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Microhabitat Effect on Iron Distribution and Transfer in *Carex pseudocuraica* in Sanjiang Plain Wetlands

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Abstract: Ten clonal units of *Carex pseudocuraica* growing in four different microhabitats (perennial flooded ditch water, perennial flooded ditch sediment, seasonal flooded ditch sediment and perennial flooded soil) of the Sanjiang Plain, Northeast China, were collected randomly for phenotypic plasticity analysis. Iron content, chemical and physical properties of substrates and the total Fe of nine plant modules were measured as well. The results show that the performance of the *C. pseudocuraica* is affected by the microhabitat, with the greatest performance score in perennial flooded ditch water, and the lowest in perennial flooded soil. The biomass allocation indexes indicate that much more mass is allocated to stems and roots to expand colonization area. The distribution of the total Fe in plant modules appears as pyramids from the tip to the root, while marked differences are observed in the distribution proportion of stems, tillering nodes and roots that are allometrically growing. Iron transfer from substrates to the plant is mainly controlled by the substrate type. The differences of iron distribution and transfer in the plant in different microhabitats are attributed to the iron contents of the substrates as well as the phenotypic plasticity of the plant.

Keywords: iron distribution; iron transfer; *Carex pseudocuraica*; Sanjiang Plain

1 Introduction

Iron is an essential redox-active transition metal and trace metal required by plants, which participates in many physiological processes such as photosynthesis, respiration and biological nitrogen fixation (Guerinot and Yi, 1994; Gurzau *et al.*, 2003; Nenova, 2009). Severe lack of iron will reduce the chlorophyll synthesis and cause acute biomass reduction (Lindsay and Schwab, 1982; Sahrawat, 2005; Yousfi *et al.*, 2007; Audebert and Fofana, 2009; Diaz *et al.*, 2009). However, excessive iron will be toxic to the root system and the growth of various wetland plants, which depends upon their tolerance mechanisms (Ponnamperuma *et al.*, 1955; Wheeler *et al.*, 1985; Snowden and Wheeler, 1993; 1995; Lucassen *et al.*, 2000; De Dorlldot *et al.*, 2005). Therefore, iron is a double-edged sword for plants and regulates the performances of certain species. These performances can be expressed as their phenotypic plasticity which endows plants with strong invasiveness and competitiveness to colonize in favourable microhabitats (Schlichting, 1986; Scheiner, 1993; Dorken and Barrett, 2004; Hulme, 2008).

The iron availability in wetland soils, for their reduced condition and enriched organic matter, is usually greater than any other soil (Liesack *et al.*, 2000; Ratering and Schnell, 2000; Roden and Wetzel, 2002). Therefore, the main problem of iron uptake by wetland plants is how to prevent iron toxicity. As an evolution strategy of some wetland plants, ferrous iron entering into rhizosphere through diffusion can be oxidized by the oxygen released from roots, and then precipitated on the root surface (Lemanceau *et al.*, 2009). The iron plaque is formed consequently, which not only controls the uptake and accumulation of iron, but also affects the uptake of other elements such as phosphorus, arsenic and cadmium (Zhang *et al.*, 1999; Chen *et al.*, 2005; Liu

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et al., 2008). Because of the significant redox gradient surrounding roots, wetlands are considered as the "hotspots" of ferric rion reduction and ferrous iron oxidation with a rapid iron cycling (Weiss *et al.*, 2003).

On a larger scale, wetlands are characterized by their microhabitat effect for the acute environmental gradients and great spatial heterogeneity within a relative limited space (Reddy and DeLaune, 2008). Therefore, different performance, as well as the iron uptake and distribution, of the same plant growing in different wetland microhabitats will be observed in the field (Batty and Younger, 2003), and we hypothesize that there may exist a relationship between plant phenotypic plasticity and iron nutrition. However, studies focused on this issue are still rare at present.

As one of the typical freshwater wetland plant in Northeast China, *Carex pseudocuraica* is a rhizomatous perennial herbaceous plant in the sedge family and the dominant species in static rivers and flooded wetlands (Fu, 1995). Sexual reproduction strategy is rare to be adopted and the plant usually forms guerilla-type colonies by adventitious shoots from stubborn rhizomes (Fu, 1995). The morphological adaptability of the plant with soil water gradient is documented recently (Luan *et al.*, 2006). However, little is known about how the iron contents of different microhabitats influence the performance of this wetland plant and whether the environmental adaptability can influence the transfer of iron from substrates to the plant and the distribution of iron in the plant.

The aim of this study is to examine the microhabitat effect on the iron distribution and transfer from wetland substrates to *C. pseudocuraica*, and analyze the relationship between the plant′s phenotypic plasticity and iron nutrition, which can provide researchers with reference for studying other wetland plants and is useful to further understand the biogeochemical cycle of iron in wetlands.

2 Materials and Methods

2.1 Study area and sampling sites

The study area was located at the Sanjiang Mire Wetland Experimental Station, Chinese Academy of Sciences (47º13"50'N, 133º13"10'E), which represents the typical landscape of the Sanjiang Plain wetlands. The wetland in the study area developed from a dish-shaped depression. The mean annual precipitation is 550–600 mm, the mean annual temperature is approximately 1.9℃, and the frost-free period is 120–125 d (Song *et al.*, 2006). The main soil types are marsh soil, meadow soil and albic soil. The main plant species are *Carex* spp., *Calamagrostis angustifolia*, *Betule fruticosa*, *Salix brachypoda* and so on (Yang *et al.*, 2004). These plants are distributed annularly in the wetland according to hydrological regime. *C. pseudocuraica* grows in the central wetland with standing water of 10–30 cm as well as the ditches attached to the wetland. Four different microhabitats with dominant species of *C. pseudocuraica*, i.e. perennial flooded ditch water (PW, the plants here were floating and not rooted in sediment), perennial flooded ditch sediment (PSed), seasonal flooded ditch sediment (SSed) and perennial flooded soil (PS), were selected as the sampling sites because they represented the different substrate types and water regimes. The chemical and physical properties of the four microhabitats are listed in Table 1.

2.2 Plant analysis

Ten clonal units of *C. pseudocuraica*, which develop from the same tillering node and interconnect each other through a rhizome, were collected randomly from each of the four different microhabitats in October 2007, to study the performance of *C. pseudocuraica* at the late autumn when the plant stops growing.

Table 1 Chemical and physical properties of four wetland microhabitats

Microhabitat	Available N (mg/kg)	Available P (mg/kg)	Available K (mg/kg)	Organic C (g/kg)	Available Fe (mg/kg)	Total Fe (g/kg)	pH
PW*	0.93	0.05	4.06	27.93	0.48	0.10	7.51
PSed	201.60	53.80	45.08	23.38	276.58	18.80	6.01
SSed	151.20	16.90	271.37	16.59	350.49	25.75	5.74
PS	445.20	20.76	190.14	76.51	140.87	15.65	5.66

Notes: PW, perennial flooded ditch water; PSed, perennial flooded ditch sediment; SSed, seasonal flooded ditch sediment; PS, perennial flooded soil. * The contents of nitrogen, phosphorus, potassium, carbon and iron in the substrate were measured as dissolved N, dissolved P, dissolved K, dissolved organic carbon (DOC), dissolved Fe^{2+} and Fe^{3+}, with the unit of mg/L

The morphological indicators studied in this paper included number of tillers (NT), number of internodes (NI), number of branches (lateral buds included) (NB), stem height (SH), length of bottom internode (LBI), maximum length and stem diameter of internode (MLI, MDI), number of adventitious roots attached to tillering node (the roots with a length over 2 cm or a diameter over 0.2 mm) (NRN), maximum length of adventitious roots attached to tillering node (MLR), number of adventitious roots attached to stem (NRS), and biomass aboveground, belowground and their sum (BA, BB, B). In this paper, BB was the sum of tiller node and root system. BA was the sum of the rest parts. Five biomass allocation indexes, i.e. leaf mass to total mass (L/M), tillering node mass to total mass (T/M), root mass to total mass (R/M), leaf mass to shoot mass (L/S) and root mass to shoot mass (R/S), were calculated based on the data above to indicate the growth strategies of *C. pseudocuraica* in different microhabitats.

The plants collected were divided into nine modules, i.e., apical stems (four or five apical internodes with light colour, AS), middle stems (MS), basal stems (two or three basal internodes with dark colour, BS), leaves (L), sheaths (S), tillering nodes (junctions attached with stems and roots, T), lateral adventitious roots (with many root hairs but without obvious root axis, LR), primary adventitious roots (with obvious root axis but less root hairs, PR) and dead adventitious roots (dark colour, without root hairs, DR), and the total Fe of the plant modules were determined according to the method suggested by Shi (1986). All modules were oven-dried at 80℃, incinerated at 550℃, and dissolved in 1∶1 HCl, and then the total Fe contents of the modules were determined with atomic absorption spectrometry (AAS) (GBC-906, Australia).

2.3 Substrate analysis

The details in the following chemical measure processes were referred to soil agrochemical analysis method (Shi, 1986). Water samples from PW were pre-filtrated through 0.45 μm filter membrane. Dissolved N and dissolved P were determined with SAN^{++} Continuous Flow Analyzer (CFA) (SKALAR, Netherland). Dissolved K was measured with AAS. Dissolved organic carbon (DOC) was measured with TOC-V_{CPH} (Shimazu, Japan) and pH was measured with composite electrode. Dissolved Fe^{2+} and Fe^{3+} were measured with 1,10-phenanthrollne-iron spectrophotometry (UV-2500, Shimazu, Japan).

Soil and sediment samples were air-dried and sieved with 1-mm sieve for available nutrients analysis and with 0.25-mm sieve for organic matter analysis, respectively. Available N was measured with CFA after extraction with NaOH (1 mol/L). Available P was measured with CFA after extraction with NH_4F-HCl (0.03 mol/L and 0.025 mol/L, respectively). Available K was measured with AAS after extraction with NH_4OAC (1 mol/L). Organic C was measured with TOC-V_{CPH}. pH was measured with composite electrode after dilution 1∶5 with distilled water. Available Fe was measured with AAS after extraction with 0.1 mol/L HCl. Total Fe was measured with AAS after digestion with HNO_3-HF-$HClO_4$ for 0.5 h.

2.4 Statistical analysis

One-way analysis of variance (ANOVA), factor analysis and correlation analysis were performed using SPSS 11.0, Standard Version (SPSS Inc., Chicago, US), and graphics using OriginPro 7.5 (OriginLab Corp., Northampton, US).

3 Results

3.1 Plant morphology

Generally, *C. pseudocuraica* growing in PW has long stems, many tillers and long roots, while that in PSed has many branches and stubbed roots with little root hairs. In SSed the plant has thick stems and many dark roots, and in PS the plant has dwarfish ramets, less tillers and short and thin roots with dense root hairs.

The measured values of the 13 plant morphological indicators are listed in Table 2. The mean differences among LBI, MLI, NRS, BA, BB and B are significant (one-way ANOVA, P = 0.033, 0.003, 0.002, 0.008, 0.013, 0.005, respectively), and those among MDI and MLR are significant extremely ($P < 0.001$).

Based on the correlation matrix of the total 13 morphological indicators, factor analysis method was applied and four factors (eigenvalue > 1, Varimax rotated) were selected and the cumulative variance was up to 73.53%. Factor 1 had the largest load in BA, which indicated that factor 1 represented biomass aboveground. Factor 2 had the largest load in NT, which indicated that factor 2 represented morphology aboveground. Factor 3 had the largest load in MLR, which indicated that factor 3 represen-

Table 2 Plant morphological indicators of four wetland microhabitats (Mean ± S.E.)

	PW	PSed	SSed	PS
NT	4.60±0.56 ^{a}	6.30±0.50 ^{a}	6.90±1.31 ^{a}	3.80±0.73 ^{a}
NI	12.10±1.99 ^{a}	9.10±0.72 ^{a}	11.80±0.98 ^{a}	10.80±0.37 ^{a}
NB	3.90±0.99 ^{a}	3.80±0.79 ^{a}	3.20±0.61 ^{a}	3.60±0.87 ^{a}
SH (cm)	57.14±9.25 ^{a}	35.52±2.13 ^{a}	64.10±23.27 ^{a}	29.66±1.86 ^{a}
LBI (cm)	3.22±0.19 ^{b}	2.32±0.17 ^{a}	2.84±0.28 ^{ab}	2.48±0.23 ^{ab}
MLI (cm)	7.80±0.38 ^{a}	6.02±0.47 ^{ab}	6.11±0.32 ^{b}	5.48±0.48 ^{b}
MDI (mm)	1.84±0.06 ^{b}	1.21±0.77 ^{a}	1.66±0.11 ^{b}	1.18±0.08 ^{a}
NRN	41.20±3.82 ^{a}	30.80±3.77 ^{a}	49.50±8.40 ^{a}	32.00±8.99 ^{a}
MLR	20.14±1.08 ^{b}	12.64±0.98 ^{a}	13.09±0.88 ^{a}	13.88±1.72 ^{a}
NRS	7.20±2.31 ^{b}	0 ^{a}	1.50±0.90 ^{a}	0 ^{a}
BA (g)	1.92±0.41 ^{b}	0.74±0.11 ^{a}	1.21±0.27 ^{ab}	0.42±0.06 ^{a}
BB (g)	0.72±0.10 ^{b}	0.38±0.05 ^{a}	0.53±0.11 ^{ab}	0.27±0.07 ^{a}
B (g)	2.64±0.48 ^{b}	1.12±0.12 ^{a}	1.73±0.36 ^{ab}	0.68±0.12 ^{a}

Notes: Data shared the same letter are not different at $P = 0.05$. NT, number of tillers; NI, number of internodes; NB, number of branches; SH, stem height; LBI, length of the bottom internode; MLI, maximum length of internode; MDI, maximum stem diameter of internode; NRN, number of adventitious roots attached to tillering node; MLR, maximum length of adventitious root attached to tillering node; NRS, number of adventitious roots attached to stem; BA, biomass aboveground; BB, biomass belowground; B, total biomass

ted dmorphology belowground. Factor 4 had the largest load in BB, which indicated that factor 4 represented biomass belowground (Table 3).

Table 3 Rotated factor matrix

	Factor			
	1	2	3	4
NT	0.084	0.894	–0.207	–0.112
NI	0.739	0.202	–0.095	0.307
NB	0.005	0.160	0.180	0.181
SH	0.329	–0.094	–0.083	0.668
LBI	0.689	–0.003	0.213	0.003
MLI	0.672	–0.135	0.318	0.119
MDI	0.418	0.286	0.568	0.069
NRN	0.087	0.746	0.376	0.188
MLR	0.175	–0.077	0.877	0.023
NRS	0.574	0.330	0.396	–0.285
BA	0.787	0.437	0.238	0.238
BB	0.406	0.568	0.602	0.842
B	0.734	0.492	0.340	0.237

The total factor score of each clonal unit is calculated as:

$$S = (0.4363S_1 + 0.1170S_2 + 0.1033S_3 + 0.0787S_4) / 0.7353 \quad (1)$$

where, S is total socre; S_1, S_2, S_3 and S_4 are the scores of facor 1, factor 2, factor 3 and factor 4, respectively.

In the equation, the coefficient of each factor is the percentage of its variance. The performance score of each microhabitat, defined as the mean of the total scores of ten colonal units, shows that the greatest value appears in PW (0.55), the second one in SSed (0.06), the third one in PSed (–0.38), and the lowest in PS (–0.46).

3.2 Biomass allocation

From the biomass allocation index, the leaf mass to total mass (L/M), tillering node mass to total mass (T/M), and leaf mass to shoot mass (L/S) in PW are the lowest in all microhabitats, while the biomass in PW is the greatest, which indicates that more mass are allocated to stems and roots to expand colonization area. The maximum of root mass to total mass (R/M) and root mass to shoot mass (R/S) appear in PS, while the minimum of these indexes appear in SSed (Table 4).

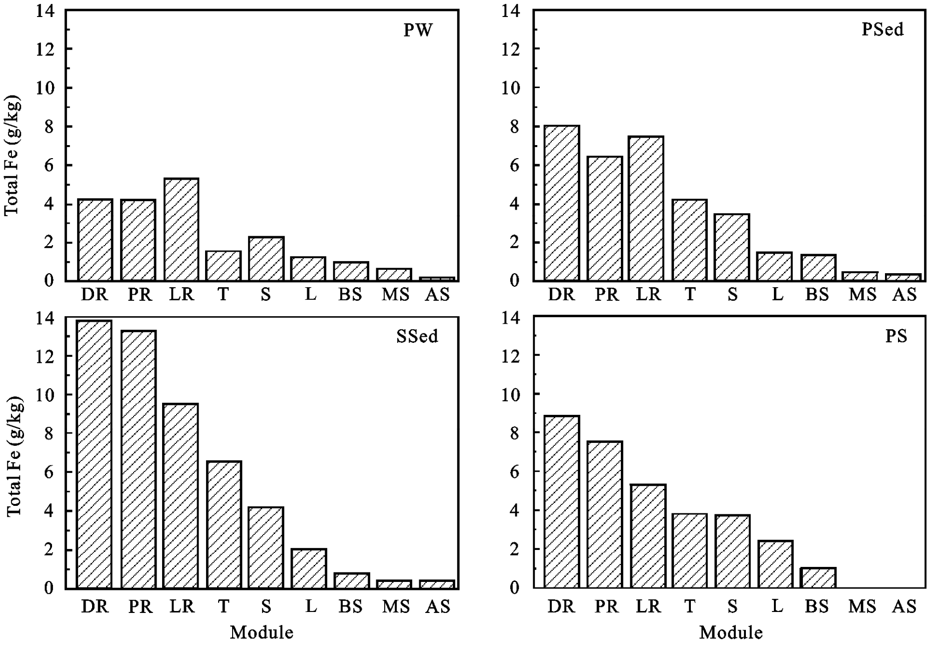
3.3 Iron distribution

The total Fe distribution in the nine modules in all microhabitats shares the same configuration just like a pyramid from the tip to the root (Fig. 1). The modules underground have the greater total Fe than that aboveground. Within a certain root system or stem system, the old modules have the greater total Fe than the young ones. Marked inter-microhabitat differences are observed in the plant modules in PW with relatively low concen-

Table 4 Biomass allocation index in four wetland microhabitats

Microhabitat	L/M	T/M	R/M	L/S	R/S
PW	0.15	0.016	0.21	0.20	0.30
PSed	0.27	0.051	0.20	0.36	0.34
SSed	0.20	0.050	0.17	0.26	0.28
PS	0.26	0.033	0.30	0.38	0.49

Notes: L/M, leaf mass to total mass; T/M, tillering node mass to total mass; R/M, root mass to total mass; L/S, leaf mass to shoot mass; R/S, root mass to shoot mass



DR: dead adventitious roots (dark colour with litter root hairs); PR: primary adventitious roots (obvious root axis with any root airs); LR: lateral adventitious roots (many root airs without obvious root axis); T: tillering nodes (junctions attached with stems and roots); S: sheaths; L: leaves; BS: basal stems (2 or 3 basal internodes with dark colour); MS: middle stems; AS: apical stems (four or five apical internodes with light color)

Fig. 1 Total Fe of *C. pseudocuraica* modules in four wetland microhabitats

tration in T and relatively great concentration in LR.

When multiplied by the biomass of each module, the total Fe distribution is transformed into an iron mass distribution (Fig. 2), which suggests that the iron distribution is influenced by allometric biomass allocation. Roots are the main pools of iron, which occupy approximately 60% of the total iron mass for all the microhabitats. Meanwhile, marked inter-microhabitat differences are still observed among microhabitats, especially the distribution proportion of stems, tillering nodes and roots that are allometrically growing (Fig. 2).

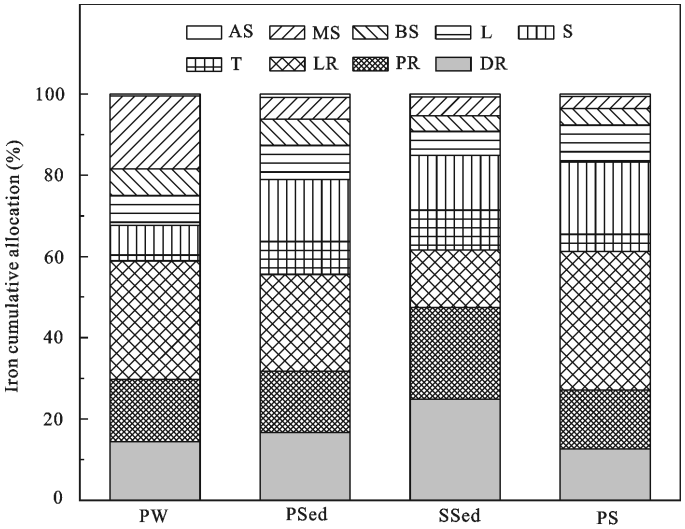
3.4 Iron transfer

When the biomass and iron mass of the nine modules of each microhabitat are added respectively, the total Fe of the plant can be calculated by the ratio of iron mass to biomass (Fig. 3). The variations of biomass and iron mass show the similar trends, however, the total Fe of the plant shows a different curve from the biomass curve and iron mass curve.

4 Discussion

4.1 Influencing factors of performance of *C. pseudocuraica*

The performance of a specific plant is controlled by several factors, including genetic aspect (Schlichting, 1986; Scheiner, 1993) and environmental aspect (Jurjavcic *et al.* 2002; Pan *et al.*, 2006). According to the performance score, it is found with one-way ANOVA



AS: apical stems (four or five apical internodes with light color); MS: middle stems; BS: basal stems (2 or 3 basal internodes with dark colour); L: leaves; S: sheaths; T: tillering nodes (junctions attached with stems and roots); LR: lateral adventitious roots (many root airs without obvious root axis); PR: primary adventitious roots (obvious root axis with any root airs); DR: dead adventitious roots (dark colour with litter root hairs)

Fig. 2 Iron allocation to each module of *C. pseudocuraica* in four wetland microhabitats

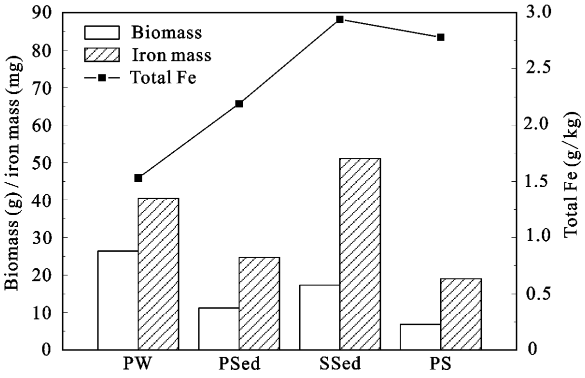


Fig. 3 Variations of biomass, iron mass and total Fe in *C. pseudocuraica* in four wetland microhabitats

that the substrate types (water, sediment and soil) and content level (four microhabitats with four levels) are the main factors deciding the performance of the plant (eight and seven of the 13 indicators are significant, respectively), while the flooding regime does not influence significantly (only 1 indicator) (Table 2).

It is interesting to find that the performance score is negative correlated to available N, available P, organic C and pH (*R* = –0.737, –0.458, –0.697, –0.160; *P* = 0.473, 0.697, 0.509, 0.898, respectively), while positive to available K, available Fe and the total Fe (*R* = 0.857, 0.853, 0.986; *P* = 0.345, 0.349, 0.106, respectively), based on the correlation analysis between the performance scores (PW is exclusive for its special substrate) and the substrate contents (Table 1). The K and Fe contents of the substrates, therefore, might be the limiting factors influencing the plant's performance, though all the correlation coefficients are not significant for the sample number is too small (*n* = 3).

Biomass allocation index can reflect the limit of substrate nutrient (Wang and Yu, 2007). The maximum of root mass to total mass (R/M) and root mass to shoot mass (R/S) appear in PS, which adapts the nutrient condition of the lowest available K (Table 1). This plastic biomass allocation demonstrates the preferentiality of the plant to favourable nutrient-rich microhabitat.

4.2 Iron distribution and transfer in plant modules

Our results show that the total Fe distribution in nine modules in four wetland microhabitats shares the same configuration. However, some modules (i.e. tillering nodes and roots) have significant inter-microhabitat differences (Fig. 2). The tillering nodes that connect underground parts and aboveground ones may serve as the sieve or choke point that inhibits the upper iron transfer from roots (Wang, 1995), thus defending the plants from iron toxicity. The activity of roots is demonstrated to be the main factor contributing to the rapid iron cycling in wetlands (Weiss *et al.*, 2004). As the inner iron pool, roots play an important role in the plant physiology. Iron is released from roots when the plant is lack of iron, but is excluded from roots when iron is exceeding (Gurzau *et al.*, 2003).

In this paper the roots are sorted into three groups for special concern. The total Fe orders are LR > DR > PR, DR > LR > PR, DR > PR > LR, DR > PR > LR for PW, PSed, SSed, PS, respectively (Fig. 2). The order in PW, different from the others completely, may attribute to the water substrate for its low available Fe, and the LR with the highest total Fe may indicate that the continued production of young roots is the main channel to take up dissolved iron when the background is negligible. DR with the largest total Fe in SSed, PSed and PS may serve as the iron excretion parts, and PR may serve as the inner iron sink for the iron reuse (Weiss *et al.*, 2003).

4.3 Microhabitat effect on iron distribution and transfer in *C. pseudocuraica*

Iron is vital to wetland plants for its nutritional function and toxic effect, while the distribution and transfer of iron in plants are affected by the plants′ performance. Our results suggest that the total Fe in PW is the lowest, while the biomass and iron mass in PW is the greatest and the second greatest respectively, which indicates that the phyto-accumulation of iron is decided mainly by the biomass other than the total Fe of plant, through which the microhabitat effect is embodied.

Besides, the total Fe of the plant is not directly proportional to the total Fe in the substrates (Table 1). The transfer coefficients (i.e. the ratio of the total Fe in plant to substrate) are 2 642.82, 7.96, 8.40 and 19.72 for the four microhabitats respectively (Zou *et al.*, 2009), which shows that iron transfer is mainly controlled by the microhabitat with different substrate types, with the greater coefficient in water and the lower one in sediment.

Furthermore, based on the correlation analysis, it is found that the total Fe of the plant is positive to available K, available N, organic C, available Fe and the total Fe in the substrate (R = 0.051, 0.150, 0.206, 0.044, 0.414; P = 0.968, 0.904, 0.868, 0.972, 0.729, respectively), while negative correlated to available P and pH (R = –0.993, –0.908; P = 0.074, 0.275, respectively). The available P and pH in the substrate may limit the iron transfer other than iron content, though the correlation coefficients are not significant in this study resulting from the sample number is too small (n = 3).

5 Conclusions

Wetland habitat is characterized by its extensive heterogeneity. With the in-situ sampling methods, the iron distribution and transfer in *C. pseudocuraica* in four microhabitats were observed. The best performance appears in perennial flooded ditch water, while the lowest in perennial flooded soil. Substrate type and iron content are the main factors deciding the performance of the plants. Furthermore, the available K and Fe in substrates might be the limiting factors influencing the plant′s performance.

All the total Fe distribution in the plant modules appear as pyramids from the tip to the root. Roots are the main pools of iron, which occupy approximately 60% of the total iron mass for all the microhabitats, and marked difference is observed in the distribution proportion of stems, tillering nodes and roots that are allometrically growing. The phyto-accumulation of iron is decided mainly by the biomass other than the total Fe of the plant. Iron transfer from substrates to plants is mainly controlled by the substrate type, with the greater transfer coefficient in water and the lower one in sediment. The available P and pH in the substrates may limit the iron transfer other than iron contents. The microhabitat effect plays a great role of within-species variation in the ability to tolerate abiotic stress and the plant′s intelligence in foraging and persisting in the changeful wetland habitats.

In this study, it is concluded that the different iron distribution and transfer in the plant in different microhabitats are attributed to the iron content in the substrates as well as the phenotypic plasticity of *C. pseudocuraica*. Considering the phytophysiology of the plant is not deeply studied, the inner mechanisms resulting in this microhabitat effect remain unclear, and further controlled experiments are needed to reveal the key processes of iron transfer from substrates to plants at greater confidence level.

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