

Full Length Research Paper

Phenotypic plasticity, clonal architecture and biomass partitioning in *Myriophyllum spicatum* L. across different lentic and lotic ecosystems of Kashmir

Shahzada Arshid* and Aijaz A. Wani

Cytogenetics and Reproductive Biology Laboratory, Department of Botany, University of Kashmir, Srinagar, 190 006.

Accepted 17 April, 2013

During the present study we measured plastic adjustments in morphological traits, clonal architecture and biomass partitioning for an aquatic clonal species (*Myriophyllum spicatum*) under two contrasting conditions in the field that is, standing vs. running waters. A significant difference in morphological traits, clonal architecture and biomass partitioning to different plant parts was observed between standing and running water populations. The species produces longer and narrower leaves in running water but smaller and broader ones in standing water populations. Spike and peduncle length, number of spikes and flowers per ramet were significantly higher in standing water populations. Moreover, a high seed set was observed in standing water populations while as running water populations did not produce any seeds. Total length of rhizome, branching of ramets, spacer length and average length of ramets per plant were highest in standing water populations. However, number of ramets per plant and number of branches per rhizome were highest in running water populations. The percentage dry mass allocation was highest to shoots followed by seeds and spikes and much less was allocated to under sediment parts in standing water populations, whereas, in running water populations allocation was highest to shoots followed by under sediment and spikes. The reduction in size, higher biomass allocations to belowground organs and a more compact growth form (reduced spacer lengths) in case of running water populations as compared to standing water populations contributed to reduce the damage risk in running water populations due to mechanical stress caused by the flow of running water.

Key words: Plant architecture, resource allocation, standing water, running water, ramet, spacer length.

INTRODUCTION

Aquatic plants, many of which propagate vegetatively, tend to possess lower genetic diversity than terrestrial plants, implying an increased role for phenotypic plasticity in aquatic habitats (Grace, 1993; Hofstra et al., 1995; Barrett et al., 1993). Many plant species exposed to environmental stresses display plastic responses in their developmental, morphological, physiological, anatomical, or reproductive traits that can support functional adjustments, possibly compensating for the detrimental effect of stress

(Sultan, 2000, 2003). Phenotypic plasticity elicited by stresses has been widely studied, but mainly in regard to resource stresses such as light, nutrients, water availability, or inorganic carbon (Chapin, 1991; Gleeson and Tilman, 1992; Hutchings and De Kroon, 1994; Hutchings and John, 2004). However, under natural conditions, plants are also subjected to stresses that do not directly limit resource availability (e.g., flooding, wind etc.). Plant responses to these stresses cannot be simply predicted by

*Corresponding author. E-mail: shahzada194@gmail.com.

models linked to resource use (Chapin, 1991). Mechanical stresses from wind, current or wave action affect plants physically and act on the plant's spatial organization rather than directly on resource acquisition (e.g. many aquatic plants escape from the stress through a prostrate growth form). Such stresses are widely encountered by plants and are ecologically very important because they act on plant growth and survival, seedling recruitment and species distribution (Foote and Kadlec, 1988; Ennos, 1997; Hudon et al., 2000; Gantes and Caro, 2001). Permanent exposure to mechanical stress can lead to altered morphologies and allocation features of individual plant parts (Strand and Weisner, 2001; Jaffe et al., 2002; Boeger and Poulson, 2003) leading to reduced size (height, leaf area, biomass and petiole length) and generally resulting in a reduced drag (Henry and Thomas, 2002; Boeger and Poulson, 2003; Hik et al., 2003; Puijalon et al., 2005). In this framework, the aim of the present study was to measure the patterns of plastic adjustments in morphological traits, clonal growth and biomass allocation between five natural populations (three standing waters and two running waters) of an aquatic plant species, *Myriophyllum spicatum* L., in response to hydraulic stress (permanent exposure to current). We also aimed to compare the plant growth patterns under stressful conditions (running waters) and comparatively less stressful (standing waters) conditions.

MATERIALS AND METHODS

In the present study three standing water sites namely Dal Lake (DL), Mansbal Lake (ML) and Hygam Wetland (HW) and two running water sites namely Shalimar stream (SS) and Chanderhama irrigation canal (CIC) were selected as study sites (Arshid and Wani, 2012).

Phenotypic variability

A Random sample of 25 plants of the *Myriophyllum spicatum* were drawn from each population (both running and standing waters) and the plants were analyzed for morphological features and phenotypic variability. The characters studied include number, shape and dimensions of leaves; petiole length; rhizome size and length; stem shape and inter-node length; spike shape and length; peduncle length and number of flowers per spike; shape and dimensions of flowers, seed morphology and size and number of seeds per spike and per flower. The variations were statistically analyzed; using SPSS 10. For microscopic studies Olympus stereo Zoom Trinocular microscope was used.

Architectural analysis

For description of patch characteristics, terminology used by Wolfer and Straife, (2004) was followed, according to which plant is defined as a complete unit of ramets connected by rhizomes originating from a single primary shoot. Ramet is a single module of a clonal plant, consisting of shoots, rhizome and roots. Spacer length is the rhizome length between two consecutive shoots of the same plant. In order to analyse the growth architecture of the species in various populations (both standing and as well as running), a random sample of 25 plants from each population was analysed for

spatio-temporal dynamics and plasticity of clonal architecture. The characters studied include: total length of rhizome, number of ramets per plant, branching frequency, ramet length, spacer length and branching frequency of rhizome. The variation if any was analysed statistically using statistical software SPSS 10.

Biomass allocation

Individual plants from natural populations were harvested at maturity (both pre and post pollinated), washed in the tap water and dried using blotting paper. The ramets were divided into individual parts (shoots, rhizomes and roots, spikes and seeds). Oven dried at 100° for 48 h (Kawano and Masuda, 1980) and the dry mass (representing the amount of resources allocated) of each component was calculated using an electronic balance.

RESULTS

Phenotypic variability

Myriophyllum spicatum inhabits both standing and running waters and is highly variable in respect of its quantitative traits. The various morphological traits analyzed in the present study are summarized in Table 1. It is clear from Table 1 that a significant amount of variability exists for various morphological traits between standing and running water populations as compared to among standing or running water populations. *Myriophyllum spicatum* produces larger (3.05 ± 0.29 cm) and narrower (0.39 ± 0.02 cm) leaves with longer petioles (0.40 ± 0.05 cm) in running water populations but smaller (2.21 ± 0.11 cm) and broader (0.84 ± 0.08 cm) leaves with smaller petioles (0.11 ± 0.01 cm) in standing water populations. Mature spike length (5.13 ± 0.5 cm), peduncle length (1.41 ± 0.22 cm), number of spikes (3.33 ± 0.49) and flowers (53.93 ± 5.17) per ramet were significantly higher in standing water populations as compared to running water populations where values for mature spike length (2.73 ± 0.24 cm), peduncle length (0.72 ± 0.08 cm), number of spikes (1.20 ± 0.41) and flowers (23.5 ± 2.77) were significantly lower. On the other hand internodal length was found higher in running water populations. Moreover seeds were not formed in running water populations whereas high seed set (93.5 ± 5.93 per ramet) was recorded in standing water populations. So the three standing water populations (Dal Lake, Mansbal Lake and Hygam Wetland) were almost at par with each other with respect to various morphological features analyzed, but significant differences were found between the standing and running water populations in these features as clearly evident by different Tukey's test values.

Growth architecture

M. spicatum shows clonal growth form, consisting of a branched rhizome and from which arises a network of leafy shoots called ramets. The whole network of rhizome and ramets arising from it is called as genet. The number of ramets on each rhizome and the spacer length between

Table 1. Phenotypic variability in morphological traits of *Myrriophyllum spicatum* from various populations of Kashmir valley.

Feature	Population				
	Standing water (Mean± SE)			Running water (Mean±SE)	
	Dal lake	Mansbal lake	Hygam wetland	Shalimar stream	Chanderhama irrigation canal
Internodal length(cm)	1.89 ^b ±0.06	1.74 ^a ± 0.03	1.99 ^c ±0.07	3.0 ^d ±0.12	2.69 ^d ±0.15
Length of leaves (cm)	2.41 ^b ± 0.26	2.21 ^a ± 0.11	2.48 ^b ±0.12	3.28 ^c ±0.32	3.05 ^c ±0.29
Breadth of leaves(cm)	0.84 ^d ±0.08	0.76 ^c ±0.09	0.64 ^b ±0.04	0.40 ^a ±0.03	0.39 ^a ±0.02
Length of apical leaves(cm)	1.92 ^b ±0.07	1.74 ^a ±0.04	2.06 ^b ±0.08	2.88 ^c ±0.22	2.83 ^c ±0.10
Breadth of apical leaves(cm)	0.59 ^c ±0.06	0.55 ^c ±0.02	0.49 ^b ±0.03	0.39 ^a ±0.01	0.39 ^a ±0.01
Number of leaflets per leaf	30 ^{ab} ±3.21	28 ^a ±2.26	32 ^{bc} ±3.35	34 ^c ±3.17	33 ^c ±2.08
Number of leaflets per apical leaves	29 ^b ±2.76	24 ^a ±1.51	31 ^b ±2.47	31 ^b ±2.03	31 ^b ±2.03
Petiole length(cm)	0.14 ^a ±0.02	0.11 ^a ±0.01	0.20 ^b ±0.04	0.40 ^c ±0.05	0.39 ^c ±0.05
Mature spike length(cm)	5.13 ^c ±0.50	4.98 ^c ±0.43	4.13 ^b ±0.35	2.86 ^a ±0.17	2.73 ^a ±0.24
Peduncle length(cm)	1.41 ^c ±0.22	1.11 ^b ±0.10	1.00 ^b ±0.21	0.74 ^a ±0.04	0.72 ^a ±0.08
Number of spikes per ramet	3.26 ^b ±0.7	3.33 ^b ±0.49	3.2 ^b ±0.41	1.73 ^a ±0.35	1.20 ^a ±0.41
Total number of flowers per ramet	50.86 ^c ±5.46	53.93 ^c ±5.17	46.4 ^b ±4.98	23.5 ^a ±2.77	24.5 ^a ±2.53
Number of male flowers per ramet	20.8 ^c ±2.90	21.53 ^c ±2.34	18.13 ^b ±1.64	9.66 ^a ±1.60	10.26 ^a ±0.96
Number of female flowers per ramet	30.06 ^{bc} ±3.58	32.40 ^c ±3.85	28.26 ^b ±3.84	13.86 ^a ±1.93	14.26 ^a ±1.73
Number of seeds per ramet	93.5 ^c ±5.93	92 ^c ±5.22	85 ^b ±4.50	-	-

Letters a, b, c, and d depicted in the table indicate means that are significantly different (Tukey's test ≤ 0.05).

Table 2. Growth architecture of *Myrriophyllum spicatum* in different populations of Kashmir valley.

Feature	Population				
	Standing water			Running water	
	Dal lake	Mansbal lake	Hygam wetland	Shalimar stream	Chanderhama irrigation canal
Total length of rhizome (cm)	18.02±1.26 ^c	18.59±1.20 ^c	16.01±1.05 ^b	12.26±1.04 ^a	13.17±1.27 ^a
Number of ramets per plant/genet	5.86±0.35 ^a	5.80±0.25 ^a	5.40±0.28 ^a	14.2±0.94 ^b	15.0±1.06 ^c
Number of branches per ramet	0.86±0.01 ^d	0.93±0.02 ^e	0.66±0.01 ^c	0.33±0.01 ^b	0.26±0.01 ^a
Spacer length (cm)	3.0±0.14 ^b	3.20±0.15 ^c	2.96±0.17 ^b	0.83±0.03 ^a	0.86±0.03 ^a
Average length of ramets(cm)	109.46±5.85 ^c	111.53±5.85 ^c	84.6±3.65 ^b	64.33±3.37 ^a	66.6±3.68 ^a
Number of branches per rhizome	2.13±0.35 ^a	2.06±0.25 ^a	2.26±0.45 ^a	3.0±0.37 ^b	3.13±0.35 ^b

Letters a, b, c, and d depicted in the table indicate means that are significantly different (Tukey's test ≤ 0.05).

two consecutive ramets are the important features in *M. spicatum* allowing the plant to some extent to adapt to heterogeneous environments such as running and standing waters. As the species inhabits both standing and running waters, it showed significant variability in almost all growth architectural features analysed between standing and running water populations (Table 2). It was observed that total length of rhizome (18.59±1.20 cm), branching of ramets (0.93±0.02 branches per ramet), spacer length (3.20±0.15 cm) and average length of ramets (111.53±5.85 cm) per plant were highest in three standing water populations as compared to two running water populations where the total length of rhizome (12.26±1.04 cm),

branching of ramets (0.26±0.01 branches per ramet), spacer length (0.83±0.03 cm) and average length of ramets (66.6±3.68 cm) showed significantly lower values. However number of ramets per plant (15.0±1.06) and number of branches per rhizome (3.13±0.35) were highest in running water populations as compared to standing water ones thus reducing the spacer length in running waters.

Biomass allocation

The allocation of dry mass to different plant parts in the species across different populations is summarized in

Table 3. Resource allocation to different parts in *Myriophyllum spicatum* across different standing and running water populations in the Kashmir valley.

Dry weight (mg)↓	Population									
	Standing water					Running water				
	Dal lake	Percentage	Mansbal lake	Percentage	Hygam wetland	Percentage	Shalimar stream	Percentage	Chanderhama irrigation canal	Percentage
Shoots	4048±58.15 ^b	87.80	4028.2±54.37 ^b	88.33	4042.1±54.51 ^b	88.15	2295.7±33.17 ^a	95.15	2305±35.74 ^a	95.03
Under-sediment part	34.33±1.70 ^a	0.74	32.6±1.64 ^a	0.71	33.2±1.09 ^a	0.72	63.8±3.04 ^b	2.64	65.4±3.77 ^b	2.69
Spikes	91.6±5.96 ^b	1.98	86.2±5.41 ^b	1.89	90.9±5.48 ^b	1.98	53±2.58 ^a	2.58	55.00±2.58 ^a	2.26
Seeds	436.1±19.84 ^c	9.45	413±18.66 ^b	9.05	419±18.77 ^{bc}	9.13	0 ^a	-	0 ^a	-

Different letters a, b, c, d in the table indicate means that are significantly different (Tukey's test ≤ 0.05).

Table 3. The dry mass allocation to different plant parts differed significantly across standing and running water populations. The percentage allocation of dry mass to shoots (4028.2±54.37 mg) was highest followed by seeds (436±19.84 mg) and spikes (91.6±5.96 mg) and much less was allocated to under-sediment parts (32.6±1.64 mg) in standing water populations. However, in running water populations the percentage dry mass allocation was higher to shoots (2295.7±33.17 mg) followed by under-sediment parts (65.4±3.77 mg) and spikes (53±2.58 mg). Seeds were not formed in these populations. So, in standing water populations were percentage allocation of dry mass to under-sediment parts was 0.71%, running water populations allocated higher resources to under-sediment parts that is, 2.69% as compared to standing water ones.

DISCUSSION

Aquatic plants, many of which propagate vegetatively tend to possess lower genetic diversity than terrestrial plants, implying an increased role for phenotypic plasticity in aquatic habitats for diversity (Sculthrope, 1967; Barrett et al., 1993). During the present investigation it was observed that *M.*

spicatum inhabited both standing as well as running waters. This species has developed distinct morphological characters with respect to its rhizome/ramet/genet, leaf, floral and seed characteristics to adapt itself in different habitats. It was observed that leaf dimensions of the species did not vary much within different standing/running water populations but differ significantly between standing and running water populations. The species produced narrow and longer leaf blades as well as longer petioles in running waters to prevent these leaves from being detached from the stem and branches of the main plant due to the flow of water, whereas in standing waters wider and smaller leaf blades with short petioles were produced due to the absence of this stress of flowing water. Such a variation in leaf morphology has been earlier reported in *Potamogeton* by Kaplan (2002, 2008). Puijalon and Bornette (2006) also observed that leaf breadth reduces significantly in plants exposed to stress of water currents. Mature spike and peduncle length varied significantly across standing and running water populations. Mature spike and peduncle length was found smaller in running water populations as compared to standing water populations. This is because pressure of the flowing waters impairs the deve-

lopment of spikes due to mechanical stress (Gants and Caro, 2001; Riis and Biggs, 2003). The number of spikes per ramet and the number of flowers per ramet in running water populations were more as compared to standing water population showing significant differences because of stress of flowing water. Similar results were obtained by Kautsky (1987) who observed that in *Potamogeton pectinatus* flower number per m² was highest in sheltered populations and the number decreased from 945 to 672 per m² with increasing exposure to waves. In standing water populations copious amount of seeds were formed whereas no seed set was observed in running water populations, because the plants growing in running waters failed to accomplish sexual reproduction and did not produce seeds (Kaplan, 2002, 2008).

Majority of the submerged macrophytes form clones, consisting of complex network of ramets interconnected by rhizome. Clonal morphology changes in response to environmental factors, both at the level of individual ramet as well as at clonal level (Puijalon et al., 2008). The present study reveals that *M. spicatum* showed considerable and significant variation in clonal growth between standing and running waters, however various growth architectural features did not vary much among

different standing water populations or running water populations.

In standing water populations, number of branches per ramet and spacer length was more as compared to the plants of running water populations. The ramets in running water populations did not produce many branches because fast flowing water impaired the development of branches and there was also a risk of getting detached from the main axis by pressure of flowing water. However in running waters, the number of ramets per plant (clone) and the number of branches per rhizome were more in number as compared to the plants of standing waters. Thus in running waters increased number of ramets per plant, reduced spacer length and increased number of branches per rhizome could help in the formation of dense canopy and enhance anchorage efficiency; a strategy of resistance that reduces the effect of pressure of flowing waters. This dense growth form described as Phalanx growth form by Lovett-Doust (1987) due to reduced spacer length and increased branching could allow the plants to occupy favourable patches in a heterogeneous environment (De Kroon et al., 1994; Dong and De Kroon, 1994; De Kroon and Hutchings, 1995). The present study is quite in agreement with the earlier findings for *Mentha aquatica*, where the species produces increased number of creeping stems and dense canopy in running waters to reduce the stress of flowing water (Puijalón et al., 2008). The increased number of creeping stems, enhanced anchorage and formation of dense canopy are responsible for reducing the effect of aero or hydrodynamic forces in many other plant species (Sand-Jensen and Mebus, 1996; Speck, 2003; Lui et al., 2007).

The length/height of ramets in standing water populations mostly depend upon the depth of water body; while in running waters ramets grow in the direction of flow. The alignment of creeping stems with flow direction may be induced by different mechanisms. First it could be due to drag forces exerted by water currents pushing the stems in the flow direction (Vogel, 1994; Kotshy and Rogers, 2008). Secondly, the stems will be detached if they grow in any direction other than the flow of water resulting in higher mortality of the creeping stems, for instance due to damages by sandblasting and drifting particles (Cleugh et al., 1998). Third factor is the different activity of the meristems. The meristems could grow perfectly in the downstream direction that is partly sheltered from the water current and submitted to less stressful conditions (Sand-Jensen and Pedersen, 1999), where as the other growth directions could be inhabited (Puijalón et al., 2008). Total length of rhizome in different populations could not be measured precisely as it depends upon the nature of substratum of water body and handling of plant material during collection (plucking of plant material). Every organism allocates its resources for various essential activities, like maintenance, growth and reproduction (Willson, 1983). The analysis of resource allocation to different plant parts is useful in predicting allocation patterns

and survival strategies of plants (Madsen, 1991).

The dry mass allocation to different plant parts in *M. spicatum* varies significantly between standing and running water populations. The dry mass allocation to shoots and spikes was less as compared to under-sediment parts in plants inhabiting running waters, whereas, in standing water populations the trend was reverse. It was presumably because the ramets in running waters do not produce more branches required to avoid the risk of getting detached by the pressure of running waters. Similarly the development of spikes got impaired in such stressful environments. The under-sediment parts (rhizome, roots) spread between the stones and sediment and in turn provide strong anchorage and protect the plants from completely being washed away. The rhizomes are mostly the means of propagation in running waters (Barrett et al., 1993). Permanent exposure of plants to mechanical stress usually results in reduced size of leaves, height and consequently biomass allocation (Niklas, 1998; Henery and Thomas, 2002; Boeger and Poulsan, 2003) and increased allocation to undersediment parts. Puijalón and Bornette, (2006) also observed higher allocation to below ground organs in running waters. This results in better resource accumulation in the parts protected from the water currents and is considered to improve anchorage efficiency (Crook and Ennos, 1996; Niklas, 1998). A lower allocation to sexual reproduction associated with delayed flowering is also often observed in running water populations (Niklas, 1998; Hodges et al., 2004). The plants in standing waters allocate much of the resources to shoots, seeds and spikes followed by under-sediment parts.

Acknowledgement

The first author is thankful to CSIR New Delhi, for providing fellowship in the form of SRF

REFERENCES

- Arshid S, Wani AA (2012). Pollen biology and stigma receptivity in *Myriophyllum spicatum* L. an invasive species in Kashmir Himalayan aquatic ecosystems. *Int. J. Adv. Life Sci.* 3: 13-20.
- Barrett SCH, Eckert DG, Husband BC (1993). Evolutionary processes in aquatic plant populations. *Aquat. Bot.* 44: 105-145.
- Boeger MRT, Poulsan ME (2003). Morphological adaptation and photosynthetic rates of amphibious *Veronica angallis-aquatica* L. (Scrophulariaceae) under different flow regimes. *Aquat. Bot.* 75: 123-135.
- Chapin FS (1991). Effects of multiple environmental stresses on nutrient availability and use. In: Mooney HA, Winner WE, Pell EJ (eds.) Responses of plants to multiple stresses. Academic Press, New York. pp. 67-88.
- Cleugh HA, Miller JM, Böhm M (1998). Direct mechanical effect of deweeding on crops. *Agroforest. Syst.* 41: 85-112.
- Crook MJ, Ennos AR (1996). Mechanical differences between free-standing and supported wheat plants *Triticum aestivum* L. *Ann. Bot.* 77: 197-202.
- De Kroon H, Hutchings MJ (1995). Morphological plasticity in clonal plants: the foraging concept revisited. *J. Ecol.* 83: 143-152.
- De Kroon H, Stueffer JF, Dong M, During HJ (1994). On plastic and non-plastic variation in clonal plant morphology and its ecological significance. *Folia Geobot.* 29: 123-138.

- Dong M, De Kroon H (1994). Plasticity in morphology and biomass allocation in *Cynodon dactylon*, a grass species forming stolons and rhizomes. *Oikos* 70: 99-106
- Ennos AR (1997). Wind as an ecological factor. *Trends Ecol. Evol.* 12: 108-111.
- Foot AL, Kadlec JA (1988). Effects of wave energy on plant establishment in shallow lacustrine wetlands. *J. Freshwater Ecol.* 4: 523-532
- Gantes HP, Caro AS (2001). Environmental heterogeneity and spatial distribution of macrophytes in plain streams. *Aquat. Bot.* 70: 225-236
- Gleeson SK, Tilman D (1992). Plant allocation and the multiple limitation hypothesis. *Am. Nat.* 139: 1322-1343
- Grace JB (1993). The adaptive significance of clonal reproduction in angiosperms: an aquatic perspective. *Aquat. Bot.* 44: 159-180.
- Hik DS, Brown M, Dabros A, Weir JJ, Cahill JR (2003). Prevalence and predictability of handling effects in field studies: results from field experiments and a meta-analysis. *Am. J. Bot.* 90: 270-277.
- Hofstra DE, Adam KD, Clayton JS (1995). Isozyme variation in New Zealand populations of *Myriophyllum* and *Potamogeton* species. *Aquat. Bot.* 52: 121-131
- Hudon C, Lalonde S, Gagnon P (2000). Ranking the effects of the site exposure, plant growth form, water depth, and transparency on aquatic plant biomass. *Can. J. Fish. Aquat. Sci.* 57: S31-S42.
- Hutchings MJ, De Kroon H (1994). Foraging in plants: the role of morphological plasticity in resource acquisition. *Adv. Ecol. Res.* 25: 159-238
- Hutchings MJ, John EA (2004). The effects of environmental heterogeneity on root growth and root/shoot partitioning. *Ann. Bot.* 94: 1-8
- Jaffe MJ, Leopold AC, Staples RC (2002). Thigmo responses in plants and fungi. *Am. J. Bot.* 89: 375-382
- Kaplan Z (2002). Phenotypic plasticity in *Potamogeton* (Potamogetonaceae). *Folia Geobot.* 37: 141-170.
- Kaplan Z (2008). A taxonomic revision of *Stuckenia* (Potamogetonaceae) in Asia, with notes on the diversity and variation of the genus on a worldwide scale. *Folia Geobot.* 43:159-234.
- Kautsky L (1987). Life cycles of three populations of *Potamogeton pectinatus* L. at different degree of wave exposure in the Askö area, Northern Baltic Proper. *Aquat. Bot.* 27: 177-186.
- Kawano S, Masuda J (1980). The productive and reproductive biology of flowering plants. VIII. Resource allocation and reproduction capacity in wild population of *Heloniopsis orientalis* (Thunb) C. Tanaka (Liliaceae). *Oecologia* 45: 307-317.
- Kotshy K, Rogers K (2008). Reed clonal characteristics and response disturbance in a semi-arid river. *Aquat. Bot.* 88: 47-56.
- Lovett-Doust L (1987). Population dynamics and local specialization in a clonal perennial (*Ranunculus repens*). I. The dynamics of ramets in contrasting habitats. *J. Ecol.* 69: 743-755.
- Lui Y, Schieving F, Stuefer JF, Anten NPR (2007). The effects of mechanical stress and spectral shading on the growth and allocation of ten genotypes of stoloniferous plant. *Ann. Bot.* 99: 121-130.
- Madsen JD (1991). Resource allocation at the individual plant level. *Aquat. Bot.* 41: 67-86.
- Puijalon S, Bornette G (2006). Phenotypic plasticity and mechanical stress: biomass partitioning and clonal growth of an aquatic plant species. *Am. J. Bot.* 93: 1090-1099.
- Puijalon S, Bornette G, Sagnes P (2005). Adaptations to increasing hydraulic stress: morphology, hydrodynamics and fitness of two higher aquatic plant species. *J. Exp. Bot.* 56: 777-786.
- Puijalon S, Bouma TJ, Van Groenendael J, Bornette G (2008). Clonal plasticity of aquatic plant species to mechanical stress: Escape versus resistance strategy. *Ann. Bot.* 102: 989-996.
- Riis T, Biggs BGF (2003). Hydrologic and hydraulic control of macrophyte establishment and performance in streams. *Limnol. Oceanogr.* 48: 1488-1497.
- Sand-Jensen K, Mebus JR (1996). Fine-scale patterns of water velocity within macrophyte patches in streams. *Oikos* 76: 169-180.
- Sand-Jensen K, Pedersen O (1999). Velocity gradients and turbulence around macrophyte stands in streams. *Freshw. Biol.* 42: 315-328.
- Speck O (2003). Field measurements of wind speed and reconfiguration in *Aurundo donax* (Poaceae) with estimates of drag forces. *Am. J. Bot.* 90: 1253-1256.
- Strand JA, Weisner SEB (2001). Morphological plastic responses to water depth and wave exposure in an aquatic plant (*Myriophyllum spicatum*). *J. Ecol.* 86: 166-175.
- Sultan SE (2000). Phenotypic plasticity for plant development, function and life-history. *Trends Plant Sci.* 5: 537-542
- Sultan SE (2003). Phenotypic plasticity in plants: a case study in ecological development. *Evol. Dev.* 5: 25-33.
- Willson MF (1983). *Plant Reproductive Ecology*. John Wiley & Sons Inc. New York. pp. 5-32.
- Wolfer SR, Straite D (2004). Saptio-temporal dynamics and plasticity of clonal architecture in *Potamogeton perfoliatus*. *Aquat. Bot.* 78: 307-318.