

Does the response of leaf stomata to light and vapour pressure follow from limitations in long distance transport?

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The Water transport capacity of the soil-plant - atmosphere- continuum restricts leaf gas-exchange. The quantity of transpired water cannot exceed that transported from soil to leaves on sustained bases. The plant properties that influence the transport rate are permeability and path length of the conducting tissue and the area of conducting and uptaking tissue relative to the area of the transpiring surface. When trees transpire excessively relative to the supply capacity the tension in the water column rises and air is drawn into the conducting tissue leading to embolism. If the transpiration remains high, this may lead to a so called runaway embolism resulting into permanent dysfunction of xylem. To avoid these negative impacts, plants seem to regulate stomatal opening before a threshold tension, or minimum leaf water potential, is reached (Sperry et al. 2002). As tree height increases, the minimum leaf water potential is reached with lower transpiration rate as the maintenance of same transpiration rate with increasing length requires larger pressure difference, i.e. lower water potential at the leaf (Ryan and Yoder 1997). The hydraulic limitation may thus decrease the productivity of large trees (Ryan and Yoder 1997).

Less attention has been paid to the implications of phloem transport to stomatal regulation and tree productivity although sink limitation has been suggested to be one important restriction for photosynthetic production. Continuous phloem transport requires that the sugar loading to phloem is able to draw water osmotically from the surrounding cells at the source tissue (i.e. leaves) while it is lost to surrounding tissue at sinks as response to sugar unloading. If this was not the case, the phloem sieve tubes would lose the turgor pressure gradient and sugar translocation from the leaves would stop. In practise this means that phloem transport is competing with transpiration for water in leaves. In principle, the sugar loading rate could compensate any transpiration rate. However, very high sugar concentration in phloem sap would make too viscous preventing the transpiration. Like runaway embolism also the latter phenomena has very strong positive feedback resulting into very abrupt stop in the phloem transport (Hölttä et al. 2005).

We studied how stomata should regulate leaf gas exchange to maintain as high assimilate transport in phloem as possible in a coupled tree xylem - phloem transport model (Hölttä et al. 2005). From the point of view of trees this means maximizing the available assimilates at the sites of carbon utilisation (i.e. sinks). We kept the stomata as open as possible while maintaining the xylem and phloem fluxes and kept phloem turgor positive throughout the phloem and observed how variation in the main driving variables of photosynthesis, intercepted radiation and air vapour pressure deficit influenced stomatal opening. For the sake of simplicity, we assumed a simple Michaelis-Menten light response and linear response to leaf internal CO₂ for photosynthetic rate. The sugar loading at the source was considered directly proportional to photosynthetic rate and unloading at the sink was assumed proportional to phloem sugar concentration. We also assumed increased xylem embolism with increasing water tension in the stem according to the air-seeding hypothesis.

Figure 1 shows the variation of stomatal conductance as a function of light and vapour pressure deficit. The form of the response is very close to observed variation of stomatal conductance to variation of these variables. In low light the stomata are kept closed due to low photosynthetic rate that allows only very low osmotic pressure to develop in the phloem tissue. If stomata would be

opened more, transpiration would start to draw water also from the phloem leading to loss of turgor there. At high light, excessive sugar loading would make the viscosity of the phloem sap so high that it would prevent transport of sugars, leading to so called feed-forward response of the stomata.

The above model is applied to realistic tree structures using the model LIGNUM (shading and transport pathway) to study how variation in leaf position as regards to light and transport pathway should influence the stomatal behaviour relative to the top of the tree.

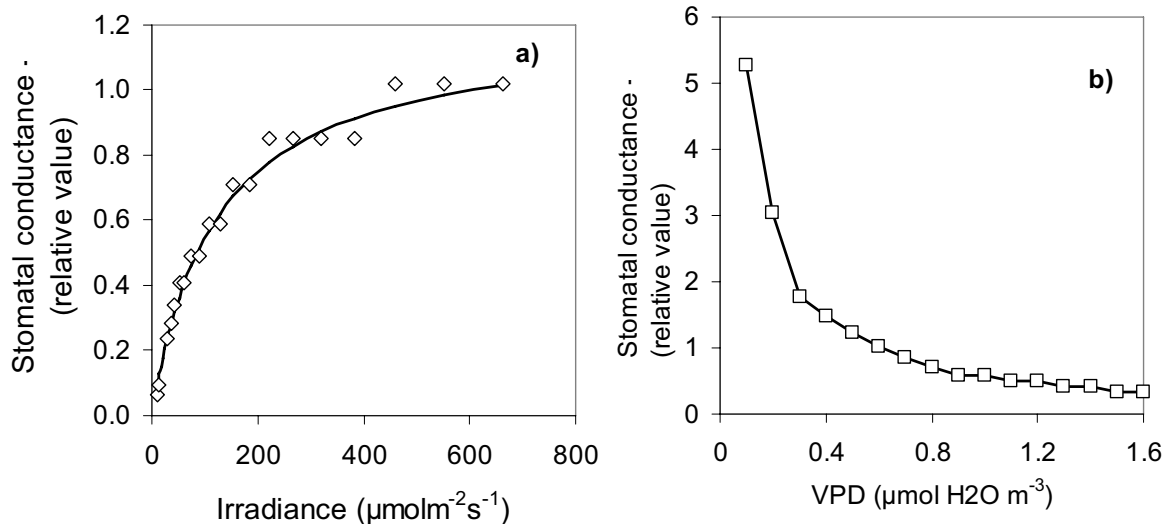


Figure 1. a) Simulated response of stomatal conductance to irradiance on the leaf surface and b) Simulated response of stomatal conductance to leaf vapour pressure deficit when leaf absorbed irradiance was kept at $400 \mu\text{molm}^{-2}\text{s}^{-1}$. The stepwise increase in the stomatal conductance in figure a) is due to used numerical method. The used trend line is fitted using Michaelis-menten type function.

References

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