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Canopy-top measurements do not accurately quantify canopy-scale leaf thermoregulation

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Leaf traits and climate interact via energy budgets, enabling leaf temperature (T_{leaf}) to depart from ambient air temperature (T_{air}) (1). When quantified as the slope β of T_{leaf} vs. T_{air}, three types of thermoregulatory behavior are possible: limited homeothermy ($\beta < 1$), poikilothermy ($\beta = 1$), and megathermy ($\beta > 1$) (2). Characterizing thermoregulation across the entire leaf area of real-world plant canopies remains an important challenge for Earth systems science, as T_{leaf} is a primary driver of carbon and water fluxes.

Recently, Still et al. (3) contributed an important dataset that advances our understanding of leaf thermoregulation. Canopy-top thermal imaging data spanning entire growing seasons at six forested sites across North and Central America

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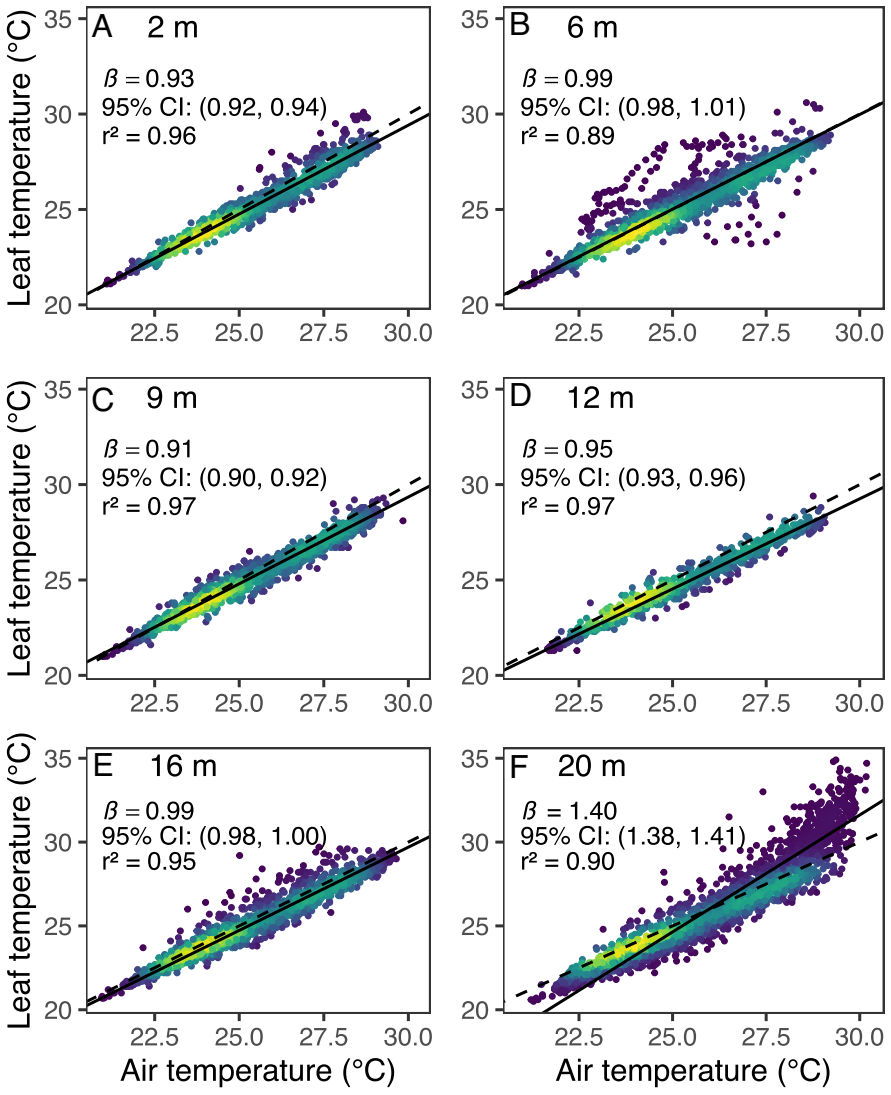

Fig. 1. Relationships between leaf and air temperature along a vertical profile in a tropical wet forest canopy. Leaf and air temperatures were measured in Luquillo, Puerto Rico at heights within the canopy of (*A*) 2 m, (*B*) 6 m, (*C*) 9 m, (*D*) 12 m, (*E*) 16 m, and (*F*) 20 m (top of canopy). Points represent leaf and air temperatures averaged in 30-min intervals. Colors correspond to the density of observations, with warmer colors indicating more observations. Solid lines show major axis (Model II) regression, with slope values (β), corresponding CIs, and r^2 values reported in each panel. Dashed line is 1:1. Full description of the site and data may be found in Miller et al. (6).

all exhibited $\beta > 1$, leading the authors to conclude that limited homeothermy does not occur in forest canopies.

However, canopy-top thermal imaging does not tell the full story of leaf thermoregulation. Due to the high infrared absorptance of water, the foremost leaves in view dominate infrared signals received by radiometers. These signals largely exclude lower canopy leaves, which generally comprise most of the leaf area (4) and contribute substantially to gross primary production (5) in forest canopies. Solar radiation dominates the energy balance of upper-canopy leaves, which are more likely to exhibit midday depression that reduces transpiration and increases T_{leaf} (4). Subcanopy leaves are largely shielded during these periods due to the "parasol effect" (4, 6) and microclimate buffering (7) of the canopy. Thus, radiometers mounted above canopies as in Still et al. primarily measure sun-exposed, upper-canopy leaves and are unable to describe thermoregulation across the entire canopy.

To demonstrate variation in leaf thermoregulation throughout a forest canopy, we reanalyzed the time series of T_{leaf} and T_{air} along a vertical profile of a tropical wet forest in Puerto Rico (6). In these data, only canopy-top leaves (20 m height) exhibited megathermy ($\beta > 1$; Fig. 1). Leaves at 2, 9, and 12 m exhibited limited homeothermy ($\beta < 1$), while those at 6 and 16 m exhibited poikilothermy ($\beta = 1$). Importantly, T_{air} was measured at the same heights as T_{leaf} in this study. Using T_{air} from outside the canopy, as in Still et al., would further increase the apparent homeothermy in lower canopy layers. Thus, despite observed megathermy in the upper canopy, most lower canopy layers exhibited limited homeothermy (Fig. 1), thus maintaining leaf temperatures closer to photosynthetic optima (5). This is consistent with prior work showing generally reduced T_{leaf} and different thermoregulation strategies in lower canopy layers (8, 9). Further, limited homeothermy has been observed even in sun-exposed upper-canopy leaves during certain times of day and in colder environments (10).

Though we applaud Still et al.'s contribution to our understanding of leaf thermoregulation, our analyses suggest that thermoregulation may be common throughout forest canopies. Accurately quantifying leaf thermoregulation requires techniques that go beyond relating average canopy-top T_{leaf} to T_{air}. Whole-canopy vertical leaf temperature distributions, though difficult to measure, will improve our understanding of why different thermoregulation behaviors occur and the attendant effects on ecosystem functioning.

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