Microfluidics of sugar transport in plant leaves and in biomimetic devices

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The physical mechanisms underlying vital plant functions constitute a research field with many important, unsolved problems. Some of these research topics gaining attention in recent years are concerned with the fluid transport in plants. Plants photosynthesize sugars in their leaves for energy production and growth. These sugars are taken up into the veins of the leaf and then transported efficiently to other parts of the plant via the vascular system. The vascular system of plants has two types of tissue: the xylem brings water from the roots up to the leaves, and the phloem transports sugars from the sources in the leaves to the sinks in roots, fruits and regions of growth. The transport of sugar solution in the phloem is driven by an osmotic pumping mechanism. The uptake of water from the xylem into the phloem generates a hydrostatic pressure difference between sources and sinks which results in a bulk flow of sugar solution. It is not clear where in the leaf this bulk flow starts, especially in plants that have intercellular connections (plasmodesmata) between the phloem and the cells surrounding the veins. In these plants bulk flow could be involved in the process of sugar loading into the veins.

We studied the physics of two basic mechanisms for sugar loading: the polymer trap and passive loading. The polymer trap is an active mechanism, which is characterized by an elevated concentration of sugars inside the veins compared to the rest of the leaf. This is achieved with the help of enzymes combining sucrose molecules entering the vein through plasmodesmata into larger sugar molecules. These molecules are then too large to move back out of the vein. In order for this system to work, the plasmodesmata have to act as extremely precise filters. Microscopy studies show that these plasmodesmata are very small, in fact they are too small to resolve their exact cross section available to transport. In our theoretical model, we approximated the plasmodesmata as cylindrical slit pores and investigated whether the pores could be small enough to fulfill the filtering function, and at the same time large enough to allow for sufficient transport of sucrose. We found that this mechanism is indeed feasible. We could further conclude that sugar is not only transported by diffusion, but is partly advected through the plasmodesmata by a bulk flow. This bulk flow is actually enough to drive the export from the leaf, meaning that no additional water has to be taken up into the phloem in order to drive the flow.

Plants that use passive loading instead, the concentration of sugars inside the veins is lower than in the surrounding tissue, and the plasmodesmata connecting the phloem with the cells surrounding the veins are larger than in the polymer trap case. We suspected, that in passive loading the advective transport contribution to sugar loading could be even more important than in the polymer trap. We demonstrated advective loading of sugars in experiments with biomimetic devices, modeling the leaf as a system of three compartments: phloem, xylem and sugar producing tissue. We further developed a theoretical model of passive loading, enabling us to identify the key parameters that determine the sugar uptake into the phloem. Assuming values typically found in plants for the three key parameters sugar concentration, interface areas between the three compartments and pore size of the plasmodesmata, the uptake of sugar can be dominated by either advection or diffusion. Of these key parameters, the pore size has the largest influence on the ratio of advective to diffusive loading. The next step in the transport of sugars is the export from the leaf. We studied the case of conifer needles, which are linear leaves with unbranched venation. Most conifer leaves are not longer than 6 cm, which is rather short compared to broad leaves with sizes spanning from millimeters to meters. In order to understand this limitation we modeled the phloem conduits in linear leaves as cylindrical, osmotic pipes running from the tip to the base of the needle. Using a simple analytical model we calculated the sugar export rate from these conduits assuming a constant concentration of sugars along the pipe. We found that in needles longer than a characteristic length the fluid close to the tip becomes stagnant and sugars can no longer be exported efficiently. This means, that very little output can be gained from making a leaf longer than the efficient leaf length. Our prediction for an efficient leaf length matches well with the mean needle lengths from a data set comprising 519 of the 629 currently known conifer species.

We further calculated the energy dissipated by the export of sugar solution from linear osmotic pipes. There are two main contributions to the dissipation of energy, one due to the resistance of membrane pores and one due to Poiseuille resistance inside the pipe. We found simple and general analytical solutions for flow rates and dissipation of energy for single pipes, generalizing the normal Poiseuille expression and showing that the driving force is not only the pressure, but the "water potential", which is a combination of concentration and pressure. We also treated a system of coupled parallel pipes with a power law distribution of lengths, as found in linear leaves. The results for the system of coupled pipes are surprisingly similar to the single pipe solutions, and likewise show the emergence of the stagnant zone for leaves longer than the effective length.

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