PNAS LETTER

Reply to Garen et al.: Within-canopy temperature data also do not support limited homeothermy

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We thank Garen et al. (1) for their comment and agree that there are many issues related to plant thermoregulation that require further study. We do not dispute that our thermal imaging (2) primarily measured the temperature of upper-canopy leaves (T_{can}) at our sites, and we support additional vertical leaf temperature (T_{leaf}) studies in various forest types to better understand the microclimate and metabolism of shade leaves. However, our imaging in combination with ecosystem-scale CO_2, H_2O, and energy flux observations support our rejection of limited homeothermy in forest canopies. Importantly, we did not assert that canopy-scale thermoregulation is not happening, just that there is no evidence for it leading to canopy temperature cooling below T_{air} as would be expected by homeothermy. Part of the discrepancy is perhaps related to thermoregulation terminology, in particular the unfortunate application of terms from the animal physiology literature implying active behavior by plants (3).

Despite areas of agreement, we dispute the assertion by Garen et al. that the data they present from a single site is evidence for limited homeothermy occurring in shade leaves. It's unsurprising that lower-canopy leaves are slightly cooler than air, a phenomenon noted in our paper. Shade leaf temperatures would be expected to stay near air temperature (T_{air}) or slightly cooler based on energy balance considerations given the lower and more diffuse solar irradiance absorbed by shade leaves, as well as microclimate buffering. It's puzzling to argue that subcanopy leaves are more actively thermoregulating than canopy-top leaves, as shade leaves don't regulate stomatal conductance, and thus T_{leaf}, as much as leaves at the top of the canopy do (4) given the different hydraulic constraints and microclimates they experience (5, 6); additionally, larger leaf sizes and lower stomatal densities in shade leaves (7) combined with lower wind speeds would decrease leaf boundary layer conductance and further reduce stomatal control of transpiration (8). Finally, Garen et al. provide no evidence that shade leaves actively modify their temperature relative to the site mean photosynthetic optima (T_{opt} = 30.2 C); indeed, raising T_{leaf} above T_{air} might be expected if homeothermy were occurring, given that T_{air} is always below T_{opt}.

The use of nonaspirated T_{air} sensors in ref. 7 could lead to overestimated T_{air}under high insolation (canopy top) and in the subcanopy where wind speeds are lower (9), likely influencing T_{leaf}/T_{air}slopes. Also, the slopes Garen et al. do provide are well above values reported previously as evidence of homeothermy: While their slopes are quite close to 1 (range 0.91 to 0.95), earlier analyses arguing for limited homeothermy suggested values of 0.67 and 0.74 (10, 11). Garen et al.'s slopes better approximate poikilothermy, with leaves closely tracking T_{air}. Indeed, the study which they use for their data also found no evidence of limited homeothermy at any canopy height and inferred a limited ability for tropical trees to thermoregulate (7).

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Author contributions: C.J.S. designed research; C.J.S. performed research; C.J.S. contributed new reagents/analytic tools; C.J.S. analyzed data; G.F.M.P., B.R., D.M.G., D.M.A., Y.K., S.P.B., C.V.H., H.K., L.H., F.C.M., S.S., D.A.R., M.G., S.P., M.D., B.R.H., and A.D.R. co-author of reply; and C.J.S., G.F.M.P., B.R., D.M.G., D.M.A., Y.K., S.P.B., C.V.H., H.K., L.H., F.C.M., S.S., D.A.R., M.G., S.P., M.D., B.R.H., and A.D.R. wrote the paper.

The authors declare no competing interest.

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Published April 3, 2023.

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