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OPINION

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Equivalence of foliar water uptake and stomatal conductance?

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There is a consensus emerging that foliar water uptake (FWU) may be the norm rather than the exception in plants globally (Berry, Emery, Gotsch, & Goldsmith, 2019) and that it may influence our understanding of how plants are coupled with the physical environment. Evidence suggests that FWU may result in significant fluxes of water at the ecosystem scale (Binks et al., 2019) and could play a fundamental role in determining the hydraulic vulnerability of plants both in terms of partially decoupling canopies from the soil water status (Binks et al., 2019; Schreel & Steppe, 2019; Simonin, Santiago, & Dawson, 2009) and of the potential of branch-level uptake to refill embolized conduits (Mayr et al., 2014). The mechanism of water ingress into leaves is of wide interest, and various pathways have been proposed. These include water movement directly through the cuticle (Goldsmith, Matzke, & Dawson, 2013), either through pores (Schonherr, 2006), abrasion-related cracks (Hoad, Jeffree, & Grace, 1992), or adsorption onto, and transport through, the cuticular matrix (Schönherr & Schmidt, 1979); water movement through specialized structures such as trichomes (Eller, Lima, & Oliveira, 2016; Nguyen, Meir, Wolfe, Mencuccini, & Ball, 2016) or hydathodes (Martin & von Willert, 2000); and pathways for liquid water moving through stomata (Berry, White, & Smith, 2014; Burkhardt, Basi, Pariyar, & Hunsche, 2012).

In order to quantify the impact and magnitude of water taken up via FWU, it is necessary to determine the conductance to FWU, K_{FWU} ($\text{g m}^{-2}\ \text{MPa}^{-1}\ \text{s}^{-1}$) which, defined using Ohm's law analogy (van den Honert, 1948), is the flux into the leaf normalized by the water potential difference between the source and the leaf.

$$K_{FWU} = \frac{dM}{dt\ A\ \Delta\Psi} = \frac{F}{\Delta\Psi}, \tag{1}$$

where dM is the net water exchange between the leaf and atmosphere or surface water (g), A is leaf area (m^2), dt is time elapsed (s), $\Delta\Psi$ is the difference in water potential between the surface water and the leaf (MPa), and F is the flux ($\text{g m}^{-2}\ \text{s}^{-1}$). A "flux" here is defined as the net exchange of water over time normalized by cross-sectional area, and while in the context of FWU, it is water moving into the leaf from the external environment, we use the term to include transpiration in which the flux occurs in the opposite direction, where transpiration is positive and FWU is negative. K_{FWU} is required to estimate the total amount of water taken into the leaves over time and how foliar water uptake may change in response to changing climate. To date, however, only two publications have measured and reported this value: Guzman-Delgado, Earles, and Zwieniecki (2018) reported values of $0.084\ \text{mmol m}^{-2}\ \text{s}^{-1}\ \text{MPa}^{-1}$ for *Prunis dulcis* and $0.021\ \text{mmol m}^{-2}\ \text{s}^{-1}\ \text{MPa}^{-1}$ for *Quercus lobata*, while Binks et al. (2019) reported $0.122\ \text{mmol m}^{-2}\ \text{s}^{-1}\ \text{MPa}^{-1}$ as an average for six common Amazonian tree genera.

In this *Opinion*, we aim to show that the magnitude of the K_{FWU} values reported above are consistent with the diffusion of vapour into stomata under commonly occurring environmental conditions. Thus, we introduce the possibility that FWU could be partly, or even wholly, accounted for by vapour uptake in some species. The potential for this vapour flux into the leaf has been proposed previously and was intuitively referred to as "reverse transpiration" (Vesala et al., 2017), which is the terminology we adopt here.

K_{FWU} can be considered as fundamentally the same biophysical property as stomatal conductance: the flux of water between the leaf and the atmosphere normalized by a difference of water "concentration." For the derivation of stomatal conductance, g_s, the concentration of water vapour is expressed in the dimensionless units of mole fraction vapour pressure deficit, therefore giving g_s the same units as transpiration, E, mmol m^{-2} s^{-1}. Thus, the equation for g_s, assuming that boundary layer conductance is non-limiting and that there is a negligible difference between leaf and air temperature (Nobel, 1999), is

$$g_s = \frac{E}{D} = E\frac{P_a}{\mathrm{VPD}}, \tag{2}$$

where D is the mole fraction vapour pressure deficit (unitless), P_a is air pressure (kPa), and VPD is vapour pressure deficit (kPa). For measurements of stomatal conductance, the humidity in the leaf air spaces is always assumed to be at 100% relative humidity (RH), and thus, VPD = SVP (100 − $\mathrm{RH_{air}}$)/100, where SVP is saturation vapour pressure (kPa). In fact, the humidity in leaves is not always 100% but in equilibrium with the leaf water potential (Vesala et al., 2017), this assumption is addressed quantitatively later on in the text.

Because relative humidity has a water potential equivalent (e.g., 100% RH = 0 MPa, and 95% RH = −6.8 MPa at 20°C, Figure 1), it is possible to express g_s in the same units as K_{FWU} (becoming g_Ψ) by substituting D in Equation (1) for the water potential of the air (Ψ_a) making the two values directly comparable (see the Supporting Information for discussion of the limitations of expressing humidity as water potential):

$$g_\Psi = \frac{E}{\Psi_a}, \tag{3}$$

where Ψ_a is derived by (Pickard, 1981; Spanner, 1951)

$$\Psi_a = \frac{RT\,ln(\mathrm{RH}/100)}{V_w{\cdot}10^6}. \tag{4}$$

R is the universal gas constant (8.13 J mol^{-1} K^{-1}), T is the temperature (K), V_w is the molar volume of liquid water (1.80 × 10^{-5} m^3 mol^{-1}), and 10^6 is a conversion factor to express units in MPa. Thus, by combining Equations (1)–(4), we can convert the units of g_s to normalize by water potential difference (g_ψ, mmol m^{-2} s^{-1} MPa^{-1}):

$$g_\psi = -g_s\frac{VPD\,V_w{\cdot}10^6}{P_a\,RT\,ln(\mathrm{RH}/100)}. \tag{5}$$

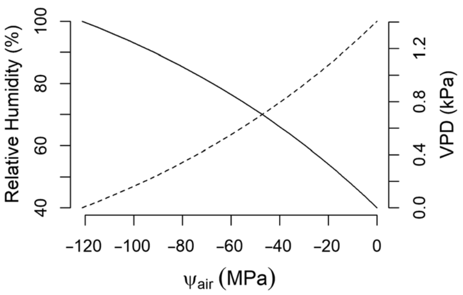

FIGURE 1 The equivalence between relative humidity (dashed line), vapour pressure deficit (VPD, solid line), and water potential

In a recent meta-analysis, Hoshika, Osada, de Marco, Peñuelas, and Paoletti (2018) found that g_{max} ranged from 70 to 360 mmol m^{-2} s^{-1} in woody plants and up to 610 mmol m^{-2} s^{-1} in crop plants, which is equivalent to g_ψ values of 0.010, 0.053, and 0.090 mmol m^{-2} s^{-1} MPa^{-1}, respectively (assuming g_s values measured at an average of 20°C and 70% RH, see the Supporting Information for sensitivity analysis). This range overlaps with the reported values for K_{FWU} listed above, showing that the measured FWU could have been partially or wholly due to vapour uptake (i.e., −E, Figure 2).

As stated previously, standard measurements of stomatal conductance make the assumption that the internal air spaces in leaves are at saturated vapour pressure (Cernusak et al., 2018; Gaastra, 1959). Therefore, the diffusion gradient considered for g_s is the difference between the saturated vapour pressure at leaf temperature and the actual vapour pressure of the air. However, this assumption is seldom correct as leaf water potentials <0 MPa result in equilibrium vapour pressures lower than saturation (Buckley & Sack, 2019; Vesala et al., 2017). Rearranging Equation (4) to find RH for a given water potential shows that, at 20°C, a leaf water potential of −1 MPa leads to an equilibrium vapour pressure equivalent of 99.2% RH. Therefore, while the

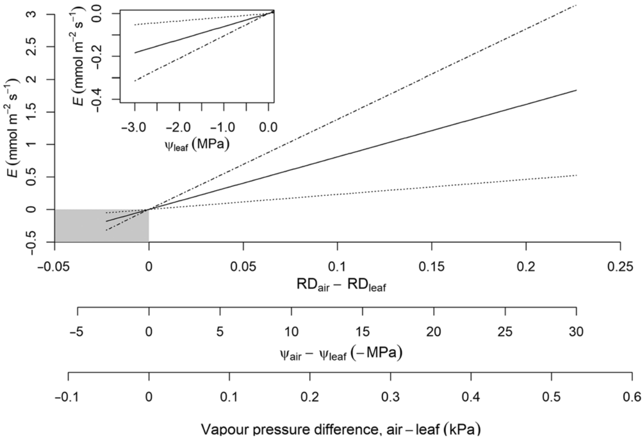

FIGURE 2 The relationship between water vapour flux between the leaf and atmosphere (E) at different leaf and atmospheric water contents. The three x-axes show different ways to express the difference in water content/concentration of the leaf and atmosphere. The first axis represents the difference in "relative deficit" between the leaf and the air, where RD is 1-(relative humidity/100). The second axis is the difference between air and leaf water potential, where air vapour pressure is expressed as its water potential equivalent. The third axis is the vapour pressure difference between the air and the leaf, which is equivalent to vapour pressure deficit, taking into account that VPD in the internal air spaces of the leaf is >0. The inset graph shows the detail of the shaded region in which the flux becomes negative (i.e., water vapour goes into the leaf, −E) over different leaf water potentials assuming that the $\mathrm{RH_{air}}$ = 100%. The different lines show representative values for stomatal conductance, where the dotted line is g_s = 100 mmol m^{-2} s^{-1}, the solid line is g_s = 350 mmol m^{-2} s^{-1}, and the dot dash line is g_s = 600 mmol m^{-2} s^{-1}

assumption is rarely correct, it generally has a minor effect on the calculation of stomatal conductance under conditions that favour photosynthesis. Other evidence suggests that internal leaf humidity may occur as much as 10% to 20% below saturation due to hydraulic limitations on liquid water movement through leaves (Cernusak et al., 2018). Under these conditions, when the leaf boundary layer is at saturated vapour pressure, as it would be when the leaves are wet or when dew is forming, the vapour pressure gradient is reversed favouring vapour movement into the leaf: reverse transpiration.

In order for reverse transpiration to occur, the following three conditions must be met:

1. leaf water potential of <0 MPa;
2. atmospheric humidity close to 100% RH (as it would be when leaves are wet or dew is forming); and
3. $g_s > 0$ mmol m^{-2} s^{-1}.

Due to the effect of gravity on the water column in trees, coupled with hydraulic resistance in the xylem, leaf water potentials are usually significantly less than 0 MPa in the absence of foliar water uptake (Binks et al., 2019); hence, Condition 1 of the three criteria above is very often met. In a study of 28 sites worldwide, Kim et al. (2010) show that leaves are wet for an average of 8.7 hr day^{-1}, during which time the leaf boundary layer humidity must be close to saturation, meaning that Condition 1 is met on average for around 30% of the time at the sampled sites. Finally, because of the methodological challenges to measuring stomatal conductance on wet leaves, few studies have measured this process. However, the effect of leaf wetting on g_s differs between species and has been variously reported to reduce, having no measureable effect on, or to increase stomatal conductance (Ishibashi & Terashima, 1995; Smith & McClean, 1989). Moreover, there is good evidence to suggest the widespread occurrence of positive g_s at night (Caird, Richards, & Donovan, 2007; de Dios et al., 2015). These factors together indicate that stomatal behaviour may vary outside the normal constraints of photosynthetic stomatal optimization (Mencuccini, Manzoni, & Christoffersen, 2019), suggesting that g_s does not always equal zero while leaves are wet, and therefore, Condition 2 is also expected to be met at least some of the time. Therefore, it seems highly likely that all three conditions will co-occur under natural conditions leading to the occurrence of reverse transpiration. Using the definition for K_{FWU} described in Equation (1), it is possible to determine the amount of water vapour that could theoretically diffuse into stomata under given conditions (Figure 3).

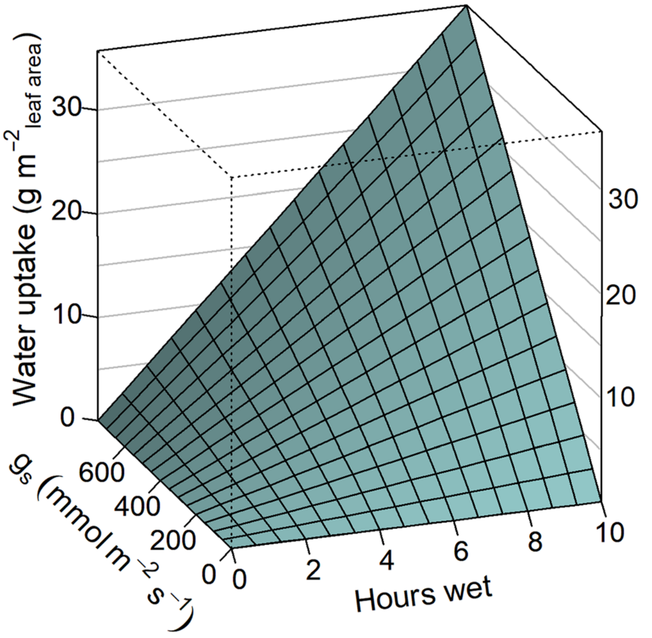

FIGURE 3 Relationship between the amount of water vapour diffusing into leaves, the duration of leaf wetness (or 100% atmospheric humidity), and stomatal conductance (g_s), given a mean leaf water potential of −0.5 MPa. This figure combines the outcomes of Equations (1) and (5) demonstrating the effect of stomatal conductance on water vapour uptake

There is some clear evidence, primarily from dye tracer experiments, for the existence of non-stomatal pathways for liquid water to move into leaves (Eller, Lima, & Oliveira, 2013; Gouvra & Grammatikopoulos, 2003; Nguyen, Meir, Wolfe, Mencuccini, & Ball, 2016). Moreover, films of liquid water have been reported to connect apoplastic water inside the leaf with free water on the leaf surface, facilitated by the presence of certain solutes (Burkhardt, 2010; Eichert & Goldbach, 2008). It therefore appears likely that there are multiple pathways of water entry into leaves, and these are likely to vary among species (Berry, Emery, Gotsch, & Goldsmith, 2019). What is different about the stomatal pathway, if it occurs, is that it could be highly dynamic and this would need to be taken into account in the method for determining K_{FWU}. Consequently, establishing the proportion of FWU that is accounted for by reverse transpiration may help with future investigation into this topic, and ultimately being able to represent K_{FWU} accurately in land-atmosphere models. The occurrence of reverse transpiration could have a number of significant implications: principally that the flux is under stomatal control and that evolutionary selection pressure may have acted on stomatal behaviour to increase the potential for water vapour uptake.

In conclusion, the purpose of this *Opinion* is to make researchers aware that—biophysically—g_s and K_{FWU} can be considered equivalent conductance terms. In order to determine the significance of FWU at canopy to global scales, it is necessary to measure a term for K_{FWU}, but future research should also aim to determine if (and in what taxa and climate regimens) this pathway is fundamentally different to g_s. The finding that reverse transpiration contributes significantly to foliar water uptake, and plant water status in general, may provide a fast-track route to the incorporation of atmosphere-leaf-atmosphere water fluxes into our existing understanding and models of plant-environment water relations.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Sensitivity of the conversion of gs to gψ on temperature (left) and relative humidity (right). gψ is expressed as a percentage of the value at 70% relative humidity and 20 oC on the y axes to enable an easy conversion of the figures presented in the main text to those derived from alternative values of temperature and humidity

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