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The significance of lateral roots in phosphorus (P) acquisition of water hyacinth (*Eichhornia crassipes*)

Yonghong Xie, Dan Yu*

Institute of Ecology, School of Life Science, Wuhan University, Wuhan 430072, PR China

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Abstract

The morphology of lateral root and plant growth in relation to phosphorus (P) acquisition of water hyacinth (*Eichhornia crassipes*) were examined in lakes with different nutrient levels and in mesocosm tanks with two levels of P supply (4.8 and 0.6 g m⁻² per year). Lateral root was 2.43 times longer and 1.97 times denser at low-P than at high-P treatments, while the diameter decreased by 20% when the P application rate was lowered from 4.8 to 0.6 g m⁻² per year. Specific root length (SRL) and specific root area (SRA) of water hyacinth were significantly higher and plant allocated more biomass to lateral root when grown in low-P environments. Although only accounting for 85.35% of total root biomass in condition with low-P availability, lateral roots constituted 99.8% of total root surface area. In natural habitats, plant displayed the same tendency as in experimental tanks. Biomass increased during the experimental period and plant P concentration declined with time under either high- or low-P conditions, the total plant P, however, remained constant at low-P treatment ($P > 0.05$). These results indicate that the variation in lateral roots of water hyacinth can be considerable and the plant can satisfy P requirements for growth by redistribution of internal P source and increase of P absorption capability in low-P waters.

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1. Introduction

One of the worst weeds in temperate and tropical regions is water hyacinth (*Eichhornia crassipes* (Mart.) Solms). This floating weed has been recognized as an aquatic nuisance due to covering many lakes, rivers and ponds. Performed studies have confirmed that the detrimental effects of water hyacinth are closely linked to its capacity of multiplying and

* Corresponding author. Tel.: +86-27-87686834; fax: +86-27-87882661.

E-mail address: yudan01@public.wh.hb.cn (D. Yu).

spreading very rapidly (Gopal, 1987; Mehra et al., 1999). The growth and nitrogen (N) and phosphorus (P) content of water hyacinth are positively related to the N and P levels of the water (Sastroutomo et al., 1978; Taheruzzaman and Kushari, 1989). Water hyacinth can clean sewage, so most studies on growth characteristics and nutrient uptake were performed in eutrophic water (Center and Spencer, 1981; Dunigan et al., 1975; Reddy and DeBusk, 1984). In contrast, much less interest has been raised in low nutrient water. In low nutrient habitats water hyacinth just can maintain itself. If the plant escapes from it, and arrives at a new, nutrient-rich habitat, new problems emerge. The overall nutrient requirement of water hyacinth such as P is very low (Chadwick and Obeid, 1966; Reddy et al., 1990). This suggests that the plant can survive in low-P environment. Some experimental results indicated that internal P cycling within water hyacinth is adequate for maintenance in low-P water (Reddy et al., 1990). However, plant nutrient concentration cannot decrease unlimitedly, and a part of nutrients such as N and P will be lost with senescing tissues (Arts, 1996). Study on the mechanisms to explain why water hyacinth can survive in low-P water is, therefore, insufficient.

Morphological plasticity is an important adaptive mechanism to acquire resources (Hutchings and de Kroon, 1994). Root growth is important for uptake of water and nutrients, storage of carbohydrates and synthesis of growth regulators (Heeraman and Juna, 1993). Woody and herbaceous roots can account for as much as 60–80% of total plant biomass (Jackson et al., 1996). The root growth pattern is genetically controlled but can be modified by the environment (Taylor and Arkin, 1981). Thinner and longer root enhance geometry for uptake of nutrients from the environment, hence, P uptake depends on root length and diameter and surface area in contact with the environment (Nielsen and Barber, 1978; Anghinoni and Barber, 1980). Morphological plasticity in root system is, thus favorable for water hyacinth to adapt to low-P environment.

Morphological plasticity of water hyacinth in leaf has been well known (Center and Spencer, 1981; Jennifer and David, 1986; Richards, 1982), but is not clear in root. This plant only has first order lateral root and forms colossal root system (Fig. 1), and a root type of 'herringbone' (one single main root with many laterals). Because each lateral root



Fig. 1. Morphological variation in lateral root of water hyacinth as a response to P availability. The results showed that the morphology of lateral root changed significantly as a functional response to P availability: H indicates high-P application rate (4.8 g m^{-2} per year), and L indicates low-P application rate (0.6 g m^{-2} per year).

has a root tip, water hyacinth may possess sufficient morphological plasticity in lateral root to exploit nutrient in low-nutrient water body. In this study, the morphology of lateral root and plant growth in relation to P acquisition of water hyacinth were estimated in mesocosm tanks with high and low levels of P addition to test following hypotheses. First, water hyacinth may display significant morphological variations in lateral root to increase root surface area to adapt to low-P environment. Second, the mechanism for water hyacinth to satisfy P requirements for growth in low-P water is to increase P absorption capability and redistribution of internal P sources.

2. Methods

Young plants of water hyacinth were collected from the site in Donghu Lake (30°33.118'N 114°21.198'E) in Wuhan City, Hubei, China. Some were placed in outdoor tanks, and the others were introduced into the fish net (3 cm mesh) in Liangzi Lake (30°15.791'N 114°33.455'E) near Ezhou City, Hubei, China. Donghu Lake is a eutrophic lake (total N 148.57 mmol m⁻³, total P 9.03 mmol m⁻³), while Liangzi Lake is an oligotrophic Lake (total N 50.71 mmol m⁻³, total P 1.32 mmol m⁻³). These two lakes (separated by about 60 km) both belong to subtropics. The average annual temperature is about 16.8 °C. The average annual rainfall is about 1820.0 mm in Liangzi Lake and 1862.2 mm in Donghu Lake. Water hyacinth can overwinter with rhizomes in this area.

In the mesocosm experiment, there were two levels of P (as NaH₂PO₄) supply (high P, 4.8 g m⁻² per year; low P, 0.6 g m⁻² per year). N, K, Ca, Mg, Fe (as Fe-EDTA), Mn, Cu, Mo, B, Zn were 60, 72, 80, 30, 7.2, 0.84, 0.03, 0.01, 0.72, 0.08 g m⁻² per year, respectively. All nutrients were added on 10th and 25th of every month. The size of outdoor tanks was 1 m × 1 m × 0.5 m. Each tank started with 200 liters of water, and put apart 30 cm height to avoid nutrients discharged from the tanks for precipitation.

Each tank was divided into four equal parts, and two mesh baskets (0.25 m², 2.5 cm opening), loaded with water hyacinth, were placed in each tank diagonally. Starting density for each treatment was two plants, or fresh weight 200 ± 10 g m⁻². Initial plant density in the baskets was the same as outside the baskets. Two tanks were used for each treatment, and each tank contained two baskets, so each treatment was replicated four times. The experiment was conducted from 25 April to 25 August 2001. On 25th of every month, after dead leaves and leaf stalks were removed, baskets were taken out from the tanks, drained for 5 min, weighed, then placed back into their respective tanks. The plants were sampled outside the mesh baskets, removed dead leaves and leaf stalks, separated into leaves, roots, leaf stalks and rhizomes, oven dried at 65 °C for 72 h, and dry weights recorded. After collected, all samples were digested with H₂SO₄–H₂O₂, then analyzed for total P concentration using colorimetry (Murphy and Riley, 1962).

Lateral root parameters were assessed at the end of the experiments. Lateral root length was measured by vernier caliper, diameter by microscope with micrometer and density by count. Despite the need of some indirect estimations, this manual technique was considered to give reliable results (Anders, 2000). After harvested, water hyacinth was placed in plastic salvers with water. Complete lateral roots were nipped randomly from the basal

with tweezers, placed in a microscope slides with water film, drew straight. Subsequently, 10 lateral roots on each root were randomly selected and length, diameter and density of lateral roots as well as the diameter of main roots were measured.

Relative growth rate (RGR) was calculated as the slope of the regression between the ln-transformed plant weight and time. Specific root length (SRL) was calculated as the total root length divided by root biomass, and estimated from the density and average length of root and lateral root. Specific root area (SRA) was defined as the root surface area per gram root, and calculated as following formula:

$$SRA = \pi \xi (D_l \times L_l + D_r \times L_r),$$

where ξ defined as means of specific root length (SRL), D_l as the mean diameter of lateral root, L_l as the mean total length of lateral root per gram root, D_r as means of root diameter, and L_r as the means of total length per gram root.

The effects of P availability on morphological parameters were tested by analysis of variance (F -ratios) and the differences of total P of each treatment in 4 months were compared by least significance deviation (LSD).

3. Results

3.1. Morphological plasticity in lateral roots

Root characteristics of water hyacinth differed significantly with P application rate or nutrient levels, in either outdoor tanks or lakes (Table 1, Fig. 1). In mesocosm experiment, lateral roots were 2.43 times longer and 1.97 times denser in low-P than in high-P treatments. Lateral root diameter decreased when grown in low-P condition. Lateral root constituted 99.8% of total root surface area under low-P condition, and 91.5% under high-P condition. In natural habitats, this plant displayed the same tendency as in outdoor tanks. As a result of the variation in root characteristics, specific root length (SRL) increased 2.82 times, and specific root area (SRA) increased 2.46 times when the P application rate lowered from 4.8 to 0.6 g m⁻² per year (Fig. 2).

As an important strategy of resource acquirement for plants, root:shoot ratio reflects adaptive response to carbon or nutrients availability. When the amount of available P decreased, root:shoot ratio increased 1.89 times in outdoor tanks, 2.68 times in the field, and lateral root:total root ratio increased 1.74 times in outdoor tanks, 1.32 times in lakes (Table 1). The plants allocated more biomass to lateral roots as a response to low-P availability.

3.2. Growth and dead biomass

Plant growth increased with P availability (Fig. 3). RGR was 3.67 times higher at high-P (22 mg g⁻¹ per day) than at low-P treatments (6 mg g⁻¹ per day) (Fig. 4). The ln-transformed yield differed significantly in any 2 months excluding in July and August under low-P condition, indicating the plants was arriving at steady stage of growth.

Table 1
 Root characteristics of water hyacinth in outdoor experiments and field study in response to P availability^a

	<i>n</i>	Outdoor experiment			Field study		
		High P	Low P	<i>F</i> -values	High P	Low P	<i>F</i> -values
Lateral root length (cm)	132	1.66 ± 0.59	4.04 ± 0.73	853.127*	1.82 ± 0.31	3.41 ± 0.57	796.616*
Lateral root diameter (mm)	132	0.15 ± 0.01	0.12 ± 0.01	143.742*	0.14 ± 0.01	0.13 ± 0.01	8.654**
Lateral root density (number of cm ⁻¹ in root)	48	62 ± 10	122 ± 11	397.827*	87 ± 7	123 ± 7	320.710*
Root diameter (mm)	132	1.14 ± 0.22	0.96 ± 0.09	12.494***	0.97 ± 0.11	0.86 ± 0.08	5.004**
Lateral root constitute total root surface area (%)	–	91.5	99.8		95.8	98.5	–
Lateral root:total root ratio	8	0.49 ± 0.05	0.85 ± 0.03	234.212*	0.67 ± 0.02	0.88 ± 0.02	270.070*
Root:shoot ratio	8	0.32 ± 0.02	0.61 ± 0.04	142.606*	0.29 ± 0.03	0.79 ± 0.04	655.844*
Lateral root:total plant ratio		0.09	0.20	–	0.12	0.22	–

^a Means ± S.D.

* *P* < 0.05.

** *P* < 0.01.

*** *P* < 0.001.

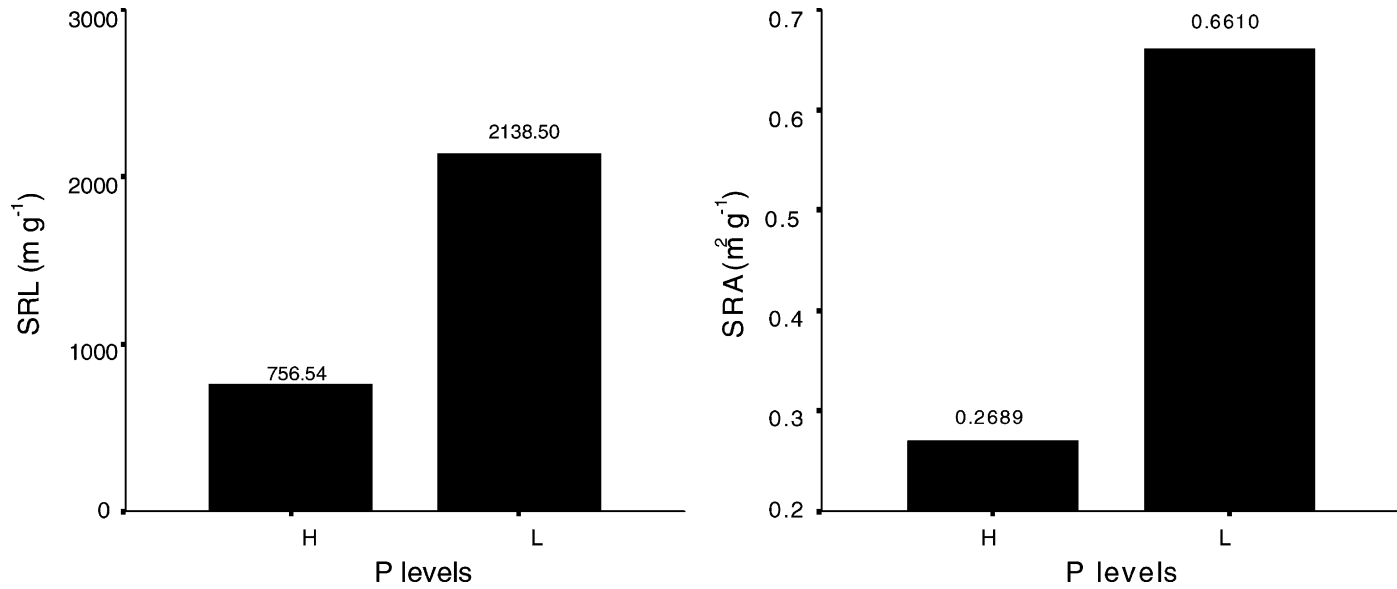


Fig. 2. Specific root length (SRL) and specific root area (SRA) affected by P application rate: H and L as shown in Fig. 1.

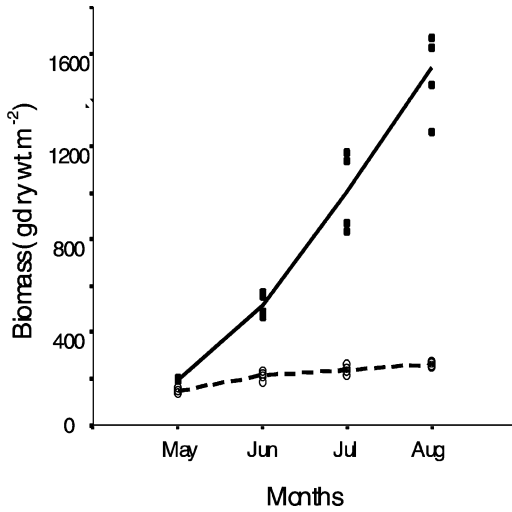


Fig. 3. Biomass of water hyacinth cultured in mesocosm tanks with high- or low-P conditions during the experiment period. Black dots with solid lines indicate high-P condition, and open dots with dashed lines indicate low-P condition.

Total biomass of dead parts was higher at high-P (80.67 g m^{-2}) than at low-P treatments (67.49 g m^{-2}). Comparatively, water hyacinth quickened renewal of leaves and leaf stalks for maintenance, namely the longevity of leaf and leaf stalk was shorter under low-P environment (Fig. 5).

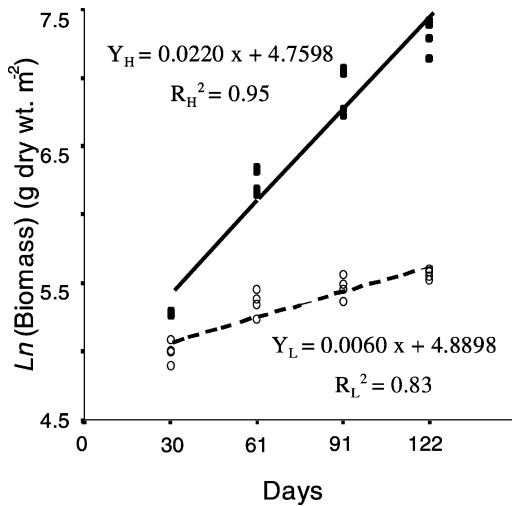


Fig. 4. The time dependence of relative growth rate (RGR) of water hyacinth grown in high- and low-P conditions. The linear regression equation for the plants was fitted between the ln-transformed plant weight and time. Black dots with solid lines indicate high-P condition, and open dots with dashed lines indicate low-P condition.

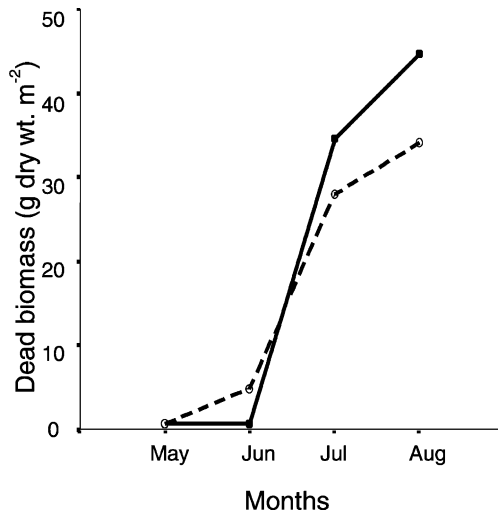


Fig. 5. Dead biomass (leaves and leaf stalks) of water hyacinth during the experimental period in high- and low-P conditions. Black dots with solid lines indicate high-P condition, and open dots with dashed lines indicate low-P condition.

3.3. Plant P concentration and total plant P

Plant P concentration declined during the experimental period, but more quickly at high-P (from 9.97 to 5.76 mg g⁻¹) than at low-P treatments (from 5.73 to 3.91 mg g⁻¹) in the second month of the experimental period, and almost at the same rate in the succeeding 3

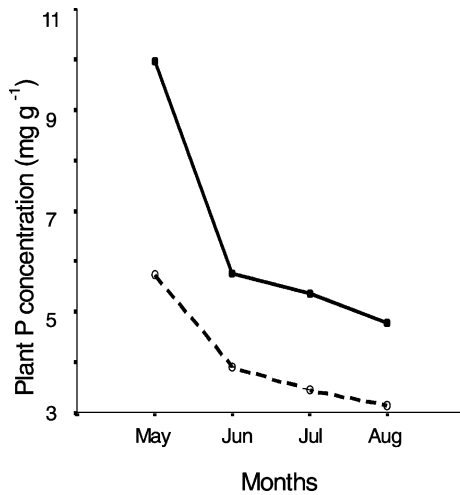


Fig. 6. Plant P concentrations of water hyacinth during the experimental period in high- and low-P conditions. Black dots with solid lines indicate high-P condition, and open dots with dashed lines indicate low-P condition.

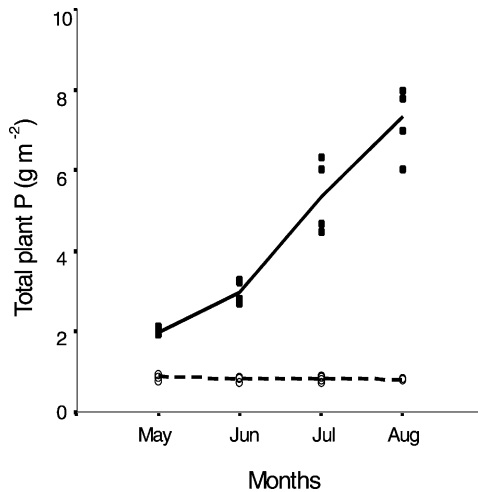


Fig. 7. Total plant P of water hyacinth during the experimental period in high- and low-P conditions. Black dots with solid lines indicate high-P condition, and open dots and dashed lines indicate low-P condition.

months (Fig. 6). Total plant P increased almost linearly under high-P condition, but remained constant under low-P condition (Fig. 7).

4. Discussion

Lateral roots of water hyacinth were longer and denser at low-P than at high-P treatments, while the diameter decreased when grown in condition with low-P availability. Consequently, SRL and SRA decreased significantly with the increase in P application rate. These results indicated that the variation in lateral root of water hyacinth can be considerable and the changes of lateral root parameters depend on the amount of available P. In high nutrient environment, maybe lateral root growth was inhibited by high-N concentration in the plant (Zhang and Forde, 1998). In their review, Robinson and Van Vuuren (1998) indicated that fast-growing species display on average a higher degree of root morphological plasticity than slow-growing species. Such difference may be the results of growth rate differences (Fransen et al., 1999). The growth rate of water hyacinth is among the highest of any plant known, so the reason for high morphological plasticity in lateral root may be of high productivity.

Our experimental results showed that the variation in lateral root of water hyacinth (including length, density and diameter) can be considerable. Such morphological variations will help to adapt to low-P environments. There are three reasons accounting for this. First, a plant with long, fine roots should be more efficient in acquiring P than a plant with short, thick ones (Ciro et al., 1999). So, the formation of thin, long roots is favorable for plants to adapt to low-P environment (Shenk and Barber, 1977). Second, higher SRA and SRL are more favorable for nutrient acquisition in low-P environment (Eissenstat, 1992). Third,

increase in lateral root density under low-P condition may reflect that root proliferation is important when plants are grown in environments with low available nutrients (Robison, 1994). Morphological plasticity in lateral roots is, thus a functional response to P availability. In addition, higher SRA and SRL may indicate that the costs of constructing root system are lower in low-P environment (Eissenstat, 1992).

P uptake of water hyacinth are influenced by plant N and P concentrations, N and P availability, and N resource in the environment (Sastroutomo et al., 1978; Reddy and Tucker, 1983; Taheruzzaman and Kushari, 1989). But the roles of morphological variations in lateral roots in P acquisition are often neglected. This study showed that morphological plasticity in lateral roots plays an important role in P acquisition for water hyacinth. Especially in low-P treatments, lateral roots constituted 99.8% of total root surface area, which substantially increase root-water contact. Therefore, higher lateral root allocation ratio with colossal root surface area may be an important factor for water hyacinth to adapt to low-P environments. In addition, root morphological plasticity is important for the acquisition of nutrient in heterogeneous environment (Fransen et al., 1998). Plants that do not display root plasticity acquire less, instead of more, nutrients in heterogeneous than in homogeneous environments (Ryel and Caldwell, 1998).

Although biomass increased during the experimental period and plant P concentration declined with time, total plant P remained constant under low-P condition. These results suggested that water hyacinth can acquire enough P to satisfy the requirements for growth. In addition, dead leaves and leaf stalks were collected before weighing, so the P acquired by water hyacinth compensated the P loss from senescing tissues in low-P waters. The mechanisms for water hyacinth to survive in low-P environments is through economical use of internal P sources and increases in P absorption capability by morphological variation in root system, which supports our initial hypothesis. However, some experimental results indicated that internal P cycling within water hyacinth is adequate for maintenance because the plant P concentration reached a steady state in a low-P water (Reddy et al., 1990). We did not observe this relationship. The difference may be caused by different ways of nutrient addition and the duration of experiments.

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