

Morphological and Physiological Responses to Sediment Type and Light Availability in Roots of the Submerged Plant *Myriophyllum spicatum*

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• **Background and Aims** Both sediment and light are essential factors regulating the growth of submerged macrophytes, but the role of these two factors in regulating root morphology and physiology is far from clear. The responses of root morphology and physiology to sediment type and light availability in the submerged plant *Myriophyllum spicatum* were studied and the hypothesis was tested that a trade-off exists in root growth strategy between internal aeration and nutrient acquisition.

• **Methods** Plants were grown on two types of sediment (fertile mud and an infertile mixture of mud and sandy loam) and under three levels of light availability (600, 80 and 20 $\mu\text{mol m}^{-2} \text{s}^{-1}$) in a greenhouse.

• **Key Results** The significantly higher alcohol dehydrogenase (ADH) activity in root tissues indicated that oxygen deficiency existed in the plants growing in fertile mud and low (or high) light environments. Significantly, low plant N and P concentrations indicated that nutrient deficiency existed in the mixed sediment and high light environment. As a response to anoxia, plants did not change the porosity of the main roots. The effect of sediment type on root morphology was insignificant under higher light environments, whereas root diameter generally decreased but specific root length (SRL) increased with decreasing light availability. Both low light and fertile mud jointly led to lack of second-order laterals. More biomass was allocated to lateral roots in infertile environments, whereas mass fractions of laterals were lower in low light and mud environments.

• **Conclusions** These data indicate that this plant can achieve the trade-off between internal aeration and nutrient acquisition by adjusting the structure of the root system and the pattern of biomass allocation to different root orders rather than root morphology and root porosity.

Key words: Adaptation, aeration, anoxia, biomass allocation, nutrient, morphological plasticity, oxygen, root system, submerged macrophytes, *Myriophyllum spicatum*.

INTRODUCTION

Sediment plays an important role in the supply of nutrients for submerged macrophytes, since it is the primary source for the uptake of N, P, Fe, Mg and micronutrients (Barko and Smart, 1981; Barko *et al.*, 1991). However, sediment properties affecting the growth of aquatic macrophytes, such as density, organic matter content and redox status, are numerous and complex (Barko and Smart, 1986b; Barko *et al.*, 1991). In most natural situations, unfavourable and favourable conditions for plant growth usually co-occur in the same sediment. For example, fertile mud contains high organic matter content with anaerobic conditions, and infertile sandy sediment contains low organic matter content with aerobic conditions. Hence, nutrient acquisition and oxygen supply might be a trade-off for the growth of roots in aquatic macrophytes. However, little is known about how aquatic plants adjust their root traits to adapt to the dilemma in the sediment environment.

In submerged macrophytes, light availability is fundamental to primary production, not only because light facilitates inorganic carbon acquisition and plant growth, but also because light regulates photosynthetic oxygen evolution and allows plants to survive in anoxic sediments via root aeration (Sand-Jensen *et al.*, 1982; Smith *et al.*,

1984; Barko and Smart, 1986a; Sorrell, 2004). Recently, Sorrell (2004) reported that photosynthetic oxygen evolution in *Isoetes alpinus* is closely related to light availability and plays an important role in regulating root anaerobiosis. The lack of oxygen usually leads to typical anoxic symptoms in plant tissues, such as a high ethanol content and alcohol dehydrogenase (ADH) activity. Therefore, the capacity to transport sufficient oxygen to underground tissues to sustain aerobic metabolism is critical to plant survival (Sorrell, 1994; Geigenberger, 2003; Sorrell, 2004). Root porosity is usually used as an indicator of the capacity to deliver oxygen to below-ground tissues, since root aeration occurs by virtue of the lacunar gas transport system (Jensen *et al.*, 1969). Additionally, plants cannot transport photosynthetic oxygen to roots and do not have enough building material to make morphological changes under lower light because of inactive photosynthesis and limited oxygen production. Thus, light availability might also be an important factor adjusting root morphology and physiology.

Root growth is highly responsive to conditions that stress the plant in nutrient and oxygen shortage. A fine and long root, a high lateral root density and a high root : shoot ratio are favourable for nutrient acquisition by increasing total root length and root area (Eissenstat, 1992; Barber, 1995; Wahl *et al.*, 2001; Xie and Yu, 2003; Xie *et al.*, 2005).

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However, thin roots can hamper root function in supplying oxygen (Fitter, 1996). Under anaerobic environments, plants would enhance the ability for oxygen supply and/or reduce the loss of oxygen by growing thicker roots and fewer laterals, and having a low root: shoot ratio (Armstrong, 1979; Visser *et al.*, 1996). Therefore, root traits favouring nutrient acquisition might be disadvantageous in conducting oxygen.

In submerged macrophytes, root growth is usually related to nutrient acquisition rather than internal aeration, and light availability is generally linked to photosynthesis rather than root biology. The aim of this study is to elucidate how submerged macrophytes combine these conflicting traits into an optimal root growth strategy. To this end, *Myriophyllum spicatum* L., a perennial submerged plant with two orders of lateral roots, was chosen for this experiment because this plant is a common species of freshwater lakes in the world (Grace and Wetzel, 1978) and can grow on different sediment types and in relatively low light environments, such as extra-eutrophical waters. The plant was grown on two sediment types and under three levels of light availability to test the following hypotheses. First, in infertile mixture and high light conditions, it is expected that the root will become thinner and longer and more biomass will be allocated to roots (especially laterals) to increase root–sediment contact because of the low nutrient status of a mixture. Secondly, in fertile mud and high light conditions, roots will be thicker and shorter and they will have higher porosity to increase transportation of oxygen because of anaerobic conditions in the mud and active photosynthesis under high light. Thirdly, in fertile mud and low light conditions, less biomass will be allocated to roots (especially laterals) to reduce the loss of oxygen because of inactive photosynthesis under low light.

MATERIALS AND METHODS

Plant material

Myriophyllum spicatum was collected from Liangzi Lake (30°6′–30°18′N, 114°24′–114°36′E), Hubei Province, China. Upon collection, the apical 20 cm of the shoots were cleaned, transported to a greenhouse in the Northeast Institute of Geography and Agricultural Ecology, the Chinese Academy of Sciences, and pre-incubated in tap water for 7 d, during which time the temperature was controlled at $30 \pm 1^\circ\text{C}$ during the day and $22 \pm 1^\circ\text{C}$ at night. Light was provided at $300 \mu\text{mol photons m}^{-2} \text{s}^{-1}$ (PPFD) in a 14 h light/10 h dark cycle.

Experimental set-up

After pre-incubation, two 12-cm long apical shoots were planted in each sediment-filled plastic tray (3 L, 8.5 cm in height) with the lower 2 cm buried in the sediment. After the shoots had grown for 5 d, the light treatment was started. Experimental treatments consisted of two sediment types [mud and a 5:95 (v/v) mixture of mud and sandy loam] and three levels of light availability (600, 80 and $20 \mu\text{mol photons m}^{-2} \text{s}^{-1}$). The three light regimes were

TABLE 1. Chemical characteristics of the two types of sediment used in the experiment (means \pm s.e., $n = 3$)

	Organic matter (mg g^{-1})	Exchangeable N ($\mu\text{g g}^{-1}$)	Exchangeable P ($\mu\text{g g}^{-1}$)	Eh values at 5 cm depth (mV)
Mud	30.0 ± 1.2	135.3 ± 12.4	37.1 ± 2.1	-76 ± 10
Mixture	1.2 ± 0.0	17.7 ± 1.8	6.9 ± 0.8	270 ± 32

chosen on the basis of relationships between light intensity and photosynthesis and between light intensity and oxygen evolution of some submerged species (Salvucci and Bowes, 1982; Frost-Christensen and Sand-Jensen, 1995; Sorrell, 2004). Compared with the mixture, the mud had high contents of organic matter, exchangeable N and P, and the Eh value at 5 cm sediment depth was lower (Table 1). A total of 36 trays were placed into six 300 L plastic bins (65 cm in height, six trays per bin). For each light treatment, two bins were used and each bin contained three trays per sediment type. Tap water (containing $4.3 \mu\text{M NH}_4^+\text{-N}$, $16.8 \mu\text{M NO}_3\text{-N}$, $1.9 \mu\text{M PO}_4^{3-}\text{-P}$) was supplied during plant growth, and was replaced completely every 3–4 d. Sodium bicarbonate was added to reach $20 \mu\text{mol L}^{-1}$, and the pH was adjusted daily to 7.0 using 0.1 M NaOH or HCl during the experimental period.

Root characteristics

The plants were harvested after 35 d. After removal from the sediments they were carefully cleaned with tap water, divided into leaves, stems and roots, and were separately weighed. Biomass per plant in each tray was the mean of the two plants. Some root tissues were used for measurement of root porosity and the activity of ADH (see below), and the others were used for estimation of root characteristics. For each treatment, 12–15 representative intact adventitious roots were chosen and divided into six groups (2–3 roots per group). Adventitious roots in each group were then divided into main roots, and first- and second-order laterals, and were weighed separately. The diameter of main roots, and first- and second-order laterals was evaluated using a microscope with an ocular micrometer, and was replicated 30, 50 and 50 times, respectively. The specific root length (SRL) of different orders of roots was calculated as the ratio of root length to root mass. For each measurement, 3–4 main roots and 5–7 laterals (first- and second-order) were randomly chosen from different plants as a group to determine the SRL. Each treatment and each order of root was replicated six times. Plant parts were then oven dried at 85°C for 48 h to a constant weight. All fresh weights were transformed into dry weights.

Biomass allocation

The lateral root: main root mass ratio was calculated as the ratio of total lateral root (first- and second-order) mass to main root mass; and the second-order: first-order

lateral root mass ratio as the ratio of second-order lateral root mass to first-order lateral root mass. The mass of main root, total lateral root, and first- and second-order lateral root in each plant was calculated from the root mass and the mass ratio of different orders of roots. In order to perform a functional growth analysis on biomass allocation to correct for size differences between plants, adjusted allometric analysis (biomass fractions in allocation) suggested by Poorter and Nagel (2000) was applied. An advantage is that biomass fractions are less sensitive to small changes in allocation when roots form <20% of the biomass. Biomass fractions can be calculated as the mass of each organ relative to the biomass of the total plant. In this experiment, an analysis of allocation was applied using six compartments: shoots, roots, main roots, total laterals, and first- and second-laterals.

Root porosity

Roots from different treatments were examined for porosity (percentage of air-filled volume) by the pycnometer method (Jensen *et al.*, 1969). Representative fresh adventitious roots (>5 cm in length) were removed intact, and were separated into main roots and laterals. The porosity of the main roots was determined using 0.1–0.3 g of root tissues and a 25 mL pycnometer. Three determinants per treatment were made using a vacuum pump.

The activity of ADH

ADH activity was measured in roots as a direct indicator of oxygen deficiency in root tissues (Mendelssohn and McKee, 1992), since oxygen is essential as the terminal electron acceptor in the oxidative phosphorylation pathway (Geigenberger, 2003). For extraction and assay of ADH activity, 1.0–1.5 g of fresh root were homogenized (ice bathed) with a mortar in 5 mL of 50 mM HEPES buffer (pH 7.3), which contained 5 mM MgCl₂ and 1 mmol L⁻¹ phenylmethyl sulfonyl fluoride (PMSF). The plant extracts were centrifuged at 22 942 g for 20 min at 4°C using a Sigma 3–18 k high-speed refrigerated centrifuge (Sigma Company, Germany). ADH activity was tested at 30°C as follows: 0.1 mL of extract was added to a reaction cuvette containing 2.85 mL of assay buffer [constituted by 15% of 1.0 M Tris (pH 8.0), 3% of 0.01 M NAD⁺ and 82% of distilled water] and 0.03 mL of 95% ethanol, and read against a reference cell containing all components except ethanol. The rate of NAD⁺ deoxidation was followed for 10–20 min on a TU-1901 spectrophotometer (Beijing Puxitongyong Company, China) at 340 nm (Tang, 1999).

Plant N and P concentrations

Upon collection, plant parts were ground into powder, and mixed together for measurement of plant chemistry. All samples were digested with H₂SO₄–H₂O₂, and analysed for plant N and P concentrations using colorimetric analysis on a TU-1901 spectrophotometer (Shi, 1994). Three replicates were used to determine plant N and P concentrations.

Statistical analysis

Multiple comparisons of means were performed by Duncan's test at the 0.05 significance level. A two-way analysis of variance (ANOVA) was used to determine the effects on root characteristics, root porosity, ADH activity, and plant N and P concentrations. Data were log₁₀-transformed if necessary to reduce heterogeneity of variances, and homogeneity was tested using Levene's test. All biomass fractions were square-root-transformed to meet with the assumptions of normality and homoscedasticity. Normality was assessed by Kurtosis test, and homoscedasticity was tested using Levene's test. The experiment was a split-plot design, so two split-plot ANOVAs were applied. First, an ANOVA with light as the main plot and bin as the sub-plot was performed to identify the effect of bin on biomass accumulation and biomass allocation. Secondly, if bin had insignificant effects, another ANOVA with light availability as the main plot and sediment type as the sub-plot was applied to test for the combined effects on biomass accumulation and biomass allocation to different plant organs.

RESULTS

Biomass accumulation

Split-plot ANOVAs with light as the main plot and bin as the sub-plot showed that biomass accumulation and biomass allocation to different plant organs were unaffected by bin, without interaction with light availability ($P > 0.05$). Both sediment type and light availability significantly affected biomass accumulation ($P < 0.001$, Fig. 1, Table 2). In the same sediment, biomass decreased with decreasing light availability ($P < 0.05$). Under high light environments, plants in mud accumulated the highest biomass ($P < 0.05$), whereas sediment effects were insignificant under medium or low light availability ($P > 0.05$).

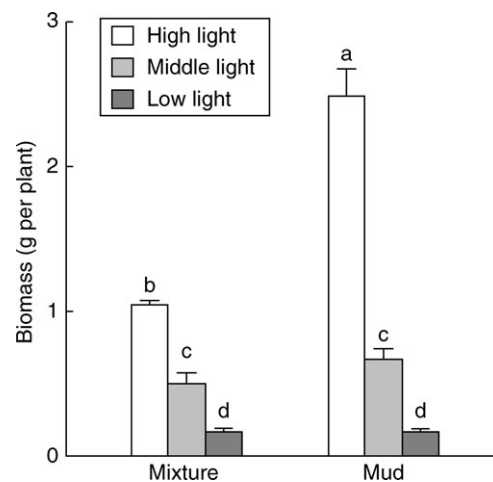


FIG. 1. Biomass accumulation (means \pm s.e., $n = 6$) of *Myriophyllum spicatum* growing on two types of sediment and under three levels of light availability. Different letters indicate significant differences among treatments. Multiple comparisons of means were performed by Duncan's test at the 0.05 significance level.

TABLE 2. Summary of split-plot ANOVAs on biomass accumulation and biomass allocation, and two-way ANOVAs on root characteristics and plant nutrient concentrations of *Myriophyllum spicatum* growing on two types of sediment and under three levels of light availability

Dependent variables	Sediment type (S) (F-values)	Light availability (L) (F-values)	S × L (F-values)
Split-plot ANOVA			
Biomass per plant (g)	38.875***	38.312***	183.999***
Shoot mass fraction	2.514 ^{ns}	1.206 ^{ns}	2.263 ^{ns}
Root mass fraction	12.777**	6.832*	7.874**
Mass fraction of main roots	2.717 ^{ns}	0.057 ^{ns}	4.909*
Mass fraction of total lateral roots	134.116***	39.886***	32.718***
Mass fraction of first-order lateral roots	100.687***	35.703***	22.859***
Two-way ANOVA			
Plant N concentration (mg g ⁻¹)	7.845*	70.609***	6.976*
Plant P concentration (mg g ⁻¹)	805.843***	197.514***	50.564***
ADH activity (μmol g ⁻¹ f. wt h ⁻¹)	141.058***	77.368***	10.380**
Porosity of main roots (%)	0.000 ^{ns}	0.165 ^{ns}	0.006 ^{ns}
Diameter of main roots (mm)	9.714**	16.348***	9.478***
Diameter of first-order lateral roots (mm)	3.385 ^{ns}	77.597***	0.239 ^{ns}
SRL of main roots (m g ⁻¹)	8.753**	16.634***	15.062***
SRL of first-order lateral roots (m g ⁻¹)	21.515***	72.578***	3.519*
d.f.	1	2	2

Significance: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Plant N and P concentrations

Both sediment type and light availability had significant effects on plant N and P concentrations ($P < 0.05$, Table 2). Plant N and P concentrations in the mud were generally higher than those in the mixture of mud and sandy loam, except for plant N concentration in the medium and low light ($P < 0.05$, Fig. 2).

Root physiological response

ADH activity in root tissues varied from 1.5 to 36.7 μmol g⁻¹ f. wt h⁻¹ in the six treatments (Fig. 3). Both sediment type and light availability had significant effects on ADH activity ($P < 0.05$, Table 2). Increased ADH activity indicated that oxygen deficiency in root tissues occurred in mud and low (high) light environments. The porosity of the main roots was unaffected by both sediment type and light availability ($P > 0.05$, Table 2), indicating that the capacity of root aeration in this species was independent of the environment.

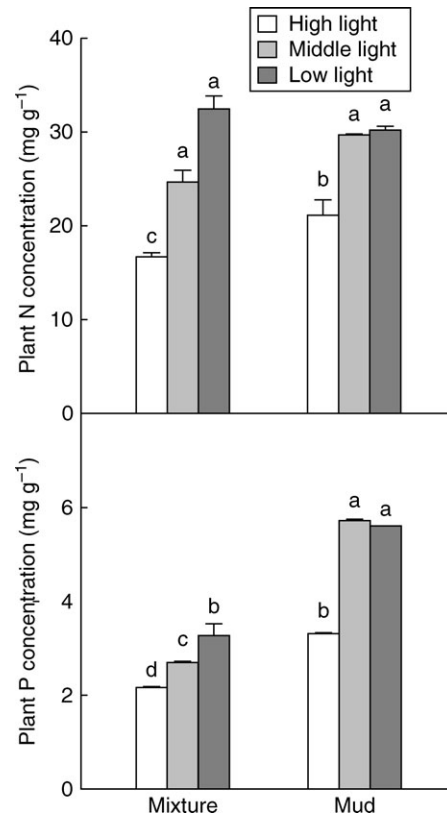


FIG. 2. Plant N and P concentrations (means \pm s.e., $n = 3$) of *Myriophyllum spicatum* growing on two types of sediment and under three levels of light availability. Different letters indicate significant differences among treatments. Multiple comparisons of means were performed by Duncan's test at the 0.05 significance level.

Root characteristics

Both sediment type and light availability had significant effects on root diameter (with significant sediment \times light interaction, $P < 0.05$) except for the diameter of first-order laterals, which was affected by light availability alone ($P < 0.05$, Tables 2 and 3). Second-order laterals only occurred in four treatments; they did not occur in medium light + mud or in low light + mud. Furthermore, second-order laterals in the mixture + low light were $\ll 5\%$, so these were disregarded in all the statistics (Table 3). Under high or medium light conditions, the diameter and SRL of different orders of roots were unaffected by sediment type ($P > 0.05$, Tables 2 and 3), except for second-order laterals. Root diameter generally decreased but SRL increased with decreasing light availability ($P < 0.05$), except for the diameter and SRL of main roots in mud.

Biomass allocation

Biomass allocation to shoots was unaffected by both light availability and sediment type ($P > 0.05$, Tables 2 and 3). However, the allocation to roots and different root orders was affected by both sediment type and light availability ($P < 0.05$, Tables 2 and 3), except for the mass fraction of main roots, in which just an interaction was found

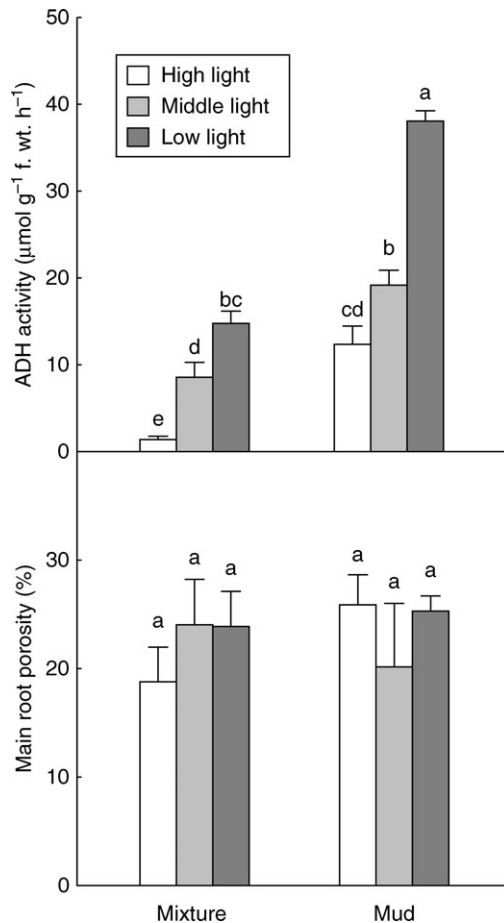


FIG. 3. ADH (alcohol dehydrogenase) activity and porosity of main roots (means \pm s.e., $n = 3$) in *Myriophyllum spicatum* growing on two types of sediment and under three levels of light availability. Different letters indicate significant differences among treatments. Multiple comparisons of means were performed by Duncan's test at the 0.05 significance level.

($P < 0.05$, Table 2). The effects of light availability on the mass fraction of the main roots depended on sediment type. Plants generally allocated more biomass to main roots and less to first-order laterals in mud and low light environments ($P < 0.05$), and more biomass was allocated to lateral roots (especially second-order laterals) in the infertile mixture and high light availability ($P < 0.05$).

DISCUSSION

Compared with the treatment of mud and high light, lower biomass accumulation, plant N and P concentrations and ADH activity suggest that the factor limiting plant growth in the mixture and high light environments was nutrient supply rather than oxygen. It was surprising that the effects of sediment type on the diameter and SRL of main roots and first-order laterals were undetectable under high light environments. These results largely contradict our initial hypothesis that roots are finer and longer in the mixture and high light environment due to nutrient deficiency. Literature data on other species are also controversial regarding the responses to infertile environments in

terms of root diameter and SRL. Many studies have shown that a fine root and a high SRL are functionally adaptive responses to infertile environments, by increasing total root length and root-sediment contact (Eissenstat, 1992; Barber, 1995; Xie and Yu, 2003; Xie *et al.*, 2005). These results indicate that the root morphological responses are species specific, and that characteristics other than root morphology might account for a plant's adaptation to nutrient availability.

Compared with the treatments of mixture and low (or high) light, significantly higher ADH activity in root tissues indicates that oxygen deficiency existed in the plants growing in mud and low (or high) light environments, although oxygen in water may diffuse into the shoot lacunae and to the roots in this type of experiment (Sorrell and Dromgoole, 1987; Pedersen *et al.*, 1998). As a response to anoxia, the porosity of the main roots of *M. spicatum* was unaffected by both sediment type and light availability, indicating that the oxygen transportation capacity was not enhanced due to anoxia. Actually, sediment oxygen demand has little effect on aeration of the main roots due to their low wall permeability and high surface impedance (Sorrell *et al.*, 2000), which is consistent with our study. In low light regimes, the accumulation of N and P in plant tissues and a higher ADH activity in roots indicated that the factors limiting plant growth in low light environments were light and oxygen, rather than nutrients. Therefore, the fact that no changes in root porosity occurred may be a result of inactive photosynthesis, which in turn cannot provide enough building material to make changes. However, the responses in high light environments completely reject our hypothesis, which predicts that root porosity will increase in high light and mud environments as a result of anaerobic conditions in the mud and active photosynthesis under high light.

In high or medium light regimes, root diameter and SRL were also unaffected by sediment type, although root diameter generally decreased but SRL increased with reduced light availability. These responses are also inconsistent with some wetland or emergent species. For example, most *Rumex* plants produce unbranched adventitious roots with a large diameter in response to flooding (Visser *et al.*, 1996), and flooding usually leads to a large number of short fine laterals in rice near the surface soil (Kirk, 2003). Xie *et al.* (2005) reported that fertile sediments led to no variation in SRL and an increase in root diameter of *Vallisneria spiralis*, a submerged plant without lateral roots. These responses are beneficial for a plant's adaptation to anoxia, by increasing oxygen transportation to root rhizosphere or by placing roots in the top soil of relatively high oxygen concentrations (Armstrong, 1979; Kirk, 2003). However, our study is consistent with another study, which found that none of the three grasses *Spartina anglica*, *Puccinellia maritima* and *Elymus pycnanthus* showed an increased root diameter due to flooding or to reducing soil conditions (Bouma *et al.*, 2001). Therefore, neither root porosity nor morphology can explain the root's adaptation to anoxia.

Another interesting finding is that *M. spicatum* can adjust biomass allocation to different orders of roots and the

TABLE 3. Root characteristics and biomass allocation of *Myriophyllum spicatum* as affected by sediment type and light availability (means \pm s.e.)

Dependent variables	n	Mixture			Mud		
		High light	Medium light	Low light	High light	Medium light	Low light
Root characteristics							
Diameter of main roots (mm)	30	0.63 \pm 0.02 ^{ab}	0.64 \pm 0.03 ^{ab}	0.60 \pm 0.03 ^b	0.68 \pm 0.03 ^a	0.57 \pm 0.02 ^b	0.43 \pm 0.01 ^c
Diameter of first-order lateral roots (mm)	50	0.23 \pm 0.01 ^a	0.18 \pm 0.01 ^b	0.17 \pm 0.01 ^b	0.22 \pm 0.01 ^a	0.17 \pm 0.00 ^b	0.16 \pm 0.00 ^b
Diameter of second-order lateral roots (mm)	50	0.14 \pm 0.02 ^a	0.13 \pm 0.00 ^a	–	0.13 \pm 0.00 ^a	–	–
SRL of main root (m g ⁻¹)	6	744 \pm 41 ^b	706 \pm 61 ^b	742 \pm 73 ^b	660 \pm 52 ^b	720 \pm 31 ^b	1203 \pm 42 ^a
SRL of first-order lateral roots (m g ⁻¹)	6	4636 \pm 120 ^c	7949 \pm 394 ^b	9580 \pm 848 ^b	5544 \pm 117 ^c	9535 \pm 503 ^b	13169 \pm 598 ^a
SRL of second-order lateral roots (m g ⁻¹)	6	34396 \pm 1186 ^a	16181 \pm 1211 ^b	–	12819 \pm 342 ^b	–	–
Biomass allocation							
Shoot mass fraction	6	0.92 \pm 0.00 ^a	0.96 \pm 0.00 ^a	0.95 \pm 0.01 ^a	0.96 \pm 0.00 ^a	0.97 \pm 0.00 ^a	0.96 \pm 0.00 ^a
Root mass fraction	6	0.079 \pm 0.004 ^a	0.038 \pm 0.004 ^{bc}	0.047 \pm 0.005 ^b	0.041 \pm 0.002 ^{bc}	0.035 \pm 0.003 ^c	0.043 \pm 0.003 ^{bc}
Mass fraction of main roots	6	0.025 \pm 0.001 ^{bc}	0.019 \pm 0.002 ^c	0.029 \pm 0.003 ^b	0.022 \pm 0.001 ^c	0.024 \pm 0.002 ^{bc}	0.034 \pm 0.002 ^a
Mass fraction of total lateral roots	6	0.054 \pm 0.003 ^a	0.019 \pm 0.002 ^b	0.018 \pm 0.002 ^b	0.019 \pm 0.001 ^b	0.011 \pm 0.001 ^c	0.009 \pm 0.001 ^c
Mass fraction of first-order lateral roots	6	0.040 \pm 0.002 ^a	0.016 \pm 0.002 ^b	0.018 \pm 0.002 ^b	0.017 \pm 0.001 ^b	0.011 \pm 0.001 ^c	0.009 \pm 0.001 ^c
Mass fraction of second-order lateral roots	6	0.014 \pm 0.001	0.003 \pm 0.000	–	0.002 \pm 0.000	–	–

Different superscript letters indicate significant differences among treatments ($P < 0.05$).
SRL, specific root length.

structure of the root system according to the light and sediment environment. These responses support our initial hypothesis on the response of biomass allocation, which predicts that more biomass will be allocated to roots (especially laterals) in infertile and high light environments and less to roots (especially laterals) under fertile mud and low light conditions. In infertile (high light and mixture) environments, the development of lateral roots was stimulated and more biomass was allocated to lateral roots (especially second-order laterals). Although root morphology was independent of sediment type, the increased biomass allocation to lateral roots can considerably increase total root length and root–sediment contact in infertile environments, since SRL was highest in second-order laterals, intermediate in first-order laterals and lowest in the main roots. Therefore, a high mass fraction of lateral roots is favourable for nutrient acquisition in infertile environments (Eissenstat, 1992; Xie and Yu, 2003). In high (or low) light and mud environments, the aeration capacity of the main roots was independent of environmental factors, but the development of lateral roots was inhibited and less biomass was allocated to laterals. It is known that radial oxygen loss can take place in different amounts and at different locations in the roots, but it often occurs at the laterals and close to the root tip (Armstrong and Armstrong, 2001; Colmer, 2003). Therefore, fewer (or lack of) second-order laterals, a low mass fraction of laterals and a high mass fraction of main roots in anoxic environments can substantially reduce total root length and the number of root tips, which in turn reduces radial oxygen loss of root systems. The mechanism of adaptation to anoxia in this species might be

closely related to reduced radial oxygen loss rather than increased capacity of oxygen transportation to root systems. Taken together, this plant can achieve the trade-off between internal aeration and nutrient acquisition by adjusting the structure of the root system and the pattern of biomass allocation to different root orders.

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