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A PRELIMINARY EXPLORATION: WHY *MYRICARIA LAXIFLORA* SO IMMERSION-RESISTANT AND SO SOIL-SELECTIVE?

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Abstract

Myricaria laxiflora is a shrub and also an endemic, rare and endangered plant species in Three Gorges Reservoir Area. It is of highly immersion resistant and soil selective. In this paper, the probable immersion-resistant structures of stem were identified, and the relationships between components of its inhabiting soil and the structures of stem were explored. Results showed that the parenchyma cells in cortical and pith could produce lysigenous intercellular lacuna acting as aerenchyma. The compact periderm, as well as loose-arrayed and star-shaped xylem parenchyma cells might be two fortifications of the stem to isolate water from inner tissues. We estimated that the vessel cavitation conducive to oxygen-store might likely be arisen.

Our result indicated that the plant stem structures greatly depended on the soil particle fractions, especially the fractions of coarse sand and above. The fractions of residual parent rock and fine gravel of soil predominated structures of stem which could act as barriers of radial oxygen loss when plant immersed in flood. This suggested that the sand-gravel soil might play an important role in determining whether survival or not of *M. laxiflora* when immersed.

Of all 7 studied mineral elements i.e. N, P, K, Ca, Mg, Mn, Zn, P and K contents of soil were positively predominant factors of vessel, especially vessel diameter which directly related to the likelihood of vessel cavitation and the capacity of water transportation. This also indicated that they played an important role in determining immersion resistance and the post immersion growth of the species. Therefore, for *M. laxiflora*, the traits of immersion-resistance and soil-selection were closely interrelated. The immersion-resistance ability of *M. laxiflora* would be stronger when soil has larger fractions of coarse sand and gravels.

Introduction

Myricaria laxiflora (Tamaricaceae), a shrub with a height about 1.5m , is an endemic, rare plant species that narrowly and inconsecutively established in the medial or lower sites of the water-level fluctuation zone of the Yangtze River valley, from Banan district of the Chongqing City to Yichang of Hubei province, China. It only grows in sand-gravel soil patches and has a long inflorescence from September to November and could produce small, light and large quantity of seeds, each of which with an aristiform pole covered with hair on the top. The flood season of the Yangtze River is usually from later March to September. Therefore, the species generally suffers from inundation for 4~6 months every year. When flood befell, the plant was always entire submerged. However, when flood receded, a part of bald branches protruded out of water, and the sprouts in the bald branches burst forth within 2-3 days and rapidly resumed growth (unpublished observations). So, it could be seen that the withering-like branches virtually possessed strong vitality, although they had undergone long time immersion. Hence its immersion-resistant characters and its potential utility of bank revetment had caught great concerns of botanical scientific workers. Unfortunately, Three-Gorge Dam’s enclosure had resulted in complete submergence of whole natural populations of the species and its habitats. This, early before, had evoked great concern within China Society of Plant Protection, and attracted enthusiastic attention among the public and government agencies for rescuing this species.

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Plant response to flooding or soil waterlogging had been studied for many years. A major constraint resulted from excess immersion was an inadequate supply of oxygen to submerged tissues. In addition to this, excess immersion also led to other changes in the soil that influence plants (Jackson & Colmer, 2005). Mechanisms that underlie short and long-term tolerance of plants to flood had been attributed to many factors. These included physiological responses, morphological adaptations and anatomical changes (Vartapetian and Jackson, 1997). Many reports, since commence of 21st century, addressed and emphasized molecular, biochemical and developmental processes that impacted on flooding tolerance of plants, such as sensing and transduction of signals of low oxygen supply (Bailey-Serres & Chang, 2005; Igamberdiev *et al*., 2005), molecule-mediated stimulation of morphological changes under water (Pierik *et al*., 2005; Finlayson, 2005), aerenchyma development and structural variations related to underwater photosynthesis (Seago *et al*., 2005; Mommer and Visser, 2005), and gene expression and regulation that characterized oxygen-deficient cells (Branco-Price *et al*., 2005; Gonzali *et al*., 2005; Harada *et al*., 2005). Up to date, these corresponding researches were based on plants inhabiting marine, aquatic, salt marsh, wetland and terrestrial ecosystems subjected to seasonal episodes of water-logging or submergence (including crop species and agricultural systems) or on model plant species such as amphibious plants *Rumex palustris*.

Almost all of these studied plants were herbaceous. However, to resolve a long-standing question in flood-resistance of woody species remained a future goal (Jackson & Colmer, 2005). In addition, no matter the preciously studied plants were herbaceous or woody, they were in following alternative conditions: (1) their roots were in waterlogged/ submerged soil, but their stems were above water surface, (2) they were aquatic submerged plants. Therefore, these plants still have capacity of photosynthesis in the adverse condition.

The habitat that *M. laxiflora* lives is very distinct. The period of its vegetative growth just overlaps with dry season of the Yangtze River, and thereby the sand-gravel soil that with poor water-holding capacity often suffers from drought. However, when flood befall, the whole-plant body is generally immersed for several months in turbidity current, thus photosynthesis would be completely impossible. So, as such an amphibious woody plant, it might be certain that this species possessed particular submergence- resistant mechanisms comparing with the above plants. Otherwise, it would not be able to survive such a long time of immersion. There should be no doubt that, relative to existent studies on flood resistance of woody plants, *M. laxiflora*, as a new material, would be sure to inaugurate a novel scope in the corresponding discipline.

Trescevskij (1966) reported that the tolerance limits of many species directly relate to the soil type (Wallace *et al*., 1996; Majid *et al*., 2007). The very fact that *M. laxiflora*'s only selecting sand-gravel soil to establish had betrayed a certain connections between immersion-resistance traits and its standing soil. However, the reasons for such a life feature remain unknown up to date. What had in our mind at first is that, was there any special anatomical structure in the vegetative organs of *M. laxiflora* to resist flood injuries? Did the sand-gravel soil have anything to do with the flood-resistant anatomical structures, if it did, how? In this paper our objectives were: 1) to identify probably anatomical features of stem that promote underwater survival, 2) to explore the relationships of functional coordination between soil components and anatomical structures of stem in order to provide an orientational guidance for the experimental designs of far-reaching studies on flood resistance of this species.

Materials and Methods

Sampling and disposal of plant material: Sampling was conducted in 10 populations from Banan, Chongqing City to Zigui, Hubei province from October to December, 2002. In each population, 15 mature individuals with age 3-5 years were sampled. The interval distance between individuals was more than 20m. A piece of branch (5-7mm length) with florid cuticle, robust growth, and diameter 3-5mm was cut down and plunged into FAA fixation fluid immediately. In September, 2003, the cross sections of stems with thickness of 25µm were prepared using xylotomic microtomy. The 11 measured parameters from each cross section were listed in Table 1. The average value from the 15 individuals for parameters was regarded as the phenotypic characters of corresponding population.

Sampling of soil material: According to the depth of root extent, 5 soil profiles were openned close to 5 plants in each population. Soil samples of 5cm, 15cm, 25cm on each profile were collected and mixed, and brought them to lab for the measuring of particle fractions and element contents i.e. N, P, K, Ca, Mg, Mn, Zn of each population. Using mean value of 5 profiles as the soil characters of corresponding population, soil predominant factors were analyzed.

Analysis of soil material: K_2SO_4-$CuSO_4$-Se digestion and TN-110 were used for measuring N contents of soil, $HClO_4$-H_2SO_4 digestion and Mo-Sb-Vc colorimetry for measuring P, Na_2CO_3 alkali dissolution, flame spectrometry for measuring K, Na_2CO_3 alkali dissolution, atomic absorption spectrometry for measuring other elements.

Data disposal: The predominant factors of soil fractions and soil nutrition contents over anatomic parameters of stem were defined using stepwise regression. In this process, the P-value level of F-statistic was set in 0.15-0.5 (Fang *et al*., 2000). Before statistic analysis, the statistical transformations (arcsine square root) were applied to the frontal 5 parameters in Table 1. All work was done in SPSS software.

Results

Secondary structure straits of stem: Fig. 1 indicated that stem of *M. laxiflora* consisted of the following layers: periderm comprising 10-12 layers of cells, which were rectangular in across-section and arranged compactly. Under the periderm there were 3-4 layers of prothenchyma cells, each of which with similar form and less or equal size to the periderm cells. Lenticels were often observed in the periderm (Fig. 2), and the parenchyma cells in cortex below the lenticels formed cavities by cell autolysis. The parenchyma cells between xylem rays were star-like or multiangular and loosely arranged with obviously intercellular spaces (Fig. 4). The vessel diameter differed with each other and larger vessel located in inner part of a growth ring (Fig. 1, D1, D2, H). The stem had larger pith and the pith diameter occupied about 30% of the stem. Similar with the parenchyma cells below lenticels, the parenchyma cells within the pith also formed cavities by cell autolysis (Fig. 3).

Table 1. The studied parameters in this paper.

Periderm thickness /stem diameter
Collenchyma cell layer thickness / stem diameter
Cambium width / stem diameter
Diameter of pith /stem diameter
Thickness of cortical layer / stem diameter
Diameter of phloem fiber cell
Diameter of vessel lumen
Frequency of multiseriate ray
Vessel frequency
Width of multiseriate ray
Ray length

Predominant factors of soil particle fraction: In Table 2, the predominant factors of soil particle fractions over structures of stem were presented. Eight to total eleven structural characters were affected by soil particle fractions. The fraction of d10 (rudimental parent rock) was the predominant factor that affected periderm thickness, collenchyma cell layer thickness, thickness of cortical layer and ray length. It had significant positive correlation with periderm thickness and cortical layer thickness. Moreover, it had positive correlation with collenchyma cell layer thickness, significant negative correlation with ray length. The fraction of d2 (fine gravel) affected periderm thickness and diameter of pith and had significant positive correlation with diameter of pith. The fraction of d425 (coarse sand) mainly influenced frequency of multiseriate ray and width of multiseriate ray, and had positive correlation with frequency and negative correlation with width, but the relativities were not significant. The fraction of dx250 (fine sand and the minor diameter particles than fine sand) mainly affected diameter of vessel lumen and thickness of cortical layer. Some characters such as cambium width, vessel frequency, and diameter of phloem fiber cell were not affected by soil granulation under the *P*-level.

Predominant fractions of soil nutrition: Table 3 indicated that among N, P and K, element K predominated the majority of structural characters (9 characters), followed by P (6 characters). Nitrogen only affected 2 i.e. width of multiseriate ray and vessel frequency. Mg affected width of multiseriate ray and diameter of phloem fiber cell. Ca affected cortical layer thickness and vessel frequency. Mn and Zn of trace elements mainly affected width and frequency of ray. According to standard partial regression coefficients, P played an important role in predominating periderm thickness/stem diameter, diameter of vessel lumen, and thickness of cortical layer/stem diameter. Similar to this, K is important than Mg in affecting diameter of phloem fiber cell and P. N was more important than K in affecting width of multiseriate ray. P played a more important role than Zn in predominating frequency of multiseriate ray.

le 2. Predominant factors of soil particle fractions and their correlation coefficients with corresponding structural parameters.

tural parameter	Predominant factor	Correlation coefficient	Multiple correlation coefficient R^2	Partial regression coefficient
erm thickness/ stem diameter	d10	0.80**	0.63	0.00
	d2	-0.48	0.76	-0.00
nchyma cell layer thickness /stem diameter	d10	0.53	0.28	0.00
eter of pith /stem diameter	d2	0.85**	0.72	0.00
n of multiseriate ray	d425	-0.62	0.38	-0.02
ency of multiseriate ray	d425	0.56	0.32	0.03
eter of vessel lumen	dx250	0.58	0.33	0.00
ness of cortical layer /stem diameter	dx250	-0.07	0.43	-0.00
	d10	0.63*	0.63	0.00
ength	d10	-0.79**	0.62	-0.00

nd d2 stand for soil particle fractions of those diameter more than 10mm and 2mm respectively. d425 stand for diameter more than 425μm. stand for diameter less than or equal to 250μm. *sig. <0.05, ** sig.<0.01.

Table 3. Predominant factors of soil nutrition and their correlation coefficients with stem structural parameters.

Structural parameters	predominant factors	Multiple correlation coefficients R^2	Standard partial regression coefficients	Correlation coefficients
Periderm thickness /stem diameter	K	0.40	0.05	0.63*
	Mn	0.63	0.00	0.20
	P	0.86	-0.34	-0.41
Diameter of phloem fiber cell	Mg	0.31	0.00	0.55
	K	0.60	1.80	0.41
Diameter of pith /stem diameter	K	0.62	0.33	0.79**
Cambium width /stem diameter	K	0.32	0.00	0.57
Width of multiseriate ray	Mn	0.35	0.00	0.60
	P	0.77	-30.17	-0.44
	N	0.92	6.66	0.11
	Mg	0.96	0.00	0.40
	K	0.98	-0.58	-0.28
Frequency of multiseriate ray	Zn	0.28	-0.01	-0.53
	P	0.51	25.75	0.39
Vessel frequency	Mn	0.64	0.02	0.80**
	K	0.84	-21.50	-0.72*
	Ca	0.89	-0.00	-0.14
	N	0.94	-47.47	-0.22
	P	0.97	92.16	0.33
Diameter of vessel lumen	P	0.34	25.43	0.59
	K	0.57	-2.04	-0.55
Thickness of cortical layer /stem diameter	Ca	0.35	-0.00	-0.59
	P	0.74	-1.57	-0.56
	K	0.82	0.07	0.56
Ray length	K	0.67	-0.51	-0.82**

Explanations of plates:

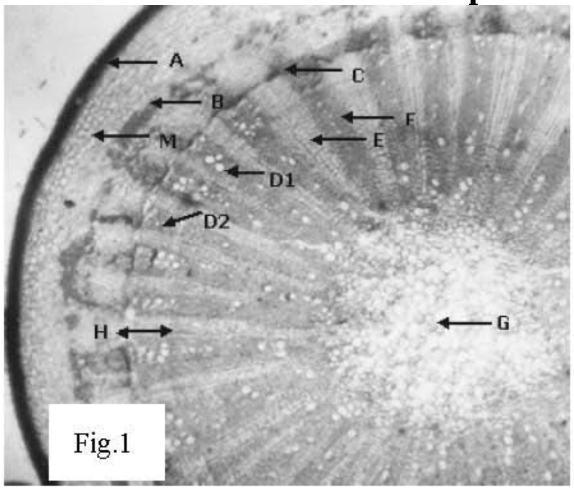

Fig.1

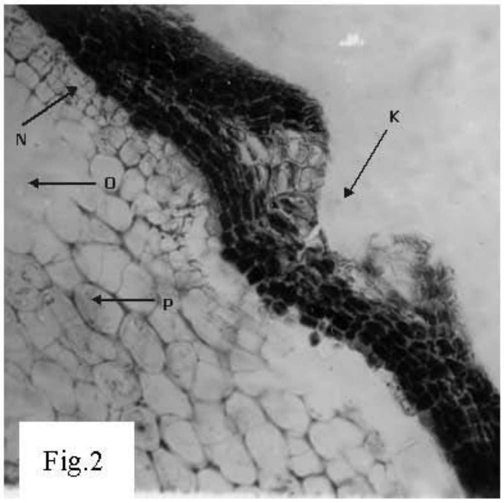

Fig.2

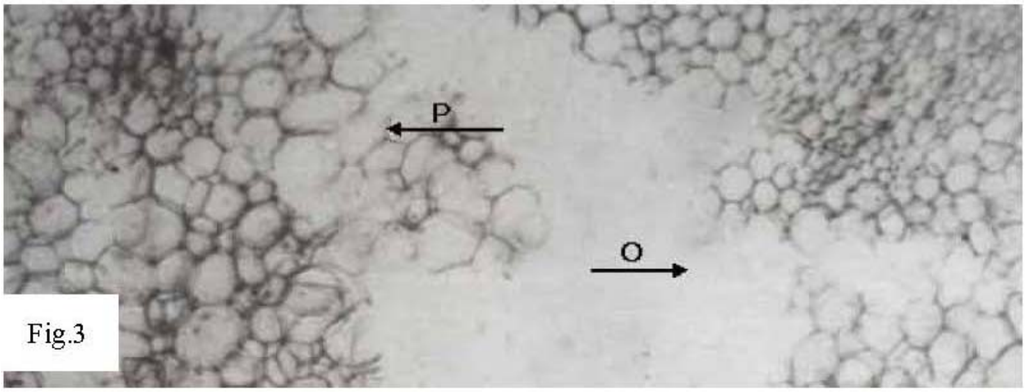

Fig.3

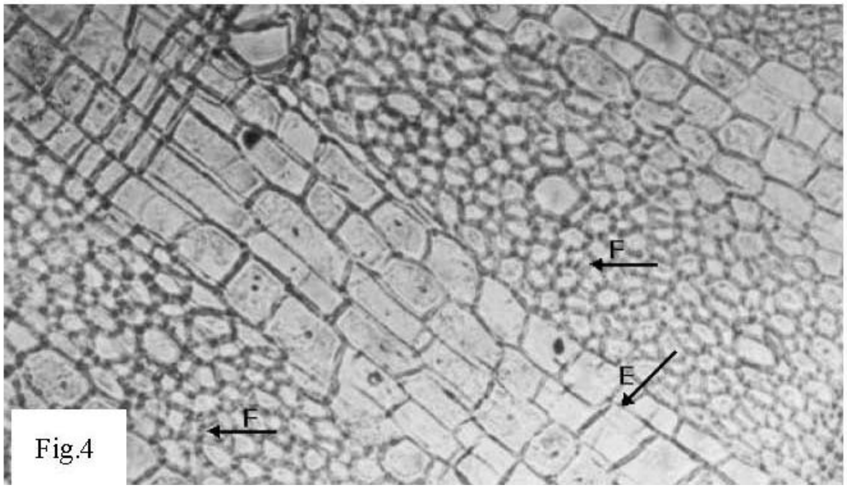

Fig.4

Fig. 1: Secondary structure of stem, ×20; Fig. 2: Stomata on the periderm and the autolysis phenomenon of the parenchymatic cells under it, × 125; Fig. 3: Autolysis phenomenon of pith cells, ×125; Fig. 4: Polygonal or stellate parenchymatic cells of stem between xylem rays and the obvious interstitial spaces, ×125; A, Periderm; B, Phloem fiber; C, Cambium; D1, Larger vessels located in inner part of a growth ring; D2, Smaller vessels located in outer part of a growth ring; E, Xylem ray; F, Parenchymatic cells betweem xylem rays; G, The expanding cells of pith cavity; H, A growth ring; K, Stomata; M, Parenchymatic cells of cuticular layer; N, Collenchyma cells under the periderm; O, The autolysis lacuna; P, Enlarged parenchyma cells.

Discussion

Immersion-resistant structures of stem: Though *M. laxiflora* is annually immersed in flood for 4-6 months, its stem, on the whole, shared general structure characters with other wooden species, without special aerating tissues or structures involved in hydrophytes or helophytes (Fig. 1). Nunez-elisea *et al*., (1999) conducted a series of experiments in four wooden species of the genus *Annona*. Results showed that flooded trees developed hypertrophied stem lenticels and did not increase air spaces in pre-existing xylem near the pith or in xylem tissue that was formed during flooding. Thus, flood tolerance did not involve aerenchyma formation in the xylem part of stem. This was similar to our results.

In the stem of *M. laxiflora,* lysigenously intercellular lacuna acting as aerating tissue could be seen in parenchyma cell area of cortex under stem lenticels (Fig. 3) and of pith (Fig. 4). These apparently should be one of submerging-resistant structure traits (Kozela & Regan, 2003).

Nowadays, it is generally agreed that plant xylem is subject to embolism very frequently, due to cavitations of xylem conduits (Milburn, 1979; Tyree & Sperry, 1989): the sudden change from liquid to vapor or gas phase within normally water-filled xylem conduits. Xylem cavitations could be triggered by tiny bubbles sucked into functioning conduits from neighboring air-filled wood compartments at critical xylem pressures. That means a cavitated vessel contains either water vapour or air. The cavitated vessel was generally regarded as the primary effect of environmental stresses (Pockman & Sperry, 2000; Davis *et al*., 2002; Tyree & Cochard, 1996; Nardini *et al*., 2000). As a rule, gas embolisms blocking the conduits and causing xylem dysfunction went against plant survival with reduction of water transport. The other way around, they would conduce to the survival of plants like *M. laxiflora*, which undergo long time of complete submergence in inundation, because gas in cavitations could be released necessarily for dealing with the absence of oxygen under deep water. In addition, distribution trait of vessel in stem indicated that timber of *M. laxiflora* should be attributed to ring-porous wood (Fig. 1; Esau, 1953), which was a kind of high specialized appearance and could only be found in a few species almost all of which being in north temperate zone (Esau, 1953), while *M. laxiflora* was just a typical plant of alpine genus in the Eurasian temperate zone. Huber (1938) reported that the high specialized vessels always had ephemeral water-transport function because of tylosis-compartmentalized and than gas-filled lacuna. In a word, for *M. laxiflora*, it was great likely that vessel lacuna might have been transferred to gas cavitations when flood forthcoming or submergence being suffered. Certainly, this needed further experimental verification.

In stem of *M. laxiflora*, the xylem parenchyma cells between xylem rays were stellate or multingular and loosely arrayed with obvious intercellular spaces (Fig. 4). Among which, vessels were arrayed (Fig. 1). When plant was immersed, in case of water having penetrated through the cortex under high water-pressure, these star-shaped and loosely arrayed cells (even if in the surface layer) could create menisci air-water interfaces to oppose the hydrostatic pressure by surface tension of the menisci interface, thereby to prevent water continuatively going ahead into living tissues and air cavities e.g. vessel lacuna and pith cavity (Armstrong, 1979). Thus gases in cavities or conduits would not be excluded and thus the living tissues would be protected. Whether the menisci air-water interfaces would be broken was determined by the pressure derived from the depth in flood.

So, this simple protective mechanism might be closely related to the under water depths where plants stood (Sorrell & Dromgoole, 1996). In fact, the thick and firm periderm and the prothenchyma layers below it (Fig. 2), as integuments of the stem, could separate water from parenchyma cells in cortex to a great extent, thereby avoiding damage of plant in deep water. The above descriptions strongly suggested that, two fortifications to isolate water have been constructed in stem of *M. laxiflora*.

Soil components matching with submerge-resistant structure: Different soil particle fractions could directly induce functional variance of soil, such as water-holding capacity, thermal property and aeration. Soil-plant-atmosphere is an integrate continuum (Willians *et al*., 2001; Arshad *et al*., 2008). Many researches had indicated that plants have capacities of short-time regulation and long-time acclimation to coordinate the functional relations between soil and themselves. The former was *via* physiological regulation and the later was through morphologies and structures (Sperry, 2000; Meinzer, 2002; Mencuccini, 2003). Membrives *et al*., (2003) reported that leaf anatomical structures of *Androcymbium* only had significant correlation with contents of clay and sand of soil. The water-holding capacity of soil decided by particle fractions was consistent with the function of leaf transpiration or hydraulic system. The plant hydraulic system had responded to variations in soil texture or evaporative demand through long-term acclimation.

As the bridge between root and leave, the stem of *M. laxiflora* need harmonize their functions in two facets with that of soil by structures. The first is to match with the aeration function of soil to prevent from the oxygen radial loss when immersed in flood. The second is to coordinate the water-holding function of soil to complete the transportation of water and mineral elements. Of which, the first one should be in a dominant position. Otherwise, it would not survive under water. Studies had revealed that a proportionally large cortical layer, thick-walled fiber layer, collenchyma cell layer, and periderm layer could act as barriers of radial oxygen loss (ROL) in stem under immersion condition and enhance oxygen transportation (Colmer, 2003; Clark & Harris, 1981; Armstrong & Armstrong, 1991). In Table 2, the fraction of d10 had extremely significant correlation with periderm thickness and significant positive correlation with cortical layer thickness. Moreover, it had positive correlation with collenchyma cell layer thickness. The fraction of d2 had significant positive correlation with diameter of pith. Actually, d10 was the content of residual parent rock in soil, and d2 was the content of fine gravel in soil. Both of them could determine soil aeration. All of the factors such as periderm thickness, cortical layer thickness, collenchyma cell layer thickness and diameter of pith are directly relate to reducing radial oxygen loss, storing and transporting oxygen when whole plant body submerged in flood (Stevens et al., 2002). So, on the part of aeration function, the plant and its standing soil was highly consistent each other. In other words, so far as soil particle fractions being concerned, the sand-gravel soil in Three-Gorge valley of the Yangtze River might have played an important role in determining whether survival or not for *M. laxiflora* under immersion condition. In addition, dx250 fraction had positive correlation with diameter of vessel lumen and negative correlation with thickness of cortical layer. As just account for that water transportation function of stem was consistent with water holding function of soil. In all 8 structural parameters affected by soil particle fraction, d10 (residual parent rock), d2 (fine gravel), and d425 (coarse sand) predominated 7 parameters. This fact implied that in the process of long-term evolution, *M. laxiflora* has adapted the barren sand-gravel soil in valley of the Yangtze River caused by frequent flood and surface runoff.

Except for collenchyma layer, all structures were restricted by studied nutrition elements of soil. K almost affected all structures, and therefore was important for keeping character stability. We know, by comparing of standard partial regression coefficients, K mainly affected diameter of vessel lumen (negative) and diameter of phloem fiber cell (positive). Phloem fiber's increase conduced to enhancing the flexibility of stem, thereby to resisting the scour of flood. In Table 3, all shared structures restricted by K and P, the action of P was always more important than that of K. Basing on which, we concluded that, similar to element K, P was also an important element to the species. What we should emphasize was that P content of soil was positively correlated with diameter of vessel lumen (R^2=0.343, *P*=0.072) and frequency of vessel (R^2=0.971, *P*=0.104). This result corresponded with previous conclusions on mangroves (Cheeseman & Lovelock, 2004; Lovelock *et al*., 2006; Lovelock *et al*., 2004; Carvajal, 1996). Previous study indicated that addition of phosphorus (P) to dwarf mangroves could stimulate increment in diameter of xylem vessel lumen and area of conductive xylem tissue. And these changes in structure were consistent with related changes in function, because addition of P also increased hydraulic conductivity (Lovelock *et al*., 2006). Mangroves and *M. laxiflora* were analogous to be flood-resistant species, but they were in different water environment. For example, mangroves grows in salt water and waterlogged soil, while *M. laxiflora* lives in fresh water and completely submerged for 3-5 months in a year, and then grows on dry land after flood receding. So, the functions of vessel structure changes might differ with each other. For mangroves, the vessel diameter increment might cause hydraulic conductivity increment, which was conductive to water and mineral substance absorption in high concentration of salt water. However, for *M. laxiflora*, to store more gas in increased vessel, when submerged in flood, might be a vital function.

Cavitation's taking place depends, in part, on conduit size (Vasellati *et al*., 2001; Atkinson & Taylor, 1996). Conduits with larger diameters are more prone to cavitation than those with smaller diameters (Zimmerman, 1983; Carlquist, 1988). Thus, a xylem with narrow vessels was physiologically better protected against cavitation. Studies showed that there were interspecfic differences in vessel diameter, which suggested its adaptive value. Generally, woody species from drier habitats had narrower vessels than species from more humid habitats (Rury & Dickinson, 1984). Therefore, we could speculate that in early time of vegetative growth (later autumn and winter), *M. laxiflora* would produce narrow vessel to promote water absorption and transportation, while in the later time of vegetative growth, (later spring before flood forthcoming) larger vessel would facilitate cavitation in order to keep underwater survival. This process should be related to P and K contents of the sand-gravel soil. In the sense of this, P and K contents of soil should be an important factor for *M. laxiflora* to resist long-time flood immersion. This certainly still needed more experimental evidences.

Conclusions

So far as structures are being concerned, the stem of *M. laxiflora* might have used the following three features to resist flood submergence. The first, two fortifications were constructed to isolate water from inner tissues, i.e. the compact periderm and the loose-arrayed and star-shaped xylem parenchyma cells, which could counteract external water pressure through air-water interfaces. The second, parenchyma cells in cortical and pith could produce lysigenous intercellular lacuna that acted as aerenchyma when stem was immersed in water. The third, vessel cavitation would be a frequent event for the stem of *M. laxiflora*, which could be induced by flood stress or arisen from intrinsic character of the specialized vessel of the species. It is necessary to design more experiments combining physiology with anatomy to study or confirm the above phenomenon.

For soil particle fractions, the particle contents of those above coarse sand (including coarse sand) of soil predominated the majority of stem structures. Especially, the fractions of residual parent rock and fine gravel of soil predominated the structures of stem which could act as barriers of radial oxygen loss when plant immersed in flood. This, to a great extent, confirmed the very fact of *M. laxiflora*'s soil option. As far as the connections between soil particle fractions and the survival submergence, further research is needed. The structural and soil parameters in Table 2 and their hiding functions might have betrayed some cues for future researches.

If vessel cavitation in submerging or at later period of vegetative growth had been proved, K and P contents of soil might play an important role in determining immersion-resistance of the species, because they pre-dominated vessel frequency, especially diameter of vessel lumen (Table 2), which directly relate to the likelihood of vessel cavitation. Whether vessel cavitation has a threshold value of its diameter, how large is it? At what levels of K and P contents, cavitation would be promoted, and what mechanism underlay? All the above questions should be solved in future study.

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References

Armstrong, J. and W. Armstrong. 1991. A convective through-flow of gases in *Phragmites australis* (Cav.) Trin. Ex Steud. *Aquatic Botany*, 39:75-88.

Armstrong, W. 1979. Aeration in higher plants. *Advances in Botanical Research*, (7):225-332.

Arshad, M., A.U. Hussan, M. Y. Ashraf, S. Noureen and M. Moazzam. 2008. Edaphic factors and distribution of vegetation in the Cholistan Desert, *Pakistan. Pakistan Journal of Botany*, 40(5): 1923-1931.

Atkinson, C.J. and J.M..Taylor. 1996. Effects of elevated CO2 on stem growth, vessel area and hydraulic conductivity of oak and cherry seedlings. *New Phytologist*, 133: 617-626.

Bailey-serres, J. and R.Chang. 2005. Sensing and signalling in response to oxygen deprivation in plants and other organisms. *Annals of Botany*, 96: 507-518.

Branco-Price, C., R. Kawaguchi, R.B. Ferreira, J. Bailey-Serres. 2005. Genome-wide analysis of transcript abundance and translation in Arabidopsis seedlings subjected to oxygen deprivation. *Annals of Botany*, 96: 647-660.

Carlquist, S. 1988. Comparative wood anatomy. Berlin: Springer-Verlag.

Carvajal, M., D.T. Cooke, D.T. Clarkson. 1996. Responses of wheat plants to nutrient deprivation may involve the regulation of water-channel function. *Planta*, 199: 372-381.

Cheeseman, J.M. and C.E. Lovelock. 2004. Photosynthetic characteristics of dwarf and fringe *Rhizophora mangle* L. in a Belizean mangrove. *Plant Cell & Environment*, 27: 768-780.

Clark, L.H. and W.H.Harris. 1981. Observations on the root anatomy of rice (*Oryza sativa* L.). *American Journal of Botany*, 68:154-161.

Colmer, T.D. 2003. Long-distance transport of gases in plants: a perspective on internal aeration and radial oxygen loss from roots. *Plant, Cell and Environment*, 26:17-36.

Davis, S.D., F.W. Ewers, J.S. Sperry, K.A. Portwood, M.C. Crocker & G.C. Adams. 2002. Shoot dieback during prolonged drought in Ceanothus (Rhamnaceae) chaparral of California: a possible case of hydraulic failure. *American Journal of Botany*, 89: 820-828.

Esau, K. 1953. Plant Anatomy. John Wiley & Sons, Inc.

Fang, J.Y., S.L. Fei, Y.J. Fan, K.M. Cui. 2000. Ecological Pattern in Anatomic Characters of Leaves and Woods of *Fagus lucida* and their climatic control in Mountain Fanjingshan, Guizhou, China. *Acta Botanica Sinica*, 42(6):636-642.

Finlayson, C.M. 2005. Plant ecology of Australia's tropical floodplain wetlands: a review. *Annals of Botany*, 96: 541-555.

Gonzali, S., E. Loreti, G. Novi, A. Poggi, A. Alpi, P. Perata. 2005. The use of microarrays to study the anaerobic response in Arabidopsis. *Annals of Botany*, 96: 661-668.

Harada, T., S. Satoh, T.Yoshioka, K. Ishizawa. 2005. Expression of sucrose synthase genes involved in enhanced elongation of pondweed (*Potamogeton distinctus*) turions under anoxia. *Annals of Botany*, 96: 683-692.

Huber, B. and E. Rouschal.1938. Anatomische und zellphysiologische Beobachtungen am Siebrohr--ensystem der Baume. *Ber. Deut. Bot. Ges.*, 56:380-391.

Igamberdiev, A.U., K. Baron, N. Manach-Little, M. Stoimenova and R.D.Hill. 2005. The haemoglobin nitric oxide cycle: involvement in flooding stress and effects on hormone signalling. *Annals of Botany*, 96: 557-564.

Jackson, M. B. and T. D.Colmer. 2005. Response and Adaptation by Plants to Flooding Stress. *Annals of Botany*, 96: 501-505.

Kozela, C., and S. Regan. 2003. How plants make tubes. *Trends in Plant Science*, 8:159-164.

Lovelock, C.E., I.C. Feller, M.C. Ball, B.M.J. Engelbrecht and M.L. Ewe. 2006. Differences in plant function in phosphorus and nitrogen limited mangrove ecosystems. *New Phytologist*, 172 : 514-522.

Lovelock, C.E., I.C. Feller, K.L. Mckee, B.M.J. Engelbrecht, M.C. Ball. 2004. The effect of nutrient enrichment on growth, photosynthesis and hydraulic conductance of dwarf mangroves in Panama. *Functional Ecology*, 18: 25-33.

Lovelock, C.E., M.C. Ball, B.Choat, B.M.J Engelbrecht, N.M.Holbrook, I.C.Feller. 2006. Linking physiological processes with mangrove forest structure: phosphorus deficiency limits canopy development, hydraulic conductivity and photosynthetic carbon gain in dwarf *Rhizophora mangle*. *Plant, Cell & Environment*, 29: 793-802.

Majid, S.A., R. Asghar and G. Murtaza. 2007. Potassium-Calcium interrelationship linked to drought tolerance in wheat (*Triticum Aestivum* L.). *Pakistan Journal of Botany*, 39(5): 1609-1621.

Meinzer, F.C. 2002. Co-ordination of vapor and liquid phase water transport properties in plants. *Plant Cell and Environment*, 25:265-274.

Membrives, N., J. Pedrola-Monfort and J.Caujape-Castells. 2003. Correlations between morphological anatomical leaf characteristics and environmental traits in southwest African species of Androcymbium (Colchicaceae). *Bot. Macaronésica*, 24: 73-85.

Mencuccini, M. 2003. The ecological significance of long-distance water transport: short term regulation long-term acclimation and hydraulic costs of stature across plant life forms. *Plant Cell and Environment*, 26:163-182.

Milburn, J.A. 1979.. Longman, London, UK.

Mommer, L. and E.J.W.Visser. 2005. Underwater photosynthesis in flooded terrestrial plants: a matter of leaf plasticity. *Annals of Botany*, 96: 581-589.

Nardini, A., S. Salleo, M.A.L. Gullo and F. Pitt. 2000. Different responses to drought and freeze stress of *Quercus ilex* L. growing along a latitudinal gradient. *Plant Ecology*, 148:139-147.

Nunez-elisea, R., B. Schaffer, J.B. Fisher, A.M. Colls and J.H. Crane. 1999. Influence of flooding on net CO_2 assimilation, growth and stem anatomy of Annona species. *Annals of Botany*, 84: 771-780.

Wallace P.M., D.M. Kent and D.R. Rich. 1996. Responses of wetland tree species to hydrology and soils. *Restoration Ecology*, 4: 33-41.

Pierik, R., F.F. Millenaar, A.J.M. Peeters, L.A.C.J.Voesenek. 2005. New perspectives in flooding research: the use of shade avoidance and *Arabidopsis thaliana*. *Annals of Botany*, 96: 533-540.

Pockman, W.T. and J.S. Sperry. 2000. Vulnerability to cavitation and the distribution of Sonoran desert vegetation. *American Journal of Botany*, 87:1287-1299.

Rury, P. and W. Dickinson. 1984. Structural correlations among woody leaves and plant habit. In:

White RA, Dickinson W, eds. Contemporary problems in plant anatomy. Orlando, Florida: Academic Press, Inc.

Seago, J.L., L.C. Marsh, K.J. Stevens, A. Soukup, O.Vortubová. 2005. A re-examination of the root cortex in wetland flowering plants with respect to aerenchyma. *Annals of Botany*, 96: 565–579.

Sorrell, B.K. and F.I. Dromgoole. 1996. Mechanical properties of the lacunar gas in *Egeria densa* Planch. shoots. Aquat. Bot, 53:47-60.

Sperry, J.S. 2000. Hydraulic constraints on plant gas exchange. *Agricultural and Forest Meteorology*, 104:13-23.

Stevens, K.J., R.L. Peterson and R.J. Reader. 2002. The aerenchymatous phellem of *Lythrum salicaria* (L.): a pathway for gas transport and its role in flood tolerance. *Annals of Botany*, 89:621-625.

Trescevskij, I. V. 1966. Afforestation in the river floodplains of droughty regions in the Volga-Din basin. *Lesnoe Khozajstvo*, 19(7):40-45.

Tyree, M.T. and H. Cochard. 1996. Summer and winter embolism in oak: impact on water relations. *Annales Des Sciences Forestiéres*, 53: 173-180.

Tyree, M.T. and J.S. Sperry. 1989. The vulnerability of xylem to cavitation and embolism. *Annual Review of Plant Physiology and Molecular Biology*, 40:19-38.

Vartapetian, B.B. and M.B. Jackson. 1997. Plant adaptations to anaerobic stress. *Annals of Botany*, 79: 3-20.

Vasellati, V., M.Oesterheld, D.Medan and J.Loreti. 2001. Effects of flooding and drought on the anatomy of *Paspalum dilatatum*. *Annals of Botany*, 88: 355-360.

Willians, M., B. J. Bond and M.G. Ryan. 2001. Evaluating different soil and plant hydraulic constraints on tree function using a model and sap flow data from ponderosa pine. *Plant Cell and Environment*, 24:679-690.

Zimmermann, M.H. 1978. Hydraulic architecture of some diffuse-porous trees. *Canadian Journal of Botany*, 56: 2286-2295.

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