Supplementary Materials 1:
Estimating the impact of reduced temperature on phloem sap

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Contents

This pdf was generated from an Rmarkdown file, which includes all R code necessary to reproduce the estimations. The Rmarkdown file is available on github (https://github.com/TTRademacher/Exp2018Analysis) and is permanently and publicly archived on the Harvard Forest Data Archive as part of the data set HF???.

1 Basics of phloem transport

Phloem flow is thought to be driven by hydrostatis forces resulting from osmotic gradients mainly caused by differences in soluble sugar cocentrations (primarily succrose) along the phloem transport pathway. This pressure flow hypothesis was first postulated by Münch (1927) and still describes phloem flow well given more recent evidence (De Schepper et al., 2013). However, trees with long distance phloem transport pathways could not be easily reconciled with the proposed theory due to the seemingly insufficient pressure gradients for long-distances transport in trees. Recent work has shown that gradual changes in phloem sieve tube anatomy along the stem can reduce pathway resistance and reconcile phloem transport in trees with Munch's hypothesis (Savage et al., 2017).

A few experiments (De Schepper et al., 2011; Johnsen et al., 2007; Peuke et al., 2006; Schaberg et al., 2017) have made use of the fact that phloem transport is temperature dependend and can be temporarily halted by chilling the phloem (Gould et al., 2004). In the following, we explain the temperature dependence of phloem flow to roughly estimate the effects of phloem chilling on phloem transport.

2 Dependence of phloem sap viscosity on temperature

To quantify the effect of chilling on dynamic viscosity of phloem sap and thus resistance to phloem transport, we estimate the effect of temperature (T_{phl}) on the viscosity of water (η_w) using the Vogel-Fulcher-Tamman equation:

$$\eta_w = \eta_0 e^{\frac{B}{(T_{phl} - T_{VF})}} \tag{1}$$

, where η_0, T_{VF} and B are empirical constants. In addition to water, phloem sap contains sugar. The sugar concentration (c in $\%weight/weight$) also affects phloem sap viscosity. According to Jensen et al. (2013), phloem sap viscosity (η_s) and density (ρ_s)can be estimated from sap sugar concentration as follows:

$$\eta_s = \eta_w e^{(Ac - (Bc)^2 + (Cc)^3)} \tag{2}$$

$$\rho_s = \rho_w (1 + Ac + (Bc)^2 + (Cc)^3) \tag{3}$$

, where A, B, and C are empirical constant, which we set to 0.032, 0.012, and 0.023 for viscosity and 0.0038, 0.0037 and 0.0033 for density according to Jensen et al. (2013). Combining the temperature and succrose dependencies of phloem sap, we obtain the response surface displayed in figure 1.

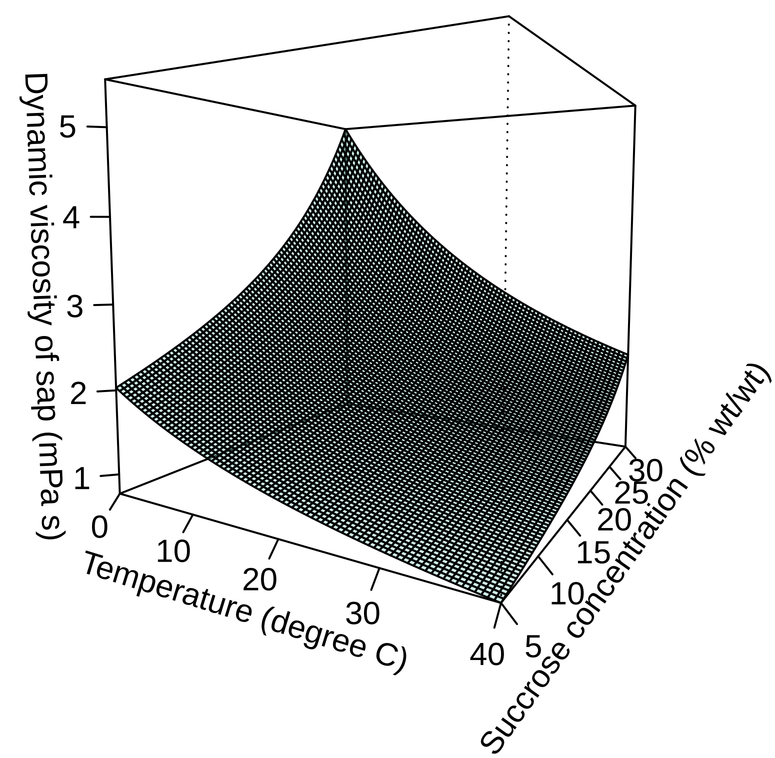

Figure 1: Surfaces of phloem sap viscosity against temperature and succrose concentration.

Knowing the sugar concentration and temperature, hence the viscosity of the phloem sap we can then estimate the resistance to flow in the lumen of sieve tubes (R_l) according to the re-arranged Hagen-Poiseuille equation.

$$\Delta P = \frac{8 \eta_s l_l Q}{\pi r_l^4} \tag{4}$$

, where r_l is the lumen radius of the sieve tube, Q is the volumetric flow rate, η_s is the dynamic viscosity of phloem sap, l_l is the length of the sieve tube, and ΔP is the resulting pressure difference. Finally, we can approximate flow (Q) through the sieve tube (Jensen et al., 2013) as a function of its resistance (R_f) and the difference in pressure (ΔP):

$$Q = \frac{\Delta P}{R_l} \tag{5}$$

This allows us to estimate temperature effects on viscosity and in turn phloem resistance and flow. Explicitly, resistance to flow in the lumen can be estimated as:

$$R_l = \frac{8\eta_s l_l}{\pi r_l^4} \tag{6}$$

This does not include the additional plate resistance in sieve tubes, but according to Jensen et al. (2012), the plate resistance in sieves tubes is roughly equal to the lumen resistance, thus the total phloem resistance to flow (R_p) can be simply approximated as:

$$R_p \approx 2R_l \tag{7}$$

3 Effects of phloem chilling on local phloem resistance to flow

During the chilling period we measured average phloem temperature in chilled trees of 5.4 ± 4.6 at 1.0 m and of 4.7 ± 3.9 at 2.0 m compared to 20.5 ± 2.3 at 1.5 m in control trees assuming a succrose concentration of 15.4%. This temperature difference causes an mean increase phloem sap viscosity from $2.8534974 \times 10^{-10}$ $Pa\,s$ for control trees to $5.0214663 \times 10^{-10}$ $Pa\,s$ at 1.0 m and $5.1387307 \times 10^{-10}$ $Pa\,s$ at 2.0 m in chilled trees, which constitutes an 76 and 80% increase, respectively. Given that the lumen resistance is proportional to the viscosity (Equ. 6) and that total phloem resistance is roughly twice the lumen resistance (Equ. 7), this translates to a proportional increase in total phloem resistance. All else being equal the increased resistance would reduce phloem flow. However, any reduced flow could eventually be overcome by higher osmotic gradient across the chilling zone due to progressive difference in succrose concentrations above versus below the chilled zone.

4 Dependence of phloem sap density on temperature

Temperature does not only affect phloem sap viscosity but also its density, further augmenting the resistance to flow at temperatures decreasing towards the freezing point of water.

As is immediately obvious from figure 2, the difference in the density due to realistic variations in temperature are substantially smaller than differences in viscosity (Fig. 1). In fact, temperture-induced density changes as a result of temperature changes are more than an order of magnitude smaller than viscosity changes and density is actually mostly affected by succrose concentration. Additionally, density does not directly affect the resistance, but rather affects the gravitational potential (Ψ_g), thus the overall pressure gradient (ΔP), which is the sum of the osmotic potential (Ψ_c)), water potential (Ψ_w) and the gravitional potential and drive phloem flow. At low Reynolds numbers, viscous forces dominate laminar flow, such as phloem flow through sieve tubes (Jensen et al., 2012). While changes in temperature do affect sap density, the effects of density on flow are comparatively negligible with about 10% variation for realistic temperatures and succrose concentrations compared to up to 500% for viscosity (see figures 1 & 2).

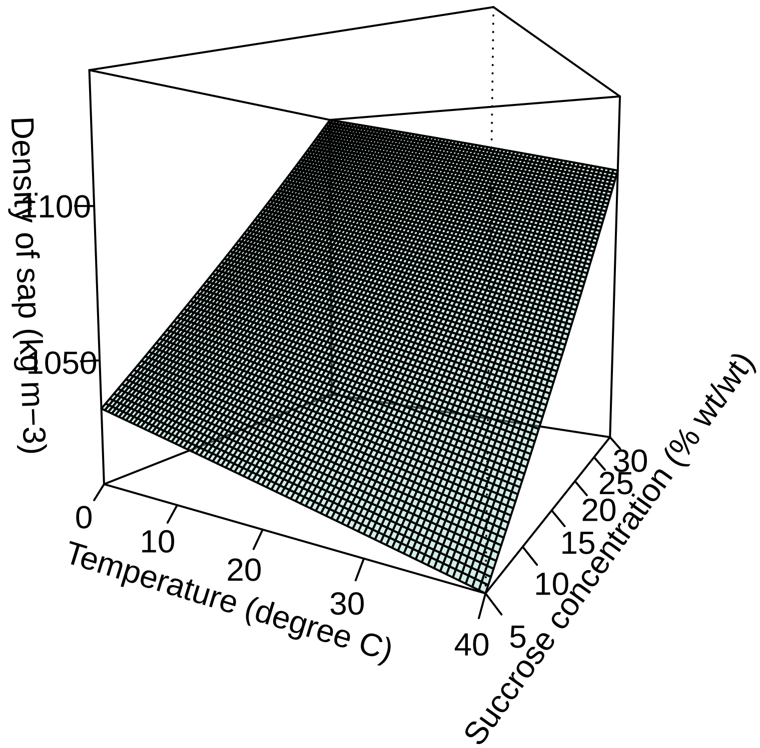

Figure 2: Surfaces of phloem sap density versus temperature and succrose concentration.

References

De Schepper, V., De Swaef, T., Bauweraerts, I., Steppe, K., 2013. Phloem transport: A review of mechanisms and controls. Journal of Experimental Botany 64, 4839–4850.

De Schepper, V., Vanhaecke, L., Steppe, K., 2011. Localized stem chilling alters carbon processes in the adjacent stem and in source leaves. Tree Physiology 31, 1194–1203.

Gould, N., Minchin, P.E.H., Thorpe, M.R., 2004. Direct measurements of sieve element hydrostatic pressure reveal strong regulation after pathway blockage. Functional Plant Biology 31, 987.

Jensen, K.H., Mullendore, D.L., Holbrook, N.M., Bohr, T., Knoblauch, M., Bruus, H., 2012. Modeling the Hydrodynamics of Phloem Sieve Plates. Frontiers in Plant Science 3.

Jensen, K.H., Savage, J.A., Holbrook, N.M., 2013. Optimal concentration for sugar transport in plants. Journal of The Royal Society Interface 10, 20130055–20130055.

Johnsen, K., Maier, C., Sanchez, F., Anderson, P., Butnor, J., Waring, R., Linder, S., 2007. Physiological girdling of pine trees via phloem chilling: Proof of concept. Plant, Cell and Environment 30, 128–134.

Münch, E., 1927. Versuche uber den Saftkreislauf. Berichte der Deutschen Botanischen Gesellschaft 17.

Peuke, A.D., Windt, C., Van As, H., 2006. Effects of cold-girdling on flows in the transport phloem in Ricinus communis: Is mass flow inhibited? Plant, Cell and Environment 29, 15–25.

Savage, J.A., Beecher, S.D., Clerx, L., Gersony, J.T., Knoblauch, J., Losada, J.M., Jensen, K.H., Knoblauch, M., Holbrook, N.M., 2017. Maintenance of carbohydrate transport in tall trees. Nature Plants 3, 965–972.

Schaberg, P.G., Murakami, P.F., Butnor, J.R., Hawley, G.J., 2017. Experimental branch cooling increases foliar sugar and anthocyanin concentrations in sugar maple at the end of the growing season. Canadian Journal of Forest Research 47, 696–701.