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1 Equivalence of foliar water uptake and stomatal conductance?

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9

10 **Abstract**

11 Foliar water uptake, the uptake of atmospheric water directly into leaves, has been reported to
12 occur in nearly 200 species spanning a wide range of ecosystems distributed globally. Until
13 recently, this flux has not been taken into consideration in land–surface models representing
14 global fluxes of water, in interpreting plant hydraulic status or in the determination of
15 species' vulnerability to drought. A key trait required to represent foliar uptake at canopy to
16 ecosystem scales is conductance to foliar uptake, K_{FWU} , which is the flux of water into the
17 leaf normalised by the water potential difference between the leaf and water source. This
18 trait is biophysically equivalent to stomatal conductance, g_s ; however, the two variables are
19 typically normalised by different measures of water 'concentration'. Here we show that
20 when converted to the same units, the typical ranges of g_s overlap with the few published
21 values of K_{FWU} suggesting that, theoretically, water vapour moving in through the stomata
22 could partially, or even wholly, account for the fluxes attributed to foliar water uptake in
23 some species. Establishing the extent to which such 'reverse transpiration' contributes to
24 foliar uptake may be key to incorporating foliar water uptake into our existing understanding
25 of plant-atmosphere interactions.

26 **Key words**

27 Reverse transpiration, vapour exchange, unsaturation, water relations, water cycle, drought,
28 plant hydraulics

30 There is a consensus emerging that foliar water uptake (FWU) may be the norm rather than
31 the exception in plants globally (Berry, Emery, Gotsch, & Goldsmith, 2019), and that it may
32 influence our understanding of how plants are coupled with the physical environment.
33 Evidence suggests that FWU may result in significant fluxes of water at the ecosystem scale
34 (Binks et al. 2019), and could play a fundamental role in determining the hydraulic
35 vulnerability of plants both in terms of partially decoupling canopies from the soil water
36 status (Binks et al., 2019; Schreel & Steppe, 2019; Simonin, Santiago, & Dawson, 2009) and
37 of the potential of branch-level uptake to refill embolised conduits (Mayr et al., 2014). The
38 mechanism of water ingress into leaves is of wide interest and various pathways have been
39 proposed. These include water movement directly through the cuticle (Goldsmith, Matzke, &
40 Dawson, 2013), either through pores (Schönherr, 2006), abrasion-related cracks (Hoad,
41 Jeffree, & Grace, 1992), or adsorption onto, and transport through, the cuticular matrix
42 (Schönherr & Schmidt, 1979); water movement through specialised structures such as
43 trichomes (C. B. Eller, Lima, & Oliveira, 2016; Nguyen, Meir, Wolfe, Mencuccini, & Ball,
44 2016) or hydathodes (Martin & von Willert, 2000); and pathways for liquid water moving
45 through stomata (Berry, White, & Smith, 2014; Burkhardt, Basi, Pariyar, & Hunsche, 2012).

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

$$50 \quad K_{fu} = \frac{dM}{dt A \Delta\Psi} = \frac{F}{\Delta\Psi} \quad (1)$$

51 Where dM is the net water exchange between the leaf and atmosphere or surface water (g), A
52 is leaf area (m^2), dt is time elapsed (s), $\Delta\Psi$ is the difference in water potential between the
53 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
54 net exchange of water over time normalised by cross sectional area and, while in the context
55 of FWU it is water moving into the leaf from the external environment, we use the term to
56 include transpiration in which the flux occurs in the opposite direction, where transpiration is
57 positive and FWU is negative. K_{FWU} is required to estimate the total amount of water taken
58 into the leaves over time and how foliar water uptake may change in response to changing
59 climate. To date, however, only two publications have measured and reported this value:
60 Guzman-Delgado et al. (2018) reported values of $0.084 \text{ mmol m}^{-2} \text{ s}^{-1} \text{ MPa}^{-1}$ for *Prunus dulcis*
61 and $0.021 \text{ mmol m}^{-2} \text{ s}^{-1} \text{ MPa}^{-1}$ for *Quercus lobata*, while Binks et al. (2019) reported 0.122
62 $\text{mmol m}^{-2} \text{ s}^{-1} \text{ MPa}^{-1}$ as an average for six common Amazonian tree genera.

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

69 K_{FWU} can be considered as fundamentally the same biophysical property as stomatal
70 conductance: the flux of water between the leaf and the atmosphere normalised by a
71 difference of water ‘concentration’. For the derivation of stomatal conductance, g_s , the
72 concentration of water vapour is expressed in the dimensionless units of mole fraction vapour
73 pressure deficit, therefore giving g_s the same units as transpiration, E , $\text{mmol m}^{-2} \text{ s}^{-1}$. Thus,

74 the equation for g_s , assuming that boundary layer conductance is non-limiting and that there
75 is a negligible difference between leaf and air temperature (Nobel, 1999), is:

$$76 \quad g_s = \frac{E}{D} = E \frac{P_a}{VPD} \quad (2)$$

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

83 Because relative humidity has a water potential equivalent (e.g. 100 % RH = 0 MPa, and 95
84 % RH = -6.8 MPa at 20 °C, Fig. 1), it is possible to express g_s in the same units as K_{FWU}
85 (becoming g_Ψ) by substituting D in equation 2 for the water potential of the air (Ψ_a) making
86 the two values directly comparable (see SI for discussion of the limitations of expressing
87 humidity as water potential):

$$88 \quad g_\Psi = \frac{E}{\Psi_a} \quad (3)$$

89 Where Ψ_a is derived by (Pickard, 1981; Spanner, 1951):

$$90 \quad \Psi_a = \frac{RT \ln(RH/100)}{V_w \cdot 10^6} \quad (4)$$

91 R is the universal gas constant (8.13 J mol⁻¹ K⁻¹), T is the temperature (K), V_w is the molar
92 volume of liquid water (1.80x10⁻⁵ m³ mol⁻¹), and 10⁶ is a conversion factor to express units in

93 MPa. Thus, by combining equations 2-4, we can convert the units of g_s to normalise by water
94 potential difference (g_ψ , $\text{mmol m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$):

$$95 \quad g_\psi = -g_s \frac{VPD V_w \cdot 10^6}{P_a RT \ln(RH/100)} \quad (5)$$

96 In a recent meta-analysis, Hoshika et al. (2018) found that g_{max} ranged from 70 to 360 mmol
97 $\text{m}^{-2} \text{s}^{-1}$ in woody plants and up to 610 $\text{mmol m}^{-2} \text{s}^{-1}$ in crop plants which is equivalent to g_ψ
98 values of 0.010, 0.053 and 0.090 $\text{mmol m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$, respectively (assuming g_s values
99 measured at an average of 20 °C and 70 % RH, see SI for sensitivity analysis). This range
100 overlaps with the reported values for K_{FWU} listed above, showing that the measured FWU
101 could have been partially or wholly due to vapour uptake (i.e., $-E$, Fig 2).

102 As stated previously, standard measurements of stomatal conductance make the assumption
103 that the internal air spaces in leaves are at saturated vapour pressure (Cernusak et al., 2018;
104 Gaastra, 1959). Therefore, the diffusion gradient considered for g_s is the difference between
105 the saturated vapour pressure at leaf temperature and the actual vapour pressure of the air.
106 However, this assumption is seldom correct as leaf water potentials < 0 MPa result in
107 equilibrium vapour pressures lower than saturation (Buckley & Sack, 2019; Vesala et al.,
108 2017). Rearranging equation 4 to find RH for a given water potential shows that, at 20 °C, a
109 leaf water potential of -1 MPa leads to an equilibrium vapour pressure equivalent of 99.2 %
110 RH. Therefore, while the assumption is rarely correct, it generally has a minor effect on the
111 calculation of stomatal conductance under conditions that favour photosynthesis. Other
112 evidence suggests that internal leaf humidity may occur as much as 10 to 20 % below
113 saturation due to hydraulic limitations on liquid water movement through leaves (Cernusak et
114 al., 2018). Under these conditions, when the leaf boundary layer is at saturated vapour

115 pressure, as it would be when the leaves are wet or when dew is forming, the vapour pressure
116 gradient is reversed favouring vapour movement into the leaf: reverse transpiration.

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

- 118 1. leaf water potential of < 0 MPa,
- 119 2. atmospheric humidity close to 100 % RH (as it would be when leaves are wet or dew
120 is forming),
- 121 3. $g_s > 0$ mmol m⁻² s⁻¹

122 Due to the effect of gravity on the water column in trees, coupled with hydraulic resistance in
123 the xylem, leaf water potentials are usually significantly less than 0 MPa in the absence of
124 foliar water uptake (Binks et al., 2019); hence, condition 1 of the 3 criteria above is very
125 often met. In a study of 28 sites worldwide, Kim et al. (2010) show that leaves are wet for an
126 average of 8.7 hour day⁻¹, during which time the leaf boundary layer humidity must be close
127 to saturation, meaning that condition 2 is met on average for around 30 % of the time at the
128 sampled sites. Finally, because of the methodological challenges to measuring stomatal
129 conductance on wet leaves, few studies have measured this process. However, the effect of
130 leaf wetting on g_s differs between species and has been variously reported to reduce, have no
131 measureable effect on, or to increase stomatal conductance (Ishibashi & Terashima, 1995;
132 Smith & McClean, 1989). Moreover, there is good evidence to suggest the widespread
133 occurrence of positive g_s at night (Caird, Richards, & Donovan, 2007; de Dios et al., 2015).
134 These factors together indicate that stomatal behaviour may vary outside the normal
135 constraints of photosynthetic stomatal optimisation (Mencuccini, Manzoni, & Christoffersen,
136 2019), suggesting that g_s does not always equal zero while leaves are wet, and therefore
137 condition 3 is also expected to be met at least some of the time. Therefore, it seems highly

138 likely that all three conditions will co-occur under natural conditions leading to the
139 occurrence of reverse transpiration. Using the definition for K_{FWU} described in equation 1 it
140 is possible to determine the amount of water vapour that could theoretically diffuse into
141 stomata under given conditions (Fig 3).

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

157 In conclusion, the purpose of this *Opinion* is to make researchers aware that - biophysically -
158 g_s and K_{FWU} can be considered equivalent conductance terms. In order to determine the
159 significance of FWU at canopy to global scales it is necessary to measure a term for K_{FWU} ,
160 but future research should also aim to determine if (and in what taxa and climate regimens)
161 this pathway is fundamentally different to g_s . The finding that reverse transpiration

162 contributes significantly to foliar water uptake, and plant water status in general, may provide
163 a fast-track route to the incorporation of atmosphere-leaf-atmosphere water fluxes into our
164 existing understanding and models of plant-environment water relations.

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279 **Figure legends**

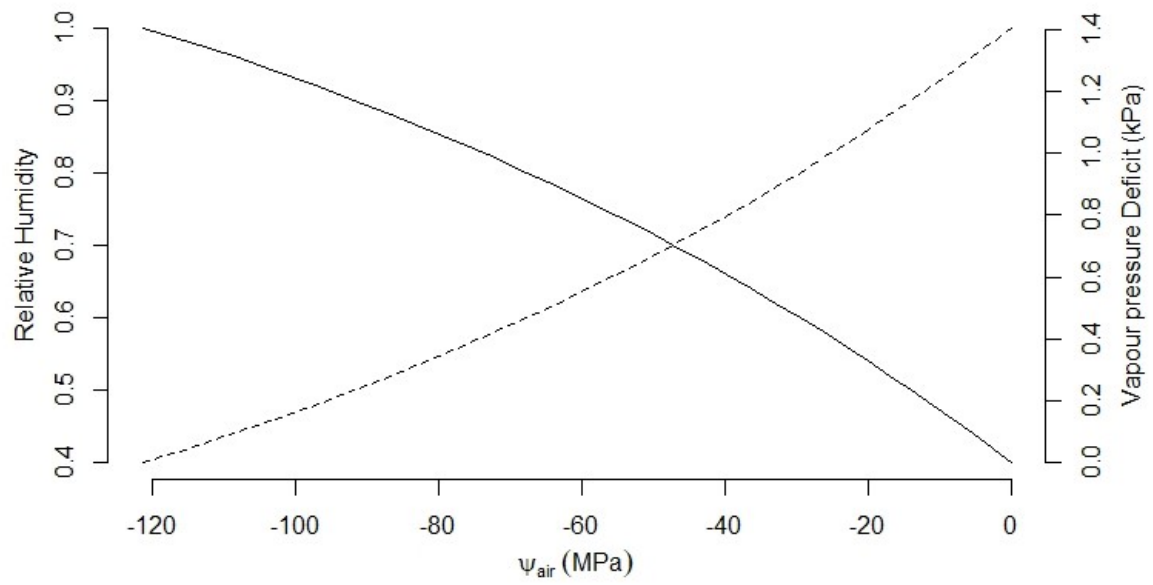
280 **Figure 1.** The equivalence between relative humidity (dashed line), vapour pressure deficit
281 (VPD, solid line) and water potential.

282 **Figure 2.** The relationship between water vapour flux between the leaf and atmosphere (E) at
283 different leaf and atmospheric water contents. The three x-axes show different ways to
284 express the difference in water content/concentration of the leaf and atmosphere. The first
285 axis represents the difference in ‘relative deficit’ between the leaf and the air, where RD is 1-
286 (relative humidity / 100). The second axis is the difference between air and leaf water
287 potential, where air vapour pressure is expressed as its water potential equivalent. The third
288 axis is the vapour pressure difference between the air and the leaf, which is equivalent to
289 vapour pressure deficit, taking into account that VPD in the internal air spaces of the leaf is >
290 0. The inset graph shows the detail of the shaded region in which the flux becomes negative
291 (i.e. water vapour goes into the leaf, $-E$) over different leaf water potentials assuming that the
292 $RH_{\text{air}} = 100\%$. The different lines show representative values for stomatal conductance
293 where the dotted line is $g_s = 100 \text{ mmol m}^{-2} \text{ s}^{-1}$, the solid line is $g_s = 350 \text{ mmol m}^{-2} \text{ s}^{-1}$ and the
294 dot dash line is $g_s = 600 \text{ mmol m}^{-2} \text{ s}^{-1}$.

295 **Figure 3.** Relationship between the amount of water vapour diffusing into leaves, the
296 duration of leaf wetness (or 100 % atmospheric humidity) and stomatal conductance (g_s),
297 given a mean leaf water potential of -0.5 MPa. This figure combines the outcomes of
298 equations 1 and 5 demonstrating the effect of stomatal conductance on water vapour uptake.

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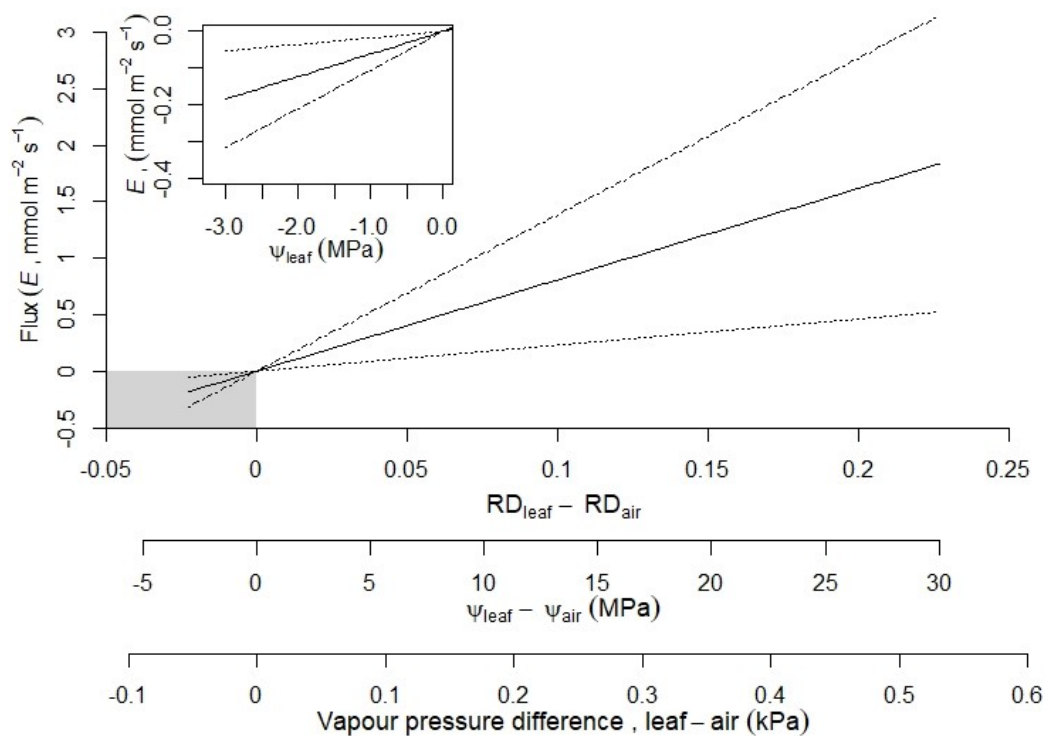
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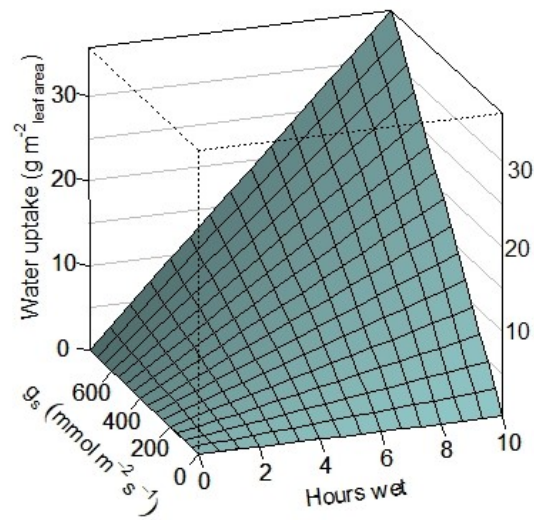
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329 **Figure 3.** Relationship between the amount of water vapour diffusing into leaves, the
330 duration of leaf wetness (or 100 % atmospheric humidity) and stomatal conductance (g_s),
331 given a mean leaf water potential of -0.5 MPa.

332

333 Equivalence of foliar water uptake and stomatal conductance?

334 **Supplementary Information**

335

336

337 **The sensitivity of g_{ψ} to temperature and humidity**

338 Stomatal conductance is the flux of water vapour (transpiration) normalised by the gradient

339 down which water vapour moves. The purpose of the normalisation is to get a

340 physiologically meaningful measure that is independent of environmental conditions.

341 However, because the relationship between saturated vapour pressure and air temperature is

342 highly non-linear, it is not possible to express stomatal conductance in a way that completely

343 negates the effect of the temperature and humidity at which the measurement was taken.

344 There are a number of different ways to represent the concentration of water vapour in air

345 including partial pressure (of vapour), mole fraction, relative humidity and water potential.

346 Of these, mole fraction (vapour pressure deficit) was chosen to normalise the transpiration

347 flux because the temperature dependence was least and differences in air pressure have no

348 effect at all, in contrast to the other measures {Nobel}.

349 In the main paper we have used water potential of the air, Ψ_{air} , to normalise the flux so that

350 transpiration can be interpreted in units consistent with plant hydraulics. However, Ψ_{air} , is

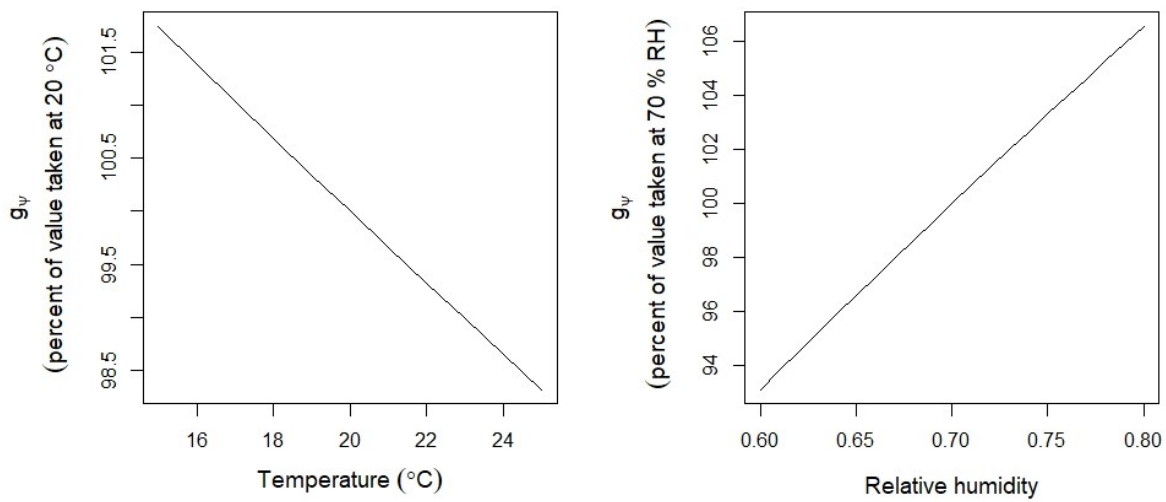
351 more sensitive to the conditions under which it is measured than mole fraction VPD.

352 Therefore, we had to assume values of humidity and temperature that represent the mean

353 conditions under which the original measures of stomatal conductance were taken in order to

354 convert them into g_{ψ} . The values of stomatal conductance in the main text were taken from a

355 meta-analysis by Hoshika et al. {Hoshika 2018} who selected data from 235 publications on
356 the basis that the “data were obtained from field measurements to represent actual field
357 conditions”. We therefore chose the values of 20 °C and 70 % relative humidity to convert
358 the values of g_s to g_ψ .



359

360 **Figure S1.** Sensitivity of the conversion of g_s to g_ψ on temperature (left) and relative
361 humidity (right). g_ψ is expressed as a percentage of the value at 70 % relative humidity and
362 20 °C on the y axes to enable an easy conversion of the figures presented in the main text to
363 those derived from alternative values of temperature and humidity.

364