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1 **Biophysical homoeostasis of leaf temperature: a neglected**
2 **process for vegetation and land-surface modelling**

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25 **ABSTRACT**

26 **Aim** Leaf and air temperatures are seldom equal, but many vegetation models assume
27 that they are. Land-surface models calculate canopy temperatures, but how well they
28 do so is unknown. We encourage consideration of leaf- and canopy-to-air temperature
29 differences (ΔT) as a benchmark for land-surface modelling, and an important feature
30 of plant and ecosystem function.

31 **Location** Tropical SW China.

32 **Methods** We illustrate diurnal cycles of leaf- and canopy-air temperature difference
33 (ΔT) with field measurements in a tropical dry woodland, and continuous monitoring
34 data in a tropical seasonal forest. The Priestley-Taylor (PT) and Penman-Monteith
35 (PM) approaches to evapotranspiration are used to provide insights into the
36 interpretation and prediction of ΔT . Field measurements are also compared to
37 land-surface model results obtained with the Joint UK Land Environment Simulator
38 (JULES) set up for the conditions of the site.

39 **Results** ΔT followed a consistent diurnal cycle with negative values at night (due to
40 negative net radiation) becoming positive in the morning, reaching a plateau and
41 becoming negative again when air temperature exceeded a “crossover” in the 24-29°C
42 range. Daily time courses of ΔT could be approximated by either the PT or PM model,
43 but JULES tended to underestimate the magnitude of negative ΔT .

44 **Main conclusions** Leaves with adequate water supply are partially buffered against
45 air-temperature variations, through a passive biophysical mechanism. This is likely
46 important for optimal leaf function, and land-surface and vegetation models should
47 aim to reproduce it.

48 INTRODUCTION

49 It has long been known that the temperature of leaves can differ by several degrees
50 (Campbell & Norman, 1998), and sometimes even by more than 10 degrees (Lange, 1959;
51 Gates *et al.*, 1964), from that of the surrounding air. Net radiation at the leaf surface must
52 be balanced by the combined fluxes of sensible and latent heat. The former is
53 proportional to the product of the leaf-to-air temperature difference (ΔT) and the leaf
54 boundary-layer conductance to heat. The latter is proportional to transpiration, which in
55 turn is proportional to the product of the leaf-to-air vapour pressure deficit (that is, the
56 vapour pressure deficit evaluated at the temperature of the leaf) and the combined
57 boundary-layer and stomatal conductances to water. ΔT adjusts rapidly to maintain this
58 balance.

59 The influence of leaf size and morphology on the leaf energy balance (through their
60 effects on boundary-layer conductance), and the implications of ΔT for photosynthesis,
61 transpiration and optimal leaf form, were active research topics in the 1960s and 1970s
62 (Linacre, 1964; Gates, 1968; Parkhurst & Loucks, 1972; Taylor, 1975; Givnish & Vermeij,
63 1976; Smith, 1978; Zangerl, 1978; Upchurch & Mahan, 1988). But Dynamic Global
64 Vegetation Models (DGVMs), first developed in the 1990s (reviewed by Prentice &
65 Cowling, 2013), have generally disregarded the biophysical effects of leaf size and
66 morphology and simply assumed $\Delta T = 0$. Biophysical land-surface models – used in
67 climate and Earth System models, and coupled to DGVMs in some cases – compute a
68 surface energy balance, and use the predicted canopy temperatures to drive leaf-level
69 physiological processes. But to our knowledge there has been no attempt to evaluate
70 these model predictions, or to analyse the implications of the modelled leaf-to-air
71 temperature differences for plant and ecosystem function.

72 As observed more than half a century ago by Gates (1964) and Linacre (1964, 1967), and
73 discussed in two recent articles (Michaeletz *et al.*, 2015, 2016), there is abundant
74 empirical evidence that under well-watered conditions in the daytime leaves are generally
75 warmer than air at low air temperatures but cooler than air at higher air temperatures – a
76 phenomenon that has been called “limited homoeothermy” (Mahan & Upchurch, 1988,
77 Upchurch & Mahan, 1988, Michaeletz *et al.*, 2015, 2016). We prefer the term
78 “biophysical homoeostasis”, which avoids any implied analogy with the metabolically
79 active process of homoeothermy in animals. Leaves are generally cooler than air during
80 the night and the periods just before sunset and just after sunrise, when net radiation is
81 negative – in other words, there is net loss of energy from the land surface. In the daytime,
82 leaf temperatures can be maintained within a narrower range than air temperatures,
83 varying around a “crossover” or “equivalence” temperature (where $\Delta T = 0$) that can vary
84 according to environmental conditions, but which generally lies within the optimum
85 range for photosynthesis (Michaeletz *et al.*, 2016). Oxygen isotope evidence suggests that
86 the effective photosynthetic operating temperature in forest canopies varies surprisingly
87 little from the boreal zone to the subtropics (Helliker & Richter, 2008) and is only a few
88 degrees greater even in the tropics (Song *et al.*, 2011), indicating that leaves are partially
89 buffered against spatial and temporal variations in the temperature of the air.

90 This Concept Paper aims to increase awareness of the biophysical causes and ecological
91 significance of leaf-temperature homoeostasis, and to point out the potential use of
92 canopy temperature as a benchmark for the evaluation and improvement of terrestrial
93 ecosystem and land-surface models. We illustrate the temperature crossover phenomenon
94 using (a) sequential field measurements on leaves of different species during two
95 consecutive sampling days at a tropical dry woodland site, and (b) continuous monitoring
96 of the upper canopy of an intact tropical seasonal forest. The Joint UK Land Environment
97 Simulator (JULES), which provides the land-surface component of the UK Met Office

98 Hadley Centre Earth System Model (Best *et al.*, 2011), was set up for the specific
99 environmental conditions and vegetation composition of the site and the results compared
100 with our field measurements.

101 **THEORY**

102 Variations in ΔT (K) on a time scale of minutes or longer (Schymanski *et al.*, 2013) are
103 closely to the steady-state energy balance (see e.g. Jones 2013, p. 225):

$$104 \quad R_n - c_p g_b \Delta T - \lambda E = 0 \quad (1)$$

105 where R_n is the net radiation at the leaf surface (W m^{-2}), c_p is the specific heat capacity of
106 air at constant pressure ($\text{J mol}^{-1} \text{K}^{-1}$), g_b is the leaf boundary-layer conductance to heat
107 ($\text{mol m}^{-2} \text{s}^{-1}$), λ is the latent heat of vaporization of water (J mol^{-1}) and E is the
108 transpiration rate ($\text{mol m}^{-2} \text{s}^{-1}$). This equation states that the leaf-level net radiation is
109 balanced by the sum of the sensible and latent heat fluxes – the sensible heat flux
110 depending on ΔT as well as on g_b , which is inversely related to the thickness of the leaf
111 boundary layer. Larger leaves generally have lower g_b , as indicated by the empirical
112 equation $g_b = 0.135 \sqrt{(u/d)} \text{ mol m}^{-2} \text{ s}^{-1}$ (Campbell & Norman, 1998, p. 101) where u is the
113 wind speed (m s^{-1}) and d is the characteristic dimension of the leaf (m) – about 0.74 times
114 the maximum width of the leaf (Taylor, 1975).

115 It follows by re-arrangement of equation (1) that:

$$116 \quad \Delta T = (R_n - \lambda E) / (c_p g_b) \quad (2)$$

117 Thus leaves are warmer than air if $R_n > \lambda E$, and more so for large leaves and at low wind
118 speeds. This explains why leaves have to be small in order to avoid overheating when air
119 temperatures are high and water is in short supply (Gates, 1968; Parkhurst & Loucks,
120 1972). However, under well-watered conditions, it is possible that $R_n < \lambda E$ if the air

121 temperature is high enough – resulting in leaves cooler than air. This cooling, relative to
122 air temperature, is also stronger in large leaves and at low wind speeds.

123 One way to predict the sign and magnitude of ΔT invokes the equation of Priestley &
124 Taylor (1972) (henceforth PT), an approximate empirical formula for evapotranspiration
125 – either from freely evaporating (wet) surfaces, or from vegetation that is well supplied
126 with soil moisture. The PT equation is based on the observation that the latent heat flux
127 (λE) is strongly determined by the available energy supply (R_n):

$$128 \quad \lambda E = \alpha [s/(s + \gamma)] R_n \quad (3)$$

129 where s is the derivative of the Clausius-Clapyeron relationship between saturated vapour
130 pressure and temperature (Pa K^{-1}), evaluated at the ambient air temperature; γ is the
131 psychrometer constant (Pa K^{-1}), equal to Pc_p/λ where P is atmospheric pressure (Pa); and
132 α is a dimensionless parameter, found empirically to take values typically in the range 1.1
133 to 1.4 and with a canonical value of 1.26 (see e.g. McAneney & Itier, 1996; Jones, 2013,
134 p. 109).

135 By combining equations (2) and (3), we obtain:

$$136 \quad \Delta T = R_n \{1 - \alpha [s/(s + \gamma)]\} / (c_p g_b) \quad (4)$$

137 The ratio $s/(s + \gamma)$ is steeply dependent on air temperature, being 0.40 at 0°C, 0.55 at 10°C,
138 0.68 at 20°C, 0.78 at 30°C and 0.85 at 40°C. Setting $\alpha = 1.26$, equation (4) implies that
139 there should be a crossover temperature (the value at which $\Delta T = 0$, implying $\alpha = 1 + \gamma/s$)
140 around 31°C (Li *et al.*, 2013).

141 The predicted crossover temperature is sensitive to the value of α , however, and this
142 parameter varies with environmental conditions. A number of studies (see e.g. Idso *et al.*,

143 1981; Michaletz *et al.*, 2016) have indicated lower crossover temperatures, in the range
144 25 to 28°C, consistent with somewhat larger values of α than the canonical 1.26.

145 There is an extensive literature (e.g. De Bruin, 1983; McNaughton & Spriggs, 1986;
146 Lhomme, 1997; Huntingford & Monteith, 1998; Raupach, 2000) devoted to explaining in
147 terms of more fundamental physical processes why α might be expected to be a relatively
148 conservative quantity. The PT equation is an expression of the large-scale average
149 evapotranspiration rate. It has also been applied successfully in the modelling of
150 transpiration by leaf canopies (e.g. Agam *et al.* 2010). At the leaf scale, however,
151 different plant species may have different traits influencing energy and water exchanges –
152 including leaf orientations influencing R_n (Chow 1994), and stomatal and boundary-layer
153 conductances – so there is likely to be variation among leaves, both above and below the
154 large-scale integrated rate.

155 A more detailed model for the leaf-level energy balance can be derived using the
156 so-called Penman linearization, which also underpins the Penman-Monteith (henceforth
157 PM) combination equation for transpiration (see e.g. Jones, 2013, pp. 104-105). The
158 Penman linearization approximates the leaf-to-air vapour pressure deficit via the initial
159 terms of a Taylor series:

$$160 \quad D(T + \Delta T) \approx D(T) + s \Delta T \quad (5)$$

161 where $D(T) = e_s(T) - e_a$ (with $e_s(T)$ the saturated water vapour pressure at air temperature
162 T and e_a the actual water vapour pressure) and $D(T + \Delta T)$ is the same quantity evaluated
163 at the leaf temperature. Equation (5) is a good approximation provided $\Delta T \ll T$. Equation
164 (2) combined with equation (5) leads to:

$$165 \quad \Delta T = [R_n - \lambda g \bullet (D + s \Delta T)/P] / (c_p g_b) \quad (6)$$

166 where g_{\bullet} is the combined (in series) stomatal and boundary-layer conductance to water,
 167 $g_{\bullet} = g_s g_b / (g_s + g_b)$ (the small difference between the boundary-layer conductances to
 168 water and heat is neglected here). Division by P is required for consistency with the
 169 molar units used for λ , g_s and g_b . As ΔT appears on both sides of equation (6), it is
 170 necessary to re-arrange it in order to solve for ΔT :

$$171 \quad \Delta T = (R_n - \lambda g_{\bullet} D/P) / [c_p (g_b + \varepsilon g_{\bullet})] \quad (7)$$

172 with $\varepsilon = s/\gamma$. Equation (7) is equivalent to formulae given by Monteith & Szeicz (1962),
 173 Linacre (1972), Paw U (1984) and others. Campbell & Norman (1998, pp. 224-229) used
 174 this formulation to show how various plausible combinations of air temperature and
 175 vapour pressure deficit can lead to negative daytime values of ΔT .

176 Additional insight can be obtained by further manipulation of equation (7). A crossover
 177 temperature T_x can be inferred from equation (7) as the air temperature for which $\Delta T = 0$,
 178 implying that $D(T_x)/P = R_n/\lambda g_{\bullet}$ or, equivalently, $e_s(T_x)/P = R_n/\lambda g_{\bullet} + e_a/P$. It is plausible
 179 that the ratio of R_n to g_{\bullet} might be relatively conservative during the daytime due to the
 180 covariation of both R_n and g_s with irradiance, leading to a relatively conservative value of
 181 T_x . (This covariance must break down at night however, or near to dawn and dusk, as R_n
 182 is then dominated by the long-wave component). The definition $\gamma = Pc_p/\lambda$ allows equation
 183 (7) to be re-written in a compact form, as follows:

$$184 \quad \Delta T = - [e_s(T) - e_s(T_x)] / [\gamma (1 + \varepsilon + g_b/g_s)] \quad (8)$$

185 if a value T_x is assumed to exist and e_a is assumed constant. Constancy of e_a is a
 186 reasonable assumption for variations in D that may be expected due to rapid air
 187 temperature changes during a day, when e_a normally varies much less than e_s . Because
 188 $e_s(T)$ increases steeply with T , equation (8) indicates that ΔT will be negative for all $T >$
 189 T_x . The rate of change of ΔT with T , evaluated at the crossover temperature T_x , is:

190
$$\partial(\Delta T)/\partial T = -\varepsilon/(1 + \varepsilon + g_b/g_s) \tag{9}$$

191 where ε is evaluated at T_x . Note that the rate of decrease in ΔT following equation (9)
192 depends only on T_x and the ratio of g_b to g_s . The variation of leaf temperature with respect
193 to air temperature (evaluated around $T = T_x$) has a slope that is less than unity by the
194 amount given in equation (9).

195 A number of simplifications have been made in the treatment above. Michaletz *et al.*
196 (2016) noted that (a) R_n is not independent of ΔT , as we have implicitly assumed so far,
197 because the long-wave radiation emitted by the leaf increases with the fourth power of
198 the leaf temperature following the Stefan-Boltzmann law; and (b) the Penman
199 linearization, appropriate for small ΔT , becomes less accurate the further the leaf
200 temperature departs from the air temperature. Point (a) is described in textbooks and a
201 standard approximation exists to correct for it (see e.g. Jones, 2013, p. 225), allowing the
202 isothermal net radiation (the value of R_n when $\Delta T = 0$) to be used in place of the true R_n in
203 a more precise formula that accounts for the first-order effect of ΔT on R_n . Point (b) is
204 dealt with in Michaletz *et al.* (2016) by representing $e_s(T)$ as a nearly exact
205 fourth-degree polynomial in T , which can be combined with the known
206 temperature-dependence of R_n leading to a quartic equation in T , which can be solved
207 analytically. The reader is referred to Michaletz *et al.* (2016) for details.

208 **METHODS AND RESULTS**

209 **Field measurements**

210 The selected field site was in a tropical dry woodland, Mandan, Yunnan province, SW
211 China (23.69° N, 101.85° E, 758 m a.s.l), with mean annual temperature 21.8°C and
212 mean annual precipitation 981 mm. Solar noon occurs at 13:00 local time. Measurements
213 were made at two topographic locations within the site, on two consecutive sunny days

214 during the dry season (October 2013). The location measured on the second day had
215 slightly denser vegetation, apparently due to run-on from surrounding slopes. However,
216 similar results were obtained for both days/locations. The canopy at both locations is
217 sparse, so most leaves receive high illumination and fully sunlit leaves were readily
218 accessible for measurement. Three species were selected. All were canopy-dominant
219 small trees or tall shrubs, having sclerophyllous, hypostomatous leaves with typical areas
220 of 25 cm² (*Terminthia paniculata*), 1 cm² (*Pistacia weinmannifolia*) and 0.9 cm²
221 (*Osteosperma schwerinae*). The smaller leaves of the two latter species were closely
222 packed along the branches, suggesting that their smaller size may not be biophysically
223 significant. Each day, the temperatures of three replicate top-canopy sunlit leaves of each
224 species were measured at half-hourly intervals using a hand-held infrared thermometer
225 (The Fluke 574, Everett, USA), pre-calibrated by the manufacturer, with emissivity set to
226 0.98. Air temperature was recorded with a mercury thermometer. The stated measurement
227 uncertainty of the infrared thermometer is ± 0.75 K and that of the mercury thermometer
228 is ± 0.1 K. The uncertainty of our estimates of ΔT is therefore small compared to the
229 range of observed ΔT (-6.2 to $+7.5$ K).

230 A consistent diurnal time course was observed across the different species and sampling
231 days/locations (Fig. 1). The data points in Fig. 1 have been smoothed using a quadratic
232 curve to highlight the characteristic diurnal pattern. ΔT was negative (reflecting negative
233 R_n) in the early morning, became positive during the morning, then peaked and began to
234 decline before solar noon (while R_n continued to increase). ΔT became negative again
235 when the air temperature exceeded a crossover value in the range 26 to 28°C. There were
236 no significant differences in observed crossover temperatures either among species or
237 between days/locations. The observed values suggest α somewhat larger than 1.26, but
238 well within the theoretically predicted range (up to 1.391 according to Huntingford &

239 Monteith, 1998). A similar diurnal time course of ΔT has been observed in other studies
240 and environments, for example by Yu *et al.* (2015) in a desert.

241 **Monitoring**

242 Canopy temperature is continuously monitored at the flux tower site located in an intact
243 tropical seasonal forest at Xishuangbanna Tropical Botanical Garden, XTBG (21.93°N,
244 101.27°E, 570 m a.s.l.), Yunnan province, China, with mean annual temperature 21.7°C
245 and mean annual precipitation 1492 mm. Solar noon occurs at 13:15. An infrared
246 temperature sensor (Apogee Instruments Inc., Logan, UT) has been installed 3 m above
247 the canopy. Air temperature is monitored using the HMP45C instrument (Vaisala,
248 Helsinki, Finland). Data are logged half-hourly.

249 We show the data from the dry season (January) of 2013 (Fig. 2). The same general
250 diurnal time course is seen at canopy level in the seasonal forest (Fig. 2) as we observed
251 at leaf level in the dry forest (Fig. 1). The observed crossover temperature was near 24°C.

252 **A test of JULES with field measurements**

253 We ran JULES in a standard configuration for stand-alone operation (i.e. not coupled to a
254 climate model) with non-limiting soil moisture prescribed in all soil layers. Driving data
255 on wind speed, relative humidity, and long- and short-wave radiation components
256 through the days of measurement were obtained from the flux tower at Yuanjiang, 2 km
257 from the field site. Appropriate values were prescribed in JULES for vegetation cover
258 broken down by plant functional types (47% broadleaf evergreen trees, 3% C₃ grasses, 25%
259 C₄ grasses, 12.5% shrubs and 12.5% bare ground) and soil properties (15% sand, 50% silt
260 and 35% clay) based on a field assessment.

261 Fig. 3 compares the JULES results to our field measurements. The model simulates
262 negative ΔT after about 14:00 local time, but the measurements show an earlier onset of
263 negative values. Measured ΔT approached -6 K for each day/location and all species
264 (Figs 1, 3), but JULES' simulated ΔT never fell below -2 K during the daytime.

265 Establishing the precise reasons for this discrepancy would require a series of sensitivity
266 experiments to be carried out. However, we note that JULES simulates a precipitous
267 decline in stomatal conductance from about 10:00 local time (Fig. 3), which would
268 restrict transpiration rates.

269 **Comparisons using simple analytical models**

270 We attempted to fit our field-observed leaf-to-air temperature differences using both the
271 PT and PM approaches (Fig. 4) by non-linear regression using the 'nls' function in R. We
272 treated α and g_b as the parameters to be estimated in equation (4) (PT), and g_b and g_{\bullet} as
273 the parameters to be estimated in equation (7) (PM). Note that these model fits are
274 approximate. A full implementation of the PM approach would require time-varying g_s ,
275 which was not measured. The assumption of constant g_b in both PT and PM models is
276 also a simplification, as wind speed variations are expected to influence g_b . The fitted
277 parameter values are given in Table 1. Negative ΔT was correctly simulated by both
278 approaches (Fig. 4), with approximately the right timing and magnitude. Fig. 4 also
279 shows JULES results for comparison and highlights the tendency of JULES to
280 underestimate negative ΔT during the hottest part of the day.

281 We fitted equations (4) and (7) in the same way to the canopy monitoring data, including
282 half-hourly measurements for each day during January 2013. For the PT model, the
283 estimated α was 1.32 ± 0.005 ($p < 0.001$), corresponding to a crossover temperature of
284 26.8°C . The fitted value for g_b in equation (4) was $0.68 \pm 0.03 \text{ mol m}^{-2} \text{ s}^{-1}$ ($p < 0.001$). In

285 comparison to monitored canopy temperature, the PT model yielded a highly significant
286 slope of 0.67 with $R^2 = 79\%$ (Fig. 5). For the PM model, we estimated a somewhat larger
287 value of g_b ($1.45 \pm 0.02 \text{ mol m}^{-2} \text{ s}^{-1}$, $p < 0.001$), and $g_{\bullet} = 0.51 \pm 0.007 \text{ mol m}^{-2} \text{ s}^{-1}$. The
288 regression between model predictions and the canopy monitoring data was again highly
289 significant, with slope 0.94 and $R^2 = 85\%$ (Fig 5).

290 We also fitted both models to the monitoring data for each day separately (Appendix S2).
291 This yielded for the PT model a median α of 1.34 (lower and upper quartiles: 1.32, 1.36)
292 corresponding to a median crossover temperature of 26.0 (24.9, 27.3) °C, and fitted
293 values for g_b in equation (4) of 0.61 (0.48, 0.68) $\text{mol m}^{-2} \text{ s}^{-1}$. For the PM model, we again
294 estimated values of g_b larger than for the PT model: 1.45 (1.26, 1.66) $\text{mol m}^{-2} \text{ s}^{-1}$, and
295 values of g_{\bullet} of 0.57 (0.50, 0.64) $\text{mol m}^{-2} \text{ s}^{-1}$. Both models fitted the monitoring canopy
296 temperature well on visual comparison (Figs 5 and S2). A general underestimation of the
297 magnitude of ΔT during the night (Fig. S2) probably relates to our simplifying
298 assumption of constant g_b , neglecting the fact that wind speeds are generally lower at
299 night than in the day. Low wind speeds would lead to smaller g_b and, accordingly, larger
300 differences between canopy and air temperatures.

301 **DISCUSSION**

302 The thermal homeostasis of sunlit leaves is a passive mechanism, dependent on ample
303 water supply for transpiration, which has the effect of keeping leaf temperatures in a
304 more limited range than air temperatures. We observed leaves to be cooler than air during
305 the midday period, even during the dry season in a tropical dry woodland (Fig. 1),
306 presumably thanks to deep roots allowing water to continue to be transpired at a
307 sufficiently high rate. However, along a gradient of declining rainfall, transpirational
308 cooling must become ineffective at some point; so that the leaves will again be warmer

309 than the air during the hottest time of day. Where this point occurs along rainfall
310 gradients remains to be determined.

311 Leaf-temperature homeostasis has important practical implications under climate
312 warming scenarios. For example, the study of urban street trees by Leuzinger *et al.* (2010)
313 projected extremely high future leaf temperatures, in scenarios where D was held
314 constant. However, D is the proximal driver of transpiration rate, and it is expected to
315 increase nearly everywhere (see e.g. Sherwood & Fu, 2014) – leading to reduced, and
316 ultimately negative, ΔT . As air temperatures rise, even in temperate regions, the
317 transpirational cooling effect of green infrastructure may become increasingly important
318 for the environment of cities. Increased transpiration rates due to high D should also help
319 to protect natural ecosystems and crops, to some extent, against potential adverse effects
320 of high temperature. In this perspective, high D is not necessarily a stress on plants.
321 Provided sufficient water is available for transpiration, high evaporative demand provides
322 a degree of leaf-temperature buffering against high air temperatures.

323 DGVMs could be modified to include leaf-to-air temperature differences with the help of
324 the theory discussed above. One key phenomenon that they currently do not capture is the
325 negative feedback (via transpiration) under well-watered conditions, which maintains leaf
326 temperatures within a more restricted range than air temperatures. DGVMs lacking this
327 feedback are likely to overestimate the direct impacts of warming on the gas exchange of
328 leaves in well-watered vegetation – including irrigated crops (Siebert *et al.*, 2017), and
329 deeply-rooted plants even in relatively dry environments, as well as in moist forests. On
330 the other hand, drought (in the sense of insufficient precipitation to support moist soils) is
331 a potential double menace to tropical moist forests (Schymanski *et al.*, 2013) as stomatal
332 closure under water limitation is expected to reduce transpiration; eventually to the point
333 where negative ΔT is no longer possible – potentially compounding the effects of

334 hydraulic failure (Rowland *et al.*, 2015) with photosynthetic inhibition and even
335 overheating damage. Deleterious effects of high leaf temperature would be felt soonest by
336 large leaves, because of their low boundary-layer conductance. How the effective
337 boundary-layer conductance actually varies under field conditions as a function of leaf
338 morphology and canopy architecture remains a topic for investigation, potentially
339 opening a route to the incorporation of more realistic plant functional diversity in
340 DGVMs.

341 Land-surface models like JULES, designed for climate-model coupling, already contain
342 the necessary equations (including explicit simulation of convective boundary layer
343 dynamics and thermodynamics) to simulate canopy temperature from physical principles.
344 However, to do so reliably, such models requires good representations of leaf
345 boundary-layer and stomatal conductances. In JULES, the irradiance absorbed by the
346 canopy follows Beer's law with a fixed light extinction coefficient based on the "big leaf"
347 approach (Clark *et al.*, 2011), thus not allowing for possible variation in leaf-angle
348 distributions. Stomatal conductance is treated as a decreasing function of vapour pressure
349 deficit, following the Jacobs (1994) equation (Cox *et al.*, 1998). Boundary layer
350 conductance is implicit, and cannot be altered in the current configuration of JULES. Our
351 example indicates that the simulation of leaf energy balance with JULES might be
352 inaccurate. In particular, the modelled cooling of leaves at high air temperatures was
353 weaker than observed. Fig. 3 also indicates that stomatal closure was predicted to occur
354 early in the day, restricting transpiration to a perhaps unrealistic extent. The "optimal
355 stomatal conductance" equation, independently derived (from different assumptions) by
356 Medlyn *et al.* (2011) and Prentice *et al.* (2014), implies that transpiration *continuously*
357 *increases* with vapour pressure deficit despite partial stomatal closure; whereas the
358 Jacobs equation used in JULES reduces g_s to a minimum value at a fixed maximum
359 vapour pressure deficit. This difference may be important. Alternatively, or additionally,

360 reductions of transpiration at high temperatures – in the field (Duursma *et al.*, 2008,
361 Medlyn *et al.* 2001), and in models like JULES that explicitly couple photosynthesis and
362 stomatal behaviour – may be caused by the exceedance of photosynthetic temperature
363 optima, prompting examination of whether the locations of these optima in current
364 models (especially for tropical plant types) are realistic.

365 Leaf and canopy temperatures are measurable at spatial scales from field measurements
366 on single leaves, through monitoring of vegetation canopies, to remotely sensed data at a
367 global scale (Li *et al.*, 2015). As a sensitive indicator of the effectiveness of
368 transpirational cooling, observations of ΔT would repay more extensive application to
369 evaluate and improve the representation of vegetation-atmosphere energy and water
370 exchanges in land-surface models, and plant functional diversity and climate-change
371 impacts in DGVMs.

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388 Imperial College initiative on Grand Challenges in Ecosystems and the Environment.

389 **SUPPORTING INFORMATION**

390 **Appendix S1** Leaf temperature measurements and climate data at two topographic
391 locations in a tropical dry woodland in Fig. 1(Mandan, Yunnan province, China).

392 **Appendix S2** Diurnal cycles of observed (Fig. 5) canopy-to-air temperature differences
393 compared with daily Priestley-Taylor (red) and Penman-Monteith (blue) simulations in a
394 tropical seasonal forest (XTBG, Yunnan province, China).

395 **Appendix S3** Parameters values in the Priestley-Taylor and Penman-Monteith models for
396 the ΔT simulations in Fig S2, estimated from half-hourly canopy temperature monitoring.

397 **DATA ACCESSIBILITY**

398 Field data used in this study can be found in Appendix S1.

399 **BIOSKETCH**

400 ND's research aims for a better understanding of temperature effects on biological
401 processes, and its application to large-scale vegetation models through a new approach
402 that emphasizes simple, theoretical models to interpret observations on the interaction of
403 traits and environment. ICP is a long-time pioneer of global vegetation modelling and is
404 currently leading the development of a next-generation trait-based model for improved
405 analysis of the coupling between biogeochemical and hydrological cycles, climate
406 impacts and climate-vegetation feedbacks. SPH works on multiple aspects of global
407 environmental and ecological data and their application to the modelling and

408 reconstruction of past environments. QHS works on ecosystem monitoring and analysis of
409 forest canopy processes. YPZ leads research on global change and ecosystems at
410 Xishuangbanna Tropical Botanical Garden.

411 **REFERENCES**

412 Agam, N., Kustas, W.P., Anderson, M.C., Norman, J.M., Colaizzi, P.D., Howell, T.A.,
413 Prueger, J.H., Meyers, T.P. & Wilson, T.B. (2010) Application of the Priestley–Taylor
414 approach in a two-source surface energy balance model. *Journal of Hydrometeorology*,
415 **11**, 185-198.

416 Best, M., Pryor, M., Clark, D., Rooney, G., Essery, R., Ménard, C., Edwards, J., Hendry,
417 M., Porson, A. & Gedney, N. (2011) The Joint UK Land Environment Simulator (JULES),
418 model description–Part 1: energy and water fluxes. *Geoscientific Model Development*, **4**,
419 677-699.

420 Campbell, G.S. & Norman, J.M. (1998) *An Introduction to Environmental Biophysics*,
421 2nd edn. Springer, New York.

422 Chow, W.S. (1994) Photoprotection and photoinhibitory damage. *Advances in Molecular*
423 *and Cell Biology* (ed. by E.E. Bittar and J. Barber), pp. 151-196. Elsevier.

424 Clark, D., Mercado, L., Sitch, S., Jones, C., Gedney, N., Best, M., Pryor, M., Rooney, G.,
425 Essery, R. & Blyth, E. (2011) The Joint UK Land Environment Simulator (JULES),
426 model description – Part 2: carbon fluxes and vegetation dynamics. *Geoscientific Model*
427 *Development*, **4**, 701-722.

428 Cox, P., Huntingford, C. & Harding, R. (1998) A canopy conductance and photosynthesis
429 model for use in a GCM land surface scheme. *Journal of Hydrology*, **212**, 79-94.

430 De Bruin, H.A.R. (1983) A model for the Priestley-Taylor parameter α . *Journal of*
431 *Climate and Applied Meteorology*, **22**: 572-578.

432 Duursma, R.A., Kolari, P., Perämäki, M., Nikinmaa, E., Hari, P., Delzon, S., Loustau, D.,
433 Ilvesniemi, H., Pumpanen, J. & Mäkelä, A. (2008) Predicting the decline in daily
434 maximum transpiration rate of two pine stands during drought based on constant
435 minimum leaf water potential and plant hydraulic conductance. *Tree Physiology*, **28**,
436 265-276.

437 Gates, D.M., Hiesey, W.M., Milner, H.W. & Nobs, M.A. (1964) Temperatures of *Mimulus*
438 leaves in natural environments and in a controlled chamber. *Carnegie Institution of*
439 *Washington Yearbook*, **63**, 418-426.

440 Gates, D.M. (1968) Transpiration and leaf temperature. *Annual Review of Plant*
441 *Physiology*, **19**, 211-238.

442 Givnish, T.J. & Vermeij, G.J. (1976) Sizes and shapes of liane leaves. *The American*
443 *Naturalist*, **110**, 743-778.

444 Helliker, B.R. & Richter, S.L. (2008) Subtropical to boreal convergence of tree-leaf
445 temperatures. *Nature*, **454**, 511-514.

446 Huntingford, C. & Monteith, J.L. The behaviour of a mixed-layer model of the
447 convective boundary layer coupled to a big leaf model of surface energy partitioning.
448 *Boundary-Layer Meteorology*, **88**, 87-101.

449 Idso, S.B., Reginato, R.J., Jackson, R.D. & Pinter, P.J. (1981) Foliage and air
450 temperatures: Evidence for a dynamic “equivalence point”. *Agricultural Meteorology*, **24**,
451 223-226.

452 Jacobs, C. (1994) Direct impact of atmospheric CO₂ enrichment on regional transpiration.
453 PhD thesis, Wageningen Agricultural University.

454 Jones, H.G. (2013) *Plants and Microclimate: a quantitative Approach to Environmental*
455 *Plant Physiology*, 3rd edn. Cambridge University Press, Cambridge.

456 Lange O.L. (1959) Untersuchungen über Wärmehaushalt und Hitzeresistenz
457 mauretanischer Wüsten- und Savannenpflanzen. *Flora*, **147**, 595-651.

458 Leuzinger, S., Vogt, R. & Körner, C. (2010) Tree surface temperature in an urban
459 environment. *Agricultural and Forest Meteorology*, **150**, 56-62.

460 Lhomme, J.P. (1997) An examination of the Priestley-Taylor equation using a convective
461 boundary layer model. *Water Resources Research*, **33**, 2571-2578.

462 Li, G., Harrison, S.P., Bartlein, P.J., Izumi, K. & Prentice, I.C. (2013) Precipitation
463 scaling with temperature in warm and cold climates: an analysis of CMIP5 simulations.
464 *Geophysical Research Letters*, **40**, 4018-4024.

465 Li, Y., Zhao, M., Motesharrei, S., Mu, Q., Kalnay, E. & Li, S. (2015) Local cooling and
466 warming effects of forests based on satellite observations. *Nature Communication*, **6**.

467 Linacre, E. (1964) A note on a feature of leaf and air temperatures. *Agricultural*
468 *Meteorology*, **1**, 66-72.

469 Linacre, E. (1967) Further studies of the heat transfer from a leaf. *Plant physiology*, **42**,
470 651-658.

471 Linacre, E. (1972) Leaf temperatures, diffusion resistances, and transpiration.
472 *Agricultural Meteorology*, **10**, 365-382.

473 Mahan, J.R. & Upchurch, D.R. (1988) Maintenance of constant leaf temperature by
474 plants I. Hypothesis – limited homeothermy. *Environmental and Experimental Botany*, **28**,
475 351-357.

476 McAneney, K.J. & Itier, B. (1996) Operational limits to the Priestley-Taylor formula.
477 *Irrigation Science*, **17**, 37-43.

478 McNaughton, K., & Spriggs, T.(1986) A mixed-layer model for regional evaporation.
479 *Boundary-layer Meteorology*, **34**, 243-262.

480 Medlyn, B.E., Barton, C.V.M., Broadmeadow, M.S.J., Ceulemans, R., De Angelis, P.,
481 Forstreuter, M., Freeman, M., Jackson, S.B., Kellomäki, S., Laitat, E., Rey, A., Roberntz,
482 P., Sigurdsson, B.D., Strassemeier, J., Wang, K., Curtis, P.S. & Jarvis, P.G. (2001)
483 Stomatal conductance of forest species after long-term exposure to elevated CO₂
484 concentration: a synthesis. *New Phytologist*, **149**, 247-264.

485 Medlyn, B.E., Duursma, R.A., Eamus, D., Ellsworth, D.S., Prentice, I.C., Barton, C.V.M.,
486 Crous, K.Y., De Angelis, P., Freeman, M. & Wingate, L. (2011) Reconciling the optimal
487 and empirical approaches to modelling stomatal conductance. *Global Change Biology*, **17**,
488 2134-2144.

489 Mercado, L.M., Huntingford, C., Gash, J.H.C., Cox, P.M. & Jogireddy, V. (2007)
490 Improving the representation of radiation interception and photosynthesis for climate
491 model applications. *Tellus B*, **59**, 553-565.

492 Michaletz, S.T., Weiser, M.D., Zhou, J., Kaspari, M., Helliker, B.R. & Enquist, B.J. (2015)
493 Plant thermoregulation: energetics, trait-environment interactions, and carbon economics.
494 *Trends in Ecology and Evolution*, **30**, 714-724.

495 Michaletz, S.T., Weiser, M.D., McDowell, N.G., Zhou, J., Kaspari, M., Helliker, B.R. &
496 Enquist, B.J. (2016) The energetic and carbon economic origins of leaf thermoregulation.
497 *Nature Plants*, **2**, 16129.

498 Monteith, J.L. & Szeicz, G. (1962) Radiative temperature in the heat balance of natural
499 surfaces. *Quarterly Journal of the Royal Meteorological Society*, **88**, 496-507.

500 Monteith, J.L. (1995) A reinterpretation of stomatal responses to humidity. *Plant, Cell &*
501 *Environment*, **18**, 357-364.

502 Parkhurst, D.F. & Loucks, O. (1972) Optimal leaf size in relation to environment.
503 *Journal of Ecology*, **60**, 505-537.

504 Paw U, K.T. (1984) A theoretical basis for the leaf equivalence point temperature.
505 *Agricultural meteorology*, **30**, 247-256.

506 Prentice, I.C. & Cowling, S.A. (2013) Dynamic global vegetation models. *Encyclopedia*
507 *of Biodiversity*, **2**, 607-689.

508 Prentice, I.C., Dong, N., Gleason, S.M., Maire, V. & Wright, I.J. (2014) Balancing the
509 costs of carbon gain and water transport: testing a new theoretical framework for plant
510 functional ecology. *Ecology Letters*, **17**, 82-91.

511 Priestley, C. & Taylor, R. (1972) On the assessment of surface heat flux and evaporation
512 using large-scale parameters. *Monthly Weather Review*, **100**, 81-92.

513 Raupach, M. (2000) Equilibrium evaporation and the convective boundary layer.
514 *Boundary-layer Meteorology*, **96**, 107-142.

515 Rowland, L., da Costa, A.C.L., Galbraith, D.R., Oliveira, R.S., Binks, O.J., Oliveira,
516 A.A.R., Pullen, A.M., Doughty, C.E., Netcalfe, D.B., Vasconcelos, S.S., Ferreira, L.V.,

517 Malhi, Y., Grace, J., Mencuccini, M. & Meir, P. (2015) Death from drought in tropical
518 forests is triggered by hydraulics not carbon starvation. *Nature*, **528**, 119-122.

519 Schymanski, S.J., Or, D. & Zwieniecki, M. (2013) Stomatal control and leaf thermal and
520 hydraulic capacitances under rapid environmental fluctuations. *PLOS One*, **8**, e54231.

521 Siebert, S., Webber, H., Zhao, G. & Ewert, F. (2017) Heat stress is overestimated in
522 climate impact studies for irrigated agriculture. *Environmental Research Letters*, **12**,
523 054023.

524 Sherwood, S. & Fu, Q. (2014) A drier future? *Science* **343**, 737-739.

525 Smith, W.K. (1978) Temperatures of desert plants: another perspective on the adaptability
526 of leaf size. *Science*, **201**, 614-616.

527 Song, X., Barbour, M.M., Saurer, M., Helliker, B.R. (2011) Examining the large scale
528 convergence of photosynthesis weighted tree leaf temperatures through stable oxygen
529 isotope analysis of multiple data sets. *New Phytologist*, **192**, 912-924.

530 Taylor, S.E. (1975) Optimal leaf form. *Perspectives of Biophysical Ecology* (ed. by D.M.
531 Gates & R.B. Schmerl), pp. 73-86. Springer, Berlin, Heidelberg.

532 Upchurch, D.R. & Mahan, J.R. (1988) Maintenance of constant leaf temperature by
533 plants II. Experimental observations in cotton. *Environmental and Experimental Botany*,
534 **28**, 359-366.

535 Yu, M.-H., Ding, G.-D., Gao, G.-L., Sun, B.-P., Zhao, Y.-Y., Wan, L., Wang, D.-Y. & Gui,
536 Z.-Y. (2015) How the plant temperature links to the air temperature in the desert plant
537 *Artemisia ordosica*. *PLOS One*, **10**, e0135452.

538 Zangerl, A.R.(1978) Energy exchange phenomena, physiological rates and leaf size
539 variation. *Oecologia*, **34**, 107-112.

540 **Table 1.** Parameter values (with standard errors) and goodness-of-fit statistics in the
 541 Priestley-Taylor and Penman-Monteith models for leaf-to-air temperature difference (ΔT ,
 542 K) as given in Fig 4, estimated from field measurements during the second day in a
 543 tropical dry woodland site (Mandan, Yunnan province, China).
 544

<i>Priestley-Taylor model</i>			
	<i>T. paniculata</i>	<i>P. weinmannifolia</i>	<i>O. schwerinae</i>
α (-)	1.27 ± 0.03	1.31 ± 0.01	1.32 ± 0.01
g_b (mol m ⁻² s ⁻¹)	0.52 ± 0.25	0.20 ± 0.03	0.24 ± 0.04
RMSE (K)	1.97	1.63	1.31
<i>Penman-Monteith model</i>			
	<i>T. paniculata</i>	<i>P. weinmannifolia</i>	<i>O. schwerinae</i>
g_b (mol m ⁻² s ⁻¹)	1.07 ± 0.35	0.86 ± 0.38	1.17 ± 0.55
g_{\bullet} (mol m ⁻² s ⁻¹)	0.53 ± 0.07	0.67 ± 0.1	0.73 ± 0.12
RMSE (K)	1.97	1.63	1.31

545

546 **FIGURE CAPTIONS**

547 **Figure 1** Diurnal time courses of the leaf-to-air temperature difference (ΔT , K) during the
548 dry season (October 2013) for three species, measured on consecutive days at two
549 topographic locations in a tropical dry woodland site (Mandan, Yunnan province, China).
550 The top panel displays measurements from the first day and the bottom panel from the
551 second day. Species: *Terminthia paniculata*, *Pistacia weinmannifolia*, *Osteosperma*
552 *schwerinae*. Vertical bars are standard errors of three replicates. Fitted smooth curves are
553 quadratic regressions against time (solid) with 95% confidence intervals (dashed). The
554 left-hand panels show measured half-hourly net radiation (R_n , W m^{-2}) from the nearest
555 meteorological station (Yuanjiang) during sampling, and field-measured ambient
556 temperatures (T_{air} , $^{\circ}\text{C}$). Vertical dashed lines mark solar noon. Horizontal dashed lines
557 mark $\Delta T = 0$.

558 **Figure 2** Diurnal time courses of the canopy-to-air temperature difference (ΔT , K) and
559 canopy temperature during the dry season (January 2013) in a continuous tropical
560 seasonal forest (Xishuangbanna Tropical Botanical Garden, Yunnan province, China).
561 Vertical bars are standard errors across the 31 days. Vertical dashed lines mark solar noon.
562 Shaded areas represent the daylight period.

563 **Figure 3** (a) Diurnal time courses of JULES-simulated canopy temperature and observed
564 leaf temperatures during the sampling days shown in Fig. 1. (d-f). Different coloured
565 symbols represent observed leaf temperatures of the three species. Air temperatures and
566 simulated soil temperatures are also shown. (b) Diurnal time courses of stomatal
567 conductance from JULES. Shaded areas represent the sampling period. Vertical dashed
568 lines mark solar noon.

569 **Figure 4** Diurnal time courses of (a) net radiation (R_n , W m^{-2}) and ambient temperature
570 (T_{air} , $^{\circ}\text{C}$), (b) vapour pressure deficit (D , in kPa) and (c) actual vapour pressure (e_a , kPa)
571 at Yuanjiang meteorological station during the sampling days shown in Fig. 1. (d-f)

572 Diurnal time courses of observed leaf-to-air temperature differences (ΔT , K) for the three
573 species, compared to modelled values obtained with the Priestley-Taylor and
574 Penman-Monteith approaches, and with the JULES land-surface model. Green circles are
575 observed leaf temperatures of the three species. Vertical dashed lines mark solar noon.
576 Shaded area represents the daylight period.

577 **Figure 5** The Priestley-Taylor and Penman-Monteith simulations for ΔT fitted to
578 half-hourly canopy-to-air temperature differences obtained from continuous monitoring
579 in a tropical seasonal forest (Xishuangbanna Tropical Botanical Garden, Yunnan province,
580 China) during the dry season (January 2013).

581

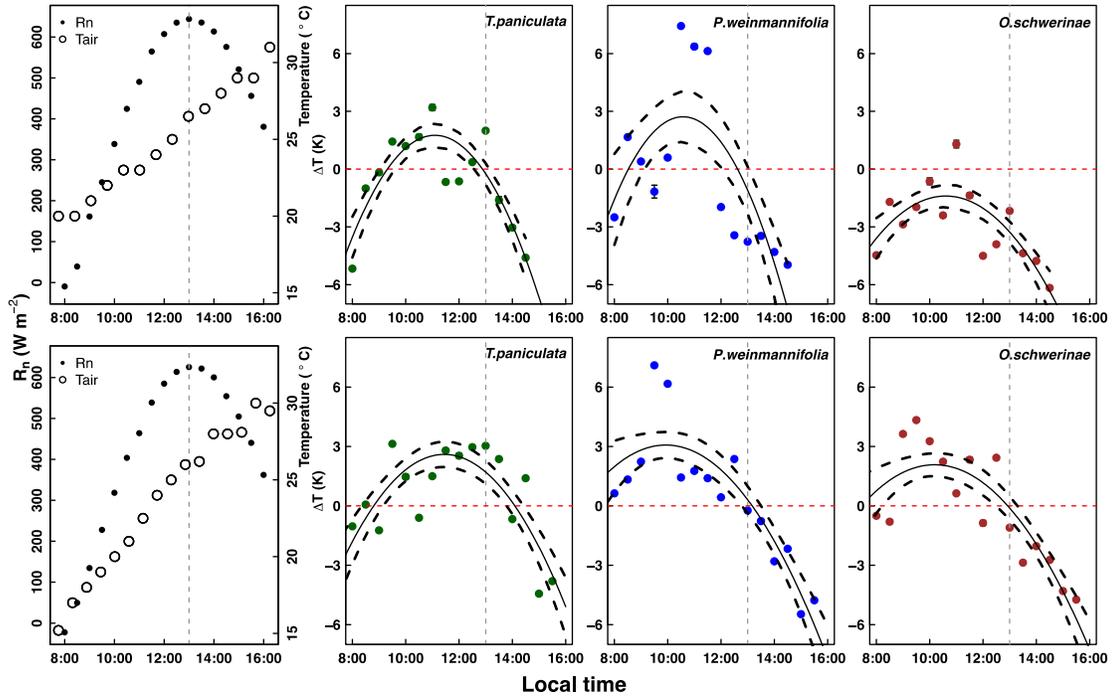
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583 FIGURES

584 Figure 1

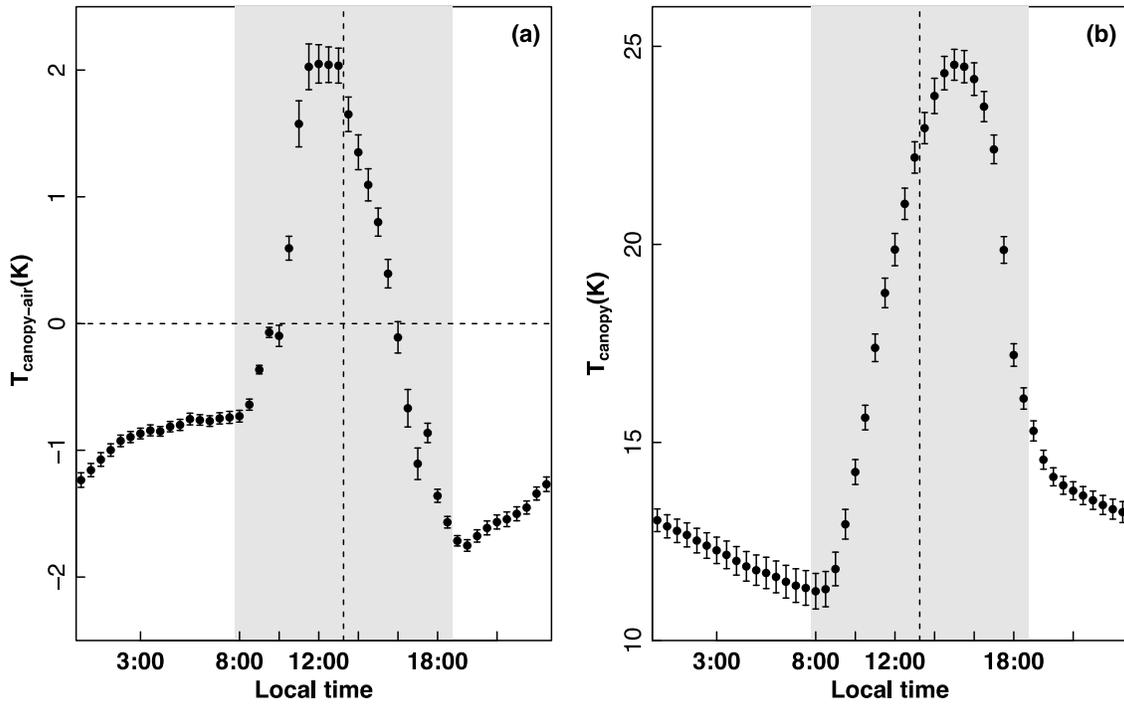
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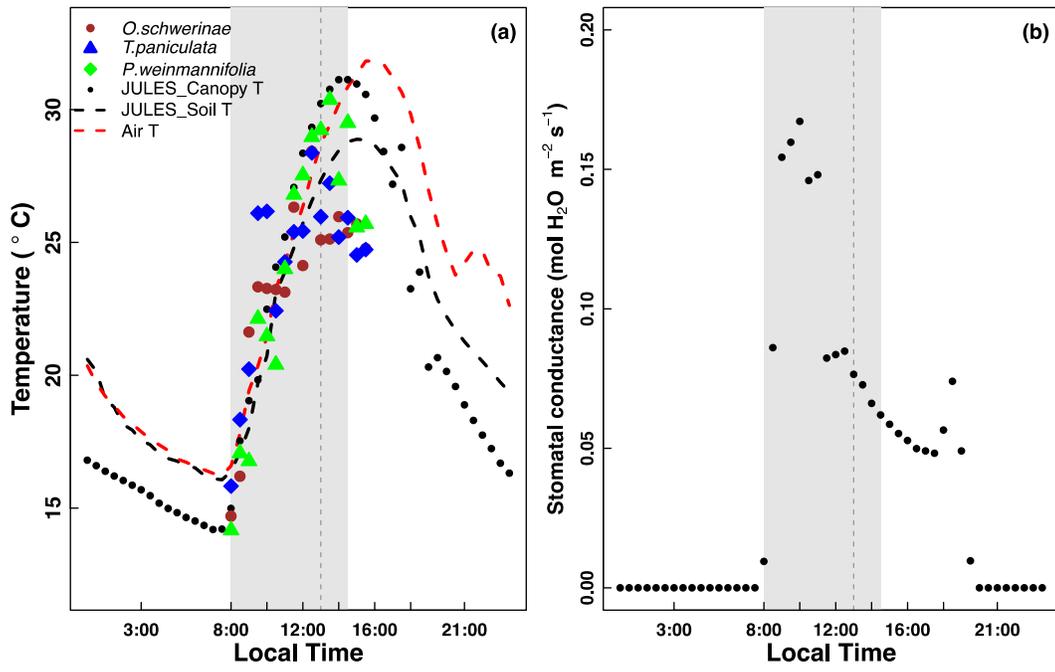
587 **Figure 2**

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590 **Figure 3**



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593 **Figure 4**

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