



# The functional dependence of canopy conductance on water vapor pressure deficit revisited

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## Abstract

Current research seeking to relate between ambient water vapor deficit ( $D$ ) and foliage conductance ( $g_F$ ) derives a canopy conductance ( $g_W$ ) from measured transpiration by inverting the coupled transpiration model to yield  $g_W = m - n \ln(D)$  where  $m$  and  $n$  are fitting parameters. In contrast, this paper demonstrates that the relation between coupled  $g_W$  and  $D$  is  $g_W = AP/D + B$ , where  $P$  is the barometric pressure,  $A$  is the radiative term, and  $B$  is the convective term coefficient of the Penman-Monteith equation.  $A$  and  $B$  are functions of  $g_F$  and of meteorological parameters but are mathematically independent of  $D$ . Keeping  $A$  and  $B$  constant implies constancy of  $g_F$ . With these premises, the derived  $g_W$  is a hyperbolic function of  $D$  resembling the logarithmic expression, in contradiction with the pre-set constancy of  $g_F$ . Calculations with random inputs that ensure independence between  $g_F$  and  $D$  reproduce published experimental scatter plots that display a dependence between  $g_W$  and  $D$  in contradiction with the premises. For this reason, the dependence of  $g_W$  on  $D$  is a computational artifact unrelated to any real effect of ambient humidity on stomatal aperture and closure. Data collected in a maize field confirm the inadequacy of the logarithmic function to quantify the relation between canopy conductance and vapor pressure deficit.

**Keywords** Transpiration · Stomata · Air humidity · Coupling

## Introduction

Evaporation of water from land dissipates 11% of the  $102 \text{ Wm}^{-2}$  multiannual average net radiant energy balance at the interface between the Earth surface and the atmosphere (Chahine 1992). Most of the evaporated water passes through vegetation modulated by the aperture and closure of stomata in the epidermal tissues of plants. Therefore, properly quantified stomatal aperture and resultant plant canopy conductance of gases is an important input for modeling weather and climate. It is also essential knowledge for managing the hydraulic balance of natural and agricultural vegetation. As stomata

are the ports for  $\text{O}_2$  and  $\text{CO}_2$  exchange, their role in biomass production is crucial.

Stomatal opening and closing occur through the change of turgor pressure that balances the matric and osmotic potential of internal plant water. Schematically, when turgor pressure of the two guard cells forming the stomata is larger than that of the epidermis cells stomata open. If it drops below they close. Environmental and endogenous stimuli that modify differentially osmolality, matric potential, or membrane permeability of guard and epidermis cells induce stomatal opening and closing.

Solar radiation by energizing soluble sugar synthesis raises the osmolality of the palisade mesophyll, drawing water from the adjacent epidermis and thereby decreases epidermis cell turgor, allowing stomata to open synchronously. If sugar production exceeds the rate of removal by the phloem, hexokinase induces stomatal closure through the sucrose content of apoplastic water (Kelly et al. 2013), offering a plausible biochemical explanation for frequently observed midday lowering of leaf conductance. Solar radiation also fuels transpiration that lowers the potential of apoplastic water, strengthening the hydraulic pull on the liquid continuum through the xylem to the medium in which roots grow, but may impair hydraulic

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conductance along the conduit. The most severe limitation develops at the soil-root contact because soil hydraulic conductivity decrease exponentially with water content (Assouline 2001). Plants grown on a confined substrate are particularly sensitive to its desiccation because of their high root density (Tardieu and Simonneau 1998). In response to deficient water supply, plants produce abscisic acid (ABA) that induces stomatal closure (Dodd 2003; Tardieu et al. 1992)

Ambient humidity drives diffusion that evacuates vapor generated in voids inside the plant. If uptake does not balance depletion, turgor loss causes stomatal closure, creating a feedback loop controlling plant water status (Monteith 1995). The effectiveness of this water conservation mechanism is specific (Tardieu and Simonneau 1998). However, if stagnant air surrounding the plant impedes dissipation of the water vapor, transpiration elevates humidity and weakens the feedback. The effect of ambient humidity on the hydraulic pull of water uptake may mask its effect on stomatal conductance. Submitting angiosperm plants to increased ambient water vapor pressure deficit  $D$  decreased leaf conductance but also elevated the ABA level in leaves (McAdam and Brodribb 2015). Treating leaves with ABA reproduced the effect of vapor pressure deficit, a possible indication that ABA and not vapor deficit induced stomatal closure.

The water potential  $\psi$  (kPa) at the sites where evaporation takes place in the plant is related to the relative humidity  $h = e_L/e(T_L)$  in the voids within the plant by:

$$\psi = \rho_{liq}RT_{KL} \ln(h) \quad (1)$$

Here,  $e_L$  is the internal vapor pressure,  $e(T_L)$  is the saturation value at Celsius leaf temperature  $T_L$ ,  $T_{KL}$  is the Kelvin leaf temperature,  $R$  is the gas constant ( $= 8.314 \text{ J mol}^{-1} \text{ K}^{-1}$ ), and  $\rho_{liq}$  is the molar density of liquid water ( $= 55.33 \text{ kmol m}^{-3}$  at  $T_{KL} = 300 \text{ K}$ ). The vital range of  $\psi$  in most plants is between  $-100$  and  $-3000$  kPa. The corresponding values of equilibrium  $h$  are from 0.999 to 0.978, higher than normal daytime ambient relative humidity. Therefore, guard cells do not sense directly ambient humidity but are in dynamic equilibrium with the humidity in the substomatal chamber.

Still, regulation of outward vapor diffusion endows ambient humidity with a stomatal control function. Experiments exposing the outer side of detached leaf epidermis to a low humidity air stream decreased reversibly stomatal aperture but only when an air space interrupted, even partially, the hydraulic contact with the inner side of the epidermis (Lange et al. 1971). Stomatal closure was weak at high relative humidity and intensified at low relative humidity of the air stream. Since  $\partial\theta/\partial\psi$ , where  $\theta$  is the relative water content of the leaf tissue, is very small as long as apoplastic water coats the cell membranes (Campbell et al. 1979; Jones 1992), a minute liquid uptake suffices to replenish the humidity of the substomatal chamber and sustain turgidity of the guard cells. Consequently, the mechanism by

which ambient humidity exerts a direct effect on stomatal aperture remained unclear. This uncertainty was resolved when Peak and Mott (2011) showed that vapor diffusion thermally enhanced by evaporative cooling transports water between the guard cells and the cells lining the substomatal chamber under control of  $\delta\chi$ , the vapor mole fraction difference between the voids in the plants and the ambient air. The resulting model predicts a weak linear response of conductance to  $\delta\chi$  changes for  $\delta\chi < 0.025$  ( $\approx 2.5$  kPa), corroborated by experimental results (Mott and Peak 2010). An additional study (Sweet et al. 2017) confirmed the gentle linear decrease of the combined stomatal and viscous boundary-layer conductance to increasing  $\delta\chi$ . This occurs when the increased  $\delta\chi$  is achieved by lowering  $\chi_a$ , the ambient vapor mole fraction, while keeping leaf temperature constant, a procedure that relates  $\delta\chi$  to ambient vapor pressure deficit  $D$ . Moreover, combined leaf and viscous layer conductance of single *Hydrocotyl* leaves isolated in a cuvette, while the rest of the foliage was maintained at high humidity, decreased almost imperceptibly in response to increases of  $D$  in the range from 1 to 3 kPa (Overdieck and Strain 1981).

Foliage water vapor conductance ( $g_F$ ) integrates the conductance of all transpiring organs. From studies of transpiration from soybean (Sinclair et al. 2008) and wheat (Schoppach et al. 2016) conducted in climate-controlled chambers, it can be inferred that vapor pressure deficit  $D$  had no detectable effect on foliage conductance  $g_F$  below a value of 2 kPa. Above this threshold, increasing  $D$  intensifies progressively the decrease of  $g_F$ , associated with a drop of leaf hydraulic conductance.

A widely adopted alternative search for linkage between stomatal conductance and ambient humidity derives a canopy conductance  $g_w$  from field measurements of transpiration, by way of a transpiration model inversion and correlates it to ambient vapor pressure deficit  $D$  through an empirically fitted mathematical function. These investigations yield remarkably consistent results that take on the following form (Oren et al. 1999):

$$g_w = m - n \ln(D) \quad (2)$$

where  $m$  and  $n$  are fitting parameters.

Accordingly, the sensitivity of  $g_w$  to a change of  $D$ :

$$\frac{\partial g_w}{\partial D} = -\frac{n}{D} \quad (3)$$

is steepest at low values of  $D$  and diminishes when  $D$  increases toward its physical limit, a behavior contrary to model (Peak and Mott 2011) and experimental findings (Lange et al. 1971; Overdieck and Strain 1981; Sinclair et al. 2008; Mott and Peak 2010; Schoppach et al. 2016; Sweet et al. 2017). Despite the contradiction, Eq. (2) has become the axiomatic paradigm used or emulated in numerous studies of the relation between canopy conductance and ambient humidity (Granier

and Loustau 1994; Granier et al. 1996; Martin et al. 1997; Ocheltree et al. 2014; Igarashi et al. 2015; Hernandez-Santana et al. 2016).

This paper contests the validity of Eq. (2) and of the interpretation of experiments that led to its inception by showing they are the result of a computational fallacy. The argument is strictly mathematical and has no bearing on the evidence of a direct response of stomata to changing ambient humidity.

## Theoretical analysis

The prevailing procedure to compute canopy conductance  $g_w$  from transpiration measurements assumes that the transpiring leaves are highly coupled with the air stream above the canopy (McNaughton and Jarvis 1983):

$$\begin{aligned} g_w &= E \frac{P}{D} \\ D &= e(T_a) - e_a \end{aligned} \quad (4)$$

Here,  $E$  is the transpiration obtained by an independent measurement,  $P$  is the barometric pressure,  $e(T_a)$  is the saturated vapor pressure at  $T_a$  the Celsius (C) air temperature, and  $D$  is the ambient vapor pressure deficit (Granier et al. 1996; Cohen and Naor 2002; David et al. 2004). The value of  $g_w$  is then fitted to an empirical function of  $D$ . As the independent variable  $D$  is used to calculate the dependent variable  $g_w$ , this numerical link invalidates the statistical significance of the regression.

The physical formulation of transpiration  $E$  as latent heat flux density  $\lambda E$  derives from a linearized solution of the energy balance of foliage, known as the Penman-Monteith (P-M) equation (Penman 1948; Monteith 1965; Campbell and Norman 1998) symbolically written as follows:

$$E = A + B \frac{D}{P} \quad (5)$$

where  $A$  stands for the radiative component of the equation and  $B$  is the coefficient of its convective component. Both  $A$  and  $B$  depend also on air temperature and on foliage conductances that govern heat and water vapor exchange between vegetation and air, but are mathematically independent of  $D$ . With all inputs (except  $D$ ) kept constant, the P-M equation shows that transpiration  $E$  is a linear function of  $D$  with a non-zero  $y$ -axis intercept equal to equilibrium transpiration (Slatyer and McIlroy 1961; Eichinger et al. 1996). The input parameters of  $A$  and  $B$  are mathematically independent as detailed in Eq. (A.29) of the Appendix. This mathematical independence does not preclude correlative links between these parameters. However, the parameters can be assigned independent values because the links are loose and do not establish unique functional relations. The total vapor diffusive

conductance through the epidermis of the transpiring surfaces  $g_F$  defined by Eq. (A.17) expresses the physiological control of transpiration in  $A$  and  $B$ .

If wind speed  $u(z) \rightarrow \infty$ , the laminar layer resistances in Eqs. (A.20) and (A.22), and the turbulent layer resistance in Eq. (A.19) vanish leading to  $A \rightarrow 0$  and  $B \rightarrow g_F$  so that Eq. (5) becomes:

$$E_\infty = g_F \frac{D}{P} \quad (6)$$

The assumption needed to derive Eq. (6) sets the theoretical validity limits of Eq. (4). For foliage made of leaves with very small characteristic dimension  $l$ , and with small inherent stomatal conductance of individual leaves,  $E_\infty$  is an approximate estimate of  $E$ . Equation (6) was used to determine the transpiration of a Douglas Fir plantation with an estimated 5% accuracy (McNaughton and Black 1973). Still, Eq. (6) remains an approximation of the real value of  $E$  formulated in Eq. (5). Accordingly, when conditions for allowing  $g_w$  to approximate adequately  $g_F$  are fulfilled,  $g_w$  should respond as  $g_F$  to environmental and endogenous stimuli.

As Eq. (4) uses measured transpiration  $E$  to determine  $g_w$ , it can be combined with Eq. (5) that models accurately the real value of transpiration yielding:

$$g_w = A \frac{P}{D} + B \quad (7)$$

If radiation, air temperature, wind speed, barometric pressure, and leaf conductance  $g_{Lj}$  (the index  $j=0$  or 1 refers to shaded or sunlit leaves) are kept constant,  $D$  is the only variable parameter in the right-hand side of Eq. (7). It shapes  $g_w$  as a descending rectangular hyperbolic function of  $D$ . The hyperbola resembles the curve described by Eq. (2) with a negative slope steepest at low values of  $D$  that flattens rapidly as  $D$  increases toward its physical upper limit:

$$\frac{\partial g_w}{\partial D} = -A \frac{P}{D^2} \quad (8)$$

The decrease of canopy conductance  $g_w$  as a function of  $D$  in Eq. (7) is derived with the premise that the leaf conductance  $g_F$  is kept constant, therefore mathematically independent of  $D$ . The diverging responses to  $D$  prove that Eq. (4) creates an artificial relation between  $g_w$  and  $D$ . Lohammar et al. (1980) derived a hyperbolic leaf conductance function of  $D$  by setting transpiration directly proportional to  $D$  which disregards the intercept in the P-M formulation. This setting is in general invalid. It is restricted to the rare natural absence of sensible heat exchange between the foliage and the air, corroborating that the hyperbolic response is an artifact.

The mathematical independence between  $g_F$  and  $D$  may seem to conflict with the established physical effect of  $D$  on the mechanism of stomatal aperture and closure (Peak and

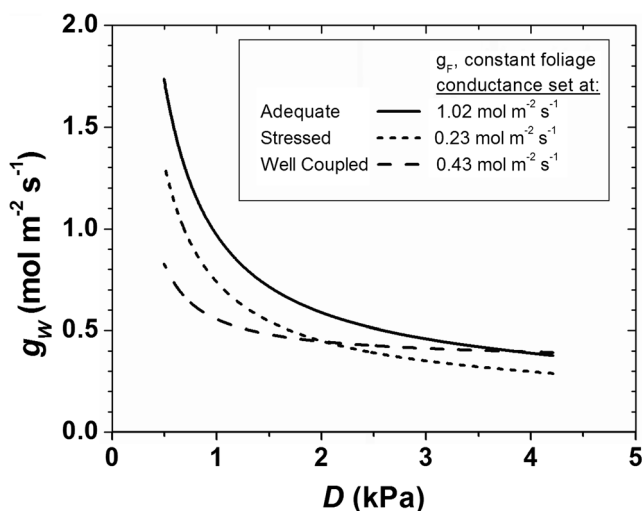
Mott 2011). However, as stomata respond also to light, carbon dioxide, temperature, sugar content, hormones, and soil moisture, leaf conductance  $g_{Lj}$  can take on many values for a single value of  $D$ . Conversely,  $D$  can take on many values for a single value of  $g_{Lj}$ . Therefore, over a wide domain the formal assignment of values for  $g_{Lj}$  and  $D$  may be independent.

## Numerical results

The artificial relation between  $g_w$  and  $D$  revealed by Eq. (7) is illustrated in Fig. 1 using constant values of solar zenith angle, air temperature, and wind speed. The vegetation parameters are for a broad-leaved cotton crop. The leaf conductances  $g_{Lj}$  ( $j = 1$  for sunlit,  $j = 0$  for shaded) characterizing adequate and stressed water supply (Petersen et al. 1991) were kept constant. Table 1 lists the numerical values.

Ambient relative humidity was varied between 15 and 90% to generate the rectangular hyperbolas. The relation between  $g_w$  and  $D$  shown by the curves diverges from the constancy assigned to  $g_{Lj}$  that implies independence from  $D$ . Inputs representative of a well-coupled hypothetical canopy with narrow leaves, low inherent leaf conductance  $g_{Lj}$ , and high wind speed (Table 1) produce the curve in Fig. 1 displaying a weak relation between  $g_w$  and  $D$ . In this case,  $g_w$  is in the vicinity of foliage conductance  $g_F$  calculated by Eq. (A.17) from the input values of  $g_{Lj}$ . The example delineates the conditions for which the coupling assumption is acceptable.

Random meteorological and leaf conductance inputs were used to simulate the results of experimentally determined relations between  $g_w$  and  $D$  in two studies of vegetation growing



**Fig. 1** Canopy conductance  $g_w$  calculated by assuming full coupling for a broad-leaved cotton crop, either adequately supplied with water or submitted to water stress, responds to changes of the ambient water vapor deficit  $D$  despite constant leaf conductance input. The response nearly vanishes for a well-coupled canopy with narrow leaves, low leaf conductance, and windy conditions

in contrasting conditions. For each simulation, a random number generator assigned 50 values to solar zenith angle, air temperature, wind speed, relative humidity, and leaf conductance within the range specified in Table 1. In both studies, sap flow was the measure of instantaneous transpiration  $E$ .

The first test is for a humid tropical forest (Granier et al. 1996). The paper adopts the coupling assumption implied in Eq. (4) to calculate canopy conductance  $g_w$  and plots it versus vapor pressure deficit  $D$ . The justification of the procedure is that it matches results derived from the inverted P-M equation to within 6%.

A digitized reproduction of the original plot is shown in Fig. 2a. The plot indeed appears to show a dependence of canopy conductance  $g_w$  on  $D$ . It displays a very high variability of conductance data at low values of  $D$ . Data points in the original plot were segregated in net radiation classes in an unsuccessful attempt to explain the variability by stomatal response to light. In Fig. 2b, random meteorological data and leaf conductance values in the range representative of the experimental conditions described in the paper (Table 1) were used as inputs to Eq. (4). The resulting plot of  $g_w$  versus  $D$  reproduces the features of Fig. 2a including the large variability of  $g_w$  at low  $D$ .

Figure 2c shows that the random input values of conductance used to generate the scatter plot of Fig. 2b are independent of  $D$ ; therefore, the relation appearing in Fig. 2b is artificial.

In their inversion of the P-M equation Granier et al. (1996), arbitrarily set the convective conductance of heat and vapor to  $0.1 \times \rho u(z)$ . Using this setting,  $g_w$  was recalculated to verify the claim that Eq. (4) approximates closely the inverted P-M equation. The resulting data points in Fig. 2b indeed display a trend like that obtained with the fully coupled model, but with a weaker response to  $D$ . Excluding the highly variable data at  $D < 1$  kPa, the two sets match within 10% similar to the 6% quoted in Granier et al. (1996). With the proper convective air conductance, the inversion of the P-M equation would generate a  $g_w$  distribution matching that of the random input values of foliage conductance  $g_F$  in Fig. 2c and be independent of  $D$ . Consequently, the apparent dependence of  $g_w$  on  $D$  results from the overestimated convective conductance. In many studies, the apparent link between  $g_w$  and  $D$  is the result of discarding the boundary-layer conductance in the computation of the inverted P-M equation (Granier and Breda 1996; Igarashi et al. 2015; Renninger et al. 2015). Including the boundary-layer conductance blurs the dependence between  $g_w$  and  $D$ , see Fig. 3A in (Martin et al. 1997).

The response of conductance  $g_w$  to variations of  $D$  was examined for an drip irrigated apple orchard grown in an arid environment (Cohen and Naor 2002). The trees in the study included Golden Delicious scions grafted on two rootstocks M9 and MM106 with different water uptake capabilities. To avoid the effect of stomata opening or closing in response to

**Table 1** Inputs used in Eq. (7) to generate the artificial relation between canopy conductance  $g_w$  and water vapor pressure deficit  $D$

	Symbol	Unit	Value	Value	Value	Value
Figure			1	1	2	3
Vegetation			Field crop (cotton)	Well-coupled field crop	Tropical forest	Apple irrigated
Input values			Set to:	Set to:	Set to or random within range:	Set to or random within range:
Height	$Z$	m	1.2	1.2	25.0	3.0
Leaf area index	$L$		4	6	7	2.5
Leaf dimension	$L$	m	0.08	0.002	0.05	0.05
Solar zenith	$H$	Radian	0.524	0.524	0 to 1.57	0.087 to 0.70
Air temperature	$T_a$	C	33	33	20 to 35	27 to 38
Wind speed	$U$	$m\ s^{-1}$	5	12	0.5 to 4.0	2 to 5
Humidity	$H$	%	15 to 90 <sup>a</sup>	15 to 90 <sup>a</sup>	40 to 90	12 to 90
Sunlit leaf $g^b$	$g_{L1}$	$mol\ m^{-2}\ s^{-1}$	0.5 <sup>c</sup>	0.1	0.03 to 0.12	0.5 to 1.5 <sup>d</sup>
Shaded leaf $g^b$	$g_{L0}$	$mol\ m^{-2}\ s^{-1}$	0.1 <sup>c</sup>	0.05	0.01 to 0.05	0.3 to 0.5 <sup>d</sup>
Sunlit leaf $g^b$	$g_{L1}$	$mol\ m^{-2}\ s^{-1}$	0.1 <sup>e</sup>			0.05 to 0.2 <sup>f</sup>
Shaded leaf $g^b$	$g_{L0}$	$mol\ m^{-2}\ s^{-1}$	0.05 <sup>e</sup>			0.05 to 0.10 <sup>f</sup>

<sup>a</sup> In 50 even spaced increments

<sup>b</sup>  $g$  = conductance

<sup>c</sup> Adequately watered

<sup>d</sup> Rootstock MM106

<sup>e</sup> Water stressed

<sup>f</sup> Rootstock M 9

increasing or decreasing levels of photosynthetic photon flux density, only midday data were used to establish the experimental dependence of  $g_w$  on  $D$ .

Experimental data points reproduced in Fig. 3a exhibit a rapid drop of  $g_w$  at low values  $D$  and a weakening response with increasing  $D$ . The ranges of the random inputs data used in Eq. (4) were adapted to mimic the experimental conditions (Table 1). Generated data points in Fig. 3b duplicate closely the apparent relation between  $g_w$  and  $D$  shown in Fig. 3a in contradiction with the independence between  $g_F$ , derived from random  $g_{Lj}$  input and  $D$  displayed in Fig. 3c.

Sap flow measurements of maize transpiration in an experimental field located in Bet Dagan, Israel were used to compare how well Eq. (5) models transpiration when  $g_L$  is assumed to decrease either linearly with increasing  $D$  as established by (Sweet et al. 2017) or logarithmically as expressed in Eq. (2). An automated meteorological station installed above the maize canopy at a height of 5.00 m logged 30-min averaged values of global radiation, air temperature, relative humidity, and wind speed. The data were collected one day after an irrigation had replenished the soil moisture profile to field capacity. At that time, the maize canopy was 3.03 m tall. Its leaf area index was 6.02. The characteristics leaf width was 0.06 m. Additional information about the site and the instrumentation can be found in

(Langensiepen et al. 2009). On the same day, leaf conductances were measured with a LI-1600 porometer (LICOR, Lincoln, NE) that recorded also intercepted photosynthetic photon flux density  $Q$  ( $\mu mol\ m^{-2}\ s^{-1}$ ) in the morning when vapor pressure deficit was 0.865 kPa and in the afternoon when vapor pressure deficit was 1.794 kPa. The porometer data served to derive leaf conductance  $g_{Lj}(1)$  and  $g_{Lj}(2)$  response to  $Q$  as follows:

$$g_{Lj}(1) = \frac{0.886}{1 + \frac{620}{Q}} \quad \text{at } D = 0.865 \text{ kPa}$$

$$g_{Lj}(2) = \frac{0.725}{1 + \frac{512}{Q}} \quad \text{at } D = 1.794 \text{ kPa} \tag{9}$$

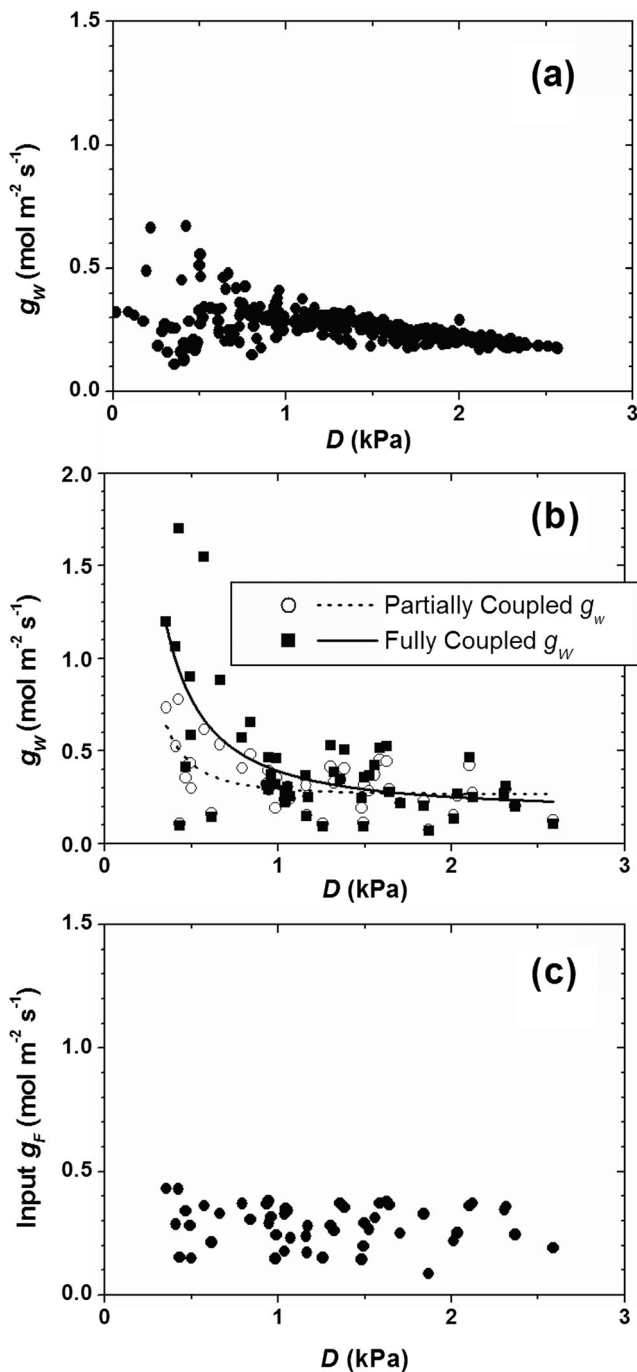
The linear dependence was calculated as follows:

$$g_{Lj} = \frac{g_{Lj}(1) - g_{Lj}(2)}{865 - 1794} (D - 865) + g_{Lj}(1) \tag{10}$$

The logarithmic dependence of Eq. (2) was fitted to values of  $g_w$  generated from Eq. (7). The results were normalized to the maximum value  $g_{w\ max}$ :

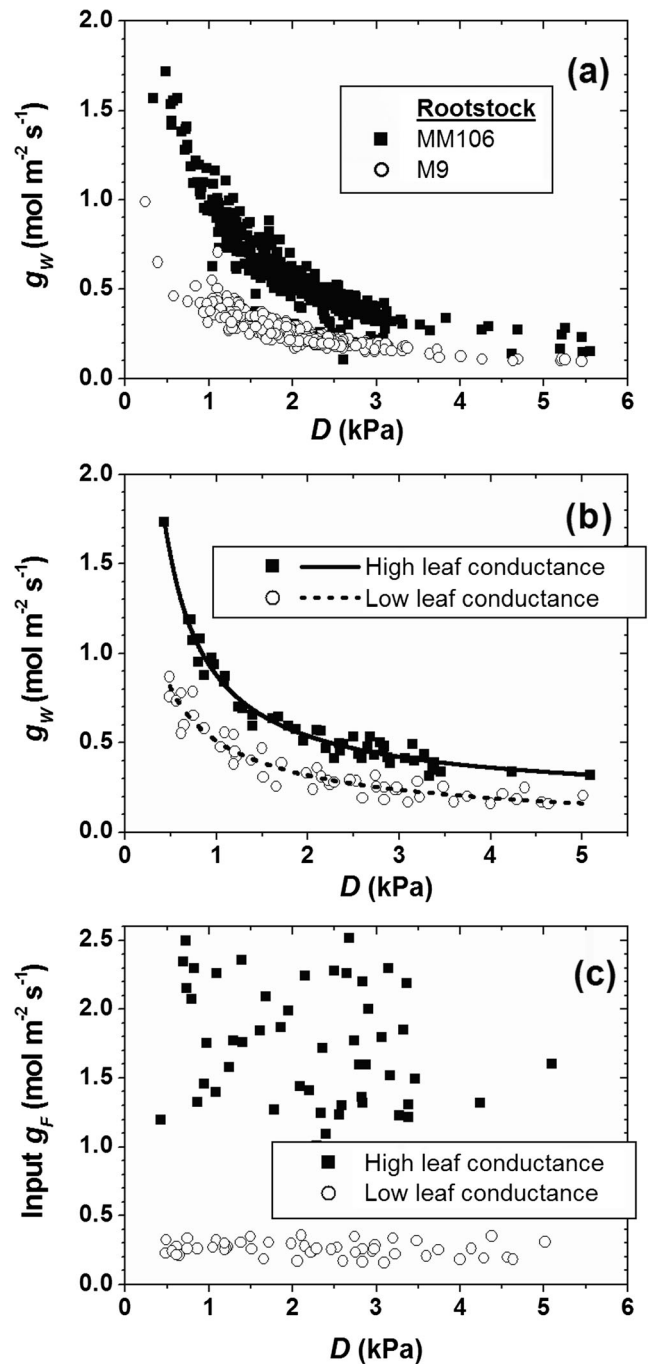
$$g_w / g_{w\ max} = 0.4693 - 0.2613 \ln(D) \quad \text{with } D \text{ in kPa} \tag{11}$$

Because  $D$  is not dimensionless, the numeric values in Eq. (11) depend on the units of  $D$ .



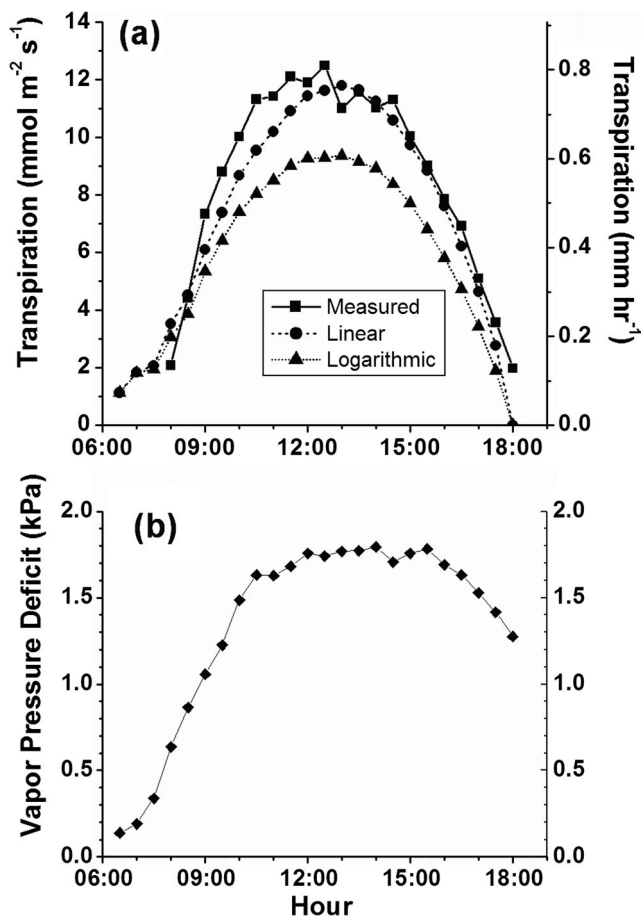
**Fig. 2** **a** Digitized reproduction of Fig. 7 in (Granier et al. 1996): scatter plot of coupled canopy conductance  $g_w$  versus ambient water vapor pressure deficit  $D$ . **b** Scatter plot of conductance  $g_w$  generated with random meteorological data and foliage conductance  $g_F$  mimics the experimental response in contradiction with the randomly distributed input shown in **c**

Figure 4 shows that the transpiration model in which the gentle linear dependence given in Eq. (10) adjusts leaf conductance to current vapor pressure deficit simulates very closely the daily course of measured transpiration. With the steeply decreasing logarithmic function, the model



**Fig. 3** **a** Scatter plot redrawn from Figure 3 in (Cohen and Naor 2002) using original midday data illustrating the response of coupled apple tree canopy conductance  $g_w$  to ambient water vapor pressure deficit  $D$ . **b** Scatter plot generated with random meteorological inputs and foliage conductance  $g_F$  mimics experimental response in contradiction with the randomly distributed input shown in **c**

underestimates transpiration. The defective performance worsens as the vapor pressure deficit intensifies. The linear dependence estimates that daily transpiration is 5.68 mm in good agreement with the measured 5.87 mm. With the logarithmic dependence, the predicted value drops to 4.56 mm.



**Fig. 4** **a** Using diurnal sap flow measurements as a reference to compare the performance of the Penman-Monteith transpiration model assuming either a linear dependence between leaf conductance and vapor pressure or a logarithmic dependence. **b** Diurnal course of the vapor pressure deficit

**Conclusion**

The assumptions leading to the coupled canopy model of transpiration imply stringent conditions on the transport characteristics of the air layers surrounding the foliage. If these conditions are not met, canopy conductance calculated by inverting this model appears to depend on vapor pressure deficit. When the correctly implemented P-M equation with a constant leaf conductance serves as input for inverting the coupled model, the resulting canopy conductance is a down sloping rectangular hyperbolic function of vapor pressure deficit similar in shape to the commonly accepted logarithmic dependence. The contradiction between output and input proves that this result is a fallacy. When conditions for which the approximation implied in the coupled model are closely met, the apparent effect of vapor pressure deficit on the calculated canopy conductance weakens. Using random inputs that preclude any relation between conductance and ambient humidity also produces the fallacious response of the calculated conductance to changing vapor pressure deficit. The

generated scatter plots duplicate closely those derived from published experimental data, strengthening the conclusion that the functional relation claimed by these studies is without basis. However, neither the mathematical reasoning nor the random simulations imply denial of a direct stomatal response to ambient humidity. Assuming enhanced vapor pressure deficit diminishes linearly leaf conductance, the transpiration model matches closely the measurements. By contrast, using the logarithmic relation between leaf conductance and vapor pressure deficit leads to a considerable underestimate of transpiration.

**Acknowledgements** We thank Dr. Shabtai Cohen for providing us the original data used in Fig. 3.

**Appendix**

The calculation of transpiration uses the approach and numerical values given in (Campbell and Norman 1998). Sunlit and shaded leaves were treated separately because of differences in the way they intercept radiation and differences in leaf conductance values (Jagtap and Jones 1989). In the following development index,  $j$  designates the class to which the considered leaves belong:

$$\begin{aligned} j = 0; & \text{ shaded leaves} \\ j = 1; & \text{ sunlit leaves} \end{aligned} \tag{A.1}$$

**Radiation balance**

The global radiation intercepted by the foliage in class  $j$ ,  $R_{g,j}$  is:

$$R_{g,j} = j f R_r L_j + x \frac{L_j}{L} (R_d + S_d) \tag{A.2}$$

The symbols of Eq. (A.2) are defined here below:

The ray interception factor  $f$  by leaves with random inclination and orientation is:

$$f = 0.5 \sec(\eta) \tag{A.3}$$

where  $\eta$  is the solar zenith angle.

$L$  is the leaf area index,  $L_j$  is:

$$\begin{aligned} L_j \text{ for } j = 1 \rightarrow L_1 &= \frac{[1 - \exp(-fL)]}{f} \\ L_j \text{ for } j = 0 \rightarrow L_0 &= L - L_1 \end{aligned} \tag{A.4}$$

The diffuse interception  $x$  of uniformly distributed hemispherical rays is:

$$x = \frac{1}{\pi} \int_0^{2\pi} \int_0^{\pi/2} [1 - \exp(-fL)] \sin(\eta) \cos(\eta) \partial\eta \partial\varphi \tag{A.5}$$

( $\eta$  = zenith angle,  $\varphi$  = azimuth angle, of an incident ray).

The beam  $R_r$  and diffuse  $R_d$  components of global radiation through a cloudless sky are calculated from the extraterrestrial solar constant  $R_o = 1356 \text{ W m}^{-2}$  (List 1966):

$$\begin{aligned} R_r &= R_o \cos(\eta) \times 0.65^{P_{\text{sec}}(\eta)/101.3} \\ R_d &= R_o \cos(\eta) \times 0.34 \times \left(1 - 0.65^{P_{\text{sec}}(\eta)/101.3}\right) \\ P &= \text{barometric pressure, (kPa)} \end{aligned} \quad (\text{A.6})$$

The foliage also intercepts  $S_d$ , the secondary scattering of global radiation approximated as:

$$S_d \approx 0.22 \times \{R_r [1 - \exp(-fL)] + xR_d\} \quad (\text{A.7})$$

Assigning a value of 0.55 to leaf solar radiation absorptivity,  $\varepsilon_s = 0.767 \times e_a^{1/7}$  ( $e_a$  = air vapor pressure in kPa) to sky emissivity of terrestrial radiation (Brutsaert 1982) and assuming the canopy emissivity of terrestrial radiation is close to unity (Fuchs and Tanner 1966),  $R_{nj}$  the net radiation of leaves in class  $j$  is:

$$\begin{aligned} R_{nj} &= 0.55R_{gj} + x \frac{L_j}{L} \left( \varepsilon_s \sigma T_{aK}^4 - \sigma T_{FKj}^4 \right) \\ \sigma T_{FKj}^4 &\approx \sigma T_{aK}^4 + 4\sigma T_{aK}^3 (T_{Fj} - T_a) \end{aligned} \quad (\text{A.8})$$

Here,  $\sigma = 5.67 \times 10^{-8} \text{ W m}^{-2} \text{ K}^{-4}$ ;  $T_{aK}$  and  $T_{FKj}$  are the Kelvin air and foliage temperatures;  $T_a$  and  $T_{Fj}$  are the Celsius air and foliage temperatures.

We define an intermediate radiation term  $R_{mj}$ :

$$R_{mj} = 0.55R_{gj} + x \frac{L_j}{L} (\varepsilon_s - 1) \sigma T_{aK}^4 \quad (\text{A.9})$$

Equation (A.8) becomes:

$$R_{nj} = R_{mj} - 4x \frac{L_j}{L} \sigma T_{aK}^3 (T_{Fj} - T_a) \quad (\text{A.10})$$

## Energy balance

We define a radiative conductance  $g_{rj}$  as:

$$g_{rj} = 4x \frac{L_j}{L} \frac{\sigma T_{aK}^3}{c_p} \quad (\text{A.11})$$

Here,  $c_p$  is the specific heat of air ( $= 29.3 \text{ J mol}^{-1} \text{ C}^{-1}$ ). Setting radiative flux density  $H_{rj}$  as:

$$H_{rj} = c_p g_{rj} (T_{Fj} - T_a) \quad (\text{A.12})$$

leads to the energy balance of the leaves in class  $j$ :

$$R_{mj} = \lambda E_j + H_{cj} + H_{rj} \quad (\text{A.13})$$

where  $\lambda$  is the latent of vaporization ( $= 43,384 \text{ J mol}^{-1}$  at  $T = 300 \text{ K}$ ) and  $\lambda E_j$  is the latent heat flux density:

$$\lambda E_j = \frac{\lambda}{P} g_{vj} [e(T_{Fj}) - e_a] \quad (\text{A.14})$$

where  $e(T_{Fj})$  is the saturated vapor pressure at  $T_{Fj}$  and  $e_a$  is the vapor pressure in the air.

$H_{cj}$  is the convective sensible heat flux density:

$$H_{cj} = c_p g_{Hj} (T_{Fj} - T_a) \quad (\text{A.15})$$

## Transport coefficients

In Eq. (A.14),  $g_{vj}$  is the conductance of the vapor path from the evaporating locations within the plant tissues to the free air above the canopy:

$$g_{vj} = \frac{L_j}{r_{vc} + r_{Lj}} \quad (\text{A.16})$$

$r_{vc}$  is the convective resistance per unit leaf area ( $r_{vc} = 1/g_{vc}$ ) of air for water vapor transport from the outer surface of a leaf to freely moving air above the canopy.

$r_{Lj}$  is the parallelly connected diffusive leaf resistance per unit leaf area through stomata and cuticle of the adaxial and abaxial faces of the leaves ( $r_{Lj} = 1/g_{Lj}$ ,  $g_{Lj}$  is the leaf conductance).

The foliage conductance  $g_{Fj}$  is then defined as:

$$\begin{aligned} g_{Fj} &= L_j g_{Lj} \frac{L_j}{r_{Lj}} \\ g_F &= g_{F0} + g_{F1} \end{aligned} \quad (\text{A.17})$$

The convective resistance  $r_{vc}$  is made of:

$$r_{vc} = r_a + 0.5 r_{vb} \quad (\text{A.18})$$

Here,  $r_a$  is the convective resistance of the turbulent air layer above the canopy assigned to a unit leaf area:

$$r_a = \frac{\ln\left(\frac{z-d}{z_0}\right) \ln\left(\frac{z-d}{0.2z_0}\right) L}{\rho k^2 u(z)} \quad (\text{A.19})$$

where  $z$  is the level above the canopy taken from the ground at which wind speed  $u(z)$  is measured,  $d = 0.66 \times Z$  is the wind profile displacement level,  $z_0 = 0.13 \times Z$  is the roughness length,  $Z$  is the canopy height,  $k$  is the von Kármán constant ( $= 0.40$ ), and  $\rho$  is the air molar density [ $= 44.6 \times (T_{aK}/273.2) \times (P/101.3) \text{ mol m}^{-3}$ ].

$r_{vb}$  in Eq. (A.18) is the one-sided convective resistance per unit leaf area for vapor transport in the laminar air boundary



layer of a leaf surface. The factor 0.5 halves the resistance because leaves are two-sided.

$$r_{vb} = 6.8 \left( \frac{\rho_s}{u_\ell^{0.5}} \right) \tag{A.20}$$

$l$  is the characteristic length of the leaf and  $\overline{u_\ell^{0.5}}$  is defined in Eq. (A.25).

Heat convective conductance  $g_{Hj}$  in Eq. (A.15) is:

$$g_{Hj} = \frac{L_j}{r_a + 0.5 r_{Hb}} \tag{A.21}$$

where  $r_{Hb}$  is the one-side convective resistance per unit leaf area for heat transport in the laminar air boundary layer surrounding a leaf:

$$r_{Hb} = 7.4 \left( \frac{\rho_s}{u_\ell^{0.5}} \right) \tag{A.22}$$

The combined conductance of heat  $g_{Tj}$  is:

$$g_{Tj} = g_{Hj} + g_{rj} \tag{A.23}$$

The boundary-layer convective resistance is proportional to  $1/\overline{u_\ell^{0.5}}$ . The mean value  $\overline{u_\ell^{0.5}}$  in the canopy is derived from the shear that foliage skin friction and form drag exert on wind:

$$\frac{\partial u_\ell}{\partial \ell} = a u_\ell \tag{A.24}$$

Here,  $\ell$  is the leaf area index (LAI) depth at which the wind has penetrated (at the top of the canopy  $\ell = L = \text{LAI}$ ;  $\ell = 0$  at the bottom of the canopy),  $u_\ell$  is the wind speed at  $\ell$ , and  $a$  is the combined drag and friction coefficient set at 0.4. The mean  $\overline{u_\ell^{0.5}}$  adjusted to the wind profile in the canopy is:

$$\overline{u_\ell^{0.5}} = \frac{2u_Z^{0.5}}{aL} [1 - \exp(-aL/2)] \tag{A.25}$$

Here,  $u_Z$  is the wind speed at canopy height  $Z$ :

$$u_Z = u(z) \frac{\ln\left(\frac{Z-d}{z_0}\right)}{\ln\left(\frac{z-d}{z_0}\right)} \tag{A.26}$$

### Additional definitions

The additional elements needed to complete the calculation of  $E_j$  are listed here.

The saturated water vapor pressure function of temperature  $T$  is (Tetens 1930):

$$e(T) = 0.6018 \times \exp\left(\frac{17.27 \times T}{T + 237.3}\right); \quad (\text{kPa}) \tag{A.27}$$

The slope of the molar fraction vapor saturation function of temperature is:

$$\Delta = \frac{1}{P} \frac{\partial e(T_a)}{\partial T_a} = \frac{e(T_a)}{P} \times \frac{17.27 \times 237.3}{(T_a + 237.3)^2} \approx \frac{e(T_{Fj}) - e(T_a)}{P(T_{Fj} - T_a)}; \quad (C^{-1}) \tag{A.28}$$

### Finalizing

Combining Eqs (A.12), (A.13), (A.14), (A.15), and (A.28) leads to the P-M equation:

$$E_j = \frac{\Delta R_m j / \lambda \Gamma_j + g_{vj} D / P}{1 + \Delta / \Gamma_j} \tag{A.29}$$

Here,  $\Gamma_j$  is the psychrometric constant ( $C^{-1}$ ) adjusted to the conductance of heat  $g_{Tj}$  and vapor  $g_{vj}$  for the leaves in class  $j$ .

$$\Gamma_j = c_p g_{Tj} / \lambda g_{vj} \tag{A.30}$$

The resulting value of foliage transpiration is:

$$E = E_0 + E_1 \tag{A.31}$$

The coupled model of transpiration is obtained when  $u(z) \rightarrow \infty$ . This condition draws in Eqs. (A.20), (A.19), (A.18), (A.17), (A.16),  $r_{vb}$ ,  $r_a$  and  $r_{vc} \rightarrow 0$ , and  $g_{vj} \rightarrow g_{Fj}$ .

Coupling also implies that in Eq. (A.22),  $r_{Hb} \rightarrow 0$  and in Eq. (A.21)  $g_{Hj} \rightarrow \infty$ . Consequently in Eq.(A.23),  $g_{Tj} \rightarrow \infty$  leading to  $\Gamma_j \rightarrow \infty$  in Eq.(A.30). The implications on convection deriving from coupling transforms Eq. (A.29) into:

$$E_j \rightarrow E_{\infty j} = g_{Fj} \frac{D}{P} \tag{A.32}$$

leading through Eqs. (A.17) and (A.31) to Eq. (6).

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