ISSN 2616-5910 Vol. 3, Issue 1: 7-11, DOI: 10.25236/AJALS.2022.030102

Effects of Cortical Photosynthesis on NSC Content in *Salix matsudana* Branches

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Abstract: *Embolism destroys the water conveyance function of ducts, reduces the hydraulic conductivity of xylem, and leads to the closure of stomata and the obstruction of photosynthesis in leaves. Therefore, in-situ repair of xylem embolism is very important to ensure the water conveyance function of catheter. Osmotic adjustment is the main driving force for in-situ repair of xylem embolism. Soluble sugars act as apoplast chemical signals and act as osmotic adjustment substances to mediate osmotic driving force during osmotic adjustment-driven catheter refilling. In this study, the isolated branches of Salix matsudana were treated with light and darkness at different times after natural drought and water loss, reaching the preset water potential. By analyzing the NSC changes of branches under different treatment conditions, the dynamics and mechanism of cortical photosynthesis on in-situ repair of woody plant embolism were analyzed. It was found that cortical photosynthesis increased the starch and soluble sugar content in bark and xylem of Salix matsudana branches, and provided a non-structural carbohydrate source for embolic catheter refilling.*

Keywords: *Cortical Photosynthesis, NSC Content, in-situ repair*

1. Introduction

When the tension of xylem exceeds the tensile strength of water column in the duct due to drought stress, the water column breaks to form a cavity, and the gas in the surrounding tissue fluid enters through the striate membrane, resulting in air pockets blocking water transport and causing embolism. Embolism destroys the water conveyance function of ducts, reduces the hydraulic conductivity of xylem, closes stomata of leaves, hinders photosynthesis, weakens productivity, and in severe cases, leads to the death of whole plants [1].

Photosynthesis provides material and energy for the growth and development of plants. It is generally believed that all green tissues of plants exposed to light can carry out certain photosynthesis, including petioles, bark, roots and some green reproductive organs. Chloroplasts in branches of many woody plants can recover and fix CO_2 released by mitochondrial respiration and diffused in transpiration flow. Because green photosynthetic cells are mainly located in cortical tissues, chloroplasts in branches are called cortical chloroplasts, and photosynthesis in branches is called cortical photosynthesis[2]. Cortical photosynthesis is an important part of plant trunk physiological activities, and the chlorophyll content of bark can reach 750 mg/m^2. Cortical photosynthesis can reduce transpiration flow, vascular rays, cambium and CO_2 excretion from bark, and convert CO_2 originally released into the atmosphere into carbohydrates, which makes plants more economical in carbon utilization. It has been proved that photosynthesis of branch cortex can promote xylem embolism repair and play a key role in maintaining water conveyance function of branches. The green photosynthetic cells were abundant in cortex, ray and pith of *Avicennia marina* branches, and the hydraulic conductivity of xylem decreased significantly after shading the branches. Under drought stress, xylem embolism of *Populus deltoides* x *nigra 'Monviso'* was detected by ultrasonic technique. The results showed that cortical photosynthesis could repair xylem embolism induced by drought stress [3].

It is generally believed that osmotic adjustment is the main driving force for in-situ repair of xylem embolism. Soluble sugar acts as apoplast chemical signal and mediates osmotic driving force as osmotic adjustment substance in the process of osmotic adjustment driving embolization catheter refilling[4]. Cortical photosynthesis can provide non-structural carbohydrates such as soluble sugar for branches in situ[5]. At present, the repair effect of cortical photosynthesis on xylem embolism and its

ISSN 2616-5910 Vol. 3, Issue 1: 7-11, DOI: 10.25236/AJALS.2022.030102

driving mechanism are still unclear. From the correlation between green photosynthetic cells in branch cortex and spatial distribution of xylem vessels (they are connected with annular parenchyma cells through vascular bundle rays), Considering the function of cortical photosynthesis in compensating non-structural carbohydrate and energy and the role of soluble sugar in osmotic regulation driving embolization catheter refilling, we speculate that cortical photosynthesis plays a key role in in-situ repair of xylem embolism during the whole growth period, especially before leaf bud germination during the greening period.

In this study, the isolated branches of *Salix matsudana* were treated with light and darkness at different times after natural drought and water loss, reaching the preset water potential. By analyzing the NSC changes of branches under different treatment conditions, the dynamics and mechanism of cortical photosynthesis on in-situ repair of woody plant embolism 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 Experimental design

The branches of *Salix matsudana* were taken and naturally dried to-1.9 ± 0.05 MPa on the experimental bench. The middle branch segment with a length of 80 cm was reserved for each branch. After being cut off 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 numbers of branches from the upper end to the lower end were ①-⑧, respectively). The average value of ① and ⑧ branch segments was taken as the initial value. Both ends of other branches are sealed with silicone acrylic gel and wrapped with sealing film. After the processing is completed, The branch segments (②, ④ and ⑥) are placed in a glass container filled with oxygen saturated deionized water and the light intensity is 200 μmol m^{-2} s^{-1} for illumination treatment, ③, ⑤ and ⑦ Branch segments are put into glass containers filled with oxygen saturated deionized water with the same volume for dark treatment. During dark treatment, the containers are wrapped with three layers of black plastic bags, the upper ends of all branches are located 5 mm below the water surface, and the hydrostatic pressure of the two treated branches is kept consistent. Saturated deionized water is changed every 2h during treatment. ② and ③ branches were taken out after treatment for 2 h, ④ and ⑤ branches were taken out after treatment for 4 h, ⑥ and ⑦ branches were taken out after treatment for 6 h. Each branch is taken as 1 repetition, with 6 repetitions.

2.2.2 Determination of NSC content in bark and xylem

Soluble sugar content was determined by Plant Soluble Assay Kit (Solarbio, China) kit method; the content of starch was determined by Plant Starch Assay Kit (Solarbio, China) kit.

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

Non-structural carbohydrates (NSC) produced by cortical photosynthesis are the material basis for maintaining the hydraulic function of plant xylem. After soaking in water for 2h, there was no significant difference in soluble sugar content of bark among different treatments. After soaking in water for 4h, the soluble sugar content of bark treated by light and dark increased by 65.36% and 18.63%, and the soluble sugar content of bark treated by light increased by 39.38% compared with that treated by dark. After soaking in water for 6h, the soluble sugar content of bark treated by light and dark increased significantly

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by 91.09% and 35.78% compared with the initial sugar content, and the soluble sugar content of bark treated by light increased significantly by 40.72% compared with that treated by dark (Fig. 1, a). The change trend of starch content in bark was opposite to that of soluble sugar content. After soaking in water for 2h, there was no significant difference between the starch content in bark treated by light and the initial starch content, but the starch content in bark treated by dark decreased by 13.67% and 14.53% respectively compared with the initial starch content and light treatment. After soaking in water for 4h, the starch content of bark treated with light and dark decreased by 4.95% and 21.90%, while that of bark treated with dark decreased by 17.83% compared with that treated with light. After soaking in water for 6h, the starch content of bark treated by light and dark decreased significantly by 22.28% and 34.21% compared with the initial starch content, and the starch content of bark treated by dark decreased significantly by 15.34% compared with that treated by light (Fig. 1, b). The total amount of NSC in bark treated by light was significantly higher than the initial value and dark treatment. Compared with the initial total amount of NSC, the total amount of NSC increased by 6.14%, 15.88% and 11.31% after 2 h, 4 h and 6 h of light treatment; Compared with dark treatment, light treatment increased by 16.25%, 28.60% and 28.63% after 2 h, 4 h and 6 h; Compared with the initial NSC, the total NSC of the dark treated bark decreased by 8.69%, 9.88% and 13.46% (Fig.1, c). The results showed that carbohydrates were only degraded under dark conditions, while cortical photosynthesis was beneficial to carbohydrate synthesis and increased NSC reserves.

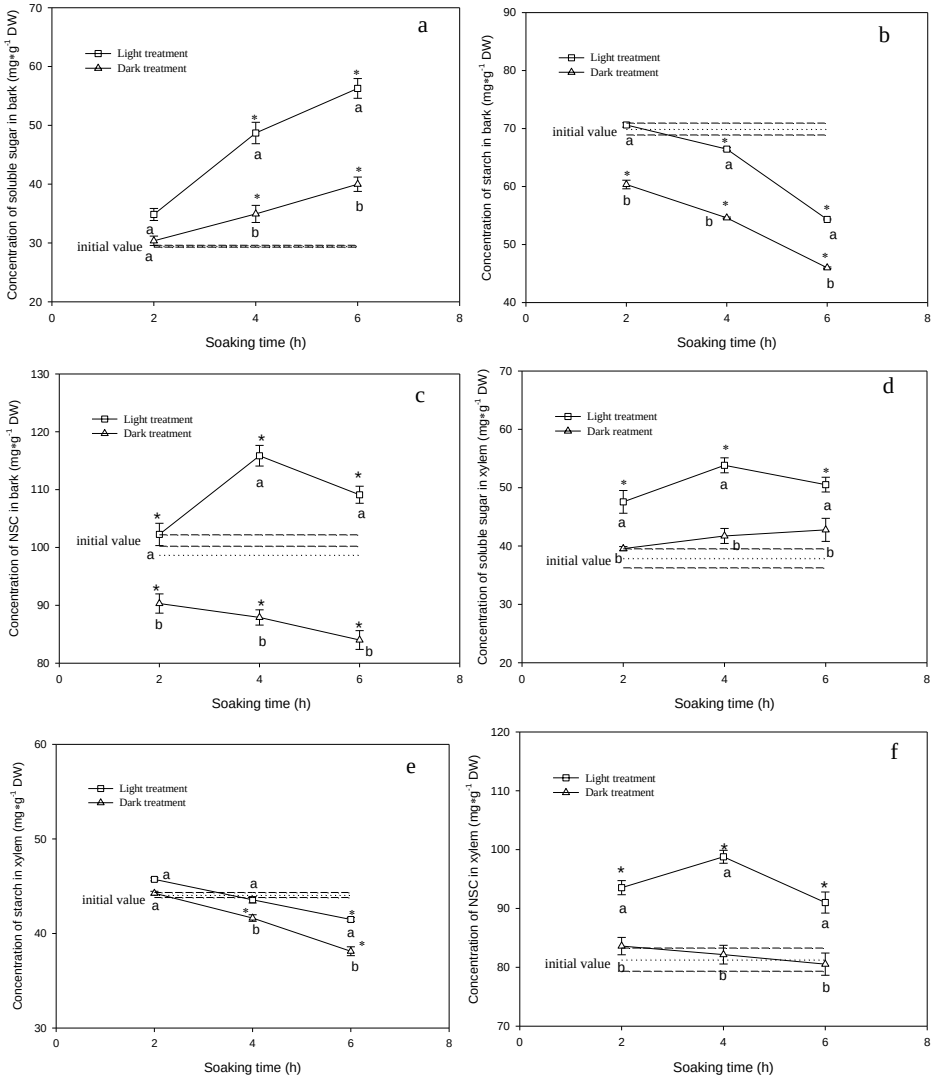

Fig.1 Concentration of NSC in bark and xylem under light and dark treatment

*Note: Data in the figure were mean ±SE (n=3). 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 light and dark treatment, * indicates significant differences (P < 0.05) between initial and treatment.*

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After soaking in water for 2h, the soluble sugar content of xylem treated by light increased by 25.51% and 20.25% respectively compared with the initial sugar content and the dark-treated xylem, but there was no significant difference between the soluble sugar content and the initial sugar content of xylem treated by dark. After soaking in water for 4h, the soluble sugar content of xylem treated by light increased by 42.05% and 29.01%, respectively, compared with the initial sugar content of xylem treated by dark, but there was no significant difference between the soluble sugar content of xylem treated by dark and the initial sugar content of xylem. After soaking in water for 6h, the soluble sugar content of xylem treated by light increased by 33.32% and 18.12% respectively compared with the initial sugar content and dark sugar content, but there was no significant difference between the soluble sugar content and initial sugar content of xylem treated by dark (Fig. 1, d). After soaking for 2h, there was no significant difference in xylem starch content among the treatments. After soaking in water for 4h, the starch content of xylem treated by light had no significant difference with the initial starch content, but the starch content of xylem treated by dark decreased by 5.51% and 4.43% respectively compared with the initial starch content and light treatment. After soaking in water for 6h, the starch content of xylem treated by light and dark decreased significantly by 5.86% and 8.81% compared with the initial starch content, respectively, and the starch content of xylem treated by dark decreased significantly by 8.09% compared with that treated by light (Fig. 1, e). Similar to the content of NSC in bark, the total amount of NSC in xylem treated by light was significantly higher than the initial value and dark treatment. Compared with the initial total amount of NSC, the total amount of NSC increased by 12.09%, 18.83% and 12.25% after 2 h, 4 h and 6 h of light treatment; Compared with dark treatment, light treatment increased by 9.62%, 16.83% and 13.73% after 2h, 4h and 6h; There was no significant difference between the total amount of NSC in xylem treated by darkness and the total amount of NSC in initial xylem (Fig. 1, f).

4. Conclusions and discussions

Because green cells containing chloroplasts are mainly distributed in the cortex of stems and branches, cortical photosynthesis becomes the main source of non-structural carbohydrates (NSC) in leafless stage or blocked photosynthesis of leaves, so as to meet the material and energy requirements of local growth of plants. The role of cortical photosynthesis in maintaining plant hydraulics has been confirmed, and most studies believe that the regulation mechanism of soluble sugar can explain the relationship between NSC content changes and hydraulics function [6]. The ability of xylem to transport water depends not only on its anti-embolism ability, but also on its ability to repair embolism. Embolic repair under tension is an energy-consuming process, which requires the formation of necessary osmotic potential gradient, which requires sufficient NSC supply[7]. In addition, NSC produced by cortical photosynthesis may make the structural characteristics of xylem more conducive to resisting cavitation caused by drought, such as forming smaller pore size or dense cell tissue. It is suggested that the bubbles in xylem ducts can be stabilized by surfactant under tension, thus inhibiting and delaying the occurrence of embolism. C is the key component of surfactant and protein chemical structure, and the carbon fixation function of cortical photosynthesis improves the bubble stabilization function to a certain extent. However, the mechanism of cortical photosynthesis in embolization repair is still unclear. Embolic repair under tension is an energy-consuming process, which is regulated by the gradient of water, sugar and ions between xylem and phloem cells. This study suggests that soluble sugar is the main driving force for the formation of osmotic potential gradient, and cortical photosynthesis can provide non-structural carbohydrate (NSC) supply for branches in situ, so as to meet the energy demand of plants for embolization repair and improve the ability of embolization repair.

There have been many researches on the generation and repair of embolism, but the specific process of the generation and repair of embolism has not been solved, and there are still many controversies about the frequency, seasonal characteristics, position effect and repair ability of embolism under negative pressure. Under drought stress, soluble sugars in plants not only participate in osmotic adjustment, but also provide carbon support and energy for the synthesis of other organic compounds. At the same time, they play an important role in protecting various enzymes and maintaining membrane stability under high ion concentration in cells. A large number of studies have found that, The soluble sugar content of plants increased significantly during embolization repair, This study also found the same results, Embolism repair under negative pressure requires the participation of parenchyma cells around embolism catheter, Starch in parenchyma cells or starch transported by xylem ray cells is hydrolyzed into soluble sugar, which enters the embolization catheter under the action of sugar transporter, reduces the osmotic potential of the embolization catheter, and drives the water in parenchyma cells or functional catheter to transport to the embolization catheter.

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Acknowledgements

The study was financially supported by "Innovation Driving and Leading Promotion of Seedling and Flower Industry in Mount Tai" of industrial upgrading project of Science and Technology Park in Shandong Province (2019YQ012).

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