

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

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## **1 Biophysical homoeostasis of leaf temperature: a neglected**

### 2 process for vegetation and land-surface modelling

3 N. Dong<sup>1,3\*</sup>, I.C. Prentice<sup>1,2\*</sup>, S.P. Harrison<sup>1,3</sup>, Q.H. Song<sup>4</sup>, Y.P. Zhang<sup>4,5</sup>

<sup>1</sup>Department of Biological Sciences, Macquarie University, North Ryde, NSW 2109,
Australia

<sup>2</sup>AXA Chair Programme in Climate and Biosphere Impacts, Imperial College London,
Department of Life Sciences, Silwood Park Campus, Buckhurst Road, Ascot, SL5
7PY, UK

<sup>3</sup>Centre for Past Climate Change and School of Archaeology, Geography and
Environmental Sciences (SAGES), University of Reading, Whiteknights, RG6 6AH,
Reading, UK

<sup>4</sup>Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical
Garden, Chinese Academy of Sciences, Menglun, 666303, China

<sup>5</sup>National Forest Ecosystem Research Station at Ailao Mountains, Jingdong 676200,
China

16 \*Joint first authors

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19 Corresponding author: <u>ning.dong@students.mq.edu.au</u>

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#### 25 ABSTRACT

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

31 **Location** Tropical SW China.

32 **Methods** We illustrate diurnal cycles of leaf- and canopy-air temperature difference 33 ( $\Delta T$ ) 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  $\Delta T$ . 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**  $\Delta T$  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  $\Delta T$  could be approximated by either the PT or PM model, 43 but JULES tended to underestimate the magnitude of negative  $\Delta T$ .

Main conclusions Leaves with adequate water supply are partially buffered against
air-temperature variations, through a passive biophysical mechanism. This is likely
important for optimal leaf function, and land-surface and vegetation models should
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 ( $\Delta T$ ) 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.  $\Delta T$  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  $\Delta T$  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 -a76 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 Hadley Centre Earth System Model (Best *et al.*, 2011), was set up for the specific
environmental conditions and vegetation composition of the site and the results compared
with our field measurements.

101 **THEORY** 

102 Variations in  $\Delta T$  (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):

$$104 \quad R_n \quad - \quad c_p g_b \Delta T \quad - \quad \lambda E \quad = \quad 0 \tag{1}$$

where  $R_n$  is the net radiation at the leaf surface (W m<sup>-2</sup>),  $c_p$  is the specific heat capacity of 105 air at constant pressure (J mol<sup>-1</sup> K<sup>-1</sup>),  $g_b$  is the leaf boundary-layer conductance to heat 106 (mol m<sup>-2</sup> s<sup>-1</sup>),  $\lambda$  is the latent heat of vaporization of water (J mol<sup>-1</sup>) and E is the 107 transpiration rate (mol  $m^{-2} s^{-1}$ ). This equation states that the leaf-level net radiation is 108 109 balanced by the sum of the sensible and latent heat fluxes - the sensible heat flux 110 depending on  $\Delta T$  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 equation  $g_b = 0.135 \sqrt{(u/d)} \mod m^{-2} s^{-1}$  (Campbell & Norman, 1998, p. 101) where u is the 112 wind speed (m s<sup>-1</sup>) and d is the characteristic dimension of the leaf (m) – about 0.74 times 113 114 the maximum width of the leaf (Taylor, 1975).

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

116 
$$\Delta T = (R_n - \lambda E) / (c_p g_b)$$
(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 temperature is high enough – resulting in leaves cooler than air. This cooling, relative to
air temperature, is also stronger in large leaves and at low wind speeds.

123 One way to predict the sign and magnitude of  $\Delta T$  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 ( $\lambda E$ ) is strongly determined by the available energy supply ( $R_n$ ):

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

129 where *s* is the derivative of the Clausius-Clapyeron relationship between saturated vapour 130 pressure and temperature (Pa K<sup>-1</sup>), evaluated at the ambient air temperature;  $\gamma$  is the 131 psychrometer constant (Pa K<sup>-1</sup>), equal to  $Pc_p/\lambda$  where *P* is atmospheric pressure (Pa); and 132  $\alpha$  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 
$$\Delta T = R_n \{1 - \alpha [s/(s + \gamma)]\} / (c_p g_b)$$
 (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  $\alpha$ , 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  $\alpha$  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  $\alpha$  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.

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

160 
$$D(T + \Delta T) \approx D(T) + s \Delta T$$
 (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 
$$\Delta T = [R_n - \lambda g \bullet (D + s \Delta T)/P] / (c_p g_b)$$
(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  $\lambda$ ,  $g_s$  and  $g_b$ . As  $\Delta T$  appears on both sides of equation (6), it is 170 necessary to re-arrange it in order to solve for  $\Delta T$ :

171 
$$\Delta T = (R_n - \lambda g \bullet D/P) / [c_p (g_b + \varepsilon g \bullet)]$$
 (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  $\Delta T$ .

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  $T_{\rm x}$ . (This covariance must break down at night however, or near to dawn and dusk, as  $R_{\rm n}$ 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 
$$\Delta T = -[e_{s}(T) - e_{s}(T_{x})] / [\gamma (1 + \varepsilon + g_{b}/g_{s})]$$
(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  $\Delta T$  will be negative for all T >189  $T_x$ . The rate of change of  $\Delta T$  with *T*, evaluated at the crossover temperature  $T_x$ , is:

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

191 where  $\varepsilon$  is evaluated at  $T_x$ . Note that the rate of decrease in  $\Delta T$  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  $\Delta T$ , 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  $\Delta T$ , 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  $\Delta T$  on  $R_n$ . Point (b) is 204 dealt with in Michaeletz 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

The selected field site was in a tropical dry woodland, Mandan, Yunnan province, SW China (23.69° N, 101.85° E, 758 m a.s.l), with mean annual temperature 21.8°C and mean annual precipitation 981 mm. Solar noon occurs at 13:00 local time. Measurements 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 of 25  $\text{cm}^2$  (Terminthia paniculata), 1  $\text{cm}^2$  (Pistacia weinmannifolia) and 0.9  $\text{cm}^2$ 220 221 (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  $\pm 0.75$  K and that of the mercury thermometer 228 is  $\pm 0.1$  K. The uncertainty of our estimates of  $\Delta T$  is therefore small compared to the 229 range of observed  $\Delta T$  (-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.  $\Delta T$  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).  $\Delta T$  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  $\alpha$  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  $\Delta T$  has been observed in other studies 240 and environments, for example by Yu *et al.* (2015) in a desert.

#### 241 Monitoring

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

We show the data from the dry season (January) of 2013 (Fig. 2). The same general diurnal time course is seen at canopy level in the seasonal forest (Fig. 2) as we observed 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% C<sub>3</sub> grasses, 25% 259 C<sub>4</sub> 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.

Fig. 3 compares the JULES results to our field measurements. The model simulates negative  $\Delta T$  after about 14:00 local time, but the measurements show an earlier onset of negative values. Measured  $\Delta T$  approached -6 K for each day/location and all species (Figs 1, 3), but JULES' simulated  $\Delta T$  never fell below -2 K during the daytime.

Establishing the precise reasons for this discrepancy would require a series of sensitivity experiments to be carried out. However, we note that JULES simulates a precipitous decline in stomatal conductance from about 10:00 local time (Fig. 3), which would 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  $\alpha$  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 gb 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  $\Delta T$  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  $\Delta T$  during the hottest part of the day.

We fitted equations (4) and (7) in the same way to the canopy monitoring data, including half-hourly measurements for each day during January 2013. For the PT model, the estimated  $\alpha$  was 1.32 ± 0.005 (p < 0.001), corresponding to a crossover temperature of 26.8°C. The fitted value for  $g_b$  in equation (4) was 0.68 ± 0.03 mol m<sup>-2</sup> s<sup>-1</sup> (p < 0.001). In comparison to monitored canopy temperature, the PT model yielded a highly significant slope of 0.67 with  $R^2 = 79\%$  (Fig. 5). For the PM model, we estimated a somewhat larger value of  $g_b$  (1.45 ± 0.02 mol m<sup>-2</sup> s<sup>-1</sup>, p < 0.001)), and  $g \bullet = 0.51 \pm 0.007$  mol m<sup>-2</sup> s<sup>-1</sup>. The regression between model predictions and the canopy monitoring data was again highly 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  $\alpha$  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) mol m<sup>-2</sup> s<sup>-1</sup>. For the PM model, we again 294 estimated values of  $g_b$  larger than for the PT model: 1.45 (1.26, 1.66) mol m<sup>-2</sup> s<sup>-1</sup>, and values of  $g \bullet$  of 0.57 (0.50, 0.64) mol m<sup>-2</sup> s<sup>-1</sup>. Both models fitted the monitoring canopy 295 296 temperature well on visual comparison (Figs 5 and S2). A general underestimation of the 297 magnitude of  $\Delta T$  during the night (Fig. S2) probably relates to our simplifying 298 assumption of constant g<sub>b</sub>, 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.

#### **DISCUSSION**

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

311 Leaf-temperature homoeostasis 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,  $\Delta T$ . 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  $\Delta T$  is no longer possible – potentially compounding the effects of hydraulic failure (Rowland *et al.*, 2015) with photosynthetic inhibition and even overheating damage. Deleterious effects of high leaf temperature would be felt soonest by large leaves, because of their low boundary-layer conductance. How the effective boundary-layer conductance actually varies under field conditions as a function of leaf morphology and canopy architecture remains a topic for investigation, potentially opening a route to the incorporation of more realistic plant functional diversity in 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,

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

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

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#### 389 SUPPORTING INFORMATION

Appendix S1 Leaf temperature measurements and climate data at two topographic
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  $\Delta T$  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.

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

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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 ( $\Delta T$ , 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

	T. paniculata	P. weinmannifolia	O. schwerinae	
α (-)	$1.27\pm0.03$	$1.31 \pm 0.01$	$1.32 \pm 0.01$	
$g_{\rm b} ({\rm mol} \;{\rm m}^{-2} \;{\rm s}^{-1})$	$0.52 \pm 0.25$	$0.20 \pm 0.03$	$0.24 \pm 0.04$	
RMSE (K)	1.97	1.63	1.31	

Priestley-Taylor model

Penman-Monteith model

	T. paniculata	P. weinmannifolia	O. schwerinae
$g_{\rm b} ({ m mol} { m m}^{-2}{ m s}^{-1})$	$1.07\pm0.35$	$0.86 \pm 0.38$	$1.17 \pm 0.55$
$g \bullet (\operatorname{mol} \operatorname{m}^{-2} \operatorname{s}^{-1})$	$0.53 \pm 0.07$	$0.67 \pm 0.1$	$0.73 \pm 0.12$
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 ( $\Delta T$ , 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<sup>-2</sup>) from the nearest 555 meteorological station (Yuanjiang) during sampling, and field-measured ambient 556 temperatures ( $T_{air}$ , °C). Vertical dashed lines mark solar noon. Horizontal dashed lines 557 mark  $\Delta T = 0$ .

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

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

**Figure 4** Diurnal time courses of (a) net radiation ( $R_n$ , W m<sup>-2</sup>) and ambient temperature ( $T_{air}$ , °C), (b) vapour pressure deficit (D, in kPa) and (c) actual vapour pressure ( $e_a$ , kPa) 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 ( $\Delta T$ , 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  $\Delta T$  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

582

583 FIGURES

### **Figure 1**



**Figure 2** 



590 Figure 3







