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LETTER

High water use in desert plants exposed to extreme heat

Abstract

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The peer review history for this article is available at https://publons.c om/publon/10.1111/ele.13516 Many plant water use models predict leaves maximize carbon assimilation while minimizing water loss via transpiration. Alternate scenarios may occur at high temperature, including heat avoidance, where leaves increase water loss to evaporatively cool regardless of carbon uptake; or heat failure, where leaves non-adaptively lose water also regardless of carbon uptake. We hypothesized that these alternative scenarios are common in species exposed to hot environments, with heat avoidance more common in species with high construction cost leaves. Diurnal measurements of leaf temperature and gas exchange for 11 Sonoran Desert species revealed that 37% of these species increased transpiration in the absence of increased carbon uptake. High leaf mass per area partially predicted this behaviour ($r^2 = 0.39$). These data are consistent with heat avoidance and heat failure, but failure is less likely given the ecological dominance of the focal species. These behaviours are not yet captured in any extant plant water use model.

Keywords

Cowan-Farquhar, functional trait, heat waves, Sonoran desert, stomatal regulation, thermal stress, transpiration, water use efficiency.

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INTRODUCTION

Understanding plant gas exchange is crucial for the prediction of global carbon and water fluxes (Franklin *et al.* 2016). Prolonged, drier and warmer conditions are becoming more common, as are episodic heatwaves (Herrera-Strada & Sheffield 2017; Sévellec & Drijfhout 2018). These effects can lead to reduced plant productivity, increased mortality, and reduction of carbon stocks (McDowell *et al.* 2008).

Many models are based on the hypothesis that leaves maximize net photosynthetic carbon gain (A_n) for a fixed level of stomatal conductance (g_{sw}) and subsequent water loss from transpiration (E_t) (Cowan & Farquhar 1977). Where soil water is not limiting, the ratio between these fluxes is largely governed by vapour pressure deficit (D). This theory, and its extensions (here, termed 'marginal gain') have been widely adopted (Ball *et al.* 1987; Leuning 1995; Medlyn *et al.* 2011). Other model extensions maximize carbon gain while minimizing the risk of xylem failure (Sperry *et al.* 1998). Generally, this class of model predicts that as thermal stress increases at higher D and air temperature (T_{air}), A_n , E_t and g_{sw} will all be suppressed and eventually decline to zero, as the cost of water loss exceeds the benefit of carbon gain.

These 'marginal gain' models have been implemented in all major terrestrial biosphere models (TBMs), such as ORCHIDEE (Chen *et al.* 2016) and E3SM/FATES (Golaz *et al.* 2019). Empirical evidence supports these models (Wijk *et al.* 2000; Bonan *et al.* 2014; Yang *et al.* 2019; Wu *et al.* 2020). However, the majority of tests come from temperate environments or environments where D < 3 kPa. Model predictions may become inaccurate in high D

²Department of Research, Conservation and Collections, Desert Botanical Garden, 1201 N. Galvin Parkway, Phoenix, AZ 85008, USA conditions (De Kauwe *et al.* 2015; Knauer *et al.* 2015; Grossiord *et al.* 2020). Efforts to model gas exchange at higher D have often yielded results that are at odds with 'marginal gain' predictions (Franks *et al.* 1997; Eamus *et al.* 2008).

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Divergence of data from predictions are especially relevant for dryland biomes, which currently cover more than 40% of the Earth's surface (Huang *et al.* 2016) as well as for other biomes that experience seasonal drought or heatwaves. Thus, there is an empirical knowledge gap between observations and models in hot or dry environments. Misrepresenting the water and carbon contributions of arid lands can lead to poor climate and vegetation distribution predictions. The latter is even more problematic as some of these models depend on parameters such as evapotranspiration rates (Dilts *et al.* 2015) and leaf biomass (Quevedo & Frances 2008) that are directly related to plant physiological performance.

There are two alternate scenarios for leaf gas exchange in thermally extreme environments: one for adaptive 'heat avoidance' behaviour, and one for non-adaptive 'heat failure' behaviour. Neither scenario is yet included in any major TBM (Rogers *et al.* 2017).

The 'heat avoidance' hypothesis highlights a trade-off between thermal and economic functions in leaves. Optimal strategies may change if leaves must avoid thermal stress and mortality at high temperatures, to preserve the possibility of future carbon gain (Urban *et al.* 2017b; Blonder & Michaletz 2018; Griebel *et al.* 2019). When water is transpired, cooling occurs (Crawford *et al.* 2012); when no further cooling is possible, leaf temperature (T_{leaf}) will increase, decreasing A_n through biochemical limitations (Slot & Winter 2016) potentially causing tissue damage and

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leaf mortality. To avoid this outcome, leaves may spend water by increasing g_{sw} and thus E_t . This behaviour would occur regardless of the rate of carbon gain, yielding divergent predictions under arid conditions than 'marginal gain' predictions. While low water use efficiency (WUE) at high D is already predicted by many 'marginal gain' models (due to the increase of E_t with D dominating downregulation of g_{sw} with D; Eamus *et al.* 2008), the 'heat avoidance' hypothesis proposes that WUE may be lower still, or that high E_t may occur in the complete absence of A_n . However, heat avoidance is predicted to be possible under conditions where soil water availability is high enough to meet leaf water demand (Urban *et al.* 2017b).

The 'heat failure' hypothesis suggests that minimum leaf conductance may increase with increasing T_{leaf} regardless of optimal strategy. First, g_{sw} could increase due to a range of physical effects related to the temperature-dependent fluidity of water (Urban *et al.* 2017b; Cochard 2019). Second, regulation of g_{sw} may be more challenging at high T_{leaf} when high pressure gradients occur between leaf air spaces and the atmosphere (arising from temperature-dependent water vapour concentration differences or direct temperature effects), resulting in uncontrolled stomatal opening (Bendix *et al.* 1994). Third, water may also be transpired through the leaf cuticle rather than through the stomata (Kerstiens 1996; Duursma *et al.* 2019). This effect is generally negligible at low temperatures but may be almost half of total conductance in some species at very high T_{leaf} (Eamus *et al.* 2008; Duursma *et al.* 2019).

Limited evidence supports the possibility of plants decoupling g_{sw} from A_n under extreme thermal stress to reduce T_{leaf} (Teskey *et al.* 2015; Slot & Winter 2016; Drake *et al.* 2018). However, most evidence has come from potted plants from temperate – Ameye *et al.* (2012), Urban *et al.* (2017), Bauweraerts *et al.* (2013); tropical – Slot *et al.* (2016), Lin *et al.* (2017); and subtropical – Drake *et al.* (2018), von Caemmerer & Evans (2015) regions. Less is known about species from arid regions (Rogers *et al.* 2017), under drought conditions (Anderegg *et al.* 2018), or *in situ* (Vargas & Cordero 2013; Teskey *et al.* 2015; Griebel *et al.* 2019).

Here we assessed the prevalence of alternative plant water use behaviour in hot and dry environments. We made *in situ* measurements of 11 C₃ species native to the Sonoran Desert of southwestern Arizona and northwestern Mexico. We combined diurnal measurements of leaf gas exchange and T_{leaf} with leaf structural traits and micrometeorological data. Data were collected in environments where T_{air} often reached 43 °C/110 °F and T_{leaf} reached 50 °C/122 °F. We predicted that alternative water use behaviour would reflect a heat avoidance strategy and would be most prevalent in species: (1) from heat-stressed habitats, (2) that express anisohydric stomatal behaviour and (3) with high construction cost leaves, where the carbon investment of leaf construction might counterbalance a high investment of water.

MATERIALS AND METHODS

Strategy classification

Three criteria were used to determine whether alternative water use behaviour was occurring (Fig. S1). First, under both

the 'heat avoidance' and 'heat failure' hypotheses, high water use and relatively low carbon uptake should occur (i.e. low WUE). We therefore carried out linear regressions between A_n and E_t and g_{sw} and reported the regression slopes. Second, under the 'marginal gain' hypothesis, A_n would decrease as a function of decreasing g_{sw} and E_t as T_{leaf} increases, whereas decoupling between A_n and g_{sw} would occur under alternate hypotheses. We also reported slope estimates and goodnessof-fit (r^2) for relationships among A_n , E_t and g_{sw} and T_{leaf} . Third, we assessed the goodness-of-fit of quantitative predictions of the 'marginal gain' hypothesis using equations linking observed values of E_t and g_{sw} to predicted values based on D, from Medlyn *et al.* (2011) and Lin *et al.* (2015):

$$g_{sw} = g_0 + 1.6 \cdot \left(1 + \left(\frac{g_1}{\sqrt{D}}\right)\right) \cdot \frac{A_n}{C_a}$$
(1)

$$E_{t} = \frac{A_{n} \cdot 1.6 \cdot (g_{1} \cdot \sqrt{D} + D)}{C_{a} \cdot P_{a}}$$
(2)

In these equations, D (kPa) is vapour pressure deficit at time of measurement, C_a is atmospheric CO₂ concentration (= 400 µmol mol⁻¹) and P_a is atmospheric pressure (= 96.25 kPa). The model includes two constants, g₀ and g₁, which were set to -0.007 and 6.55, respectively, based on data for a savanna site (Medlyn *et al.* 2011). Savanna coefficients were chosen as an approximation for a desert environment as no desert data were available.

Alternative water use behaviour was considered to occur when at least two of the three below criteria were met (Fig. S1):

- (1) A_n/E_t (WUE) and A_n/g_{sw} (intrinsic water use efficiency; iWUE): regression slopes and coefficient of determination (r^2) : species with low r^2 and non-significant slopes or < 500 µmol mol⁻¹;
- (2) E_t and g_{sw}/T_{leaf} regression slopes and r^2 : species with non-negative slopes and low r^2 ;
- (3) Correlation between observed E_t and g_{sw} and estimated E_t and g_{sw} using eqns 1 and 2: species with low r² and E_{t_Pre-dicted} < Et_Observed.</p>

Through these criteria alone, it is not possible to distinguish 'heat avoidance' from 'heat failure'. Doing so would require partitioning the transpiration fluxes into three major components (see Discussion). Hence, hereafter, any species meeting the above criteria are referred to as 'alternative water use(rs)'.

Predictors of alternative water use behaviour

We examined which traits predicted alternative water use behaviour across species by regressing thermal strategy indices (i.e. slopes obtained from linear regression between A_n and E_t and g_{sw} per species, and value of r^2_{ET} from eqns 1 and 2) against species mean values of leaf mass per area (LMA; g m⁻²), leaf dry matter content (LDMC; g g⁻¹), predawn and midday leaf water potential (ψ ; MPa) and hydraulic strategy (i.e. isohydric or anisohydric). Details of leaf and hydraulic trait measurements are described in Supporting Text sections *'Leaf water potentials and hydraulic strategy*' and *'Leaf structural trait determination'*. Additionally, we assessed the relationship between water use classification indices (regression slopes and r^2) and ecological parameters including habitat, leaf habit, stomata distribution and wood anatomy. All of these ecological and morphological parameters were obtained through previously published literature (Table S1).

Study site and species

Field measurements occurred in 2018 between 4 June and 6 July in natural habitat at the Desert Botanical Garden (DBG) in Phoenix, Arizona, USA (33.46° N, 111.94° W, elevation 330 m). DBG is located in the northern Sonoran Desert and is characterized by hot and dry summers (June mean

maximum $T_{air} = 44$ °C; average relative humidity (RH) = 18%), with mean annual precipitation (MAP) totalling 191 mm yr⁻¹, 35% of which falls during the summer monsoon.

We selected 11 common Sonoran Desert woody plant species (three individuals per species = 33 plants; Fig. 1 and Table S1 for names, abbreviations and authorities). Selection was based on diversity of leaf and canopy architecture (Fig. 1). Selected individuals were similar in size within species, fully exposed to sunlight, and occurred on similar terrain. All species were C_3 with no known CAM expression, in order to focus on species that do not carry out night-time gas exchange (Winter & Holtum 2014).



Figure 1 Representative photographs and list of species at the Desert Botanical Garden (Phoenix, AZ, USA). Species name abbreviation between parentheses.

Gas exchange

Three fully expanded, sun-exposed leaves were chosen from each individual (n = 99 leaves) for diurnal gas exchange measurements. The physiological parameters measured were A_n (µmol CO₂ m⁻² s⁻¹), E_t (mol H₂O m⁻² s⁻¹) and g_{sw} (mol H₂O m⁻² s⁻¹) using a portable photosynthesis system (LI6800, LI-COR Inc., Lincoln, NE, USA). The diurnal measurements were divided into five intervals: 5 AM–7 AM (predawn and dawn); 8 AM–10 AM (early morning); 12 PM–2 PM (midday); 4 PM–6 PM (late afternoon); and 7:30 PM–10 PM (night). We measured three individuals per day, re-measuring individual leaves. Plants that easily lost their leaves had neighbouring leaves chosen for subsequent measurements. For more details on LI6800 measurement settings, refer to *Supporting Text* (*'LI6800 sampling details'*).

All days had $T_{air} > 35$ °C with no rain or clouds (Fig. S2). Plants received limited irrigation during the study period. However, if plants received irrigation on the day of measurement, we postponed the measurements to another day when shallow soils were superficially dry [i.e. volumetric water content at 10 cm depth < 15% using a soil moisture meter (FieldScout TDR150, Spectrum Technologies, Aurora, IL); Table S2]. Sampled plants had rooting depths likely well beyond the depth of our soil moisture measurements, and as a result could have had access to deep soil moisture.

Environmental variables

 T_{air} (°C) and RH (%) were measured at DBG every 30 s and averaged at 30-min intervals using a weather station (S-THB-M008, Onset, Bourne, MA). Values of T_{air} and RH were used to calculate D (Monteith & Unsworth 1990). D values were consistent with LI6800 point measurements (D_{Leaf}, kPa).

 T_{leaf} (°C) was measured using an infrared camera (A615, FLIR, Nashua, NH, USA; 640 × 480 pixels, accuracy ± 1 °C). Two thermal images per sampled plant were taken before every gas exchange period at 1–2 m from the target leaves (n = 10 images per plant per day). T_{leaf} was estimated from each thermal image as the mean value within a polygon enclosing each of three leaves per image (Schindelin *et al.* 2012).

RESULTS

Prevalence of alternative water use

We identified seven marginal gain species and four alternative water users (Table S1). Alternative water use was supported in *Qutu, Rhov* and *Vaca*, as each fulfilled all three criteria, as well as in *Dovi*, which fulfilled two criteria, since E_t of this species remained constant throughout 8 AM and 4 PM even though A_n did not decline as sharply as other species within this group (34% reduction of A_n compared to $58 \pm 7\%$ of the other three species, between 8 AM and 12 PM). Classification was based on the evidence below.

Criterion 1: marginal gain species with A_n/E_t regressions with slopes above 1000 and P < 0.05, included *Chli*, *Enfa*, *Latr*, *Olte*, *Pofr*, *Prve* and *Sich* species (n = 7). Alternative water users with slopes below 1000 and P > 0.05 (*ns*), included *Dovi*, *Qutu*, *Rhov* and *Vaca* species (n = 4; Figs 2a,d and S3, Table S3). Exceptions to these criteria were made for *Enfa* (slope = 853) and *Latr* (P = 0.15) since both species did not completely suppress A_n during midday (Fig. S3) and maintained a higher E_t than the other species over the same period (thus we did not observe decoupling between A_n and g_{sw}). All species had $r^2 > 0.50$ for the correlation of A_n and g_{sw} (P < 0.05; Table S3, Fig. 2d), except *Rhov*. In most species, E_t and g_{sw} were coupled ($r^2 > 0.60$ and P < 0.01), except *Dovi*, *Prve*, *Rhov* and *Vaca* with *Prve* being the only species among those not classified as an alternative water user.

Criterion 2: Alternative water use species exhibited some of the strongest relationships between E_t or g_{sw} and T_{leaf} (Fig. 2b,e; Table S3), with exception of Qutu ($r^2 < 0.10$). Overall, the relationship between E_t or g_{sw} and T_{leaf} was mostly non-significant and had $r^2 < 0.50$, and g_{sw} was better correlated to T_{leaf} than E_t ($r^2_{gsw} = 0.22$, P < 0.001; $r^2_{Et} = 0.07$, P < 0.05). However, g_{sw} declined with increases in T_{leaf} for all species, but not enough to prevent E_t from increasing for three alternative water users (*Qutu, Rhov, Vaca*) and one marginal gain species (*Latr*).

Criterion 3: For most species, the Et predicted from eqn 1 and $E_{t observed}$ correlations were strong (P < 0.05), with exception of Dovi, Latr, Qutu, Rhov and Vaca (P > 0.05; Fig. 2c,f and Table S3). Besides Qutu, the model proposed by Medlyn et al. (2011) and Lin et al. (2015) closely estimated g_{sw} to the observed rates, with $r^2 > 0.50$ (P < 0.05) and slopes close or above 1. However, these relationships were highly dependent on the time of day and the inclusion of Enfa in the data set. The estimation of E_t and g_{sw} using eqns 1 and 2 yielded poor estimates when compared to the observed Et and gsw rates of all species $(r_{\rm Et}^2 = 0.61, P < 0.001; r_{\rm gsw}^2 = 0.51, P < 0.001),$ with model predictions on average 36 and 60% smaller than the observed E_t and g_{sw} rates respectively. These failures were not solely caused by inappropriate values of g₀ and g₁ in predictions, as the predicted and observed values were not linearly correlated.

Predictors of heat avoidance

Alternative water using behaviour was predicted by higher leaf construction costs (supporting Prediction 2; Table S4). Species with higher LMA had lower A_n/E_t slope coefficients (Criterion 1; $r^2 = 0.39$, P < 0.05; Fig. 3a) and lower r^2_{Et} (Criterion 3; LDMC - $r^2 = 0.60$, P > 0.01; Fig. 3d). However, alternative water using behaviour was not related to hydraulic strategy, as of half alternative water users and 57% of marginal gain species were anisohydric (Figs S4 and S5).

Additionally, alternative water use behaviour was also dependent on species' habitat ($r^2 = 0.77$, P < 0.05), leaf habit ($r^2 = 0.47$, P < 0.05) and stomata distribution ($r^2 = 0.41$, P < 0.05; Fig. 4a,c). All species classified as alternative water users were evergreen, and occurred naturally in mountain and canyons at higher elevations. All other species mostly occurred in lower deserts, were deciduous and were amphistomatous. Wood anatomy and leaf water potential (ψ_{pd} , ψ_{md} and $\Delta \psi$; Table S4, Figs S5 and S6) had little to no relationship with water use behaviour of the studied species, even though these traits are nominally linked to drought-tolerance.



Figure 2 Criterion 1 – (a and d) Relationship between daytime photosynthesis (A_n), transpiration rates (E_t), and stomatal conductance (g_{sw}) per water use classification (blue = alternative water user; orange = marginal gain); Criterion 2 – (b and e) relationship between T_{leaf} and E_t , and g_{sw} ; and Criterion 3 – (c and f) daytime relationship between observed and predicted E_t and g_{sw} per species, excluding *Enfa*. Statistical results for each species are in Table S2; inclusion of *Enfa* and night-time estimates of E_t and g_{sw} are shown in Figure S7.

'Marginal gain' model breakdowns

The marginal gain model performed poorly for morning and evening estimates of Et and gsw (Fig. S7). The model also did not predict positive Et and gsw during night-time and predawn periods. The model also yielded weak fits, especially for the evening $(r^2_{\rm Et 7PM} = 0.16,$ P < 0.05; $r^2_{\rm gsw 7PM} = 0.16,$ P < 0.05). When disregarding morning and evening values, the model explained 78% of the variance for g_{sw} (P < 0.001) and 59% for E_t (P < 0.001). When excluding Enfa from the data set, Et estimates were further reduced and the explained variance was only 23% (P < 0.001; Fig. S7c), while g_{sw} was similar with and without Enfa in the analysis (74%, P < 0.001; Fig. S7d). E_t was poorly estimated at midday $(r_{\text{Et 12PM}}^2 = 0.09, P = 0.12), \text{ afternoon } (r_{\text{Et 4PM}}^2 = 0.19,$ P < 0.05) and morning ($r^2_{\text{Et_8AM}} = 0.36$, P < 0.001). These poor estimates of E_t reflect the distinct and decoupled manner to which E_t increased when A_n and g_{sw} concurrently decreased with rising D (Fig. 5; Figs S8-S11).

DISCUSSION

This study is a potential proxy for future environmental change in aridlands, and for environments facing more extreme heatwaves. Under conditions of high daytime D (> 6 kPa), T_{air} (> 40 °C) and low RH (< 20%) (Figs S2, S12– S15), we found evidence that heat avoidance or heat failure is common in many desert plant species. We also found that species with high construction cost leaves were more likely to have alternative water use behaviour. These results provide empirical evidence from natural environments that current gas exchange models are in some cases insufficient for predicting plant water use under hot and dry conditions.

Heat avoidance or heat failure?

Results from the present study showed that 37% of desert species expressed gas exchange patterns of high water loss relative to net carbon assimilation, consistent with either heat avoidance or heat failure. Although data from this study do not allow us to directly test whether non-'marginal gain' species fall under the definition of heat avoidance or heat failure, our results seem most consistent with heat avoidance. In this study, the environmental conditions, while extreme globally, were locally within the range of typical summer conditions. Nevertheless, alternative water use might occur in other biomes or under episodic heatwave conditions. It is also possible that plants in this study extended their thermal tolerance threshold, thus leading to reductions of A_n as a result of increased mitochondrial respiration, increased photorespiration, reduced electron transport



Figure 3 Plant trait (leaf mass per area – LMA and leaf dry matter content – LDMC) relationship with thermal water use behaviour categories and model goodness-of-fit parameters. (a and b) A_n vs. E t slope coefficients of each water use classification; and (c and d) r^2_{Et} obtained through the Medlyn *et al.* (2011) and Lin *et al.* (2015) model fits for each species. Only significant regression lines are shown ($\alpha = 0.05$).

capacity of Photosystem II or a combination of all three. Thermal tolerances of various desert species (including half of species sampled in our current study) were found to be between 45 and 52 °C (Downton *et al.* 1984; Knight & Ackerly 2003; Gallagher 2014), with most species having the potential of recovering ~ 90% of initial A_n and E_t rates. Although some of the observed T_{leaf} values were above T_{air} or not significantly cooler than T_{air} at peak evaporative cooling capacity (Figs S12–S14), we speculate that they transpire just enough to not exceed thermal tolerance thresholds (i.e. lethal temperatures; Blonder & Michaletz 2018), or temperatures would have been even higher in the absence of transpiration.

Heat tolerance could also preclude alternate water use behaviour. While high tolerance is documented in many CAM species that do not transpire during daytime conditions (e.g. Cactaceae; Smith *et al.* 1984), it appears less common in the C_3 species studied here. High transpiration may be evolutionarily more easily achieved or lower cost than other strategies. While drought deciduousness or CAM photosynthesis could enable temporal avoidance of stressful environmental conditions (Cushman & Borland 2002; Tomlinson *et al.* 2013; Winter & Holtum 2014), many arid-adapted species do not deploy these strategies to cope with extreme aridity since they require large amounts of energy and carbon to produce organic acids or new leaves. CAM photosynthesis, dense trichomes, higher reflectance, increased thickness and higher waxiness (Ehleringer & Mooney 1978; Smith 1978; Ehleringer 1988; Schuster *et al.* 2016) all have been identified as adaptive leaf traits in desert species to cope with the extreme conditions during harsh summers. However, because these traits are metabolically costly, some species might instead increase investment of water loss for evaporative cooling (i.e. saving carbon through respiration reduction and increase of Rubisco efficiency; Carmo-Silva *et al.* 2015) than investing carbon in leaves that might be permanently lost during heatwaves. This perspective is consistent with prior findings that species with tolerance to high T_{leaf} also express low minimum midday leaf conductance (g_{min}), and subsequently reduced evaporative cooling (Schreiber 2001; Schuster *et al.* 2016).

In the present study, plants that adopted an alternative water use behaviour were mostly evergreen and had higher LMA, which suggests that these species prioritize tissue preservation instead of allocating carbon towards new leaf production after leaf mortality induced by heat stress. Desert and evergreen plants tend to have higher LMA and higher construction costs than deciduous plants and plants from more mesic biomes (Poorter *et al.* 2009), possibly due to the effects of lower water availability (de la Riva *et al.* 2016a) or high carbon investment in defensive traits against leaf desiccation (de la Riva *et al.* 2016b). The loss of leaves in response to extreme heat could result in a significant long-term carbon



Figure 4 Variation in water use classification by species' habitat, leaf habit and stomatal distribution. Colours represent the thermal water use behaviour category (orange = marginal gain; blue = heat avoidance). Non-significant relationships with other traits are shown in the supporting information (Figures S5 and S6).



Figure 5 Comparison between observed E_t rates when related to climatic parameters. Colour scale is based on the r^2_{ET} obtained between daytime observed and predicted E_t rates for each species (e.g. species with stronger fits are shown in yellow and lighter green colours). (a) T_{air} (°C), (b) T_{leaf} (°C), and (c) D_{leaf} (kPa). Analyses include all species and only daytime values (8 AM–4 PM). Only statistically significant regression lines are shown ($\alpha = 0.05$). For the comparison between observed and predicted g_{sw} , see Figure S10; and Table S1 for r^2_{ET} values for each species.

deficits and potentially reduced plant growth, which could be avoided if T_{leaf} were tightly regulated.

Implications for water availability

Heat avoidance may not be possible for extended temporal intervals in arid regions that are limited by soil moisture. For example, if we assume a leaf area index of only 1, whole-canopy water use in Enfa – the species with the highest E_t and g_{sw} in our study (Fig. S3) – extrapolated over the entire summer would exceed the incoming amount of precipitation (191 mm yr⁻¹) by a factor of three. However, E_t and g_{sw} rates in Enfa also were similar to rates previously reported for this species under well-watered and natural conditions (Smith & Nobel 1977; Ehleringer & Mooney 1978; Ehleringer 1988; Pockman & Sperry 2000).

Thus it instead seems likely that heat avoidance would only occur under high soil water availability (Urban *et al.* 2017b; Drake *et al.* 2018). All individuals in this study did receive supplemental irrigation. The four potential alternative water users in the present study all naturally occur along mountain slopes, and deep valley-bottom regolith where extensive mountain front recharge likely results in considerably higher soil moisture relative to mean annual precipitation that falls on the landscape. Rooting depths of *Qutu* have been reported to extend below 9 m, and rooting depths of a *Rhus* species closely related to *Rhov*, have been reported to extend below 13 m (Canadell *et al.* 1996). The deep roots would allow these species to forage for water throughout an extremely large volume of soil that in turn, could support high midday E_t rates during periods of high evaporative demand.

Implications for models

The decoupling of E_t and g_{sw} from A_n and D results in significant underestimations of water fluxes when using current 'marginal gain' stomatal regulation models, for example, Medlyn *et al.* (2011). These biases would then scale up to ecosystem-level predictions in TBMs, with potentially major consequences for predicting climate change impacts especially in aridlands.

The overall implication is that current models do not effectively describe many species' responses to extreme conditions. Models may need revision for plants occurring in hot and dry environments or those exposed to episodic heatwaves. Our trait-based results provide some preliminary insights into which species are mostly likely to follow the 'marginal gain' hypothesis, but the number of species predicted to be 'alternative water users' is large enough that further model development is likely necessary.

Importantly, the mathematical assumption of the portable photosynthesis system we used and most theory, is $E_t = g_{sw} \cdot D$. This is based on the assumption that water diffuses from internal air spaces through stomata and then into a boundary layer (Jones 1992). Regardless of this assumption, the values of A_n and E_t estimated from the system can be easily validated as they are estimated directly from the measured gas fluxes. However, g_{sw} is inferred based on this model, meaning that reported values should be interpreted with some

caution. More strongly, in a mixed model regression analysis, we found that E_t and g_{sw} depend statistically not only on D but also on T_{leaf} (Fig. S16). Thus there is a direct temperature effect on water transport that requires further explanation (see Fig. S17 for T_{leaf} effects on WUE and iWUE). There are several processes that would lead to model failure.

First, water may also be transpired through the leaf cuticle rather than through the stomata (Kerstiens 1996). This effect is generally negligible at low temperatures (Schuster et al. 2016; Duursma et al. 2019) but may be almost half of total conductance at T_{leaf} > 50 °C (Eamus et al. 2008; Cochard 2019; Duursma et al. 2019). Second, minimum leaf conductance has been shown to increase with T_{leaf}, due to a range of physical effects related to the temperature-dependent fluidity of water and increase in mesophyll conductances (Urban et al. 2017a; Urban et al. 2017b; Cochard 2019). Third, regulation of g_{sw} may be more challenging at high T_{leaf} , when pressure gradients occur between leaf air spaces and the atmosphere (arising from temperature-dependent water vapour concentration differences or direct temperature effects; Cernusak et al. 2018; Grossiord et al. 2020), and if this pressurization then leads to uncontrolled stomatal opening (Brix et al. 1992; Steinberg 1996; Cochard 2019). The vapour concentration effect could lead to pressurizations of approximately 4 kPa at 45 °C (Supporting text – 'Effect of temperature increases on closed stomata'). Internal leaf pressurizations have been reported of 1-2 kPa (Brix et al. 1992; Steinberg 1996; Arkebauer et al. 2001), but it seems doubtful that stomata could remain closed at much higher pressures. Fourth, damage to electron transport capacity of Photosystem II and other photo-biogeochemical processes could occur at high T_{leaf} that affect carbon assimilation but not water loss (Jiao & Grodzinski 1996; Slot & Winter 2016). Our field experiments were not designed to directly assess the relative contributions of these processes, but will be critical to advance simultaneous measurements of each in future studies.

Thus, the assumption of $E_t = g_{sw} \cdot D$ will no longer be fully valid if Et depends on Tleaf through the above mechanisms (Grossiord et al. 2020). High gc is likely to occur when Tleaf is high, due to temperature-dependence of cuticular permeability (i.e. wax barriers; Schreiber 2001). Non-diffusive transport is likely to occur when the specific humidity of water vapour is high (i.e. when the water vapour is non-negligible molar fraction of the air), in which there is significant momentum transfer and thus directional flow from water transport (Kowalski 2017). Additionally, if leaf pressurization occurs at high temperatures, then there may also be further effusive transport occurring as stomata spontaneously open to equalize pressure differences. None of these processes are captured by the LI6800's g_{sw} calculations (LI-COR 2018). More importantly, none of these processes are yet widely incorporated into gas exchange models (Kowalski 2017; Cochard 2019; Duursma et al. 2019).

To determine whether any of these processes may have influenced our conclusions, we took a heuristic approach, in which we assume an uncertainty in g_{sw} estimates that increases non-linearly with T_{leaf} , taking a value of $\pm 1\%$ at $T_{leaf} = 10$ °C, $\pm 5\%$ at $T_{leaf} = 25$ °C to $\pm 40\%$ at $T_{leaf} = 52$ °C. These values are chosen based on prior simulations of the importance of



 $E_{\text{total}} = E_{\text{stomata_diffusion}(T_{\text{leaf}}, D, A)} + E_{\text{stomata_effusion}(T_{\text{leaf}}, T_{\text{air}}, A)} + E_{\text{cuticle}(T_{\text{leaf}}, D)}$

Figure 6 Illustration of hypothesized alternative transpiration pathways (E) in a leaf in response to increases in leaf temperature (T_{leaf}), air temperature (T_{air}) and/or vapour pressure deficit (*D*) increase (dashed arrow indicates that all three variables follow the same increasing trend). E_{stomata_diffusion} is transpiration through water diffusing from stomata (red); E_{cuticle} is cuticular transpiration (blue); E_{stomata_effusion} is water loss through effusion from the stomata at high temperatures (orange); E_{total} is the sum of all components described (green). Parameters subscript between parentheses indicate drivers of that specific E component (A_n refers to photosynthesis).

 g_c (~ 40%; Eamus *et al.* 2008) and $g_{sw,effusion}$ (9%; Haynes 2014; Kowalski 2017) at the highest temperature extremes. These simulations are likely overestimating the magnitude of these potential processes, as there is evidence that some desert plant cuticles can withstand thermal stress without impacting cuticle integrity and functioning (Schuster *et al.* 2016; Bueno *et al.* 2019). Regardless, we found that the g_{sw} uncertainty did not change the fundamental conclusion that the 'marginal gain' model did not fit the data well in the heat avoidance/heat failure species (Fig. S18).

Development of high temperature gas exchange theory, in which E_t depends not only on g_{sw} and D, but also directly on T_{leaf} and T_{air} , is beyond the scope of this empirical study. It seems necessary to adapt current gas exchange models from $E = E_{stomata,diffusion(D, A)} = g_{sw(D, A)}$ ·D to a more general partitioning in terms of multiple fluxes, as $E = E_{stomata,diffusion(Tleaf, D, A)} + E_{stomata,effusion(Tleaf, Tair, A)} + E_{cuticle(Tleaf, D)}$ (Fig. 6). Such a partitioning would be challenging, as there would no longer be a single leaf conductance value that summarizes transport against a single gradient. This partitioning would also be difficult to measure with field-based gas exchange measurements that cannot easily separate transport processes. However, these advances are critical for more accurate modelling of high temperature gas exchange in plants and thus for TBMs.

Moreover, optimality models would also need to be extended to predict stomatal responses given the conflicting demands of marginal gain and heat avoidance, as well as the possibility of heat failure. Such theory remains to be developed. One immediate 'workaround solution' might be to assume that E_t always follows marginal gain theory, but also

necessarily increases due to temperature effects. This could be implemented in eqn 1 by assuming that the g_0 coefficient is an increasing function of T_{leaf} , that is, implicitly capturing some of the effects of $E_{effusion}$ and $E_{cuticle}$ (Duursma *et al.* 2019). Such a perspective is supported by other studies that have found temperature effects on this parameter (Duursma *et al.* 2019; Wu *et al.* 2020).

CONCLUSION

This study highlights the limitations of current theory in describing plant gas exchange at high temperatures under field conditions. It remains unknown how frequently this alternative water use behaviour might be occurring in other environments and for other taxa. Further studies should quantify this strategy variation at broader scales, from potted plants to experimental common gardens to naturally occurring plants in the wild. This study also highlights the need for further development of gas exchange models that can capture the full range of processes and plant responses to extreme environments. Advancing such models will provide more robust predictions for aridlands and for biomes experiencing heatwaves and drought.

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AUTHORSHIP

LA collected and analyzed the data and wrote the manuscript; BB and KH wrote the manuscript and provided scientific input. BB conceived the project and obtained funding. LA, CS and SW conducted fieldwork, and processed the samples and data. The authors declare no conflict of interest.

DATA ACCESSIBILITY STATEMENT

The data supporting these results are archived in Dryad (https://doi.org/10.5061/dryad.j9kd51c8h).

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SUPPORTING INFORMATION

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

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