The co-regulatory interaction of transpiration and water potential: Implications for stomatal conductance models and height growth in trees

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Abstract

Leaf water potential decreases with increasing transpiration rate according to an analogue of Ohm's law, while transpiration rate decreases with decreasing leaf water potential in the framework of stomatal control. This interaction is not accommodated in present-day models of stomatal conductance. We formally derive the equilibrium between these two counteracting processes for steady-state water conditions. We show that the mechanism considered causes an attenuation of the immediate effect of atmospheric variables on transpiration, which can improve existing models of stomatal conductance that presume non-interdependent variables. Parameters from European beech (*Fagus sylvatica* L.) are used to illustrate the results. Lastly, our model suggests that if height growth is limited by hydraulic constraints, then, irrespective of species, an increase of soil water potential by 1 Pa enables additional growth in height of circa 0.1 mm.

Keywords: cohesion-tension theory, hydraulic homeostasis, stomatal control, Ohm's law, hydraulic limitation hypothesis, nonlinearity

Introduction

Models of stomatal conductance g_s at the leaf level commonly postulate a one-sided dependence of g_s on different environmental factors (Damour et al., 2010). The multiplicative approach of Jarvis (1976), expressing g_s as a product of empirical functions of light intensity, leaf temperature, vapour pressure deficit, ambient carbon dioxide concentration and leaf water potential has had a lasting effect. In order to assess water stress more explicitly, follow-up work replaced the response to leaf water potential by a response to soil water deficit (Stewart, 1988), instant pre-dawn leaf water potential (Misson et al., 2004) as well as pre-dawn leaf water potential aggregated over a period of time (MacFarlane et al., 2004, White et al., 1999), the latter two variables being assumed a proxy for soil water potential.

The tendency of existing models to express stomatal conductance, g_s, as a one-sided function of leaf water potential, $\Psi(\ell)$, neglects the co-regulatory interaction between these two variables. Indeed, the response of g_s to $\Psi(\ell)$ is well documented for many species and conditions, and Damour et al. (2010) emphasise the relationship's "mechanistic basis because it is well demonstrated

that stomatal movements result from variations in leaf (or guard cell) water status, which result themselves from variations of evaporation in the substomatal cavity, and thus of the transpiration flux" (cf. also Buckley and Mott, 2002). However there is also a direct mechanistic impact of g_s on $\Psi(\ell)$. By an analogy to Ohm's law (see below), water potential along a soil-to-leaf water column is a function of leaf transpiration E, which is closely related to g_s via

$$E = \alpha \cdot \left(g_s^{-1} + g_b^{-1}\right)^{-1} \cdot \text{VPD}, \tag{1}$$

where g_b, VPD and α denote boundary layer conductance to water vapour, vapor pressure deficit and a physical parameter, respectively (Damour et al., 2010). Hence, E decreases with decreasing $\Psi(\ell)$, while $\Psi(\ell)$ increases with decreasing E. In this article, we formally determine the equilibrium between these counteracting mechanisms. We show how the result can be used with existing models for stomatal conductance, and discusses implications for height growth in trees. We illustrate our findings using parameters of European beech (*Fagus sylvatica* L.).

Model description

Let $E \geq 0$ [kg s^{-1}] denote the average transpiration rate from a leaf at a certain point in time. Let ℓ [m] denote the length of the soil-to-leaf pathway, and $K(s)$ [kg s^{-1} m^{-1} Pa^{-1}] the hydraulic conductivity of the root or shoot segment supplying the leaf and located $s \in [0, \ell]$ meters away from the soil-root interface. Under steady-state conditions, the water potential $\Psi(s) \leq 0$ [Pa] along the soil-to-leaf water column obeys

$$\frac{d}{ds}\Psi(s) = -\frac{E}{K(s)} - \rho g \cdot \frac{d\,\text{height}}{ds}, \tag{2}$$

by analogy to Ohm's law (Tyree and Zimmermann, 2002). The last term is due to gravitational force, with $\rho = 1000$ kg m^{-3} and $g = 9.81$m s^{-2} denoting density of water and acceleration due to gravity, respectively. $\Psi(0)$ and $\Psi(\ell)$ represent average soil and leaf water potential, respectively, at the given time. For leaf height h and given soil water potential $\Psi(0) = \Psi_0$, (2) solves to

$$\Psi(\ell) = -E \cdot \int_0^\ell \frac{1}{K(s)}\, ds - \rho g \cdot h + \Psi_0. \tag{3}$$

Tyree and Zimmermann (2002) established a sigmoid relationship of transpiration rate E against leaf water potential $\Psi(\ell)$. E reaches its maximum for $\Psi(\ell) = 0$, and tends to 0 as $\Psi(\ell)$ decreases. This corresponds to the closure of stomata in case of low leaf water potential in order to prevent the rupture of the root-to-leaf water column and the formation of embolisms. Depending on whether this mechanism applies sooner or later, species are characterised as isohydric and anisohydric, respectively (McDowell et al., 2008). Let the response of E to $\Psi(\ell)$ be described by an empirically obtained function

$$\Psi(\ell) \mapsto E(\Psi(\ell)). \tag{4}$$

Inserting (4) into (3) results in an equation for $\Psi(\ell)$,

$$\Psi(\ell) = -c_1 \cdot E(\Psi(\ell)) - c_2, \tag{5}$$

where for short $c_1 := \int_0^\ell \frac{1}{K(s)}\, ds > 0$ and $c_2 := \rho g \cdot h - \Psi_0 > 0$.

According to (3), $\Psi(\ell)$ decreases with increasing E, while E decreases with decreasing $\Psi(\ell)$ according to (4). The solution of (5) represents the equilibrium between these counteracting mechanisms. It exists and is unique: The right-hand side has a unique fixpoint $\Psi(\ell)^* < 0$, since it is a monotonically decreasing function of $\Psi(\ell)$, and negative at $\Psi(\ell) = 0$. The corresponding equilibrium transpiration rate follows from (4) as $E^* = E(\Psi(\ell)^*)$. Here, E^* varies only with soil-to-leaf hydraulic resistance $\int_0^\ell \frac{1}{K(s)}\, ds$, height h and soil water potential Ψ_0, which allows us to express it in terms of a species-specific function:

$$E^* = f\left(\int_0^\ell \frac{1}{K(s)}\, ds, h, \Psi_0\right). \tag{6}$$

Equilibrium stomatal conductance g_s^* follows from (1). For suitable representations of the sigmoid function (4), f can be derived explicitly (Appendix A1).

A priori, the soil-to-leaf hydraulic resistance $\int_0^\ell \frac{1}{K(s)}\, ds$ depends on individual tree anatomy. In Appendix A2, we argue that it may be approximated by a species-specific constant, in which case E^* could be expressed as a function of h and Ψ_0 alone.

Generalisation to other environmental variables Similar to Jarvis (1976) and follow-up work, the dependence of E^* (and analogously stomatal conductance) on soil water potential Ψ_0 can be readily extended to additional exogenous environmental variables such as radiation intensity, temperature, vapour pressure deficit and carbon dioxide concentration in a multiplicative way. (4) then generalises to

$$E = E(\Psi(\ell)) \cdot g(v_1, v_2, \ldots), \tag{7}$$

where $0 \leq g \leq 1$ describes the relative response, i.e. rescaled such that it equals 1 at optimal v_i values, of transpiration rate to the environmental variables v_i at fixed $\Psi(\ell) = 0$. The function g may, on its part, be the product of functions of one v_i each, as done in many models. This extension affects the calculation in above section only in that the constant c_2 in (5) changes. This is a consequence of the fact that the v_i, unlike leaf water potential, are exogenous variables. We thus obtain a species-specific function, generalising (6):

$$E^* = \widetilde{f}\left(\int_0^\ell \frac{1}{K(s)}\, ds, h, \Psi_0, v_1, v_2, \ldots\right).$$

Unlike Jarvis (1976) and followers, this is not a multiplicative approach in the narrow sense, since varying the v_i also affects $\Psi(\ell)$ by inducing a different E^*-$\Psi(\ell)^*$ balance. If the immediate effect of varying v_i is an increase (decrease) of transpiration rate, this increase (decrease) would be lessened since it leads to a small decrease (increase) in leaf water potential, which, on its turn, leads to a small decrease (increase) of transpiration rate. For instance, if g were linearly increasing (decreasing) in v_1, then $\widetilde{f}$ would be a concave (convex) function of v_1. The response of E^* to varying v_i is thus more complex than the term g alone, specifically in that its immediate effect is attenuated as a consequence of the interaction of transpiration and leaf water potential.

Simulation example We illustrate the above results using parameters for European beech (*Fagus sylvatica* L.). We use the representation in Appendix A1 to describe the response of E to $\Psi(\ell)$, for which parameters in (A1) were estimated as $p_1 = 1.7 \cdot 10^{-4}$, $p_2 = 1.8$, $p_3 = 3$, using data from Lemoine et al. (2002), and, for convenience, a linear approximation of (1), as suggested by Monteith (1995), $g_s \approx 60.24 \cdot E$, based on data from Cochard et al., 2000. $\int_0^\ell \frac{1}{K(s)}\, ds$ was set to $2.3 \cdot 10^4$ (Aranda et al., 2005). To exemplify the property described in the above paragraph, we considered an additional, hypothetical environmental variable, $v_1 \in [0, 1]$, for which the immediate response of E is assumed as $g(v_1) = v_1$, in the notation of (7). For $v_1 \equiv 1$, this reduces to the case described in (6).

Fig. 1 shows equilibrium leaf water potential and transpiration rate as a function of v_1 as well as height and soil water potential, which were combined into one term. Several nonlinearities can be observed: As described above, even though g is linear, the response of E^* to varying v_1 is concave, i.e. the ultimate effect of varying v_1 is attenuated. Similarly, $\Psi(\ell)^*$ is a nonlinear function of v_1. E^* shows a sigmoid response to $-\rho g \cdot h + \Psi_0$, which results from the qualitatively similar response of E to $\Psi(\ell)$. Lastly, the response of $\Psi(\ell)^*$ to changing Ψ_0 is nonlinear, which would not be the case if E were independent from $\Psi(\ell)$ in (2).

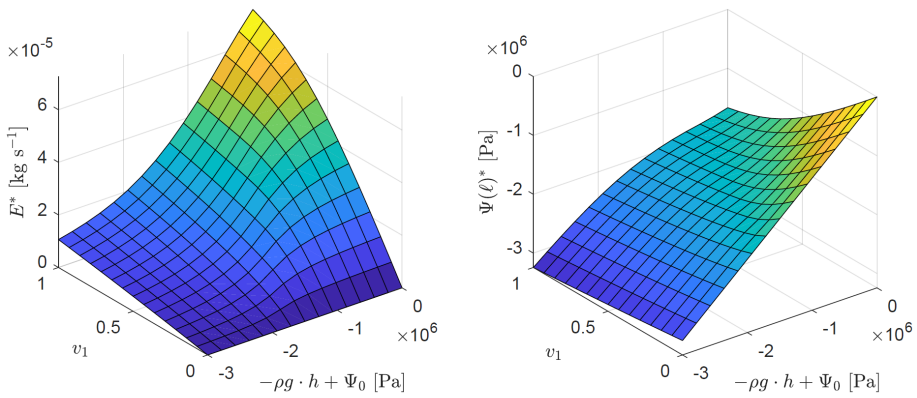

Figure 1: Equilibrium leaf water potential (left) and transpiration rate (right) in European beech as a function of two environmental variables (see text for details). Each additional 1 m in leaf height h corresponds to a reduction of $-\rho g \cdot h + \Psi_0$ by $\rho g = 9810\,\mathrm{Pa}$.

Discussion

The strong impacts that current climatic trends and weather events have on tree and forest growth require a sound understanding of the stress tolerance of trees (Hartmann, 2011). Models can help to better map stress reactions and thus offer decision support for the selection of resistant and resilient species in order to avert future damage. The interaction of water potential and transpiration described here, as well as the demonstrated effect of this regulatory circuit on the impact of other environmental variables, contributes to this strategy.

We have shown that the relationship between leaf water potential and transpiration is not unilateral as tacitly assumed in current models, but interactive. We developed a model to accommodate this mechanism, and demonstrated how it can be used with existing models for stomatal conductance, in which it proved to attenuate the immediate effect of varying exogenous environmental variables. This addresses a major criticism of multiplicative approaches, namely the supposedly independent action of the different factors (Damour et al., 2010).

According to (3), $\Psi(\ell)^*$ decreases with height h, and thus so does E^*. Because of the positive relationship between transpiration rate and photosynthesis, the same is true for the latter variable, which implies that an increase in height has a decreasing effect on carbon assimilation at the leaf level, other things being equal. The hydraulic limitation hypothesis (Ryan and Yoder, 1997) suggests that this mechanism induces the deceleration and eventual limitation of tree height growth. In (3), the roles of soil water potential, Ψ_0, and height, in terms of $\rho g \cdot h$, are interchangeable (cf. Fig. 1). Provided that the effect of height on the total hydraulic resistance $\int_0^\ell \frac{1}{K(s)}\, ds$ is negligible (which we argue to be the case in Appendix A2), this would imply that, if water were the limiting factor to height growth according to the hydraulic limitation hypothesis, an increase of Ψ_0 by 1 Pa would enable an increase in height by $\frac{1}{\rho g} \approx 0.1\,\mathrm{mm}$.

Despite further supportive evidence (Hubbard et al., 1999, Martínez-Vilalta et al., 2007), Becker et al. (2000b) and Ryan et al. (2006) questioned the hydraulic limitation hypothesis. Among several alternative reasons suggested to play a more important role (Martínez-Vilalta et al., 2007), reduced turgor pressure has been hypothesised to limit height growth in terms of cell expansion and division (Fatichi et al., 2014). This variable is affected by low leaf water potential, induced by the very mechanism described here.

We made several simplifying assumptions in our model that can be relaxed while retaining the key mechanism. The steady-state assumption of the tree's water balance is an idealisation since water storage in trees underlies diurnal fluctuations (Tyree and Zimmermann, 2002). Nevertheless, in the long term, it may be a reasonable simplification. Linked to this is the non-consideration of the horizontal transport of water within the tree (Tyree and Zimmermann, 2002) in our model. Although this is an important process, it plays a much smaller role than vertical movement, an observation that gave rise to the concept of hydraulic branch autonomy (Sprugel et al., 1991). We tacitly assumed the establishment of the E^*-$\Psi(\ell)^*$ equilibrium for given environmental conditions such as soil water potential Ψ_0 to occur instantaneously. Indeed, it has been shown that stomata open and close very quickly (Saliendra et al., 1995, Salleo et al., 2000, 2001). Nevertheless, applying the model to a much smaller time scale would require modifications e.g. in terms of a smooth change in stomata aperture over time in response to a changing environment, as well as a delay in its interaction with water potential. The balancing between the probability for embolism formation, which, in so-called vulnerability curves, is described as a function of water potential, and the repair of embolisms (Tyree and Zimmermann, 2002) is only implicitly accounted for in our model, and could be considered in a mechanistic way. Lastly, while treated as a given exogenous parameter in our model, soil water potential is, in reality, subject to the functioning of the individual tree as well as the larger stand community.

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Appendix

A1 Explicit calculation of equilibrium leaf water potential $\Psi(\ell)^*$

Let the simple algebraic sigmoid function

$$E(\Psi(\ell)) = p_1 \cdot \frac{\Psi(\ell) + p_2}{1 + p_3 \cdot |\Psi(\ell) + p_2|} + \frac{p_1}{p_3}, \tag{A1}$$

with parameters p_1, p_2, $p_3 > 0$ controlling vertical dilatation, horizontal translation and steepness, respectively, describe the empirically measured response of transpiration rate E to leaf water potential $\Psi(\ell)$. As opposed to certain alternative sigmoid function types such as the logistic function used in the regression by Tyree and Zimmermann (2002), this form allows the explicit calculation of the equilibrium leaf water potential in (5). It reads

$$\Psi(\ell)^* = \begin{cases} \frac{1}{2p_3^2}\Big(p_3 - c_3 - p_3\sqrt{1 + 4c_1p_1 + 2c_2p_3 - 2p_2p_3 + p_3^2(c_2 - p_2)^2}\Big) & \text{if } p_2 \geq c_2 \\ \frac{1}{2p_3^2}\Big(- p_3 - 2c_1p_1p_3 - c_3 + \ldots \\ \sqrt{(p_3 + 2c_1p_1p_3 + c_3)^2 - 4p_3^2(c_1p_1 + c_2p_3 + 2c_1p_1p_2p_3 + c_2p_2p_3^2)}\Big) & \text{if } p_2 < c_2 \end{cases} \tag{A2}$$

where c_1 and c_2 are as in (5), and where we abbreviated $c_3 := c_2p_3^2 + p_2p_3^2$. Inserting (A2) into (A1) yields the explicit form of the equilibrium transpiration rate, denoted f in (6).

A2 Simplifying the total hydraulic resistance $\int_0^\ell \frac{1}{K(s)}\, ds$

For shoot segments, the allometric relation $K(s) = a \cdot C^b(s)$, where $C(s)$ denotes the branch cross-sectional area at s, and $a, b > 0$ are species-specific constants, is empirically documented for a range of species (Cochard et al., 2000, Cruiziat et al., 2002, Mencuccini, 2002, Patino et al., 1995, Tyree et al., 1991, Yang and Tyree, 1993, Zotz et al., 1998). This relationship illustrates the disproportionately strong impact of the smallest and final parts of the stembase-to-leaf pathway on the total hydraulic resistance, as opposed to a much smaller effect of thicker branches and the trunk. Empirical evidence for this was presented by Yang and Tyree (1993), Yang and Tyree (1994) and Tyree and Zimmermann (2002), who found that the major part of the water flow resistance in shoots was located in the leaf blade, petiole and smallest branches (in that order). Root hydraulic conductance has been studied less (Cruiziat et al., 2002, Tyree and Zimmermann, 2002). Allometric relationships between cross-sectional area and

conductance of root segment, similar to those for shoots, have been observed in some species (Doussan et al., 1999, Kotowska et al., 2015), although the allometric coefficients may differ from the ones for shoots (Gonzalez-Benecke et al., 2010). Analogous to the results for shoots, Tyree and Zimmermann (2002) found that the smallest parts of the roots, namely the radial non-vascular pathway from the surface of the fine roots to the vessels, as well as the fine roots themselves (in that order) account for most of the resistance in the root system.

These findings show that the shoot and root parts that dominate the total soil-to-leaf hydraulic resistance, namely the very smallest parts, are present in small and large trees alike, suggesting that soil-to-leaf hydraulic resistance depends little on the leaf's position in the tree, the tree's size or its age. This is in agreement with the theoretical considerations by West et al. (1999), Enquist (2000) and Becker et al. (2000a), who demonstrated that an appropriate tapering of the vascular conduits results in a hydraulic resistance that is independent of the path length. It may motivate to approximate the a priori tree-anatomy-specific soil-to-leaf resistance $\int_0^\ell \frac{1}{K(s)}\,ds$ by a species-specific constant.

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