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HOW THE CHEMISTRY OF XYLEM APOPLAST INFLUENCES RECOVERY FROM WATER STRESS IN POPLAR

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parenchyma cells, drought, xylem sap, embolism refilling, sugars

Global climate changes are expected to intensify drought events in the near future causing plant death across natural ecosystems. One cause of tree mortality is xylem hydraulic failure due to formation of embolisms (air-filled conduits). Woody plants have evolved several mechanisms to mitigate the loss of water transport capacity and many of them are able to face embolism with a fast recovery. However, this process cannot happen spontaneously and physiological activity of living parenchyma cells is necessary to generate the osmotic gradient needed to force water influx into the void vessels.

The xylem of poplar trees was shown to dynamically counteract embolism formation by accumulating carbohydrates in the apoplast and dropping xylem sap pH, thus suggesting the occurrence of specific changes in the physiological activity of parenchyma cells in response to stress. We hypothesized that sap acidification could serve as one of the symptoms/signals of severe water stress in poplar and that the resulting accumulation of sugars can prime stems for embolism recovery when stress is relieved after re-hydration.

To test our hypothesis, we followed dynamic changes of xylem sap chemistry occurring in poplar (*P. tremula* x *P. alba*) trees exposed to drought and re-hydration treatments by applying a multidisciplinary approach involving physiological, molecular and chemical analyses at once.

Severely stressed poplars showed a drop of xylem sap pH, complete stomata closure, an increase in abscisic acid (ABA) and total soluble sugar content in the sap coupled with a significant decrease in starch concentrations. We also demonstrated that upon lower pH conditions, the most accumulated carbohydrates in the xylem apoplast were glucose and fructose followed by maltose. These findings suggest that the measured pH drop could stimulate the activity of acidic invertases and sugar transporters that promote the splitting of sucrose into monosaccharides and the subsequent sucrose efflux. To further investigate this aspect and strengthen the observed physiological and biochemical responses, we profiled the expression of a set of genes playing a key role in sugar metabolism and transport (beta-amylases, acidic invertases, sucrose and maltose transporters) and we tested the related enzyme activities.

After recovery from severe water stress, poplars showed high stomatal conductance values, low ABA content and an increase in apoplastic pH. Moreover, in this higher pH environment, although starch levels were still lower than control conditions, sugar accumulation was significantly reduced and sucrose was the primary component. This was confirmed by data obtained from transcriptomic analyses that, indeed, showed the inhibition of genes encoding specific beta-amylases and sugar transporters.

We thus propose that, as soon as transpiration is restored, new water would be delivered from roots and cellular stress reaction would be 'triggered off' by washing away sugars and changing xylem pH to more neutral values.

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