

Title: Evapotranspiration: From kinetic theory to the limits of plant life

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Abstract: In 1898, Francis Darwin noted that *“transpiration is stomatal rather than cuticular, so that other things being equal, the yield of watery vapour depends on the degree to which stomata is open, and may be used as an index to their condition”*. Curiously, Darwin was a harsh critic of cohesion-tension theory in plant xylem noting that *“To believe that columns of water should hang in the tracheals like solid bodies, and should, like them, transmit downwards the pull exerted on them at their upper ends by the transpiring leaves, is to some of us equivalent to believing in ropes of sand”*. The developments of these two ideas in parallel with progress in statistical mechanics and sucrose transport in phloem are reviewed and linked together using optimality theories. This concept has been particularly successful in explaining the form and function of terrestrial vegetation from eco-hydrological and carbon-economy perspectives, and across spatial and temporal scales. Any optimality model is based on three key ingredients: an objective function that describes the gain that needs to be maximized or loss to be minimized, a control variable that shifts the dynamics in the desired direction, and a set of constraints that account for environmental conditions and conservation laws bounding the system. All three ingredients are difficult to define and quantify – especially in complex biological and ecological systems. Despite these difficulties, optimality approaches may complement process-based approaches when mechanistic knowledge is scarce - resembling 'closure models' in turbulence theories. At the leaf scale, it is often hypothesized that carbon gain is maximized, thus providing a quantifiable objective for a mathematical definition of optimality conditions. Eco-physiological trade-offs and fluctuating resource availability introduces natural bounds to this optimization process. In particular, carbon uptake from the atmosphere is inherently linked to water losses from the soil as water is taken up by roots and evaporated. Hence, fluctuating soil moisture constrains the amount of carbon that can be taken up and assimilated into new biomass. The problem of maximizing photosynthesis at a given water availability by modifying stomatal conductance, the plant-controlled variable to be optimized, has been traditionally formulated for short time intervals over which soil moisture changes can be neglected. This simplification led to a mathematically open solution, where the undefined Lagrange multiplier of the optimization (equivalent to the marginal water use efficiency) is heuristically determined via data fitting. Here, a set of models based on different assumptions that account for soil moisture dynamics over an individual dry-down are proposed so as to provide closed analytical expressions for the carbon gain maximization problem for varying soil moisture resources, atmospheric CO<sub>2</sub> levels, and vapor pressure deficit. A blueprint of how these theories can be bridged to explain widely used empirical formulations of stomatal conductance and showing their connection to the capacity of the phloem to transmit sugar are discussed.