

RELATIVE RESPONSE TO MECHANICAL STRESS OF CO-EXISTING AQUATIC SPECIES, FLOATING-LEAVED *NYMPHOIDES PELTATA* AND SUBMERGED *MYRIOPHYLLUM SPICATUM*

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Abstract

With the increasing impact of human activities on the environment, the effects of mechanical disturbance on aquatic plants are increasingly evident. Mechanical perturbations at the upper layer and surface of water frequently damage floating-leaved and caulescent submerged plants. Here, we co-cultivated floating-leaved *Nymphoides peltata* and submerged *Myriophyllum spicatum* in mesocosms and then subjected leaf laminas of *N. peltata* and stems of *M. spicatum* to different levels of mechanical damage. Similar experiments were conducted twice, the second with having an increased intensity and frequency of disturbance. Generally, mechanical disturbances impacted the growth of these species more significantly in the second experiment than in the first. In the second experiment, the total biomass of *N. peltata* was decreased and the biomass proportion to leaf lamina increased with increasing disturbance intensity; leaf area was maintained across treatments. For *M. spicatum*, all disturbance treatments decreased total biomass and the total length of stems, compared to non-damage controls. However, in *M. spicatum* the number of ramets were increased with increasing disturbance intensity. Our results indicate that *N. peltata* has a high capacity for foliage compensation, and vegetative reproduction of *M. spicatum* may be improved by intense mechanical disturbance, though severe damage will suppress growth. Mechanical disturbances in upper water layers may change the relative performance of co-existing submerged and floating-leaved species with a repressive effect on submerged species. Management of mechanical disturbance by human activities is urgently required to maintain the function of submerged plants when restoring contaminated wetlands.

Key words: *Nymphoides peltata*, *Myriophyllum spicatum*, Mechanical damage, Biomass, Morphological traits.

Introduction

With increasing extreme climate events and anthropogenic impacts on the environment, mechanical disturbances by natural forces and human activities on aquatic plants in wetlands are predicted to climb (Lake, 2000; Eriksson *et al.*, 2004; Davenport & Davenport, 2006; Xu *et al.*, 2014). Disturbances created by natural forces such as gale-force winds, typhoons and heavy rains, include high waves, fast currents and flooding. Observed effects of these disturbances have included a decrease in species richness and cover of aquatic plants (Bailey, 1988; Riis & Hawes, 2003); a tendency to increase resource allocation to belowground biomass and storage organs (Puijalon & Bornette, 2006; Puijalon *et al.*, 2008; Wang *et al.*, 2010); shorter stems in emergent plants and decreased leaf area and leaf numbers in floating-leaved species (Wang *et al.*, 2010); subsequent increased regenerative ability following changes under stress (Puijalon *et al.*, 2008); the ability of floating plants in closed areas to block the effects of both wind-induced flows and thermal disturbances (Ozaki *et al.*, 2002); and the ability of some aquatic plants to show surprising resistance to the effects of flooding (Keruzoré & Willby, 2014). In contrast to perturbations by natural forces, mechanical disturbances resulting from human activities have received less attention.

As a result of boating and other recreational activities, fishing and aquatic plant management regimes, perturbations in the upper layer of water and the water surface by propellers and rakes occur frequently (Peng *et al.*, 2003; Davenport & Davenport, 2006; Riis, 2008; Kelting & Laxson, 2010; Hallac *et al.*, 2012; Xu *et al.*, 2014), inevitably damaging aquatic macrophytes,

especially floating-leaved plants and caulescent submerged ones with a canopy-forming growth habit (Eriksson *et al.*, 2004; West *et al.*, 2009). A few studies have found that damage by man-made implements changes competition among submerged plants (Engelhardt & Kadlec, 2001; Eriksson *et al.*, 2004; Zhang *et al.*, 2014). For instance, cutting by propellers favors Eurasian watermilfoil (*Myriophyllum spicatum* L.) over sago pondweed (*Potamogeton pectinatus* L.) (Eriksson *et al.*, 2004). Hornwort (*Ceratophyllum demersum* L.) is highly tolerant to cutting and uprooting by propellers, since it thrives free floating and mainly regenerates by fragmentation (Eriksson *et al.*, 2004). Rake slashing decreases the growth of abundant hydrilla (*Hydrilla verticillata* [L.f.] Royle) rather than four co-occurring submerged species (Zhang *et al.*, 2014). Damage to floating-leaved plants remains scantily documented. In fact, however, floating-leaved plants frequently co-exist with submerged ones in natural communities (Zhou & Chen, 1996; Nikolic *et al.*, 2007; Xu *et al.*, 2014) and have a tendency to expand populations in eutrophicated wetlands (Egertson *et al.*, 2004; Li *et al.*, 2010; Huang *et al.*, 2014). Therefore, activities in water commonly damage floating-leaved and submerged plants simultaneously. Nevertheless, damage intensities and patterns differ between the two life forms. For floating-leaved and caulescent submerged plants, the most direct damage is respectively breaking and loss of leaf laminae and stem fragmentation and commonly results in coverage decrease, biomass loss and even extending the life cycle (Eriksson *et al.*, 2004; Xu *et al.*, 2014; Zhang *et al.*, 2014).

Another concern is a possible impact of mechanical disturbances on the interactive relationship between floating-leaved and submerged plants in communities.

Fragmentary laminas of floating leaves possibly increase light penetration into water, which can promote the growth of co-occurring submerged plants. Every harvest of floating-leaved water chestnut (*Trapa bispinosa* Roxb.) has a positive impact on submerged *M. spicatum* (Xu *et al.*, 2014). In contrast, changes in the growth of submerged plants after stem fragmentation may have little impact on the growth of floating-leaved ones. Accordingly, mechanical disturbances probably change the relative performance of co-existing floating-leaved and submerged plants and community structure, thus altering the functions of wetlands such as supporting animal species diversity and ameliorating water quality (Eriksson *et al.*, 2004; Seto *et al.*, 2013).

The widespread Eurasian floating-leaved species, yellow floating heart (*Nymphoides peltata* [Gmel.] O. Kuntze), has a nymphaeid growth form with stout rhizomes anchored in the substratum, long procumbent stolons bearing adventitious roots and leaves, from whose axils flowering stems rise with the leaves to the surface and produce cover throughout most of the growing season; and can reproduce vegetatively through fragmentation of stolons or stems (Darbyshire & Francis, 2008). In eutrophicated wetlands, its populations are expanding rapidly, and even becoming invasive in some regions (Darbyshire & Francis 2008; Huang *et al.*, 2014). This species is frequently subjected to intense mechanical disturbances in tourism, fishery and aquatic plant management regimes (Qiu *et al.*, 1997). The Eurasian submerged plant, *M. spicatum*, is widespread, including in China (Sun, 1992). Long stems arise from buds at the crown of long slender rhizomes in the substratum, and branch profusely from the upper stem nodes, producing numerous whorls of feathery leaves forming a canopy just

below the water surface (Aiken *et al.*, 1979). It can reproduce vegetatively both from the root crown and from stem fragments (Cao & Wang, 2012). It is frequently found subordinate to *N. peltata* in aquatic habitats (Zhou & Chen, 1996). Here, we co-cultivated the floating-leaved *N. peltata* and submerged *M. spicatum* in mesocosms and applied different levels of mechanical damage to *N. peltata* leaf laminas and *M. spicatum* stems. Our aim was to investigate the effects of mechanical disturbance on mixed cultures containing these two species.

Materials and Methods

Experimental design: Our experiments were carried out in the experimental garden at Central China Normal University (N 30°30', E 114°21') in Wuhan, Hubei, China. We designed four intensities (treatments) of mechanical disturbance: undisturbed control, and weak, medium and severe disturbance (Table 1). Each treatment had four replicates. Sixteen mesocosms (length× width× height, 150 cm× 100 cm×110 cm) were used to cultivate plants in each experiment conducted in 2011 and 2013. Mechanical disturbances were implemented by cutting each plant of *M. spicatum* into stem fragments and removing leaf laminas of *N. peltata* to different extents according to the experimental design (Table 1). This implementation was based on our field observations. In natural communities consisting of *M. spicatum* and *N. peltata*, mechanical disturbances such as boating activities and plant harvest commonly break stems of *M. spicatum* and leaf laminas of *N. peltata* because of the canopy-forming growth habit of *M. spicatum* and the floating leaves of *N. peltata*. However, the petioles and stems of *N. peltata* are less damaged because of their flexibility.

Table 1. Methods of mechanical disturbance of *Myriophyllum spicatum* and *Nymphoides peltata* in two experiments.

Intensity of disturbance	Method of mechanical disturbance ^a	
	First experiment (2011)	Second experiment (2013)
<i>Myriophyllum spicatum</i>		
Preparation for plant materials	Three whole plants per mesocosm; no preculture	Three apical fragments per mesocosm; precultured in 27 days
Control	Undamaged	Undamaged
Weak	Cutting into 8-node fragments	Cutting into 8-node fragments
Medium	Cutting into 3-node fragments	Cutting into 3-node fragments
Severe	Cutting into 3-node fragments, one half of leaves removed	Cutting into 1-node fragments
<i>Nymphoides peltata</i>		
Preparation for plant materials	One 8-node fragment with intact leaves per mesocosm; no preculture	Two whole new-germinated plants per mesocosm; precultured in 27 days
Control	Undamaged	Undamaged
Weak	Half laminas were removed from one half of leaves, with retained midribs	Half laminas were removed from all leaves, with retained midribs
Medium	Half laminas were removed from all leaves, with retained midribs	From one half of leaves, half laminas were removed with retained midribs; from the other half of leaves, whole laminas removed
Severe	From one half of leaves, half laminas were removed with retained midribs; from the other half of leaves, whole laminas removed	Whole laminas were removed from all leaves

^aPlants of the two species in the same intensities of disturbance were mixed-cultivated in each experiment; frequencies of disturbances in the first and second experiments were one and two times with an interval of 36 days, respectively

Experimental process: Experiment one. On May 24, 2011 we collected similar sizes of materials of each species (58 whole plants of *M. spicatum* and 26 apical fragments of *N. peltata*) from a pond in our experimental garden. Of the materials, 10 plants of *M. spicatum* and 10 fragments of *N. peltata* were used to measure initial parameters. For *M. spicatum*, total length of stems, total number of nodes and total biomass were 181.2 ± 3.3 cm (mean \pm SD, the same below), 80 ± 2 , and 0.603 ± 0.014 g, respectively. For *N. peltata*, stem length, numbers of nodes, and total biomass were 88.5 ± 2.1 cm, 6, and 1.233 ± 0.023 g, respectively. In each mesocosm, fragments of *M. spicatum* cut from three whole plants and one apical fragment of *N. peltata* with leaf laminas removed partially in the same disturbance intensities were grown in mixtures (plant materials in the control treatments were not damaged). The mixed culture was used to simulate more closely the situation in natural *N. peltata*-*M. spicatum* communities, as compared to monoculture of each species. All materials were placed in water, not inserted into sediment, because we observed fragments newly produced by mechanical disturbance commonly floated in water freely. The water level was maintained at about 40 cm throughout the experiment. There was 10-cm-thick sediment (total nitrogen 1.97 ± 0.03 mg g⁻¹, total phosphorus 0.13 ± 0.02 mg g⁻¹ by dry weight) on the bottom of each mesocosm. A week after treatment, all *N. peltata* plants had developed adventitious roots and rooted in sediment. For *M. spicatum*, however, only a small percentage of fragments had rooted in sediment by the end of the experiment, others had a few short adventitious roots suspended in water throughout the experiment. We recorded water pH, temperature, electrical conductivity (Waterproof ECTest, Eutech Instruments, Thermo Fisher Scientific, Waltham, MA, USA), and underwater light intensity (LI-193SA underwater irradiance sensor, LI-COR, Lincoln, NE, USA) at a depth of 5 cm at about 13:00 h every four days. Throughout the experiment parameters in all mesocosms were in the range of 7.05–7.26 (water pH), 22.3–27.9°C (water temperature), 217–251 $\mu\text{s cm}^{-1}$ (electrical conductivity), and 112.2–633.2 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ (underwater light intensity), respectively.

Forty days after treatment, all live plants were harvested. All rotten or dead tissues were removed and discarded. Roots of plants were carefully excavated from sediment and washed. We counted the nodes and measured main stem length and the length of each branch of all plants. Leaf area of *N. peltata* was also measured. Plants of *N. peltata* were separated into roots (for nutrient uptake), stems and petioles (mainly for supporting), leaf laminas (for photosynthesis), and reproductive organs (flowers and fruits). However, *M. spicatum* plants were not separated into organs, because the function of each organ may not be exclusive, e.g. each organ (roots, leaves and stems) has a function in nutrient absorption (Best & Mantai, 1978). Then, each part of *N. peltata* and each plant of *M. spicatum* was

dried at 72°C to weigh biomass. The above parameters were recorded on a total, per-mesocosm basis. Specific leaf area (SLA) and leaf area ratio (LAR) of *N. peltata* were calculated as follows: SLA = leaf area/ lamina dry mass; LAR = leaf area/ total dry mass.

Experiment two. This experiment was started on April 1, 2013. Collections of *M. spicatum* and *N. peltata* from a pond in our experimental garden were 58 apical fragments without branches and 42 intact plants germinating from overwintered rhizomes, respectively. Initial parameters were obtained from 10 plants of each species. Stem length, number of nodes and total biomass of *M. spicatum* were respectively 22.5 ± 1.1 cm, 10 ± 1 and 0.271 ± 0.004 g. Rhizome length, number of leaves and total biomass of *N. peltata* were 15.0 ± 0.8 cm, 4 and 0.281 ± 0.003 g, respectively. Three *M. spicatum* fragments and two *N. peltata* plants were planted together in each mesocosm. The lowest nodes of *M. spicatum* fragments were inserted into sediment to favor root production. The rhizomes and roots of *N. peltata* were buried in sediment. Forty-cm-deep water was above 10-cm-thick sediment (total nitrogen 1.85 ± 0.05 mg g⁻¹, total phosphorus 0.11 ± 0.03 mg g⁻¹ by dry weight) in mesocosms. After preculture of 27 days, disturbance treatments were started (Table 1) when all plants were rooted in sediment, the canopy of *M. spicatum* was blocked from the water surface and all leaves of *N. peltata* floated on the water surface. In the process of cutting *M. spicatum* fragments and removing *N. peltata* leaf laminas (Table 1), roots of all plants were not disturbed. Thirty-six days after the first disturbance, the plants were disturbed for a second time. Thirty days after the second disturbance, all plants were harvested. The methods of harvesting and measuring plants were the same as that in the first experiment except that the number of *M. spicatum* ramets was recorded in the second experiment. Water pH, temperature, electrical conductivity and underwater light intensity were in the range of 7.12–7.27, 18.6–28.8°C, 205–245 $\mu\text{s cm}^{-1}$, and 135.5–622.7 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$, respectively. The recording methods of these environmental parameters were the same as those in the first experiment.

Data analysis: All data met assumptions of normality. One-way ANOVA was used to analyze differences in growth traits among treatments for each species in each experiment. For traits in which significant differences ($p < 0.05$) were detected, Tukey's tests among treatments were performed. Statistical analyses were performed using STATISTICA 6.0 (StatSoft, Tulsa, OK, USA) and figures were drawn in SigmaPlot 10.0 (Systat Software, Chicago, IL, USA).

Results and Discussion

Mechanical disturbance impacted the growth of *M. spicatum* and *N. peltata* more in the second experiment than in the first experiment (Table 2, Figs. 1 and 2). All growth traits except SLA of *N. peltata* were similar among treatments in the first experiment. The different results between our two experiments may be related to increased intensity and frequency of disturbance in the second experiment.

Table 2. Summary of one-way ANOVAs on the effects of mechanical disturbance treatments on growth traits of *Myriophyllum spicatum* and *Nymphoides peltata* in two experiments.

Trait	First experiment (2011)		Second experiment (2013)	
	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
<i>Myriophyllum spicatum</i>				
Total dry mass (g)	2.63	0.159	45.16	<0.001
Total length of stems (cm)	1.05	0.405	43.51	<0.001
Total number of nodes	0.72	0.561	5.57	0.012
Number of ramets	/	/	12.33	<0.001
<i>Nymphoides peltata</i>				
Total dry mass (g)	0.32	0.810	15.38	<0.001
Leaf lamina mass ratio	0.36	0.780	268.90	<0.001
Stem and leaf petiole mass ratio	1.07	0.399	7.64	0.006
Root mass ratio	1.04	0.409	21.96	<0.001
Total length of stems (cm)	0.28	0.837	2.57	0.113
Total number of nodes	0.74	0.545	0.91	0.470
Leaf area (cm ²)	0.89	0.475	0.25	0.862
Leaf area ratio (cm ² g ⁻¹)	1.87	0.188	18.39	<0.001
Specific leaf area (cm ² g ⁻¹)	10.07	0.001	0.15	0.929

The growth of floating-leaved *N. peltata* under mechanical disturbance: Under increased disturbance intensity and frequency, total biomass of *N. peltata* was decreased in the second experiment (Fig. 1). In the severe disturbance treatment, *N. peltata* plants lacked all leaf laminae for a short time after each damage event and this might retard accumulation of photosynthetic products dramatically. Surprisingly, however, at harvest the total leaf area of *N. peltata* in the disturbance treatments was not reduced compared to the control non-damage treatment, indicating that the plants have a high ability to compensate and renew foliage. The high efficiency of leaf recovery growth of *N. peltata* may benefit from its high speed of leaf recruitment (up to 24 leaves every ten days, Yu & Yu, 2011). Plants recruit leaves continually to ensure that young leaves always exist in the canopy, which is a complementary means whereby the plant is able to respond to photosynthesis reduction (Cooling *et al.*, 2001; Yu & Yu, 2011). Similarly, rapid and continual leaf recruitment has been observed in other floating-leaved species such as running marsh-flower (*Villarsia reniformis* R.Br.) when leaves are submerged and die because of rising water levels (Cooling *et al.*, 2001). Increasing the net assimilation rate is an overcompensatory response to defoliation (Oosterheld & McNaughton, 1991). Following mechanical stress removal, therefore, plants are commonly able to perform compensatory growth, which is supported by studies on *T. bispinosa* after being harvested partly (Xu *et al.*, 2014), aquatic cutleaf water parsnip (*Berula erecta* [Hudson] Coville) in flowing water (Puijalón & Bornette, 2006) and mesophytic white mustard (*Sinapis alba* L.) under wind stress (Retuerto & Woodward, 2001).

Besides the rapid recovery in leaf area, *N. peltata* plants in the second experiment increased LAR with increasing disturbance intensity (Fig. 2). LAR is positively correlated with relative growth rate (Poorter & Remkes, 1990). Increasing LAR is an adaptive strategy for many plants subjected to light limitation and favors

capturing more light (Poorter & Rozendaal, 2008), thus compensating for photosynthesis. Simultaneously, *N. peltata* plants regulated biomass allocation: increasing the proportion to leaf laminae at the cost of allocation to non-photosynthetic organs under increasing damage intensity, even with a failure to produce reproductive organs in the severe disturbance treatment (Fig. 1). Damage to leaves would reduce the plants' ability to carry out photosynthesis, the effects of which may parallel simple light limitation to a certain extent. Seemingly, that plants increased allocation to leaf laminae under increased disturbance intensity is consistent with the response of plants in a light-limited environment (Poorter, 2001) and may be explicable based on the "functional equilibrium" theory (Poorter & Nagel, 2000). However, the allocation of *N. peltata* was not consistent with the finding that in response to mechanical stress from running water aquatic plants increase allocation to below-ground biomass and storage organs to enable themselves to reduce the risk of damage (Puijalón & Bornette, 2006; Puijalón *et al.*, 2008). The different results between the present and previous studies on running water may indicate that the effect of intermittent leaf damage differs from that of continuous flowing water on aquatic plants.

It is worthwhile mentioning that in the first experiment the SLA of *N. peltata* in the disturbance treatments was reduced compared to the control non-damage treatment (Fig. 2). Correspondingly, leaf area and leaf dry mass of this species were reduced by mechanical damage to a certain extent, though the differences among treatments were not significant (Figs. 1 and 2). Lower values of SLA indicate leaves with increased lamina thickness and density, contrary to the common response of shaded and defoliated terrestrial plants (Poorter *et al.*, 2012; Pankoke & Muller, 2013). However, *N. peltata* plants may enhance their tolerability to potential mechanical damage by subsequently increasing leaf thickness and density, and this may be a tolerance strategy to mechanical disturbances (Puijalón *et al.*, 2011).

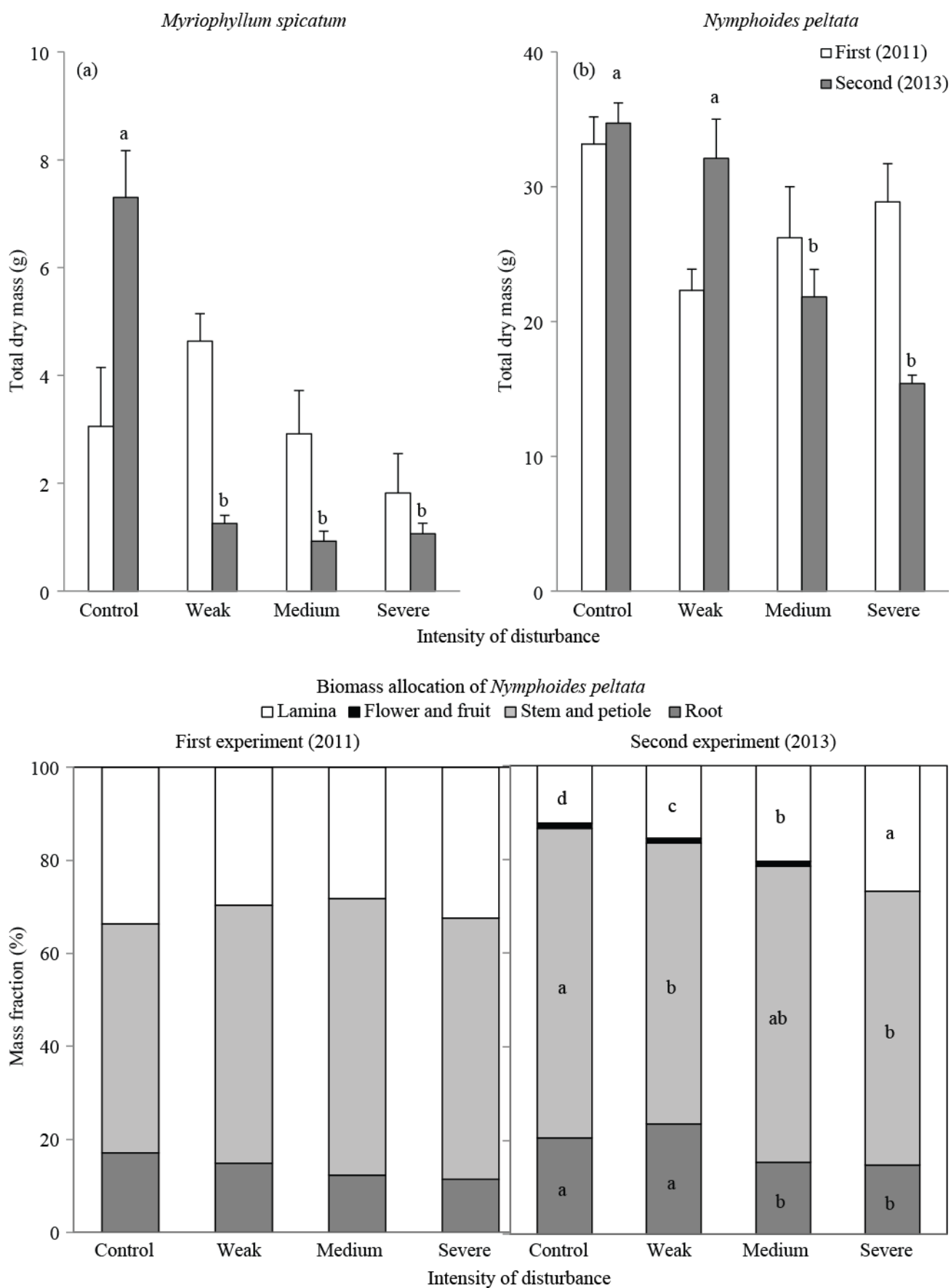


Fig. 1. Total dry mass of *Myriophyllum spicatum* and *Nymphaoides peltata* (panels: a-b) and biomass allocation of *Nymphaoides peltata* (panels: c) under different disturbance intensities (control, weak, medium and severe) in two experiments in 2011 and 2013. Different letters denote significant differences (Turkey's tests, $p < 0.05$) among the four intensities for each species in each experiment. Significance levels are not shown for traits in which no significant differences were detected using ANOVA ($p > 0.05$).

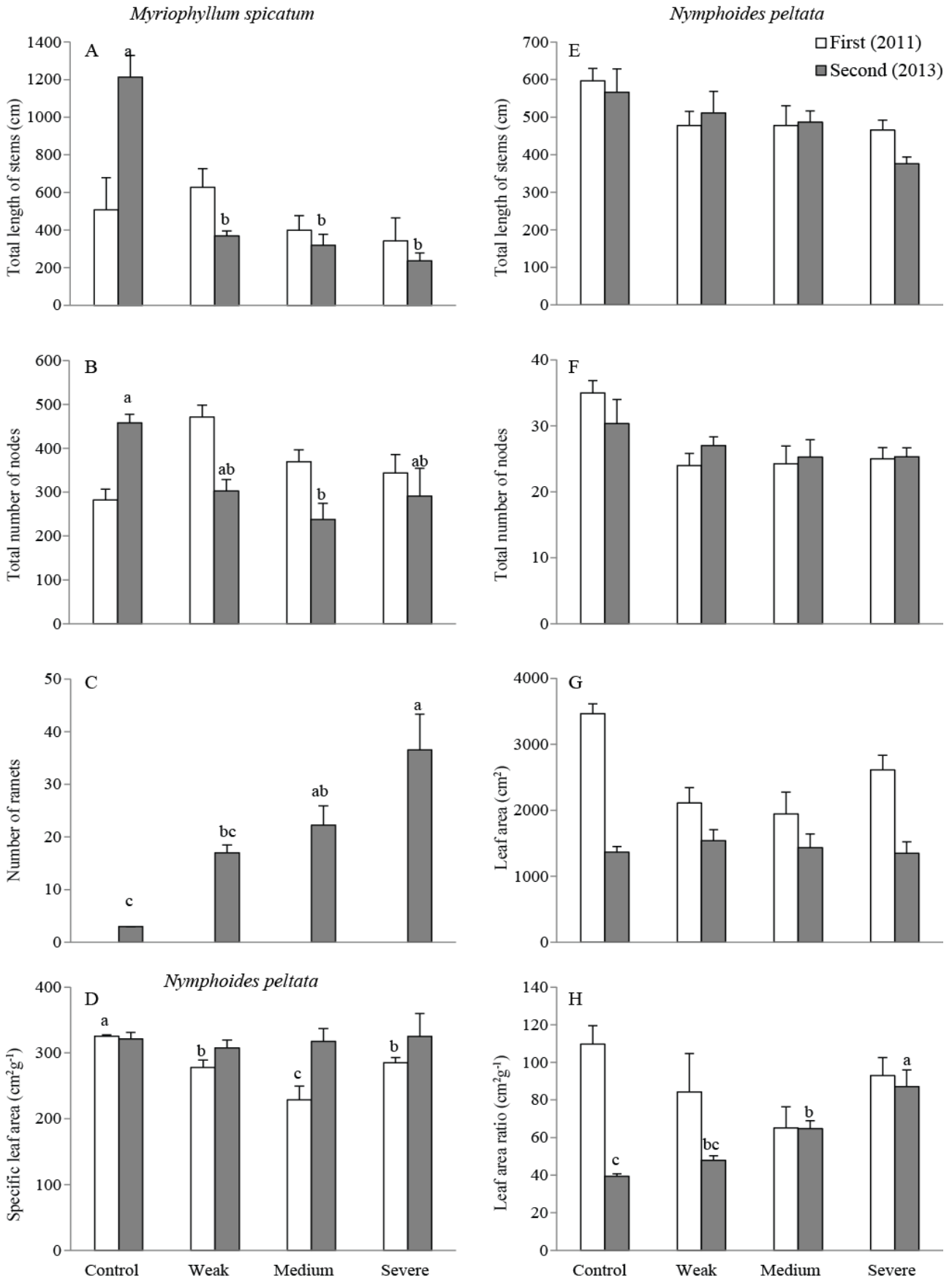


Fig. 2. Morphological traits of *Myriophyllum spicatum* (panels: a-c) and *Nymphoides peltata* (panels: d-h) in different disturbance intensities (control, weak, medium and severe) in two experiments in 2011 and 2013. Different letters denote significant differences (Turkey's tests, $p < 0.05$) among the four intensities for each species in each experiment. Significance levels are not shown for traits in which no significant differences were detected using ANOVA ($p > 0.05$).

The growth of submerged *M. spicatum* under mechanical disturbance: In the second experiment, all disturbance treatments decreased total biomass and the total length of stems for *M. spicatum*, compared to the control treatment (Figs. 1 and 2). This result indicates that mechanical fragmentation of stems can repress the growth of *M. spicatum*. A similar negative impact of mechanical cutting was observed by Mony *et al.* (2011), who found that frequent cutting decreased the number of branches in *M. spicatum*. However, in their study, *M. spicatum* displayed a tolerance strategy through maintenance of similar biomass production per initial mass despite regular cutting. Moreover, its high tolerability to mechanical disturbance was also observed in our first experiment (Table 2, Figs. 1 and 2) and previous studies (Eriksson *et al.*, 2004; Zhang *et al.*, 2014). Significant growth repression in our second experiment may be related to the more serious damage experienced, compared to the other experiments mentioned above. For example, in previous studies the disturbance methods were only cutting less than 50% of plant height (Mony *et al.*, 2011) or slashing communities by rakes (Zhang *et al.*, 2014).

Myriophyllum spicatum is considered a species of high tolerance to disturbance because it occurs preferentially in frequent flood-disturbed habitats (Amoros *et al.*, 2000) and is more common in marinas used as harbours for private boats than in inlets not exposed to boating disturbance (Eriksson *et al.*, 2004). Besides the ability to maintain growth rates (Mony *et al.*, 2011), the high vegetative reproductive capacity of *M. spicatum* may also contribute to its tolerability to disturbance, supported by our finding of an increased number of ramets with increasing disturbance (Fig. 2); stem fragmentation increased the potential of ramet production. Although fragments with more nodes develop into successful plantlets with a higher frequency, mono-node fragments have plantlet formation abilities (Gao *et al.*, 2007; Riis *et al.*, 2009). Accordingly, vegetative reproduction of *M. spicatum* may be improved by intense mechanical disturbance, though severe damage results in a substantial suppression of growth.

Relative performance of *N. peltata* and *M. spicatum* affected by mechanical disturbance: In terms of morphological traits and biomass accumulation (Figs. 1 and 2), mechanical disturbance in this study negatively influenced submerged *M. spicatum* more acutely than floating-leaved *N. peltata*. Our results indicate that mechanical disturbance in the upper water layer and at the water surface, such as boating activities and plant harvest, may change the relative performance of co-existing submerged and floating-leaved species with a repressive effect on submerged species. *Nymphoides peltata* has stolons creeping horizontal to the substratum (Darbyshire & Francis, 2008) which generally remain undamaged and vegetatively reproducible despite disturbance at the upper water layer and surface. In contrast, after being disturbed by mechanical forces, stem fragments of caulescent *M. spicatum* commonly floated in the water column for a certain period before anchoring in sediments, and sometimes remained floating throughout the experiment or died at the water surface. The growth of plantlets floating in

the water column is generally inferior to those rooted in sediments (Barrat-Segretain & Bornette, 2000; Wu *et al.*, 2007), particularly because sediments, rather than water, provide most of the nutrients for submerged plants (Barko & Smart, 1980; Carignan & Kalff, 1980; Chambers *et al.*, 1989). Thus, the speed of recovery growth may be more rapid in *N. peltata* than *M. spicatum*. Likewise, we speculate that similar effects may arise after mechanical disturbance when other nymphaeid macrophytes that co-exist with other rooted caulescent plants.

In wetlands, intense mechanical disturbance is usually accompanied by eutrophication (Eriksson *et al.*, 2004; Xu *et al.*, 2014). In eutrophicated habitats, floating-leaved plants tend to expand their populations (Huang *et al.*, 2014; Xu *et al.*, 2014), even as invasive species in some regions (Darbyshire & Francis 2008; Tall *et al.*, 2011), while populations of submerged plants shrink (Yuan *et al.*, 2012). Submerged macrophytes possess significant potential to bioconcentrate elements due in part to their greater surface area in contact with water compared to non-submerged plants (Dhir *et al.*, 2009). Population decline of these submerged plants has already made the recovery of damaged wetlands more difficult because of eutrophication, which is further exacerbated by man-made mechanical disturbance. An advisable management of mechanical disturbance by human activities is required to maintain the function of submerged plants when restoring contaminated wetland ecosystems.

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