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Testing for non-stomatal limitations to optimisation behaviour under drought on contrasting plant functional types

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Stomatal aperture is thought to operate to minimise leaf water loss per unit of carbon (C) gain. The benefit of opening stomata is to increase the concentration of CO_2 at the sites of carboxylation, but the nature of associated costs remains unclear. Water loss can be considered as a direct cost to the plant, but it also leads to non-stomatal limitations (NSL) to C gain, either through reduced carboxylation capacity ($V_{c,max}$) or mesophyll conductance (g_m), or both. According to a new formulation proposed by Dewar et al. (2018), these indirect, non-stomatal, costs of water loss would lead to different function forms of optimal stomatal response. Although in reality such a dichotomy is unlikely and both forms of NSL could coexist, we might expect a certain type of NSL to dominate for a given plant functional type (PFT) depending on leaf morphology. In PFTs with long-lived leaves and high leaf mass area (LMA), leaves are more likely to experience stress during their lifespan, thus, we expect their photosynthetic machinery to be less sensitive to fluctuations in leaf water potential and NSL should arise mainly from reduced g_m. In PFTs with shorter-lived leaves and lower LMA, NSL arising from reduced carboxylation capacity should prevail. Here, we tested the suitability of these two optimal stomatal response formulations (g_m- or $V_{c,max}$-driven) on six PFTs (C4 crop, grass, fern, conifer, broadleaved evergreen and deciduous trees) at two stages of leaf ontogeny. We measured gas-exchange over a vapour pressure deficit gradient in mature and developing leaves and in well-watered and water-stressed plants, grown under controlled conditions. We found that the marginal water cost of C gain decreased under water stress in broad-leaved trees, but not in other PFTs, and it did not change between developing and mature leaves. Both the g_m- or $V_{c,max}$-driven formulations fit our data, suggesting that stomata behaved according to optimisation theory for all PFTs, except for ferns where stomata operated optimally only when subjected to water stress. The $V_{c,max}$-driven formulation was the best fit to our gas-exchange data for all PFTs, suggesting that NSL caused by carboxylation capacity override mesophyll diffusivity, regardless of leaf morphology.

Reference:

Dewar R., Mauranen A., Mäkelä A., Hölttä T., Medlyn B. & Vesala T. 2018 New insights into the covariation of stomatal, mesophyll and hydraulic conductances from optimization models incorporating nonstomatal limitations to photosynthesis New Phytologist DOI: 10.1111/nph.14848