

Original Article

Wind increases leaf water use efficiency

Stanislaus J. Schymanski & Dani Or

Department of Environmental Systems Science, ETH Zurich, Zurich 8092, Switzerland

ABSTRACT

A widespread perception is that, with increasing wind speed, transpiration from plant leaves increases. However, evidence suggests that increasing wind speed enhances carbon dioxide (CO₂) uptake while reducing transpiration because of more efficient convective cooling (under high solar radiation loads). We provide theoretical and experimental evidence that leaf water use efficiency (WUE, carbon uptake per water transpired) commonly increases with increasing wind speed, thus improving plants' ability to conserve water during photosynthesis. Our leaf-scale analysis suggests that the observed global decrease in near-surface wind speeds could have reduced WUE at a magnitude similar to the increase in WUE attributed to global rise in atmospheric CO₂ concentrations. However, there is indication that the effect of long-term trends in wind speed on leaf gas exchange may be compensated for by the concurrent reduction in mean leaf sizes. These unintuitive feedbacks between wind, leaf size and water use efficiency call for re-evaluation of the role of wind in plant water relations and potential re-interpretation of temporal and geographic trends in leaf sizes.

Key-words: gas exchange; global stilling; leaf energy balance; leaf temperature; water use efficiency; wind speed.

INTRODUCTION

Since the seminal work by Penman (1948) that skillfully combined aerodynamic considerations and Bowen's energy balance considerations (Bowen 1926) with simplifying assumptions to eliminate leaf temperature from latent heat flux calculation, common treatments of leaf or canopy gas and energy exchange do not explicitly consider leaf temperatures (e.g. the Penman–Monteith equation (Monteith 1965)). The elimination of leaf or surface temperature from the calculation permits analytical estimates of evaporation or transpiration rates for given atmospheric and surface conditions but, at the same time, obscures important feedbacks. For example, the sensitivity of evaporation and transpiration rate to air temperature is often represented by the increasing slope of the saturation vapour pressure curve with increasing temperature (Raschke 1958, 1960; Monteith 1965; Priestley & Taylor 1972). However, the underlying diffusion equation does not feature air temperature but vapour concentration in the air, which is only very weakly dependent on air temperature. In fact, the main impact of air temperature on

transpiration rate is through its effect on sensible heat flux, which in turn is very sensitive to leaf boundary layer conductance. Consequently, temperature sensitivity of transpiration is likely dependent on leaf surface and boundary layer properties. This web of interactions poses a challenge to the intuitive understanding of leaf temperature and energy balance adjustments to environmental forcing. An additional complication arises from the effect of stomatal control, which modifies the coupling between latent and sensible heat flux. Ten years before Monteith (1965) derived the now widely used Penman–Monteith equation, Raschke (1958) recognized the effect of stomatal resistance on the sensitivity of latent heat flux to wind speed and pointed out the counter-intuitive finding that, whereas transpiration rates normally increase with wind speed, they may decrease with increasing wind speed at high stomatal resistances. The possibility of the latter behaviour and its limitation to low stomatal conductance was also mentioned by Monteith (1965), who pointed to supporting experimental results (Mellor *et al.* 1964).

Various other authors have also noted that transpiration may decrease in response to increasing wind speed under certain conditions (Kuiper 1961; Gates 1968; Drake *et al.* 1970; Nobel 1981; Dixon & Grace 1984), but the general expectation remains that increasing wind speed results in increased transpiration, based on the assumption that transpiration scales with 'atmospheric evaporative demand' (McVicar *et al.* 2012a, 2012b; McMahon *et al.* 2013; Ben Neriah *et al.* 2014).

An issue that has not received much attention in the literature is the effect of wind speed on leaf water use efficiency (WUE), which is the amount of CO₂ taken up by photosynthesis divided by the amount of water transpired. Given the high sensitivity of transpiration to leaf temperature (Ball *et al.* 1988), as illustrated in Fig. S2, whereas CO₂ assimilation responds to a lesser extent (Medlyn *et al.* 2002), we hypothesize that the effect of wind on sensible heat flux enables plants to operate at higher WUE under high wind speed relative to WUE under low wind speed. To test this hypothesis, we undertook a series of field experiments on a variety of plants grown under ambient conditions in Zurich, Switzerland. Furthermore, to separate the influences of different atmospheric drivers on leaf energy balance and to form a more complete picture across the range of feasible atmospheric conditions, we employed a physically-based model of heat and mass transfer, solving the leaf energy balance (Schymanski *et al.* 2013), and combined it with a detailed photosynthesis model, parameterised for grapevine leaves (Buckley *et al.* 2014).

Please note that references with the prefix 'S' in the below text (e.g. S1 and S2) refer to equations, figures and tables provided in the Supporting Information.

Correspondence: S. J. Schymanski. e-mail: stan.schymanski@env.ethz.ch

MATERIALS AND METHODS

All relevant symbols used in this section and their respective units are given in Table S1. All derivations and analysis were performed using the freely available software SAGE (version 6.8, <http://sagemath.org>).

Field observations

A LI-COR Portable Photosynthesis System (LI-6400XT, LI-COR Inc., Lincoln, Nebraska, USA) was used to measure leaf temperatures and gas exchange of intact leaves under constant conditions resembling ambient atmospheric conditions. The leaf boundary layer conductance was varied by varying the voltage of the fan that circulates the air inside the leaf chamber. Voltage was varied at 4 min intervals in five steps, first increasing from lowest to highest and then decreasing again stepwise back to the lowest voltage. Using a miniature constant temperature anemometer (Supporting Information), we found that wind speeds inside the original LI-6400XT leaf chamber were not stable at the different voltage settings; therefore, the air circulation in the top half of the chamber was blocked by placing a strip of adhesive tape over the respective air conduits, which is the recommended procedure for measuring flux from one side of a leaf only.¹ This resulted in stable and reproducible wind speeds on the abaxial side of the leaf, ranging between 0.3 and 3 ms⁻¹ (Tab. S2) while suppressing sensible heat flux and gas exchange from the adaxial side of the leaf. Because all investigated leaves were hypostomatous (verified by microscopic analysis), it likely weakened the observed wind effect on WUE by reducing sensible heat flux. In addition, use of the LI-6400XT LED light source chamber head likely affected the radiative environment by reducing the energy load per quantum photosynthetically active photon flux on the one hand, while absorbing and re-emitting long-wave radiation emitted by the leaf on the other hand. Therefore, in the second round of experiments, we only used the LI-6400XT transparent chamber top with a high transmissivity to both solar and emitted long-wave radiation. Correspondence of leaf temperatures in the leaf chamber with those in ambient conditions (Table S3) suggests that the chamber effect on the leaf energy balance is unlikely to have led to spurious results.

Measurements were performed on outdoor plants in Zurich, one set in September 2014 (Leaves 1–17) and another set in July 2015 (Leaves 18–30). Only leaves fully exposed to sunlight were chosen. On days with stable atmospheric conditions, a transparent chamber top was used, while on partly cloudy days, photosynthetically active radiation was generated using the LI-COR LED light source (6400-02B LED), producing a constant photon flux density set to a similar value as that measured on the outside of the chamber when angled similarly to the chosen leaf. The CO₂ concentration and air temperature inside the chamber were kept constant at the values determined outside at the beginning of each experiment, while vapour pressure was not controlled, resulting in slight co-variation with

transpiration rates and elevated values compared with ambient conditions (Table S3).

In 2015, leaf temperatures were also measured under ambient conditions, using an infrared thermometer (Steinel 11391 ThermoCheck, Steinel Inc., Bloomington, MN, USA) and an infrared camera (Model ICI 7640S; Infrared Cameras, Inc. (ICI), Beaumont, TX, USA).

For each experiment where wind speed (v_w) in the chamber was varied from lowest to highest and then back to lowest, the relative response S_0 of WUE (W_{UE}) to a relative change in wind speed was computed for each transition in wind speed as follows:

$$S_0 = \frac{\Delta W_{UE}/W_{UE}}{\Delta v_w/v_w} = \frac{\Delta W_{UE}}{\Delta v_w} \frac{v_w}{W_{UE}} = \left(\frac{W_{UE,2} - W_{UE,1}}{v_{w,2} - v_{w,1}} \right) \left(\frac{v_{w,1} + v_{w,2}}{W_{UE,1} + W_{UE,2}} \right) \quad (1)$$

where the subscripts 1 and 2 denote the median values ($n \approx 50$) before and after each transition, respectively. For the implications of this formulation and the meaning of S_0 , the reader is referred to the Discussion Section and Eqn 16. Results for each leaf are summarized as box plot in Fig. 2.

Leaf energy balance model

The mathematical model of the leaf energy balance employed in this study is described in detail elsewhere (Schymanski *et al.* 2013) and is summarized in the Supporting Information.

The leaf energy balance is determined by the dominant energy fluxes between the leaf and its surroundings, including radiative, sensible and latent energy exchange (linked to water vapour exchange). In this study, we focus on steady-state conditions (no change in leaf heat storage), considering the following energy balance equation:

$$0 = R_s - R_{ll} - H_l - E_l \quad (2)$$

where R_s is absorbed short wave radiation, R_{ll} is the net long-wave balance, that is, the emitted minus the absorbed, while H_l and E_l are the sensible and latent heat fluxes away from the leaf, respectively. As in Schymanski *et al.* (2013), this study considers spatially homogeneous, thin planar leaves, that is, full illumination and a negligible temperature gradient between the two sides of the leaf. It further focuses on conditions where convective mass and heat exchange are dominated by inertial forces, that is, wind speeds greater than 0.5 ms⁻¹ for a 5 cm wide leaf or greater than 0.3 ms⁻¹ for a 2 cm wide leaf (Supporting Information). Of the different components in Eqn 2, only sensible and latent heat flux (H_l and E_l , respectively) is directly affected by wind speed, as wind reduces thickness of the leaf boundary layer, which serves as a resistance for convective mass and heat exchange. For wet surfaces, the effect of wind is commonly reflected in the heat or mass transfer coefficients (h_c and g_{tw} , respectively) as follows:

$$H_l = 2h_c(T_l - T_a) \quad (3)$$

where h_c (W m⁻² K⁻¹) is the average one-sided convective heat transfer coefficient and

¹<http://www.licor.com/env/newslines/2008/09/making-one-sided-leaf-measurements-with-the-li-6400xt/>

$$\frac{E_l}{M_w \lambda_E} = g_{lw}(C_{wl} - C_{wa}) \quad (4)$$

where M_w is the molar mass of water, λ_E (J kg^{-1}) is the latent heat of vaporization and g_{lw} (m s^{-1}) is the mass transfer coefficient for water vapour. For a leaf, however, additional resistances need to be considered; these relate to the depth and area of stomata and the geometry and distance between stomata (Bange 1953; Assouline & Or 2013; Lehmann & Or 2015). Commonly, these are lumped into stomatal resistance or, its inverse, stomatal conductance (g_{sw} , m s^{-1}). The total leaf conductance to water vapour (g_{lw} in Eqn 4) thus becomes

$$g_{lw} = \frac{1}{\frac{1}{g_{sw}} + \frac{1}{g_{bw}}} \quad (5)$$

where g_{bw} is the leaf boundary layer conductance to water vapour. To a good approximation, h_c and g_{bw} scale with the square root of wind speed. For laminar conditions at 300 K air temperature,

$$h_c \approx 3.9 \sqrt{v_w / L_l} \quad (6)$$

where v_w (m s^{-1}) is wind speed and L_l (m) is leaf width, meaning that h_c is constant ($h_c = h_{c0}$) if leaf size scales with wind speed as $L_l \approx 15.26 / h_{c0}^2 v_w$. For details please refer to the Supporting Information, where we also explain conversion between g_{lw} in units of m s^{-1} and molar units ($\text{mol m}^{-2} \text{s}^{-1}$), more commonly used in the plant physiology literature ($g_{lw, \text{mol}} \approx 40 \text{ mol m}^{-3} g_{lw}$).

All components of the leaf energy balance except for absorbed shortwave radiation (R_s) depend on leaf temperature, whereby increasing leaf temperatures generally increase heat transfer away from the leaf, resulting in negative feedbacks. These negative feedbacks lead to a stable steady-state leaf temperature for given R_s , air temperature and humidity, wind velocity, leaf size and stomatal conductance. The steady-state temperature was obtained by numerical root finding of Eqn 2 after substitution of the equations given in the Supporting Information. By its effect on the sensible and latent heat transfer coefficients (h_c and g_{lw} , respectively), wind speed affects steady-state leaf temperature, exerting also an indirect effect on the respective fluxes (via the thermodynamic drivers) and on the net long-wave balance of the leaf (Fig. S1).

Carbon–water trade-off and water use efficiency

Adjustments in stomatal aperture affect both the transpiration flux of water from the leaf ($E_{l, \text{mol}} = g_{lw}(C_{wl} - C_{wa})$, Eqn S5) and CO_2 assimilation by the leaf (A_l , $\text{mol m}^{-2} \text{s}^{-1}$). The ratio of both fluxes ($A_l / E_{l, \text{mol}}$) gives the amount of carbon gained per unit of water lost and is commonly termed WUE as follows:

$$W_{UE} = \frac{A_l}{E_{l, \text{mol}}} \quad (7)$$

Both water vapour release and CO_2 uptake by the leaf ($E_{l, \text{mol}}$ and A_l , respectively) are diffusive fluxes, and A_l can be obtained equivalently to $E_{l, \text{mol}}$ as follows (Cowan 1977):

$$A_l = g_{lc, \text{mol}}(C_a - C_c) \quad (8)$$

where $g_{lc, \text{mol}}$ ($\text{mol m}^{-2} \text{s}^{-1}$) is the total conductance of the diffusive pathway of CO_2 from the free air to the photosynthesising sites inside the leaf, while C_c and C_a are the mole fractions of CO_2 inside the leaf and in the free air respectively (mol mol^{-1}), equivalent to the partial pressures of CO_2 divided by air pressure (Cowan 1977). The total diffusive conductance to CO_2 ($g_{lc, \text{mol}}$) is given by the following:

$$g_{lc, \text{mol}} = \frac{1}{\frac{1}{g_{bc, \text{mol}}} + \frac{1}{g_{m, \text{mol}}} + \frac{1}{g_{sc, \text{mol}}}} \quad (9)$$

where $g_{bc, \text{mol}}$, $g_{sc, \text{mol}}$ and $g_{m, \text{mol}}$ are the leaf boundary layer, stomatal and mesophyll conductance to CO_2 , respectively ($\text{mol m}^{-2} \text{s}^{-1}$). The quantities of $g_{bc, \text{mol}}$ and $g_{sc, \text{mol}}$ are directly linked to the equivalent conductances for water vapour (g_{bw} and g_{sw}), such that variations in stomatal conductance affect both $E_{l, \text{mol}}$ and A_l usually in the same direction, but by different amounts (see the Supporting Information for details on conversions between conductances to water vapour and CO_2). Note that the expression of leaf gas exchange in terms of mole fraction rather than concentration difference (Eqn 8 versus Eqn 4) is an approximation commonly used in plant physiology, but the respective quantities can readily be converted to one another, as explained in the Supporting Information, Section S3.

Photosynthesis model

CO_2 assimilation (A_l) was modelled following the photosynthesis model of Farquhar *et al.* (1980), as summarized by Buckley *et al.* (2014), also using the same biochemical parameters and their sensitivity to leaf temperature as those determined for grapevine by Buckley *et al.* (2014). For any given stomatal conductance and atmospheric forcing, the leaf energy balance model was used to simulate leaf boundary layer conductance to water vapour (g_{bw}), the energy balance components and steady-state leaf temperature, while g_{bw} (after conversion to $g_{bc, \text{mol}}$, see the Supporting Information) and leaf temperature were used in the photosynthesis model to obtain A_l expected for grapevine leaves under prescribed combinations of stomatal conductance and environmental forcing. A_l was modelled as the minimum of the RuBP carboxylation-limited and the RuBP regeneration-limited assimilation rates as functions of $g_{lc, \text{mol}}$, that is,

$$A_l = \frac{1}{2}(C_a + K_m)g_{lc, \text{mol}} - \frac{1}{2}R_l + \frac{1}{2}V_m - \frac{1}{2}\sqrt{\left((C_a + K_m)g_{lc, \text{mol}} + R_l\right)^2 - \left(2(C_a - 2\Gamma^* - K_m)g_{lc, \text{mol}} + 2R_l - V_m\right)V_m} \quad (10)$$

and

$$A_l = \frac{1}{2}(C_a + 2\Gamma^*)g_{lc, \text{mol}} + \frac{1}{8}J_e - \frac{1}{2}R_l - \frac{1}{8}\sqrt{16\left((C_a + 2\Gamma^*)g_{lc, \text{mol}} + R_l\right)^2 - \left(8(C_a - 4\Gamma^*)g_{lc, \text{mol}} - J_e + 8R_l\right)J_e} \quad (11)$$

respectively, where K_m , V_m and Γ^* are parameters related to the biochemistry of photosynthesis, J_e is light-dependent electron

transport rate and R_l is the non-photorespiratory CO_2 release in the light. In the previous equations, $g_{m,mol}$, K_m , V_m , Γ_s , J_e and R_l depend on leaf temperature, which was represented by empirical parameterisations derived elsewhere (Buckley *et al.* 2014) for grapevine leaves. See the Supporting Information for details.

Relative sensitivity of leaf water use efficiency to variations in wind speed

For any perturbation of wind speed from $v_{w,1}$ to $v_{w,2}$, the relative sensitivity S_0 of WUE to relative changes in wind speed was estimated in two ways; one is the same as described in Eqn 1, where $W_{UE} = A_l/E_{l,mol}$ at each wind speed, and A_l is computed based on the photosynthesis model described earlier, using parameter values for grapevine leaves. The second way of estimating S_0 aimed at obtaining more general results, independent of species-specific biochemical leaf properties and temperature responses, and was based on the following considerations.

If transpiration is expressed as a function of water vapour mole fractions rather than concentrations ($E_{l,mol} = g_{tw,mol}(W_l - W_a)$, Eqn S39), where the ratio of the leaf conductivities to carbon dioxide and water vapour ($g_{tc,mol}/g_{tw,mol}$) is a constant (Cowan 1977), WUE is proportional to

$$W_{UE} = A_l/E_{l,mol} \propto \frac{C_a - C_c}{W_l - W_a} \quad (12)$$

where W_a and W_l are the mole fractions of water vapour in the ambient air and inside the leaf respectively, equivalent to the partial pressures of vapour divided by total air pressure. The leaf-internal CO_2 mole fraction (C_c) is a function of the light-dependent photosynthetic sink strength inside the leaf and on $g_{tc,mol}$ itself, while W_l is a function of leaf temperature only. If we neglect the effect of leaf temperature on the photosynthetic sink strength and assume that the CO_2 uptake rate is constant if both absorbed shortwave radiation (R_s) and total leaf conductance for CO_2 ($g_{tc,mol} \propto g_{tw,mol}$) remain constant, we can estimate the potential physical wind effect on WUE by adjusting g_{sw} in Eqn 5 to maintain constant g_{tw} and hence $g_{tc,mol}$ while varying wind speed. This simulates the wind-induced change in transpiration rate for a given constant CO_2 uptake rate (A_l). If A_l is constant, that is, $dA_l/dv_w = 0$ and $\partial W_{UE}/\partial E_{l,mol} = -A_l/E_{l,mol}^2$, the sensitivity of WUE to wind speed (v_w) becomes

$$\frac{dW_{UE}}{dv_w} = \frac{\partial W_{UE}}{\partial A_l} \frac{dA_l}{dv_w} + \frac{\partial W_{UE}}{\partial E_{l,mol}} \frac{dE_{l,mol}}{dv_w} \approx -\frac{A_l dE_{l,mol}/dv_w}{E_{l,mol}^2} \quad (13)$$

Division of Eqn 13 by $W_{UE} = A_l/E_{l,mol}$ reveals that the relative sensitivity of W_{UE} to changes in wind speed is equal to the relative sensitivity of transpiration to wind speed in this scenario, with a negative sign as follows:

$$\frac{dW_{UE}/dv_w}{W_{UE}} \approx -\frac{dE_{l,mol}/dv_w}{E_{l,mol}} \quad (14)$$

For estimating the physical wind effect on WUE independently of species-specific temperature response curves, we inserted Eqn 14 into Eqn 1 and obtained

$$S_0 = \frac{dW_{UE}/W_{UE}}{dv_w/v_w} \approx -\frac{dE_{l,mol}}{dv_w} \frac{v_w}{E_{l,mol}} \approx \left(-\frac{E_{l,mol,2} - E_{l,mol,1}}{v_{w,2} - v_{w,1}} \right) \left(\frac{v_{w,1} + v_{w,2}}{E_{l,mol,1} + E_{l,mol,2}} \right) \quad (15)$$

where the subscripts 1 and 2 denote values at lower and higher wind speed, respectively.

Numerical experiments

Using the leaf energy balance model described in the Supporting Information, sensitivity of the different leaf energy balance components and leaf temperature to wind speed was examined under a wide range of environmental conditions, ranging from 10% to 90% relative humidity, 100 to 900 W m^{-2} absorbed shortwave radiation and 10–40 °C air temperatures. The model leaf in the simulations had a characteristic length scale of 5 cm. Simulations were performed either using constant stomatal conductance or constant leaf conductance, computed from initial wind speed and initial stomatal conductance. Two values of initial stomatal conductance were considered, low conductance of 0.001 m s^{-1} (equivalent to $0.04 \text{ mol H}_2\text{O m}^{-2} \text{ s}^{-1}$, roughly the 25% quartile of the range compiled by Manzoni *et al.* (2011)) and high conductance of 0.01 m s^{-1} (equivalent to $0.4 \text{ mol H}_2\text{O m}^{-2} \text{ s}^{-1}$, roughly the 75% quartile of the range compiled by Manzoni *et al.* (2011) and equivalent to the maximum observed by Buckley *et al.* (2014)). To assess the sensitivity of WUE to wind speed at constant CO_2 uptake rate, we computed the relative change in WUE resulting from a relative increase in wind speed by 1% for wind speeds of 0.5 m s^{-1} and 5.0 m s^{-1} .

RESULTS

Observed effect of wind on leaf gas exchange and water use efficiency

In order to isolate the effect of wind speed on leaf WUE, we conducted a series of measurements under controlled conditions using sun-exposed leaves in a gas-exchange leaf chamber where we could measure transpiration and CO_2 uptake rates while varying wind speed in small steps between 0.3 and 3 m s^{-1} (Figs S3 & S4). Figure 1 illustrates three experiments with contrasting responses. At very high and constant stomatal conductance (*Hibiscus sp.*), both transpiration and CO_2 assimilation rates slightly increase with wind speed, resulting in no net response of WUE to wind speed. At low stomatal conductance, on the other hand, WUE commonly increased with wind speed, regardless of stomatal responses. For little or negative stomatal response to wind speed (*Acer pseudoplatanus*), transpiration strongly declined with increasing wind speed, while CO_2 assimilation rates slightly increased, leading to strongly increasing WUE. On the other hand, even for strong positive response of stomatal conductance to wind speed (*Malus domestica*), leading to increasing transpiration rates with wind speed, CO_2 assimilation rates

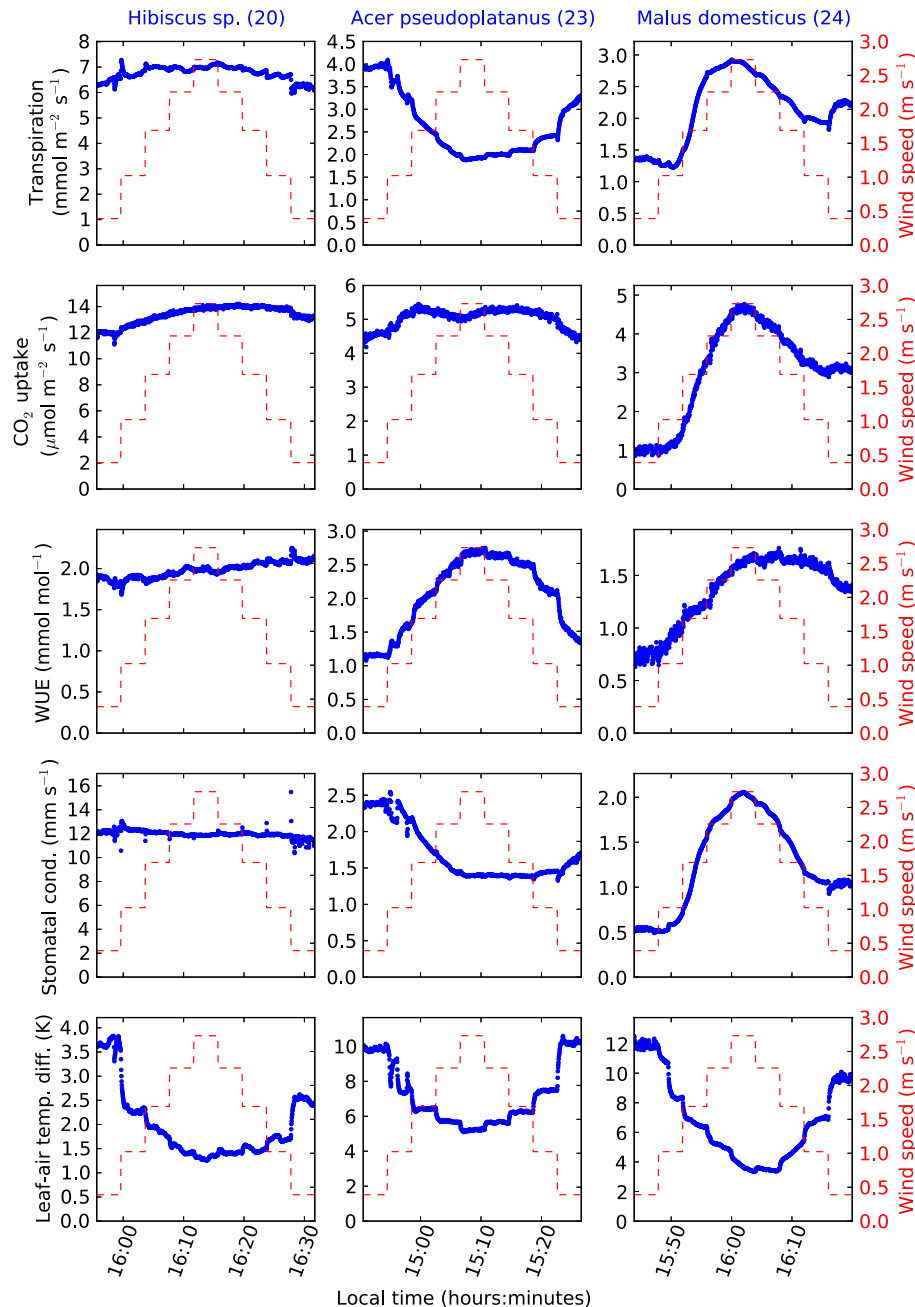


Figure 1. Observed leaf responses to varying wind speed. For each leaf, fan voltage in the leaf chamber was varied every 4 min from low to high in five steps and back again. The effective wind speed in the chamber (Table S2) is indicated by the red dashed line, corresponding to the vertical axis on the right hand side of each plot. Each column of panels corresponds to measurements on a different plant species (indicated at the top, number refers to experiment described in Table S3). To convert stomatal conductance from units of mm s^{-1} to $\text{mol m}^{-2} \text{s}^{-1}$, values need to be multiplied by roughly 0.4.

increased even more strongly with wind speed, leading to a net positive effect of wind on WUE.

Similar experiments were conducted on 30 leaves of 20 species growing in a temperate climate (Zurich), 19 of which expressed a clear positive response of WUE to wind speed (all quartiles > 0 in Experiments 1, 2, 6, 7, 9, 10, 13, 17, 19 and 21–30 in Fig. 2), while only 1 experiment shows an equivalently clear negative response (Experiment 11). The observed increases in WUE were up to 60% for a 100% increase in wind speed. The

experiments with a clear positive effect of wind on WUE included situations where stomata responded to wind speed positively (6, 7, 17, 21 and 24–27), negatively (9, 10 and 19) or not at all (1, 2 and 13) and also where assimilation responded positively (6, 7, 17, 19 and 21–30), slightly negatively (9 and 10) or not at all (1 and 2) to wind speed (Fig. S16a–f). Some of them even show an increase in transpiration with wind speed and nevertheless a positive response of WUE because of an even stronger increase in assimilation (6, 24, 25 and Fig. S16b,e).

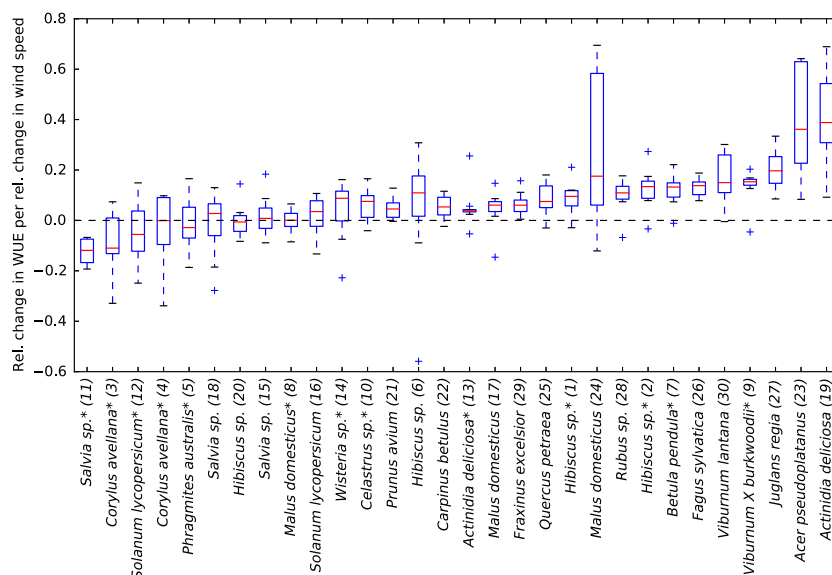


Figure 2. Relative sensitivity of water use efficiency (WUE) to wind speed for different leaves in LI-6400XT leaf chamber, sorted by 25% quartile in ascending order. Experiments are described in main text, while specific experimental conditions for each experiment (identified by index value following plant name) are given in Table S3. Each box-whisker plot summarizes eight values, where the box extends from the first to the third quartile, the red line marks the median value, while the whiskers mark the data range, excluding outliers marked as crosses. Outliers are defined as points that deviate from the quartiles by more than 1.5 times the interquartile range. Asterisks denote experiments using the standard LI-6400XT LED light source; all others were conducted using the LI-6400XT transparent chamber top and ambient light.

Leaves with roughly constant and low stomatal conductance commonly expressed decreasing transpiration rate with increasing wind speed, as also confirmed in experiments using an artificial leaf with low conductance (Fig. S5).

Numerical simulations of wind effects on water use efficiency

Simulations of steady-state leaf energy balance and gas exchange and their sensitivities to wind speed were performed for a large range of atmospheric conditions, two wind speeds (0.5 and 5.0 m s^{-1}) and two values of initial stomatal conductance (0.01 and 0.1 m s^{-1}). Two scenarios of stomatal response to wind speed were considered; one is no response, that is, *constant stomatal conductance*, and the second is an adequate stomatal closure with increasing wind speed to maintain *constant total leaf conductance*. We also used two different methods of calculating the relative sensitivity to wind speed (Eqn 1); one was using the photosynthesis model and biochemical parameters of grapevine leaves, and the other was based on Eqn 14, that is, ignoring temperature effects on photosynthesis.

In the constant leaf conductance scenario, simulations presented in Fig. 3 suggest a positive response of grapevine WUE to wind speed across a very wide range of environmental conditions, with the only negative responses simulated for low light and low relative humidity combined with high stomatal conductance. Overall, the simulated responses of WUE to wind speed are strongest for high irradiance and low stomatal conductance with relative responses of up to 0.7. Figure 4 reports the same simulations, but this time, the response of WUE to wind speed is represented by the negative response

of transpiration to wind speed at constant leaf conductance (Eqn 14), that is, neglecting any effects of leaf temperature on photosynthesis. The results are qualitatively the same, but the simulated responses are weaker at low wind speed and much weaker at low wind speed and low stomatal conductance, reaching maximum values of 0.35 only (Fig. 4a). The assumption of constant leaf conductance does not affect the results very strongly, as a comparison of Figs 3 and S9 reveals, the latter of which represents simulations for constant stomatal conductance. At high stomatal conductance, the values are lower by 0.05 to 0.1 in the absence of stomatal adjustments, but at low stomatal conductance, the results are virtually indistinguishable (compare also Figs S10 & S11). Figure 6 illustrates the effect of variations in stomatal conductance on transpiration, CO_2 assimilation and WUE at different wind speeds. Throughout the range of stomatal conductance values, assimilation is greater at high wind speed compared with low wind speed, while transpiration shows the opposite behaviour, except for very high stomatal conductance, where transpiration under high wind speed exceeds that at low wind speed. This results in a general decrease in WUE with increasing stomatal conductance, and in generally higher WUE at high wind speed across the range of stomatal conductance.

The simulated ranges of WUE sensitivity to wind speed are very similar to the sensitivity we found in our field observations, and both simulations and observations indicate a clear separation between positive sensitivities when leaves are warmer than the air and negative responses when leaf-air temperatures are near or below zero (Fig. 7). The observed relationship between leaf-air temperature difference and relative response of WUE to wind speed was best reproduced in the

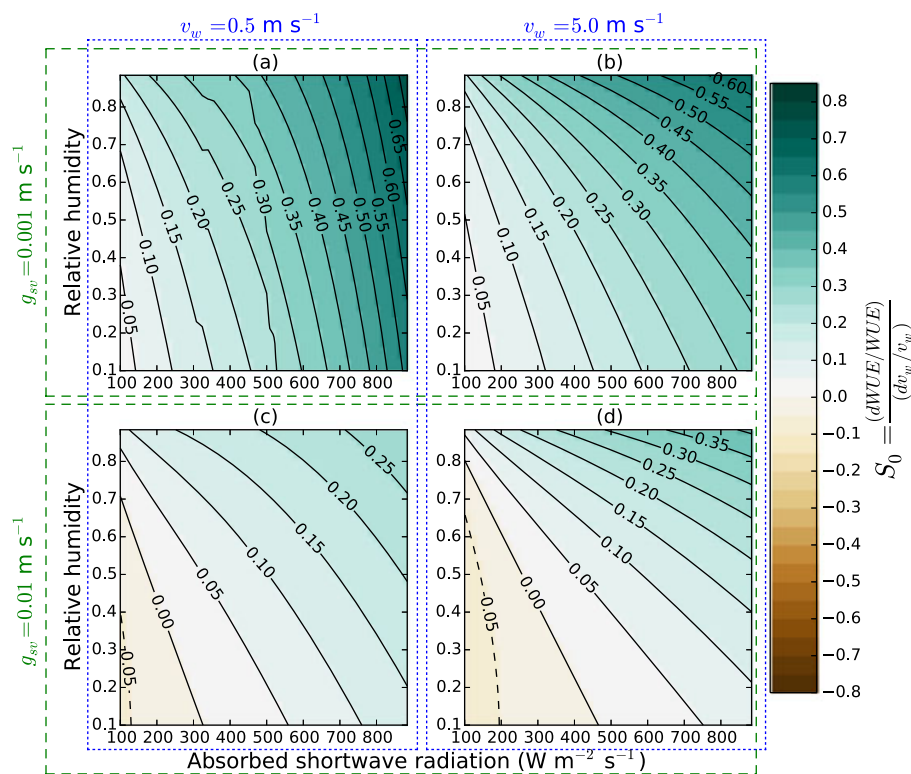


Figure 3. Simulated relative sensitivity of grapevine water use efficiency (WUE) to wind speed (v_w) at constant leaf conductance for different combinations of shortwave irradiance and vapour pressure (expressed as relative humidity). Simulations performed for a 5 cm wide leaf at air temperature of 27 °C ($T_a = 300$ K). Every point on the map represents an experiment with specified initial stomatal conductance and wind speed, from which wind speed was perturbed by 1% while stomatal conductance was adjusted to maintain leaf conductance constant. Top row (a and b): 0.001 m s⁻¹ initial stomatal conductance, bottom row (c and d): 0.01 m s⁻¹ initial stomatal conductance. Left column (a and c): 0.5 m s⁻¹ initial wind speed, right column (b and d): 5.0 m s⁻¹ initial wind speed. The contour lines and values in the colour map represent a relative change in WUE ($dWUE/WUE$) per relative change in wind speed (dv_w/v_w), for example, a value of 0.1 suggests that a 1% increase in wind speed would result in a 0.1% increase in WUE.

simulations with high wind speed and high stomatal conductance (Figs. 4b, S10b & S11b).

DISCUSSION

The model employed in this study facilitates a range of theoretical insights into the sensitivities of steady-state leaf gas exchange to environmental drivers that defy conventional wisdom and intuition. In the following, we will discuss key findings and place these into perspective with common intuition and observations.

Sensitivity of the leaf energy balance to wind speed

Wind affects the leaf boundary layer conductance for water vapour and sensible heat flux in a similar way. However, stomatal conductance decouples the leaf conductance for latent heat flux from the sensible heat transfer coefficient. As stomatal conductance decreases, leaf temperature increases and the associated sensible heat flux becomes the dominant process removing heat from an irradiated leaf surface (Bowen ratio > 1, Fig. S7). Under such circumstances, leaf temperature is most sensitive to sensible heat flux, whereas latent heat flux is most

sensitive to leaf temperature, as changes in wind speed do not strongly affect leaf conductivity to water vapour (Figs S6b & S8). Thus, leaf transpiration rate tends to *decrease* with increasing wind speed because of the increasing cooling efficiency by sensible heat flux. This unintuitive behaviour has been previously documented experimentally (Yamaoka 1958; Mellor *et al.* 1964; Dixon & Grace 1984) and attributed by Monteith (1965) to stomatal resistances greater than 100 s m⁻¹, that is, stomatal conductance below 0.01 m s⁻¹. This is consistent with our findings for atmospheric conditions represented in Fig. S6, where transpiration rate increases with wind speed for stomatal conductance greater than $g_{sw} = 0.01$ m s⁻¹, whereas transpiration rate decreases with increasing wind speed for lower stomatal conductance. As also suggested by Monteith (1965) and Monteith & Unsworth (2013, P. 231), we found that environmental conditions that increase the Bowen ratio of a leaf (higher H_l) would expand the range of stomatal conductance for reduced transpiration by higher wind (most importantly under high irradiance, but also for high relative humidity and low air temperature, Fig. S7). Conversely, conditions that reduce the leaf Bowen ratio would reduce the relevant range of stomatal conductance for reduced transpiration by higher wind. Furthermore, we note that stomatal

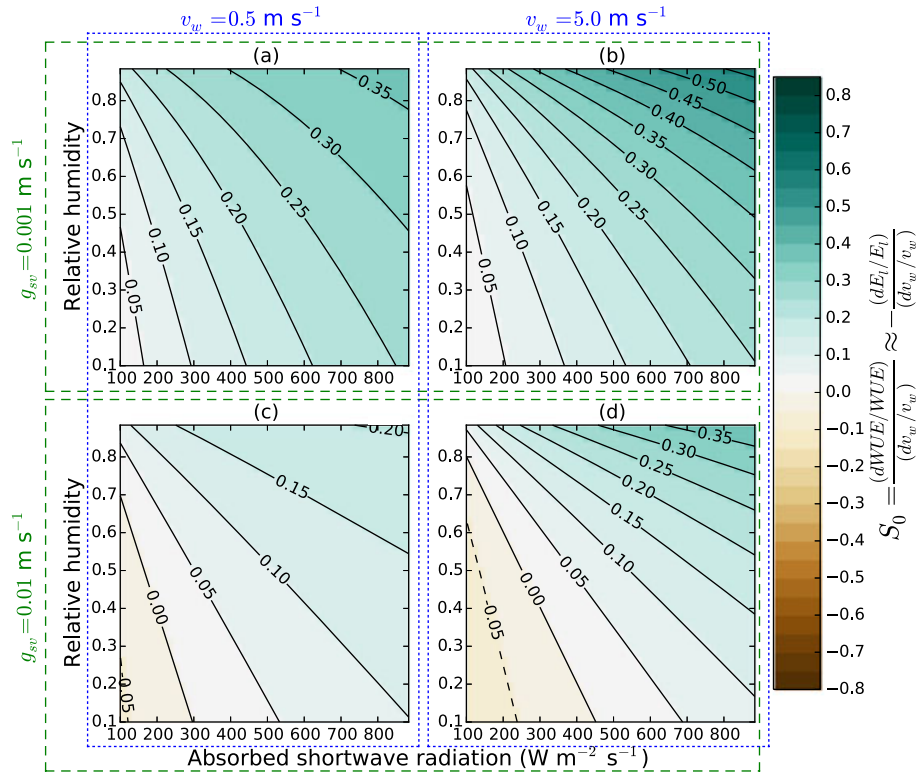


Figure 4. Simulated relative sensitivity of water use efficiency (WUE) to wind speed (v_w) at constant leaf conductance for different combinations of shortwave irradiance and vapour pressure (expressed as relative humidity). It is the same simulations as in Figure 3, but WUE is estimated based on the negative sensitivity of transpiration, that is, neglecting species-specific temperature response functions of photosynthesis.

conductance of 0.01 m s^{-1} ($\approx 0.4 \text{ mol m}^{-2} \text{ s}^{-1}$) is close to the upper end of the ranges found in our field experiments (Figs. S16a–f), in the observations by Buckley *et al.* (2014) and in the data compiled by Manzoni *et al.* (2011), implying that a decrease in leaf transpiration in response to increasing wind speed is likely more widespread than commonly considered.

Our results challenge two common assumptions related to transpiration and evaporation from wet surfaces: (1) One is that evaporation from unsaturated media and transpiration have similar sensitivity to environmental forcing as evaporation from an equivalent saturated surface (McVicar *et al.* 2012a; Ben Neriah *et al.* 2014; Milly 1992). We found that the sensitivity of wet surface evaporation to atmospheric forcing is, in general, different than that of partially dry surfaces, for example, plant leaves, and that they may exhibit opposite sensitivities to wind speed (Schymanski & Or 2015). (2) Another common assumption is that increasing air temperature enhances evaporation and transpiration because of increased atmospheric water demand (Bernacchi & VanLoocke 2015). However, the decrease in the Bowen ratio with increasing air temperature even when vapour pressure deficit is constant (Fig. S7d) suggests that the sensitivity of evaporation and transpiration to air temperature is due to suppression of convective cooling as the air temperature rises. This is an important distinction as it implies that the strength of the temperature effect depends on leaf size, surface properties and wind speed.

Relative sensitivity of water use efficiency to wind speed

The presentation of the WUE sensitivity to wind speed in relative terms, as performed in Eqn 1, is most meaningful if this relative sensitivity (S_0) is independent of wind speed, that is, if

$$S_0 = \frac{dW_{UE}/W_{UE}}{dv_w/v_w} = \frac{dW_{UE}}{dv_w} \frac{v_w}{W_{UE}} = \text{const.} \quad (16)$$

This is satisfied if WUE as a function of wind speed follows a power law of the form:

$$W_{UE} = \left(\frac{W_{UE0}}{v_{w0}^{S_0}} \right) v_w^{S_0} \quad (17)$$

where W_{UE0} is WUE at some $v_w = v_{w0}$. For a proof, please refer to the Supporting Information, Section S4. Both our simulation results and observations follow this power law relatively closely, as illustrated in Fig. S12, where Eqn 16 was fitted to exemplary simulation and observation data. The relatively narrow ranges of values reported in Fig. 2 despite a total variation in wind speed by a factor of 10 (in small steps) also support the scaling proposed in Eqn 17 and suggest that S_0 measured at one wind speed is indicative of relative WUE sensitivity to wind at a wide range of wind speeds.

Despite the short durations of our field experiments (ca. 30 min each), stomatal conductance rarely remained

constant, and yet, we observed a very common positive response of WUE to wind speed (Fig. S16a–f). This is best understood by comparing the sensitivity of transpiration and photosynthesis with stomatal conductance at high and low wind speed (Fig. 6). At low stomatal conductance, transpiration is higher for low wind speed than for high wind speed, but as stomatal conductance increases, transpiration increases less at low wind speed compared with high wind speed because of limitation by the low leaf boundary layer conductance. It appears that modest stomatal adjustments would allow the leaf to maintain constant transpiration rate as wind drops from 5 to 0.5 m s^{-1} . However, this would also incur a reduction in CO_2 uptake rates, resulting in a much lower WUE compared with high wind speed. In fact, the WUE achieved at high wind speed with a moderate stomatal conductance of 0.005 m s^{-1} cannot be matched in the simulation in Fig. 6 even with 0.001 m s^{-1} conductance. Furthermore, offsetting the positive wind effect on WUE would require a substantial reduction in stomatal conductance with decreasing wind speed, which carries the danger of reaching critically high leaf temperatures on a hot summer day (Leigh *et al.* 2012; Schymanski *et al.* 2013). In this context, we have to stress that the stomatal responses observed in our short experiments should not be used to gain insights about likely responses of stomata to changes in wind speed. As pointed out by a reviewer of this paper, stomatal responses to changes in evaporative demand may initially go in the opposite direction to that followed after 30 min and longer (Buckley *et al.* 2011). Because wind speed was altered every 4–5 min in our experiments, it is unlikely that the direction of stomatal response to wind was correctly captured.

To obtain a more complete picture of possible wind effects on WUE, we ran model simulations assuming no stomatal adjustments and simulations based on the assumption that stomata adjust in such a way as to maintain constant total leaf conductance, implying progressive reduction in stomatal conductance as wind speed increases (Fig. S6d). The simulations for grapevine leaves (Figs 3 & S10) suggest that the predominantly positive sensitivity observed in our field experiments is likely to hold over a very wide range of conditions, with the only exceptions towards the high stomatal conductance end, combined with low irradiance and low relative humidity. This was not strongly affected by assumptions of constant stomatal

or constant leaf conductance (compare Figs 3 & S9). The very strong responses at low stomatal conductance and low wind speed combined with high irradiance (Fig. 3a) are likely influenced by a decline in photosynthetic efficiency at high leaf temperatures (Fig. S13), which reached values of up to 47°C in the simulations. Such high leaf temperatures are beyond the range of data used for derivation of the temperature sensitivity by Buckley *et al.* (2014), which ended at 40°C . Comparison of Fig. 3 with Fig. 5, where WUE sensitivity to wind speed was estimated while neglecting the temperature-dependent biochemistry of photosynthesis altogether (scenario leading up to Eqn 14), reveals that the simplifying assumptions reduced the WUE-wind sensitivity at high leaf temperatures but had little effect elsewhere in this plot. This suggests that the estimates of WUE-wind sensitivity based on our mainly physical argument (Figs 4–7) may allow some general insights that are independent of species-specific and leaf-specific biochemical parameters.

We found a robust positive correlation between leaf-air temperature differences and relative sensitivity of WUE to wind speed in both our experimental and model data. This finding is consistent with the observation by Drake *et al.* (1970), who found positive response of transpiration to wind speed when leaf temperature was below ambient and negative response when it was above ambient. Likewise, the relationship went through the origin in our experimental data and in our simulations at *constant total leaf conductance* but less so for simulations at *constant stomatal conductance* (Fig. S15 cf. Fig. S14). The explanation is straightforward if one considers that at *constant leaf conductance*, transpiration is only sensitive to leaf temperature as wind speed varies. Given that increasing wind speed moves leaf temperature closer to air temperature, it decreases leaf temperatures and transpiration of leaves warmer than ambient, whereas it increases leaf temperature and transpiration of leaves colder than ambient temperature. At *constant stomatal conductance*, in contrast, varying wind speed affects transpiration both through its effect on leaf temperature and boundary layer conductance, meaning that transpiration can respond positively even if leaf temperature is already above ambient (Fig. S6). However, in this case, increasing leaf conductance would also have a positive effect on CO_2 assimilation and potentially on WUE, which complicates the interpretation.

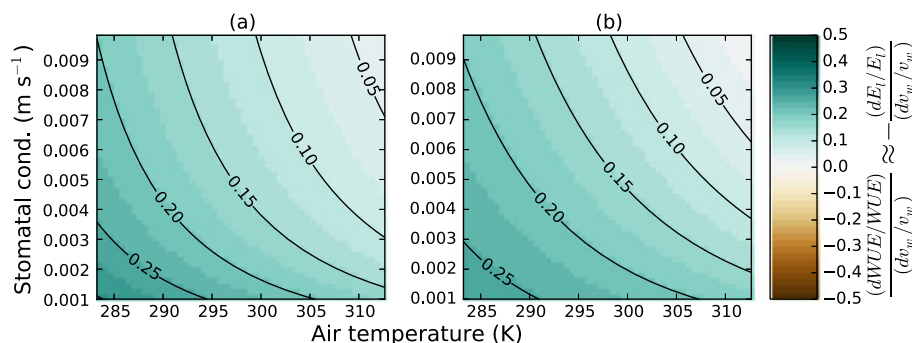


Figure 5. Relative sensitivity of water use efficiency (WUE) to wind speed (v_w) as a function of stomatal conductance and air temperature for (a) 0.5 m s^{-1} and (b) 5.0 m s^{-1} wind speed. Irradiance and relative humidity were kept constant at 500 W m^{-2} and 0.5, respectively. See caption in Fig. 3 for details.

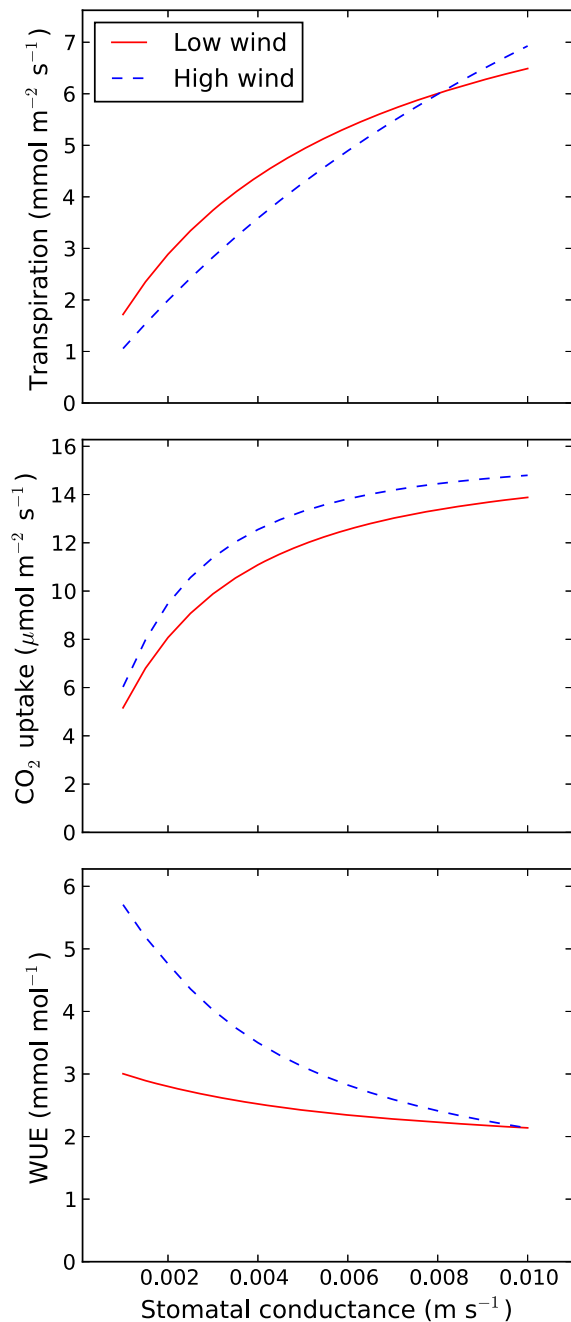


Figure 6. Simulated response of transpiration (top), CO_2 assimilation (middle) and water use efficiency (bottom panel) of grapevine leaves to stomatal adjustments for low (0.5 m s^{-1}) and high (5.0 m s^{-1}) wind speed. Atmospheric conditions correspond to those in the middle of the panels in Plot 5.

Our experimental data could lead to the interpretation that a linear regression through the origin would allow quantification of the WUE sensitivity to wind speed from leaf-air temperature differences, but our simulation data suggests that the slope of the curve is very sensitive to wind speed (Fig. 7). Nevertheless, positive leaf-air temperature differences appear to be a very strong indication for positive wind-WUE sensitivity, which could be used to assess how widespread such positive

sensitivity is within a canopy. Preliminary results of infrared-sensed leaf temperatures during our field measurements in 2015 revealed that temperatures of sun-exposed leaves (canopy edge and sunflecks) are generally above air temperature (Tab. S3), while only leaves in the deep shade of the canopy expressed temperatures at or below air temperature. The fact that all our field measurements were conducted in the mesic conditions of Zurich, Switzerland, suggests that positive leaf-air temperature differences and hence positive effects of wind speed on WUE are not restricted to water-limited environments but are likely quite widespread. Considering that canopy gas exchange is dominated by sun-exposed leaves, it is likely that canopy-scale WUE would also respond to variations in wind speed in a similar direction. However, our analysis is strictly valid at the leaf scale only, as it does not consider any feedbacks of leaf energy and gas exchange with the canopy air or any atmosphere-canopy coupling that would also be affected by variations in wind speed. Furthermore, the study only considers short-term response, where stomatal conductance is the only biological response variable, that is, the results are mainly based on physical processes. Possible longer-term effects will be discussed.

Implications for global change studies

McVicar *et al.* (2012a) reported a mean global decrease in wind speeds between -0.009 and $-0.017 \text{ m s}^{-1} \text{ a}^{-1}$ in the past 50 years, likely linked to global warming (Coumou *et al.* 2015). For wind speeds between 0.5 and 5 m s^{-1} , a trend of $-0.01 \text{ m s}^{-1} \text{ a}^{-1}$ would be equivalent to a decrease by 0.2 – 2% per year. Given increases in WUE of up to 0.35% for each 1% increase in wind speed for low stomatal conductance and low wind speed (Fig. 4a), the trend in wind speed alone could have lowered leaf-scale WUE by as much as 0.7% per year if everything else had remained unchanged. In comparison, considering a mean increase in atmospheric CO_2 concentrations (c_a) by $2 \mu\text{mol}$ per year at a current c_a of $400 \mu\text{mol}$, [that is, a relative change of 0.5% per year] and a relative response of WUE to increasing c_a in the order of 0.3 to 1.4 (Barton *et al.* 2012; De Kauwe *et al.* 2013; Tausz-Posch *et al.* 2013; Bernacchi & VanLoocke 2015), increasing c_a is likely to cause increases in WUE in the order of 0.15 – 0.7% per year. This suggests that the expected contribution of declining wind speed to changes in WUE could have the capacity to compensate for effects of increasing c_a under some conditions. For more common conditions of 50% relative humidity and 500 W m^{-2} irradiance, a 2% drop in wind speed per year could still result in roughly $0.2 \times 2 = 0.4\%$ decrease in WUE at low stomatal conductance, all else constant. At high wind speed conditions, we would obtain a relative response of 0.25 and a trend in wind speed of 0.2% per year only, resulting in 0.05% decrease in WUE per year attributable to global stilling.

The effect of long-term trends in wind speed on WUE could be affected by plant adaptation that mitigates negative effects on WUE, for example, by optimising canopy structure and leaf sizes to increase convective cooling (Smith 1978). The leaf boundary layer conductance is roughly a function of the square

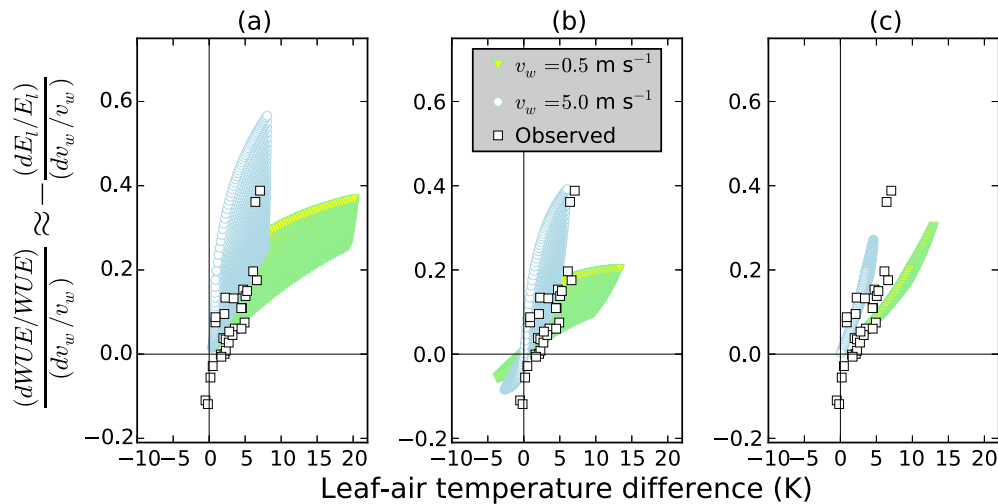


Figure 7. Observed and simulated relative sensitivity of transpiration to wind speed as a function of the leaf-air temperature difference. Panels (a), (b) and (c) correspond to simulations presented in Figs 4 (a and b), 4 (c and d) and 5, respectively. Simulations at 0.5 m s^{-1} wind speed (v_w) are plotted as green triangles, while simulations at 5.0 m s^{-1} wind speed are plotted as blue circles. Black empty rectangles correspond to median values of each observed leaf in Fig. 2.

root of the ratio of wind speed to leaf width, implying a linear scaling between leaf width and wind speed to keep heat and mass transfer across the boundary layer constant (Eqn 6). If a decline in wind speed has adverse effects on leaf WUE as suggested in the present study, ecological adaptation may result in decreasing leaf sizes with declining average wind speeds in order to mitigate this effect. In fact, leaf sizes have been observed to decline in the past century, which has commonly been explained by increasing air temperatures (Guerin *et al.* 2012). Interestingly, the observed decline in leaf widths of an Australian shrub in the past 100 years (Guerin *et al.* 2012) is quantitatively consistent with full compensation for declining wind speeds

observed in Australia during the past decades (Fig. 8). It has been proposed previously that there may be considerable selective pressure for smaller leaves under high radiation loads and limited water availability, because of the effect of leaf size on leaf temperatures and transpiration rates while maintaining high CO_2 assimilation rates (Ball *et al.* 1988). Our results suggest that this selective pressure is likely to be increased by global stilling.

CONCLUSIONS

We conclude that wind has a generally positive short-term effect on the WUE of sun-exposed leaves for a wide range of conditions, as demonstrated in the present study experimentally and on theoretical grounds. Our results are consistent with previous findings suggesting negative effect of wind on transpiration under certain conditions, but we demonstrate that the concurrent positive effect of wind on CO_2 assimilation results in positive response of WUE over most of the relevant environmental spectrum. Considering global trends in wind speed and atmospheric CO_2 concentrations, we estimated that global stilling could result in decreasing WUE in the same order of magnitude as the increase attributed to increasing atmospheric CO_2 concentrations. However, in contrast to the CO_2 effect on WUE, wind speed effects can be compensated for by adjustments in leaf sizes in the long term. Our results emphasize the ecological importance of leaf boundary layer conditions and hence leaf size and wind speed for plants in their environment and suggest that wind speed trends should not be neglected in the interpretation of trends in WUE and/or leaf sizes over time.

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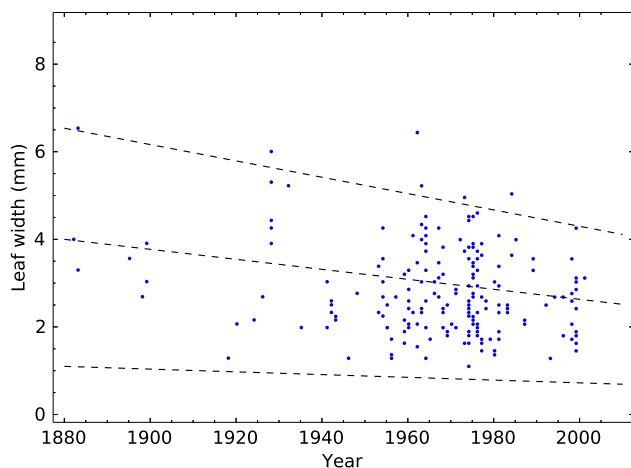


Figure 8. Trend in leaf widths of *Dodonaea viscosa subsp. angustissima* over time, as derived by Guerin *et al.* (2012) from herbarium samples. Data points were digitized from Fig. 2d in Guerin *et al.* (2012), and dashed lines represent trends in leaf (starting with different initial leaf sizes in 1880) size that would maintain constant leaf aerodynamic heat transfer coefficients (Eqn 6) as wind speed declines by $0.009 \text{ m s}^{-1} \text{ year}^{-1}$ down to 2 m s^{-1} in 2008 (McVicar *et al.* 2008).

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