The compensation growth occurred in two nutrient levels of sediments, and the damaged plants in the high-nutrient sediments show much greater compensatory ability than ones in the low-nutrient sediments.

References

Barko JW, Smart RM (1983) Effects of organic matter additions to sediment on the growth of aquatic plants. J Ecol 71:161–175
Barko JW, Smart RM (1986) Sediment-related mechanisms of growth limitation in submersed macrophytes. Ecology 67:1328–1340
Belsky AJ (1986) Does herbivory benefit plants? A review of the evidence. Am Nat 127:870–892
Carpenter SR (1981) Submersed vegetation: an internal factor in lake ecosystem succession. Am Nat 118:372–383
Carpenter SR, Elser JJ, Olson KM (1983) Effects of roots of *Myriophyllum verticillatum* L. on sediment redox conditions. Aquat Bot 17:243–249
Chapin FS, McNaughton SJ (1989) Lack of compensatory growth under phosphorus deficiency in grazing-adapted grasses from the Serengeti Plains. Oecologia 79:551–557
Chen RL, Barko JW (1988) Effects of freshwater macrophytes on sediment chemistry. J Freshwater Ecol 4:279–289
Coley PD, Bryant JP, Chapin IIIFS (1985) Resource availability and plant antiherbivore defense. Science 230:895–899

Diemonta SAW, Martina JF, Levy-Tacherb SI, Nighc RB, Lopezd PR, Golicher JD (2006) Lacandon Maya forest management: restoration of soil fertility using native tree species. Ecol Eng 28:205–212

Ferraro DO, Oesterheld M (2002) Effect of defoliation on grass growth—a quantitative review. Oikos 98:125–133

Gold WG, Caldwell MM (1989) The effects of the spatial pattern of defoliation on regrowth of a tussock grass. Oecologia 80:289–296

Gu XH, Zhang SZ, Bai XL, Hu WP, Hu YH, Wang XR (2005) Evolution of community structure of aquatic macrophytes in East Taihu Lake and its wetlands. Acta Ecol Sin 265:1541–1548 (in Chinese)

Henry-Silva GG, Camargo AFM, Pezzato MM (2008) Growth of free-floating aquatic macrophytes in different concentrations of nutrients. Hydrobiologia 610:153–160

Huang XF, Cheng WM, Cai QM (1999) Survey, observation and analysis of lake ecology. Standards Press of China, Beijing, pp 145–159 (in Chinese)

Huhta A, Lennartsson T, Tuomi J, Rutio P, Laine K (2000) Tolerance of Gentianella campestris in relation to damage intensity: an interplay between apical dominance and herbivory. Evol Ecol 14:373–392

Jin G (1995) Primary observation on restoration of Vallisneria after being fed. In: Liang YL, Liu HQ (eds) Resource, environment and ecosystem-based fisheries management of macrophytic lakes. Science Press, Beijing, pp 227–235 (in Chinese)

LaMontagne JM, Jackson LJ, Barclay RMR (2003) Compensatory growth responses of Potamogeton pectinatus to foraging by migrating trumpeter swans in spring stop over areas. Aquat Bot 76:235–244

Lennartsson T, Nilsson P, Tuomi J (1998) Induction of overcompensation in the field gentian, Gentianella campestris. Ecology 79:1061–1072

Li YK, Yu D, Xu XW, Xie YH (2005) Light intensity increases the susceptibility of Vallisneria natans to snail herbivory. Aquat Bot 81:265–275

Li KY, Liu ZW, Hu YH, Wang CH (2006) Snail Radix swinhoei (H. Adams) herbivory on three submerged plants. Acta Ecol Sin 26:3221–3224 (in Chinese)

Lorenzena B, Hans B, Mendelssohnb AI, McKeec LK, Miaod SL (2001) Growth, biomass allocation and nutrient use efficiency in Cladium jamaicense and Typha domingensis as affected by phosphorus and oxygen availability. Aquat Bot 70:117–133

Lortie CJ, Aarssen LW (2000) Fitness consequences of branching in Verbascum thapsus (Scrophulariaceae). Am J Bot 87:1793–1796

McNaughton SJ (1979) Grazing as optimization process: grass–ungulate relationships in the Serengeti. Am Nat 113:691–703

McNaughton SJ (1983) Compensatory plant growth as a response to herbivory. Oikos 40:329–336

Meyer GA (1998) Mechanisms promoting recovery from defoliation in goldenrod (Solidago altissima). Can J Bot 76:450–459

Meyer GA (2000) Interactive effects of soil fertility and herbivory on Brassica nigra. Oikos 88:433–441

Nolet BA (2004) Overcompensation and grazing optimisation in a swan-pondweed system? Freshwater Biol 49:1391–1399

Nowak RS, Coldwell MM (1984) A test of compensatory photosynthesis in the field: implications for herbivory tolerance. Oecologia 6l:311–318

Oba G, Mengistu Z, Stenseh NC (2000) Compensatory growth of the African dwarf shrub, Indigofera spinosa, following simulated herbivory. Ecol Appl 10:1133–1146

Painter E, Belsky AJ (1993) Application of herbivore optimization theory to rangelands of the western United States. Ecol Appl 3:2–9

Sanderson PL, Armstrong W (1980) Phytotoxins in periodically waterlogged forest soils. Eur J Soil Sci 31:643–653

Sand-Jensen K, Pedersen NL, Thorsgaard I, Moeslund B, Borum J, Brodersen KP (2008) 100 years of vegetation decline and recovery in Lake Fure, Denmark. J Ecol 96:260–271

Sponberg AF, Lodge DM (2005) Seasonal belowground herbivory and a density refuge from waterfowl herbivory for Vallisneria americana. Ecology 86:2127–2134

Valentine JF, Heck KL, Webb D (1997) Experimental evidence that herbivory increases shoot density and productivity in a subtropical turtlegrass (Thalassia testudinum) meadow. Oecologia 112:193–200

Van Staalduinen MA, Anten NPR (2005) Differences in the compensatory growth of two co-occurring grass species in relation to water availability. Oecologia 146:190–199

Vergés A, Pérez M, Alcoverro T, Romero J (2008) Compensation and resistance to herbivory in seagrasses: induced responses to simulated consumption by fish. Oecologia 155:751–760

Verkaar HJ, Van der Meyden E, Breebart L (1986) The responses of Cynoglossum officinale L. and Verbascum thapsus L. to defoliation in relation to nitrogen supply. New Phytol 104:121–129

Zhao W, Chen SP, Lin GH (2008) Compensatory growth responses to clipping defoliation in Leymus chinensis (Poaceae) under nutrient addition and water deficiency conditions. Plant Ecol 196:85–99