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Relationship between Streaming Potential and Sap Velocity in *Salix alba* L.

By

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With 5 Figures

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Summary

GINDL W., LÖPPERT H. G. & WIMMER R. 1999. Relationship between streaming potential and sap velocity in *Salix alba* L. – *Phyton* (Horn, Austria) 39 (2): 217–224, with 5 figures. – English with German summary.

In a laboratory experiment, a strong linear relationship ($R^2 = 0.92$) was found between the velocity of a defined liquid streaming through a stem of *Salix alba* L. and the electrochemical potential (streaming potential) measured between two inserted electrodes. Field measurements confirmed that diurnal patterns of sap velocity inferred from streaming potentials deliver reasonable estimates comparable to traditional methods.

Zusammenfassung

GINDL W., LÖPPERT H. G. & WIMMER R. 1999. Zusammenhang von Strömungspotential und Saftflußgeschwindigkeit in *Salix alba* L. – *Phyton* (Horn, Austria) 39 (2): 217–224, 5 Abbildungen. – Englisch mit deutscher Zusammenfassung.

In einem Laborexperiment mit einem *Salix alba* L. Stämmchen wurde ein enger linearer Zusammenhang ($R^2 = 0.92$) zwischen der Geschwindigkeit einer durch ihn strömenden Flüssigkeit und dem an seinen Enden gemessenen elektrochemischen Potential (Strömungspotential) gefunden. Die Ergebnisse eines Feldversuches bestätigten, daß die Abschätzung der Saftflußgeschwindigkeit in lebenden Bäumen mittels der Messung des Strömungspotentials möglich ist.

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Introduction

The streaming potential phenomenon is one of several elektrokinetic processes that include electro-osmosis and electrophoresis (HAMANN & al. 1998). A streaming potential is built up, when a liquid containing ions is forced through a capillary. In a tree, the water conducting elements of the xylem, i.e. tracheids and vessels represent the capillaries. Their diameters range from 40 μm in earlywood tracheids of conifers up to 400 μm in large vessels of deciduous trees (ZIMMERMANN & BROWN 1971). The liquid flowing through these capillaries, the xylem sap is an aqueous solution of inorganic salts, sugars, small amounts of organic acids, nitrogen compounds, growth hormones and enzymes, the driving force being the deficit of water saturation of the ambient air compared to the water saturated plant cell wall (KOZLOWSKI & PALLARDY 1997). The most important ions concerning the establishment of streaming potentials in the xylem sap are K^+ and Ca^{2+} . The concentration of these ions is in the order of 2 mmol/l for K^+ and 0.5 to 1 mmol/l for Ca^{2+} (GLAVAC & al. 1990, DAMBRINE & al. 1992). Cell walls of tracheids and vessels are composed of three main polymers: cellulose, lignin and polyoses (FENGEL & WEGENER 1989). Some polyoses, e.g. the xylans in secondary cell walls, contain uronic acid groups, which are partly dissociated, causing a net negative charge of the cell wall (BRETT & WALDRON 1996, NOBEL 1991). To preserve electroneutrality, mobile charges of opposite sign from the xylem sap will accumulate near the solid-electrolyte interface (Fig. 1) in a diffuse double layer (HAMANN & al. 1998). When a pressure gradient forces the xylem sap to move through the cell, a part of the diffuse double layer is dragged along with the sap. As the double layer

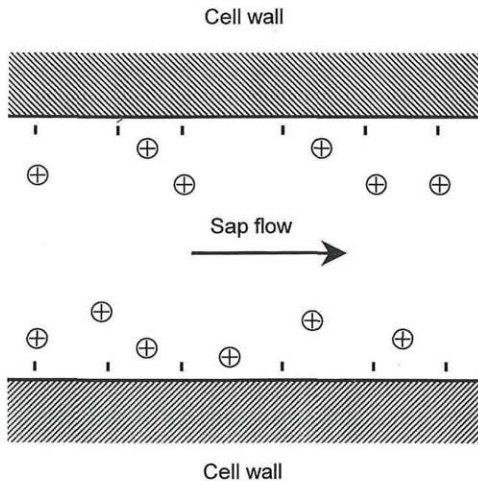


Fig. 1. Schematic representation of the distribution of charges in a conducting xylem cell. Only excess charges are displayed.

contains an excess of positive charges compared to the bulk of the xylem sap, this transport constitutes a convection current. The resulting charge separation gives rise to a potential difference, the streaming potential. In the steady state, the streaming potential drives a conduction current back through the liquid which reduces the streaming potential to a certain amount, depending on the ohmic resistance of the return path (FRIBORG 1997). When the ends of the capillary are contacted with electrodes, a potential can be measured with a high impedance electrometer amplifier. This potential is proportional to the velocity of the liquid and the distance between the measuring electrodes and is furthermore influenced by the dielectric properties of the xylem sap, by the zeta potential at the cell wall-liquid interface, by the viscosity of the liquid and its electric conductivity (eqn. 1) (WEDLER 1997). A modification of eqn. 1, using Poiseuille's law, gives a relationship between streaming potential and sap velocity (eqn. 2).

$$[1] \quad E = dp \, e \, z \, n^{-1} \, k^{-1}$$

$$[2] \quad E = 8 \, v \, e \, z \, l \, r^{-2} \, k^{-1}$$

E Streaming potential

l Distance between the measuring electrodes (= length of the capillary)

dp Pressure difference at the ends of the capillary

r Radius of the capillary

v Mean velocity of the streaming liquid

e Dielectric constant of the streaming liquid

k Electric conductivity of the streaming liquid

n Viscosity of the streaming liquid

z Zeta potential

As a consequence of eqn. 2, streaming potentials in the xylem of trees should be related to transpiration flow (FENSOM 1963). Therefore, the measurement of the streaming potential could be a valuable method for the determination of sap velocity in trees (SCHUCH & WANKE 1968, MORAT & al. 1994, KOPPAN & al. 1998). To demonstrate the usefulness of this method, we present results from experiments performed in the laboratory as well as in the fields.

Material and Methods

A two years old stem of *Salix alba* L., 9.2 mm thick was cut at the end of September 1998 in an abandoned gravel pit. The stem was taken to the laboratory where it was submerged in 90 °C hot water for 60 min to kill living cells. Then the 554 mm long stem was debarked and subsequently mounted in the experimental apparatus (Fig. 2). Compressed air was used to force a solution containing 1 mmol/l K⁺ and 0.1 mmol/l Ca²⁺, prepared with KCl, CaCl₂ and de-ionised water, through the stem. Pressures applied to the stem ranged from 0.02 MPa to 0.3 MPa. AgCl coated Ag wires, 0.2 mm thick, installed in the experimental apparatus at a distance of 15 mm from the ends of the stem (Fig. 2) and connected to an ORION-EA 920 ion analyser, were used to measure the streaming potential. The time needed for 1 ml of solution to

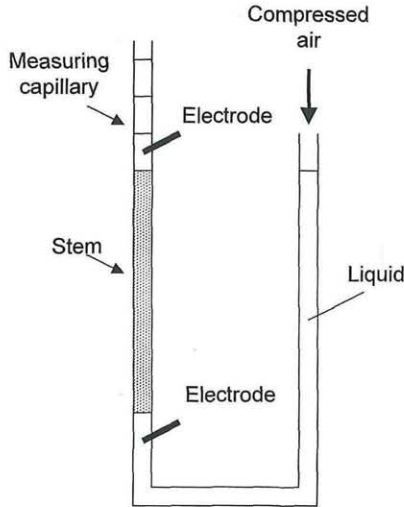


Fig. 2. Principle of the apparatus used for the measurement of streaming potential in the laboratory.

flow through the stem was determined with a measuring capillary attached to the top end of the stem and a stop clock. At the end of the experiment, thin sections of $25\ \mu\text{m}$ thickness were taken from the middle of the stem with a sliding microtome, stained with methylene blue and mounted permanently in Malinol (Chroma Ges., Köngen, Germany). The total vessel area was determined using a digital camera attached to a light microscope and the image analysis software NIH Image. From the volume flux and the vessel area, the mean velocity of the liquid flowing through the stem was calculated.

To assess the influence of different concentrations of mineral elements on the streaming potential, solutions with the previously used concentration as well as solutions 10 and 100 fold in concentration were forced through the stem at constant velocity. Six measurements were taken at each concentration.

For a field experiment, a *Salix alba* L. tree with a total height of 10 m and a diameter of 15 cm at breast height was selected. The electrodes made of stainless steel (1.2 mm in diameter, with 8 mm long blank tips) were inserted 20 mm into the xylem at a height of 80 cm and at 380 cm (at the bottom of the crown) above ground. Due to the length of its blank tips, potentials originating from numerous vessels in the vicinity of the electrode were averaged. The difference of the potential between the upper and the lower electrode was recorded with a PHYTOGRAMTM (GENSLER 1997) measuring amplifier. Measurements were taken every 15 min. Air temperature and relative humidity were recorded with a conventional thermo-hygrograph. The saturation deficit of the ambient air was calculated from these recordings.

Results

In our laboratory experiment we found a strong correlation between the velocity of a streaming liquid and the streaming potential (Fig. 3) based

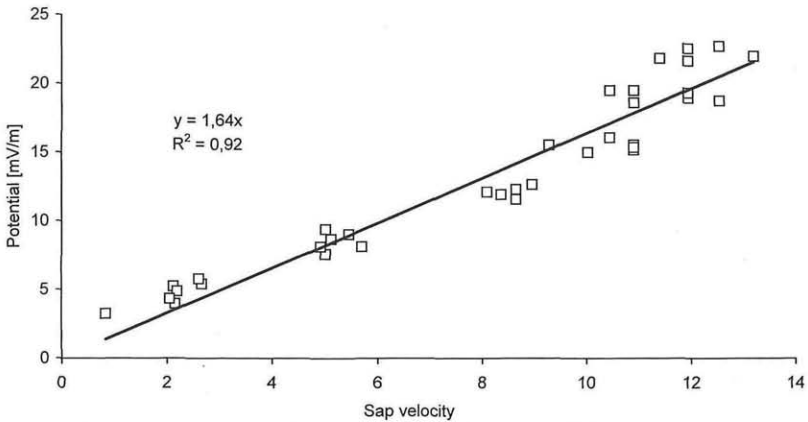


Fig. 3. Scatter plot and regression line of streaming potential in reference to the velocity of a streaming liquid.

on 37 measurements. 92 % of the variation of the potential could be explained by a linear regression. The experiment with different K^+ and Ca^{2+} concentrations showed, that a 10-fold increase of the original concentration only slightly diminished the streaming potential, but not to a statistically (t -test, $p < 0.01$) significant extent (Fig. 4). At a concentration 100 times enriched with K^+ and Ca^{2+} , the lowering effect on the streaming potential became more pronounced.

Results from the field experiment for the 24 Aug. 98 through 26 Aug. 98 period are displayed in Fig. 5. The potential measurements varied in 24 hour cycles. The amplitude of the potential variations was approx. 30 mV/m. Maximum velocities in *Salix alba* were reached between 11 and 16 o'clock, while minimum velocities were recorded between 21 and 4 o'clock.

Discussion

The laboratory experiments conducted in this study revealed an excellent correlation between the velocity of a liquid flowing through the xylem of a tree and the streaming potential (Fig. 3). However, for the applicability of the method in the field, the influence of various factors, i.e. temperature, ionic composition of the streaming liquid and the dimensions of the capillaries have to be taken into consideration.

Temperature will influence the streaming potential because of the temperature-dependence of the zeta-potential (KORTUM 1962). According to this relationship, a variation in stem temperature of 20 K would result in an inaccuracy of 7 %. But inaccuracies of this type can be easily corrected by simultaneous measurements of the stem temperature.

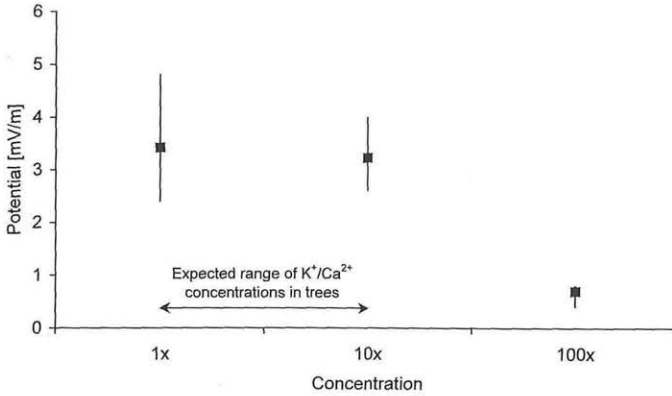


Fig. 4. Mean values of streaming potential at three different concentrations of K^+ and Ca^{2+} . Vertical bars indicate maximum and minimum values.

The streaming potential should also depend on the composition of the xylem sap. This may be concluded from the fact, that in the stationary state of sap flow, the convection current is balanced by a conduction current in the opposite direction. A variation in the conductivity of the xylem sap would therefore change the streaming potential and thus make a comparison of laboratory and field experiments difficult. However, within the concentration range of solutions comparable to the composition of xylem saps of trees (GLAVAC & al. 1990, DAMBRINE & al. 1992), only a minor influence has been observed (Fig. 4).

Finally, the streaming potential is inversely proportional to the square of the radius of the capillary (eqn. 2), and would thus depend on the structure of the wood. Therefore, measurements carried out with a particular tree species are not easily comparable to those with other species. Further experiments will be focused on this problem.

In conclusion, changes in the streaming velocity of the xylem sap can be continuously monitored by measurement of the streaming potential, as shown in Fig. 5 as a typical result from field experiments. Measurements displayed in Fig. 5 are similar to published sap flow curves for *Salix* (LINDROTH & al. 1995, CIENCIALA & LINDROTH 1995), although a characteristic period of near zero potential/sap velocity is missing during the second night. Double peaks common for sap flow curves (GRANIER 1977) are present on the second and third day.

When the streaming potentials displayed in Fig. 5 are used to calculate the maximum sap velocity according to the relationship in Fig. 3, the resulting values have to be regarded with precaution, as discussed above. The maximum sap velocity of 15 to 17 m/h is considerably above published values for *Salix*. Velocities of 3 m/h were found with the heat pulse method (ZIMMERMANN & BROWN 1971) and values of 1.8 m/h resulted from dye in-

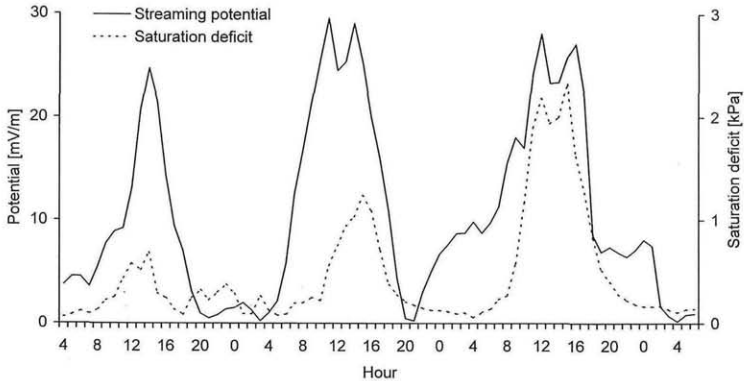


Fig. 5. Streaming potential in a *Salix alba* L. tree in reference to the saturation deficit of the ambient air from 24 Aug. 98 to 26 Aug. 98.

jection experiments (CERMAK & al. 1984). This indicates that results from small scale laboratory experiments are possibly not applicable to full scale field measurements, particularly, when the first are performed with pressurised material while the latter are done in xylem under water tension.

The measurement of sap flow with various thermal techniques is a well established method in tree physiology. All these techniques make use of the fact, that thermal energy introduced into the stem by heating is transported with the streaming sap. Either the velocity of a heat pulse applied inside the xylem or the amount of heat energy transported away from a source by the moving sap is used to calculate flow rates (SMITH & ALLEN 1996, KÖSTNER & al. 1998). The development of an electrochemical method to measure sap velocity and in a second step sap flow would provide an opportunity to re-evaluate current methods and improve the understanding of plant-water relations.

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