

## Hydraulic constraints influence the distribution of canopy photosynthetic properties

Mikko Peltoniemi<sup>1,2,3,\*</sup>, Remko Duursma<sup>4</sup> and Belinda Medlyn<sup>3</sup>

<sup>1</sup>Finnish Forest Research Institute (METLA), Vantaa, Finland. <sup>2</sup>Department of Forest Sciences, University of Helsinki, Helsinki, Finland. <sup>3</sup>Department of Biological Sciences, Macquarie University, North Ryde, NSW, Australia. <sup>4</sup>Hawkesbury Institute for the Environment, University of Western Sydney, Penrith, NSW, Australia.

\*correspondence:mikko.peltoniemi@metla.fi

**Highlights:** We showed that limited water transport capacity to upper canopy leaves leads to sub-optimal photosynthetic performance of a tree. In these cases, the widely applied assumption of optimal N distribution that follows irradiance distribution does not hold. Hydraulically constrained optimum N distribution would be flatter than the distribution of irradiance. We further showed that in order to maximize canopy photosynthesis, trees should allocate water transport capacity and N co-optimally, which means allocating both of them according to irradiance distribution.

**Keywords:** Canopy, Hydraulic conductance, Nitrogen, Optimal, Photosynthesis, Resource allocation

Leaf properties vary significantly within plant canopies, due to the strong gradient in light availability through the canopy. Leaves near the canopy top have high nitrogen (N) and phosphorus content per unit leaf area, high leaf mass per area, and high photosynthetic capacity, compared to leaves deeper in the canopy. Variation of leaf properties has been explained by the optimal distribution of resources, particularly nitrogen, throughout the canopy. Studies of the optimal distribution of leaf nitrogen (N) within canopies have shown that, in the absence of other constraints, the optimal distribution of N is proportional to light. This is an important assumption in the big-leaf models of canopy photosynthesis and widely applied in current land-surface models. However, measurements have shown that the gradient of N in real canopies is shallower than the optimal distribution. One thing that has not yet been considered is how the constraints on water supply to leaves influence leaf properties in the canopy. Leaves with high stomatal conductance tend to have high transpiration rate, which suggests that for the efficient operation of canopy, high light leaves should be serviced by more water. The rate of water transport depends on the hydraulic conductance of the soil-leaf pathway. We extend the work on optimal nitrogen gradients by considering the optimal co-allocation of nitrogen and water supply within plant canopies. We developed a simple “toy” two-leaf canopy model and optimised the distribution of N and hydraulic conductance (K) between the two leaves. We asked whether the hydraulic constraints to water supply can explain shallow N gradients in canopies. We found that the optimal N distribution within plant canopies is proportional to the light distribution only if hydraulic conductance is also optimally distributed. The optimal distribution of K is that where K and N are both proportional to incident light, such that optimal K is highest to the upper canopy. If the plant is constrained in its ability to construct higher K to sun exposed leaves, the optimal N distribution does not follow the gradient in light within canopies, but instead follows a shallower gradient. We therefore hypothesize that measured deviations from the predicted optimal distribution of N could be explained by constraints and costs on the distribution of K within canopies. Distribution of N in tall canopies would be particularly constrained unless these trees were unable to invest in the construction and maintenance of high hydraulic conductance to peripheral leaves. Further empirical research is required to the extent to which plants can construct optimal K distributions, and whether shallow within-canopy N distributions can be explained by sub-optimal K distributions. Future development of ecosystem carbon and water exchange models could benefit from integration of water supply and other constraints influencing canopy N distribution.

### LITERATURE CITED

Peltoniemi MS, Duursma RA, Medlyn BE. 2012. Co-optimal distribution of leaf nitrogen and hydraulic conductance in plant canopies. *Tree Physiology* 32: 510-519