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Wind-induced leaf transpiration

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ABSTRACT

While the significance of leaf transpiration (f_e) on carbon and water cycling is rarely disputed, conflicting evidence has been reported on how increasing mean wind speed (U) impacts f_e from leaves. Here, conditions promoting enhancement or suppression of f_e with increasing U for a wide range of environmental conditions are explored numerically using leaf-level gas exchange theories that combine a stomatal conductance model based on optimal water use strategies (maximizing the 'net' carbon gain at a given f_e), energy balance considerations, and biochemical demand for CO_2. The analysis showed monotonic increases in f_e with increasing U at low light levels. However, a decline in modeled f_e with increasing U were predicted at high light levels but only in certain instances. The dominant mechanism explaining this decline in modeled f_e with increasing U is a shift from evaporative cooling to surface heating at high light levels. New and published sap flow measurements for potted *Pachira macrocarpa* and *Messerschmidia argentea* plants conducted in a wind tunnel across a wide range of U ($2 - 8 \text{ m s}^{-1}$) and two different soil moisture conditions were also employed to assess how f_e varies with increasing U. The radiative forcing imposed in the wind tunnel was only restricted to the lower end of expected field conditions. At this low light regime, the findings from the wind tunnel experiments were consistent with the predicted trends.

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1. Introduction

The global water and carbon cycle sensitivity to stomata predicted by global climate models that employ the Ball-Berry [3] or Leuning [44] stomatal conductance formulations has been convincingly documented [6,13,21]. Likewise, detailed ecosystem models predicting gas exchange between the biosphere and atmosphere are analyzed in terms of their sensitivity to stomatal conductance [1,37]. Since water loss through stomata (i.e., transpiration) to the dry atmosphere is inevitable when CO_2 uptake (i.e., assimilation) occurs, how stomata respond to environmental factors has long been an active research area. Environmental factors governing transpiration (f_e) from leaves include, at minimum, atmospheric CO_2 concentration (c_a), air temperature (T_a), air relative humidity (RH) or vapor pressure deficit (VPD), photosynthetically active radiation (PPFD), soil moisture (or leaf water potential) and mean wind speed (U) [52]. When surveying the literature encompassing a wide range of ecosystems and environ-

mental conditions, conflicting empirical results on the sign of $\partial f_e / \partial U$ emerged [7,10,11,17,23–25,28,30,31,39,49,63]. Positive, negative or week dependency of f_e on U for numerous forested canopies has been highlighted and discussed elsewhere [39]. This is perhaps not surprising and has been foreshadowed by Monteith [52] who pointed out that wind effects on f_e are a vexing problem because of their non-monotonic effects. The thickness of the laminar boundary layer pinned to a leaf surface, which monotonically depends on U, determines the diffusive path length for the exchanges of gases between the leaf surface and the turbulent atmosphere above the laminar boundary layer. However, U also dictates the heat exchange between leaves and the overlying atmosphere as well as the degree of evaporative cooling experienced at the leaf surface depending on the radiation load.

The Penman–Monteith (PM) equation that utilizes an energy balance has been extensively used to predict f_e for more than 50 years in hydrology. The dependence of f_e on U was discussed in the original work describing the PM equation, indicating that the sign of $\partial f_e / \partial U$ is mainly governed by a competition between evaporative cooling and surface heating (or cooling). However, the biotic controls for water transport through the stomatal pathway (i.e., encoded as stomatal conductance g_s here) remain weakly dependent on U

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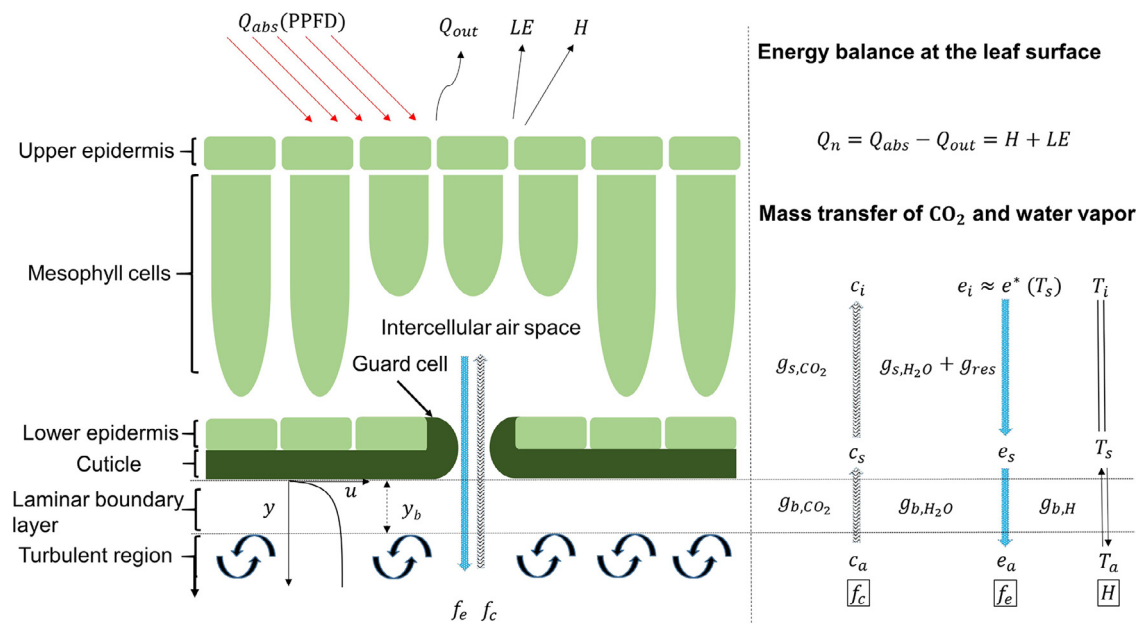
Fig. 1. Schematic of the mass (CO_2 and water vapor) and energy transfer between the leaf and the atmosphere. Note that u is the average wind velocity at the distance y from leaf surface within the laminar boundary layer and y_b is the thickness of the laminar boundary layer.

in the PM equation. To be clear, gas exchange through stomata of biologically active scalars is a complex problem given the biotic controls imposed by guard cells. The stomatal pathway serves as the main conduit for CO_2 and water vapor exchange, but this pathway can be further impacted by the laminar boundary layer (see Fig. 1). Thus, the main objective of this work is to disentangle wind effects from other exogenous environmental factors (e.g., radiative cooling) on g_s and f_e so as to explore the manifold of possible conditions promoting $\partial f_e / \partial U$ to reverse from > 0 to < 0 with increasing U.

When analyzing responses of stomata to their environment, temperature, atmospheric CO_2 concentration and water vapor pressure at the leaf surface are commonly assumed to be sufficiently close to their counterparts in the atmosphere represented by their states beyond the outer edge of the laminar boundary layer. A plausible argument for this approximation is that the thickness of the laminar boundary layer pinned to a leaf is sufficiently small so that the leaf is presumed to be 'well-coupled' to its environment. This approximation is common when interpreting leaf-gas exchange measurements in cuvettes where the flow rate through the chamber is sufficiently large to ensure the validity of the 'well-coupled' approximation. This approximation becomes also convenient when deriving relations between g_s and external environmental conditions [20]. Following this 'approximation', only monotonic increase in f_e with increasing U (i.e., $\partial f_e / \partial U > 0$ for increasing U) is expected primarily due to the reduced thickness of the laminar boundary layer. Because measurements (e.g., g_s) within such thin and disturbed laminar boundary layer adjacent to the leaf experiencing variable U are difficult to conduct, a leaf-level gas exchange model is needed and developed here for computing mass transfer of CO_2 and water vapor. The model combines biochemical demand for CO_2 as described by the Farquhar photosynthesis model [19] for C3 plants, a Fickian mass transfer including transfer through the laminar boundary layer that may be experiencing forced or free convection depending on U and the radiation load, an optimal leaf water use strategy that maximizes 'net' carbon gain for a given f_e describing stomatal aperture variations, and a leaf-level energy balance to accommodate evaporative cooling. Hence, the proposed model is able to bridge the gap between biological controls through stomata and the aerodynamic modifications due to U as may be experienced in natural settings. These calculations can be used to

arrive at a closed set of equations that predict f_e through g_s as impacted by variable U. The manifold of conditions promoting the sign reversal of $\partial f_e / \partial U$ with increasing U can therefore be numerically delineated.

To address this study objective, the manuscript is organized as follows. The model development is first presented in Sections 2.1 and 2.2 featuring the mass transfer equations for water and carbon dioxide gases through stomates and through the laminar boundary layer. The Farquhar photosynthesis model applied to the mesophyll and the energy balance at the leaf surface are then presented in Sections 2.3 and 2.4, respectively and then coupled to the mass transfer equations. The optimality hypothesis for stomatal aperture variations with variations in environmental conditions, which is used to mathematically close the overall set of equations for the model system, is discussed in Section 2.5. Other 'closure' conditions for stomatal aperture variations such as those widely used in land-surface schemes (e.g. a Ball-Berry or Leuning type closure) are briefly presented and elaborated on in an appendix. The goal of exploring these alternative and widely used stomatal conductance models is to highlight the non-linearities in $\partial f_e / \partial U$ with increasing U in such g_s model closure. A broad range of environmental conditions (mainly PPDF, soil moisture, and atmospheric humidity) are then explored in Sections 3.1.1–3.1.4 using the proposed model so as to unfold the possible environmental conditions above the laminar boundary layer promoting a sign reversal in $\partial f_e / \partial U$ from > 0 to < 0. Because the work here employs published and recent wind tunnel experiments on potted plants aimed at discerning the effects of U on measured f_e, these experimental conditions and the parameters required in model calculations are used as a case study for the model and are discussed in Section 3.2. The measured dependence of f_e on U at low PPFD is presented in Sections 3.2.1 and 3.2.2 using the published and new sap flow measurements conducted for two different potted plants with similar leaf dimensions in the wind tunnel across a wide range of U and for two different soil moisture states. The wind-tunnel setup has been described elsewhere [11] and only salient features of the experiment are summarized in Appendix A. Since physiological parameters and total leaf area for the potted plants were not directly measured in these wind tunnel experiments, comparisons between modeled and actual leaf-level f_e cannot be directly conducted (discussed later). However, the