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Effects of water absorption by bark on embolization repair of plant xylem

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Abstract: *Drought stress hinders photosynthesis and phloem transport in leaves, which limits the loading and long-distance transport of photosynthates in leaves. Especially for deciduous trees at leafless stage, non-leafy photosynthesis may be of great significance to in-situ embolization repair of stems and branches xylem. It has been proved that photosynthesis of bark of branches can promote xylem embolization repair by mediating water absorption of bark, which plays a key role in maintaining water conveyance function of branches. In this study, the isolated branches of Salix matsudana were used as experimental materials. After reaching the preset water potential and PLC gradient, they were treated with immersion in water, and the contribution of cortical photosynthesis to xylem embolism repair was studied by immersion treatment at different times. It was found that the embolism vulnerability curve of Salix matsudana was "S" shape, P50 was-1. 93 MPa, and Salix matsudana had strong anti-embolism ability; the absolute water content of bark and xylem of Salix matsudana branches was significantly increased, the volume ratio of xylem vessel sap was significantly increased, PLC was significantly reduced, and exogenous water could enter xylem vessel through bark to repair embolism.*

Keywords: *water absorption by bark, embolization repair, plant xylem*

1. Introduction

Water stress leads to the increase of xylem tension, the gas in the surrounding tissue fluid invades through the striate membrane, and the bubbles in the duct expand rapidly under negative pressure, filling the whole lumen and inducing embolism. Embolism destroys the water conveyance function of conduit, reduces the hydraulic conductivity of xylem, closes the stomata of leaves due to insufficient water supply, hinders photosynthesis, weakens carbon assimilation, and finally dies of plant tissues under the double harm of dehydration and insufficient energy supply [1]. It is found that in some conifers, embolism caused by freeze-thaw will gradually repair in late winter and early spring. For example, the PLC of branches of *Pinus contorta* and *Pseudotsuga sinensis Dod* decreased in early spring. Mayr et al. (2014) pointed out that the winter embolism recovery of these conifers began when snow still existed, and thought that these conifers and branches could mediate embolism repair by absorbing water, and the water source was snow covering the plant surface [2]. Mason et al. (2016) found that when the branches of *Sequoia sempervirens* were soaked in 18O isotope labeled water for 16 h, the labeled water could be detected in the xylem vessel[3]. Therefore, exogenous water can be transported radially into xylem duct to repair embolism. In recent years, more and more experiments have provided evidence for in-situ repair of xylem embolism, and proposed a "new refilling water" embolism repair process. In this study, the isolated branches of *Salix matsudana* were used as experimental materials, and soaked for different time after reaching the preset water potential through natural drought and water loss. The contribution of bark water absorption to xylem embolization repair was studied by low pressure sap flow method, and the pathway and motivation of in-situ embolization repair of woody plants were analyzed.

2. Materials and Methods

2.1 Experimental materials

Taking *Salix matsudana* clones (about 4 m in height and 0.03 m in diameter) with the same growth rate as experimental materials, the annual branches (50 ± 10 cm in length and 5 ± 0.5 mm in diameter) of were taken at 1.2 m height in the south direction of Salix matsudana clones.

2.2 Experimental Methods

2.2.1 Vulnerability curve of xylem embolism of Salix matsudana

Vulnerability curve (VC) of xylem embolism was measured by traditional drying method [4], and xylem embolism was measured by low pressure flow method[5]. The average value of embolism of three branches was taken as embolism of this branch.

2.2.2 Water absorption weight of Salix matsudana branches

The branches of *Salix matsudana* were taken and naturally dried to -1.9 ± 0.5 MPa on the experimental bench. The 5 cm branch segment in the middle of each branch was cut in water, and the two ends of the branch segment were sealed with silicone acrylic gel and wrapped with sealing film. After treatment, the branches were put into a glass container filled with oxygen saturated deionized water for water immersion treatment. The upper ends of all branches were located 5 mm below the water surface, and the hydrostatic pressure of the treated branches was kept consistent. During treatment, saturated deionized water was changed every 2h. The branches were taken out after 0, 0.5, 1, 2, 3, 4, 6, 8, 10 and 24h after treatment, and the surface moisture of the branches was dried with absorbent paper, and the fresh weight was weighed and the increased weight was calculated. Each branch is one repetition and six repetitions.

2.2.3 Absolute water content of bark and xylem of Salix matsudana branches

The branches of *Salix matsudana* were taken and naturally dried to-1.9 ±0.5 MPa on the experimental bench. The middle branch segment with a length of 80 cm was reserved for each branch. After cutting 20 cm at both ends with scissors in water, the middle 40 cm was cut into 8 segments with equal length, each segment was about 5 cm long (the branches from the upper end to the lower end were numbered ①-④ respectively). The absolute water content of branch ① was taken as the initial value. Both ends of other branches were sealed with silicone acrylic gel and wrapped with sealing film. After the treatment, the branches (②, ③ and ④) were immersed in glass containers filled with oxygen saturated deionized water and shaded. The upper ends of all branches were located 5 mm below the water surface, and the hydrostatic pressure of the two treated branches was kept consistent. During the treatment, saturated deionized water was changed every 2h. ② branch was taken out after treatment for 2h, ③ branch was taken out after treatment for 4h, and ④ branch was taken out after treatment for 6h. Each branch is taken as 1 repetition, with 6 repetitions.

The absolute water content was determined by Charrier (2013) [6].

2.2.4 Salix matsudana branch PLC and vessel juice volume

The experimental design is the same as 1.2. 3. The PLC of branches and the juice volume of vessels were measured, and each branch was one repeat and six repetitions.

Xylem embolization (PLC) was determined by low pressure flow method (Sperry, 1988), and xylem juice was extracted by centrifugation (Mason et al. 2016).

2.3 Data processing

Excel 2007 was used to collate the experimental data, and SPSS v.20 software was used to analyze the data of different treatments by one-way ANOVA and compare the significance of the difference. The significance level was $P<0.05$. Using SigmaPlot 10.0 software to draw charts.

3. Results and analysis

3.1 Vulnerability curve of embolism of Salix

Different tree species have different ability to resist embolism due to different water conveyance structures of xylem. The water transport function of xylem is closely related to the drought resistance of plants. Therefore, to a certain extent, the drought resistance of plants depends on the anti-embolism ability and embolism repair ability of plants. Embolism vulnerability curve is used to measure the resistance of plants to embolism. On this basis, the researchers further put forward the concept of "hydraulic safety range", and they think that the hydraulic safety range of plants is between the lowest water potential experienced by plants in natural state and the water potential when the embolism degree is 50% (P50). However, when the vulnerability of plant embolism reaches the irreparable range (P50 in gymnosperms and P88 in angiosperms), plants are easily affected by embolism and lead to death. The vulnerability curve of xylem embolism of *Salix matsudana* measured in this study is shown in Figure 1. The embolism vulnerability curve of *Salix matsudana* is "S" shape. Under water stress, when the water potential is low and maintained in a certain range, the loss rate of hydraulic conductivity remains at the original level. Only when the water potential decreases to a certain degree or the water deficit reaches a certain degree, the embolism occurs and the loss rate of hydraulic conductivity increases gradually. The P50 of *Salix matsudana* was -1.93 MPa, and the drought resistance of *Salix matsudana* was strong.

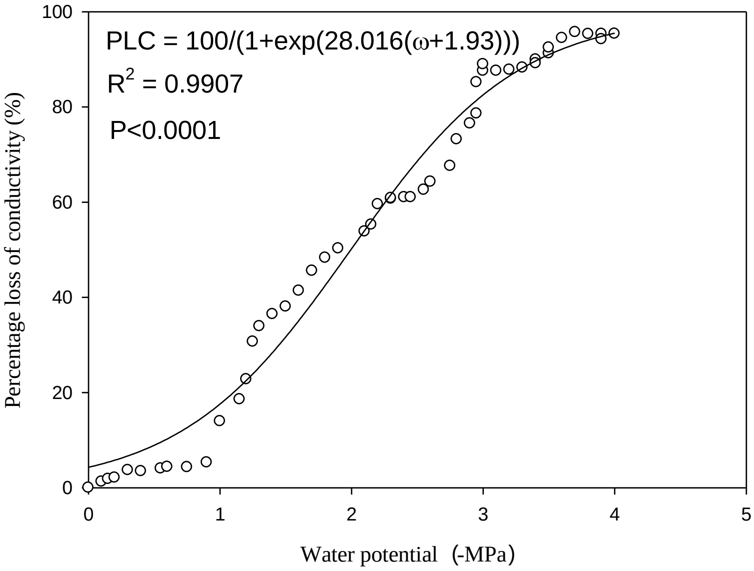

Fig.1 Xylem vulnerability curves of Salix matsudana

3.2 Repair of xylem embolism by radial water transport

With the extension of immersion time, the branch weight of Fraxinus mandshurica increased gradually. After soaking for 24 h, the branch weight increased by 111.27 mg. Among them, it increased by 85.48 mg in the first 4 hours, and the change was the most obvious (Fig. 2a). After immersion treatment for 2 h, the absolute water content of branch bark was not significantly different from the initial value, but the absolute water content of branch bark increased significantly by 10.94% and 17.63% after 4 h and 6 h treatment. With the extension of treatment time, the absolute water content of bark increased significantly. Compared with 2 h treatment, the absolute water content of bark increased by 7.13% and 14.21% after 4 h and 6 h treatment (Fig.2b). The absolute xylem water content of each treatment was significantly higher than that of the initial branch, and increased by 10.41%, 11.99% and 17.76% respectively after 2 h, 4 h and 6 h treatment. In terms of treatment time, there was no significant difference in xylem water content after soaking for 2 h and 4 h, and the xylem water content after 6 h immersion was significantly increased by 6.66% and 5.15% respectively compared with that for 2 h and 4 h (Fig. 2c). Thus it can be seen that exogenous water can enter the xylem from the bark through radial transport and increase the xylem water content. As to whether exogenous water can enter the xylem vessel, the xylem duct juice was extracted in this experiment. After 2 h, 4 h and 6 h treatment, the xylem duct sap volume of branches increased significantly by 17.28%, 21.63% and 21.74%, respectively, compared with the initial volume, but there was no significant difference between each treatment time (Fig.2d). After 2 h, 4 h and 6 h treatment, the xylem PLC of branches decreased significantly by 16.99%, 23.65% and 25.22% respectively compared with the initial PLC, but the difference between each treatment time was not significant (Fig.2e). It can be seen that exogenous water can enter the xylem catheter to repair embolism.

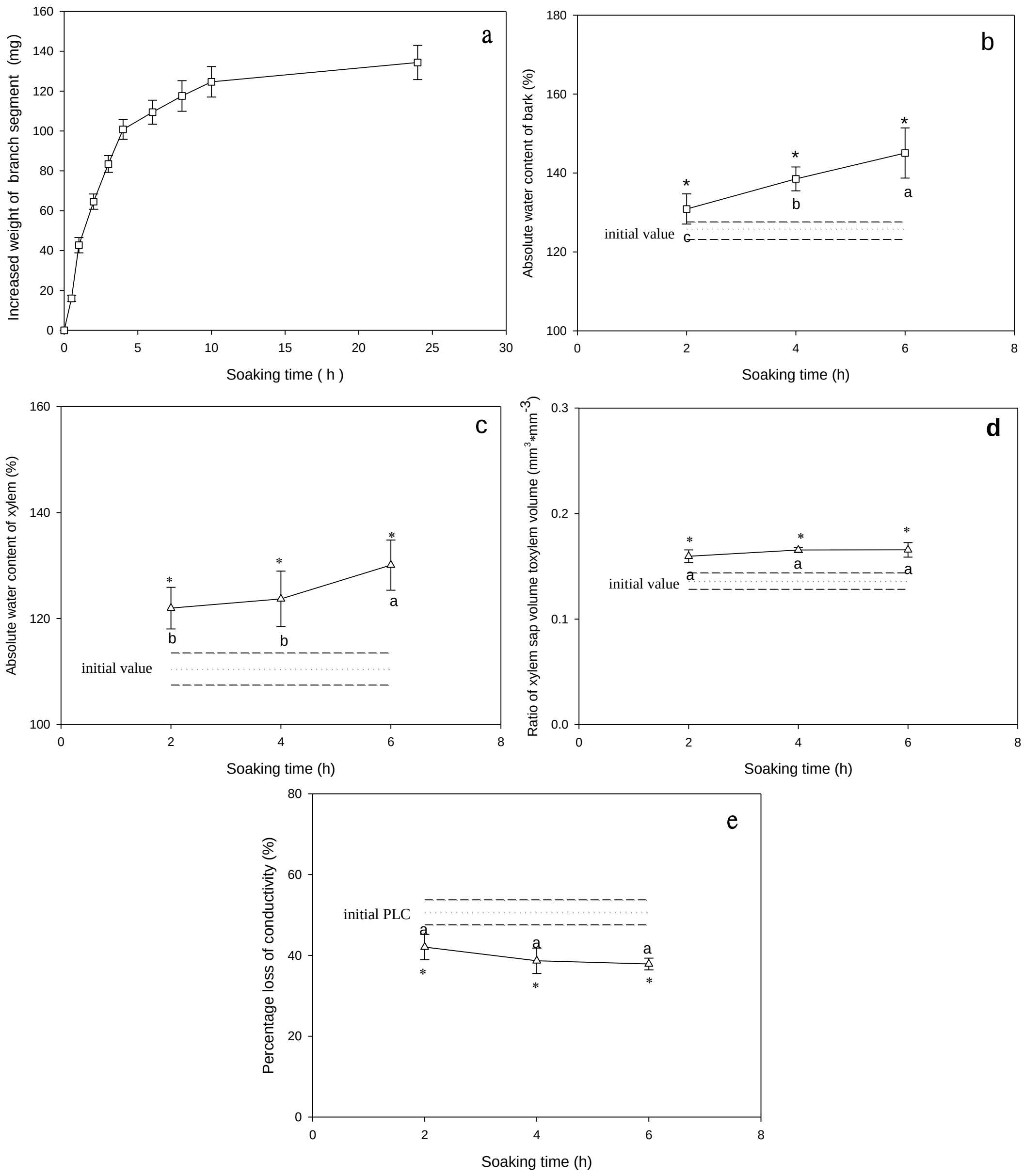

Fig.2 Hydraulic characteristics of branches after soaking of Salix matsudana

*Note: (a) Mass increment of branch segment at different soaking time. Absolute water content of bark (b), Absolute water content of xylem (c), Ratio of xylem sap to xylem volume (d) and PLC (e) at different soaking times. Data in the figure were mean ±SE (n=6). The dotted line represents the average value of initial (before soaking in the water), the dashed line indicates initial mean ±SE. Different lowercase letters denote significant differences ($P < 0.05$) between treatment time, * indicates significant differences ($P < 0.05$) between initial and after soaking.*

4. Conclusion and discussion

Salix matsudana is an important tree species for fast-growing timber, farmland protection and soil and water conservation in northern China. It has strong adaptability to difficult site conditions such as drought, flooding and saline-alkali, and has high greening, ornamental and economic value. The plant height of *Salix matsudana* is usually more than 20 m, which requires plants to have high tension (1 Mpa) to ensure the continuity of water transportation to meet the growth requirements of plants. Especially under drought conditions, in-situ repair of canopy branch embolism is very important.

4.1 Vulnerability of xylem embolism of Salix

It is generally believed that xylem embolism is inversely proportional to xylem water potential, and the relationship between water potential and embolism degree is often reflected by xylem embolism vulnerability curve. Regarding the vulnerability of embolism, scholars generally believe that the larger the diameter of xylem duct in the same tree species, the easier it is to cause embolism; Early timber catheter in the same ring is more likely to cause embolism; Roots are more prone to embolism than stems. Embolism vulnerability of branchlets is higher than that of big branches. Early studies suggest that embolism occurs only under extreme drought conditions, however, once it occurs, it will be irreversible until plants die of water shortage. Therefore, the anti-embolism ability of plants determines the tolerance of plants to drought environment. In recent years, more and more studies have found that embolism is a common physiological phenomenon in plants, and embolism can be repaired under negative pressure, and embolism is always formed and repaired in plants. It is generally believed that the decrease of hydraulic conductivity caused by xylem embolism affects stomatal movement and drought tolerance, and the anti-embolism ability of xylem is positively correlated with drought tolerance of plants. In this study, by constructing the embolism vulnerability curve, it was found that the embolism vulnerability curve of *Salix matsudana* was "S", and the P50 was-1. 93 Mpa, which had high anti-embolism ability, which was consistent with the research results of Dangwei (2016).

4.2 Repair of xylem embolism by radial transport of water

The formation of xylem embolism is a non-biological process, which is affected by water column tension of xylem and physical and chemical properties of wood. However, embolization repair is a complex biological process that requires the interaction of material metabolism and energy metabolism, and needs sufficient water supply. Studies have shown that plants can absorb water from fog, snow and rain through leaves to promote hydraulic recovery of leaves, which shows that plants can directly absorb water from the outside through non-root pathways. However, the effect of bark on hydraulics recovery is only mentioned in some coniferous plants. For example, after soaking in water for 200 min, the mass of fir branches increased by 8%, and the water potential decreased from-1. 4 MPa to-0. 2 MPa; After soaking spruce branches in water for 5 days (bark + leaves), the PLC of spruce branches decreased from 86% to 29%[2]. In this study, it was found that the weight of Salix willow branches increased by 122.82 mg after soaking in water for 24 h, which was similar to the mass change curve of some conifers, indicating that the bark could absorb water and provide water source for embolism repair. Some studies believe that embolization repair is usually carried out in a short time, and the time of embolization repair is also affected by the degree of stress [7]. *Populus trichocarpa* can repair the embolism within 2h after rehydration under moderate drought stress, but the repair time is longer than 20h after rehydration under severe drought stress [8]. The results showed that the PLC decreased by 16.99%, 23.65% and 25.22% after soaking for 2 h, 4 h and 6 h, respectively, which indicated that exogenous water could be transported radially to repair embolism in situ, but the time effect of repairing embolism remains to be further studied.

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