Tansley insight

Imaging canopy temperature: shedding (thermal) light on ecosystem processes

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Summary

Canopy temperature $T_{\text{can}}$ is a key driver of plant function that emerges as a result of interacting biotic and abiotic processes and properties. However, understanding controls on $T_{\text{can}}$ and forecasting canopy responses to weather extremes and climate change are difficult due to sparse measurements of $T_{\text{can}}$ at appropriate spatial and temporal scales. Burgeoning observations of $T_{\text{can}}$ from thermal cameras enable evaluation of energy budget theory and better understanding of how environmental controls, leaf traits and canopy structure influence temperature patterns. The canopy scale is relevant for connecting to remote sensing and testing biosphere model predictions. We anticipate that future breakthroughs in understanding of ecosystem responses to climate change will result from multiscale observations of $T_{\text{can}}$ across a range of ecosystems.

I. Introduction

Temperature is fundamentally important to almost all aspects of plant function (Berry & Björkman, 1980; Körner, 2006). The most common measurement of plant temperature is that of the leaf temperature $T_{\text{leaf}}$, given the central role leaves play in plant metabolism and in water and energy cycling. Leaves are easily measured compared with other organs, like roots. $T_{\text{leaf}}$ directly influences a variety of cellular properties and processes, including membrane fluidity, enzyme reaction kinetics, and diffusion constants and dissolution of CO$_2$ and oxygen, which together control rates of photosynthesis and respiration (Jones, 2013). Leaf and tissue temperatures also indirectly impact many aspects of plant phenology and development, from dormancy to flowering (Körner & Hiltpolnter, 2018). The temperature of any aboveground plant organ is strongly connected to air temperature $T_{\text{air}}$, but biological
and environmental variations can cause large deviations (c. 20°C) of $T_{\text{leaf}}$ above and below $T_{\text{air}}$ (e.g. Ehleringer et al., 1976; Smith & Carter, 1988; Fauset et al., 2018; Blonder et al., 2020). For example, in temperate and tropical alpine areas, plant stature and leaf traits can lead to leaves being warmer (e.g. Sage & Sage, 2002) or colder (Melcher et al., 1994) than $T_{\text{air}}$.

Though controls on $T_{\text{leaf}}$ are generally well understood, and satellite-based thermal measurements at coarse spatial resolution have been available since the 1980s, there is little information on high temporal frequency thermal regimes at canopy scales ranging from individual to multiple crowns. Understanding canopy scales is crucial to upscale biophysical process models and observations from leaves to ecosystems, and also to differentiate the responses of different species or individuals to environmental stressors in heterogeneous ecosystems.

Canopy temperature $T_{\text{can}}$, which we define here as the average temperature of multiple leaf assemblages aggregated from individual branches up to whole crowns, is rarely measured but strongly influences — and is influenced by — ecosystem–atmosphere exchanges of water, energy, and carbon (C) (Fig. 1). Techniques for measuring $T_{\text{can}}$ are more established in the homogeneous canopy structures of crops, where $T_{\text{can}}$ links directly to heat and water stress (Jackson et al., 1981; Maes & Steppe, 2012; Ballester et al., 2013). In natural ecosystems, however, $T_{\text{can}}$ measurements can include multiple crowns with heterogenous plant heights and diverse groupings of species and life forms. Wired contact sensors, like thermocouples, present multiple practical and methodological challenges for measuring $T_{\text{can}}$ from representativeness to durability (Kim et al., 2018). Given these limitations, it becomes clear why our understanding of $T_{\text{can}}$ dynamics at fine spatial and temporal scales is extremely limited.

There are multiple canopy-scale temperature measurements that can be inferred from measurements of sensible heat (Kustas et al., 2007) or upwelling longwave radiation fluxes (Norman & Becker, 1995; Kim et al., 2016), all of which are related to $T_{\text{air}}$ (Table 1). However, measuring $T_{\text{can}}$ as defined here is feasible only with thermal imaging, as multiple leaf regions — though typically not individual leaves — corresponding to different species or canopy positions can be analyzed (Pau et al., 2018: Fig. 2). The advent of relatively inexpensive and robust thermal cameras promises to transform our understanding of $T_{\text{can}}$ regimes (Costa et al., 2013; Seidel et al., 2016; Smigaj et al., 2017; Lapidot et al., 2019; Still et al., 2019). Thermal cameras mounted on above-canopy towers enable remote measurements over large areas and long time periods (Aubrecht et al., 2016; Kim et al., 2016; Yi et al., 2020). Although the images can be influenced by mid and lower canopy elements, they typically capture upper canopy branches and leaves that are directly in the camera’s field of view. Upper canopy leaves are most likely to depart from adjacent $T_{\text{air}}$, as this region is often simultaneously brighter, hotter, windier, and drier than the understory during daytime, and typically colder at night. The upper canopy absorbs most of the solar radiation in many ecosystems, and it typically accounts for the majority of C and water exchanges (Bonan, 2016). Critically, sunlit canopy leaves also occupy the zone where most climate variations and stress are likely to manifest (Hilker et al., 2008). Thus, thermal imaging of upper canopy leaves can enable new insights into plant function and stress.

II. Canopy temperature strongly influences – and is influenced by – exchanges of water, energy and CO₂ with the atmosphere

Temperature effects on carbon and water fluxes

Many metabolic and biophysical processes depend nonlinearly on temperature, particularly in the ranges experienced by most leaves during periods of physiological activity (Yamori et al., 2014; Heskel et al., 2016; Gimenez et al., 2019). For example, the catalytic
activity of leaf metabolic enzymes follows well-characterized exponential relationships with temperature (Bernacchi et al., 2001). Similarly, vapor pressure deficit (VPD), the difference in water vapor pressure between the saturated leaf intercellular spaces and the air surrounding the leaf (Jarvis & Morison, 1981), is nonlinearly related to \( T_{\text{can}} \). Since leaves often reach temperatures 5–10°C higher than \( T_{\text{air}} \) during the daytime (e.g., Aubrecht et al., 2016), estimates of processes like transpiration connected to VPD can be erroneous if modelled with \( T_{\text{air}} \). In turn, the predicted response of leaf photosynthesis to temperature will be affected (Lin et al., 2012). Indeed, Still et al. (2019) found that using measured \( T_{\text{leaf}} \) to drive a leaf-level process model produced large increases in modeled photosynthesis and transpiration compared with using \( T_{\text{air}} \) as a driver.

Because of its role in metabolic processes, various measures of \( T_{\text{air}} \) are typically used as explanatory variables in ecosystem models. Ecosystem respiration is often modeled using \( T_{\text{air}} \) as a proxy for plant and soil temperatures, which are rarely measured. However, measurements of plant temperature should be more closely related to ecosystem metabolic fluxes. Indeed, Kim et al. (2016) found that \( T_{\text{can}} \) was more strongly associated with afternoon net ecosystem \( C \) exchange than was \( T_{\text{air}} \) in a semi-arid pine forest. Similarly, Pau et al. (2018) found for a semi-deciduous tropical forest that canopy photosynthesis was more strongly correlated with \( T_{\text{can}} \) than either \( T_{\text{air}} \) or VPD. At larger scales, Sims et al. (2008) showed that a model incorporating vegetation temperature was a better predictor of gross primary productivity than more complex models were.

### III. Canopy temperature patterns and relationships to structure and function

Canopy structure plays a large role in determining canopy temperature dynamics

Stand structural characteristics strongly influence canopy temperature dynamics and the coupling between leaf and air temperatures. For example, a larger difference in \( T_{\text{can}} \) relative to above-canopy \( T_{\text{air}} \) in denser tree crowns was noted by Leuzinger & Körner (2007), Scherrer et al. (2011), and Aubrecht et al. (2016). A clear driver of these differences is the turbulent exchange of sensible and latent heat between tree canopies and the overlying atmosphere. The airspace in dense canopies can often be decoupled from air aloft (Jarvis & McNaughton, 1986) and can affect mass and energy exchanges between canopies and the atmosphere (Aubinet, 2008). Surface roughness also plays an important role, as do multiple aspects of canopy structure, including leaf area density profiles and branch patterns (Monson & Baldocchi, 2014). Decoupling is high in homogeneous and short canopies, such as crops, grasslands, or even-aged forest stands, as their low surface roughness suppresses turbulent mixing, resulting in steep temperature gradients between the canopy and surrounding air; in heterogenous canopies, greater isolation of emergent tree canopies can lead to higher coupling (Monson & Baldocchi, 2014). Canopy structure also influences radiation absorption and \( T_{\text{can}} \). Uneven canopies absorb more radiation, as scattered light not absorbed at the canopy top is likely to be absorbed by leaves lower in the canopy (Roberts et al., 2004). Leaf geometric and optical properties, as well as leaf angle distribution and clumping, will also influence radiation absorption by the canopy. Sunlit leaves can be 5–10°C warmer than shaded leaves (Doughty & Goulden, 2008), and thus \( T_{\text{can}} \) is strongly influenced by the relative proportions of sunlit and shaded foliage, which can be determined using multilangle imagery (e.g., Mu et al., 2017).

Nighttime measurements of canopy temperature can illuminate processes that are not apparent from flux and meteorological data

On clear nights, forest canopies cool by emitting more longwave radiation towards the sky and the ground than they receive. The sky is typically much colder than the canopy and has lower emissivity,
such that the longwave flux leaving the upper canopy exceeds the downwelling longwave flux from the sky, leading to large negative nocturnal net radiation $R_{\text{net}}$ fluxes on such nights (Jones, 2013; Bonan, 2016). This radiation imbalance, along with sensible heat transfers, can lead to large spatial heterogeneity in surface temperatures, as is illustrated for the upper crown of an old-growth Douglas fir tree in Oregon (Fig. 3a). The trunk and branches have higher moisture content and thermal inertia: they retain heat from the prior day’s insolation and remain considerably warmer than leaves. The cooling rate of leaves depends on canopy position: upper canopy foliage cools faster on clear and calm summer nights than the mid- and lower canopy. This radiative cooling can chill leaves below adjacent $T_{\text{air}}$ and even to the dewpoint (Fig. 3b). This leads to condensation in the upper canopy, as measured by leaf wetness sensors (Fig. 3c). This dewfall might serve to alleviate water stress of leaves in the upper canopy and thereby enhance photosynthesis, as foliar water uptake has been shown to be common and important in many species (Dawson & Goldsmith, 2018; Berry et al., 2019). Additionally, nighttime temperature plays an important role in regulating ecosystem respiration (Anderegg et al., 2015), and thus monitoring nighttime $T_{\text{can}}$ will be important to understand impacts of climate warming on productivity.

**IV. Understanding biotic and abiotic controls on canopy temperature**

The temperature that canopies experience results from a complex interplay of biotic and abiotic processes. Biotic influences on $T_{\text{can}}$ can be broadly classified as those that influence the absorption of radiation, those that influence the dynamics of leaf and canopy boundary layers, and physiological processes that influence water vapor exchanges. For example, leaf size, leaf area density and leaf clumping influence radiation absorption, but they also regulate leaf boundary-layer resistance. Physiological traits, including stomatal conductance and its sensitivity to VPD, influence canopy energy and water exchanges (Jones, 2013; Monson & Baldocchi, 2014). Though these interactions are relatively straightforward to estimate in isolated leaves, they are much more challenging to model and measure at the canopy scale. Critically, many of these properties can vary across heterogeneous canopies as a function of canopy position, species composition, and even within species and individual crowns (Leuzinger & Körner, 2007; Aubrecht et al., 2016; Yi et al., 2020).

Forecasting climate change impacts requires a firm understanding of how and why $T_{\text{can}}$ varies with these factors across canopy types and landscape positions. If $T_{\text{can}}$ equals $T_{\text{air}}$, then estimates of acclimation and adaptation of photosynthetic temperature response should scale linearly (Kumarathunge et al., 2019). By contrast, if $T_{\text{can}}$ changes at a different rate than $T_{\text{air}}$ (e.g. Pau et al., 2018) then the implications of climate warming and weather extremes are very different. Though the environmental drivers of $T_{\text{leaf}}$ are captured by energy budget theory (Jones, 2013), and these same drivers should influence $T_{\text{can}}$, their relative importance likely varies by vegetation type and season. We assessed environmental controls on $T_{\text{can}}$ at contrasting conifer sites in the Pacific Northwest, USA (an old-growth Douglas fir/western hemlock moist forest at Wind River, WA, and a mature semi-arid Ponderosa pine forest at Metolius, OR) as well as a tropical semi-deciduous forest in Panama, Barro Colorado Island (BCI; Fig. 4). A boosted regression tree analysis (Greenwell et al., 2020) of variables influencing the difference between daytime $T_{\text{can}}$ and $T_{\text{air}}$ across the growing season shows that the most important explanatory variable at Wind River is $R_{\text{net}}$, followed by VPD and soil moisture. Similarly, $R_{\text{net}}$ dominates variable importance rankings at BCI. By contrast, the most important variable explaining the difference between $T_{\text{can}}$ and $T_{\text{air}}$ at Metolius is VPD, followed by wind speed (WS) and then $R_{\text{net}}$. The primacy of VPD and WS as explanatory variables at the more coupled, semi-arid pine forest site bolsters an expectation that atmospheric and aerodynamic conditions strongly influence evaporative cooling via impacts on stomatal conductance and transpiration. By contrast, cooling at the less coupled sites with...
denser canopies and higher leaf areas should be driven more by $R_{w}$ and equilibrium evaporation (Jarvis & McNaughton, 1986; Jones, 2013). Particularly at the conifer sites, $T_{\text{can}}$ should increase more rapidly than $T_{\text{air}}$, as growing-season VPD increases if other variables remain constant. Though the importance of these drivers is not surprising given ecophysiological and energy budget theory, this analysis highlights knowledge gaps in predicting $T_{\text{can}}$ across forest types. VPD is likely to be affected by climate change (Grossiord et al., 2020), and annual WSs already exhibit trends (McVicar et al., 2012). Changes in both variables will likely influence $T_{\text{can}}$ and ecosystem function.

V. Future opportunities

Upscaling canopy temperature measurements with near-surface and satellite-based thermal remote sensing

The improved accessibility of thermal imagers, in terms of cost, physical footprint, and power requirements, promises a rapid development of our understanding of leaf and canopy-scale function. In particular, the combination of fixed-mount, unmanned aerial-vehicle-based, and satellite remote sensing presents opportunities to understand variations in $T_{\text{can}}$ at spatiotemporal scales that were previously unmeasurable. Fixed-mount imagers are already providing high spatial and temporal resolution data sets of $T_{\text{can}}$ (Still et al., 2019), although they are restricted to a relatively small field of view. Though UAV-mounted cameras also capture high-resolution imagery across larger spatial scales, short flight times limit temporal resolution, which is particularly important given the dynamic nature of $T_{\text{can}}$. Satellite measurements of land surface temperature (LST) do not capture similarly high spatial and temporal resolutions, although geostationary satellite platforms provide coarse-scale LST estimates multiple times per hour (Freitas et al., 2013). However, satellites do provide global-scale coverage and long-term records (Li et al., 2013). Some of the most exciting future research opportunities will result from combining these platforms, and from connecting thermal data with visible and near-infrared bands from other sensors. Upscaling thermal, visible, and other spectral imagery from fixed mounts using temporally sparse but higher resolution UAV imagery will help reveal how $T_{\text{can}}$ responds to environmental variability across a range of landscape positions, species mixtures, canopy structures, and management histories. Canopy and landscape-scale thermal imaging can also be related to satellite LST for upscaling to regions. Relationships between $T_{\text{can}}$ and LST are likely to vary with biome, season, and climate (Table 1). Some of this variation is due to the mixing of typically hotter soil and/or colder water in vegetated pixels.

Measurements of canopy temperature can help benchmark land surface models

Land surface models (LSMs) are complex biophysical process models that simulate land–atmosphere exchanges of momentum, energy, and greenhouse gases, and they are used to represent terrestrial ecosystems in Earth system models (Fisher & Koven, 2020). Leaf energy budget theory is embedded in most LSMS. However, LSMS underestimate observed temporal and spatial variability in $T_{\text{can}}$ (Dong et al., 2017; Jiang et al., 2019), which implies that they are not capturing aspects of canopy structure and function. We suggest that $T_{\text{can}}$ observations can be used to help benchmark LSMS (Collier et al., 2018) and test the accuracy of modeled $T_{\text{can}}$ and its implications for temperature-dependent water and C cycling predictions.
Variable importance rankings of net radiation ($R_{net}$), vapor pressure deficit (VPD), soil water content (SWC), and wind speed (WS) from a boosted regression tree analysis of the difference between canopy temperature ($T_{can}$) and air temperature ($T_{air}$) during daytime at contrasting forest sites in the Pacific Northwest, USA (a dense old-growth Douglas fir/western hemlock moist forest at Wind River, WA, and a mature, relatively open canopy semi-arid Ponderosa pine forest at Metolius, OR) and a tropical semi-deciduous forest on Barro Colorado Island, Panama. Data used in analysis when $T_{air}$ $>$ 5°C and downwelling shortwave radiation $>$ 25 W m$^{-2}$ across the growing season. Cross-validation $R^2$ for Wind River is 0.7, for Metolius it is 0.7, and for BCI it is 0.76; calibration $R^2$ for Wind River is 0.81, for Metolius it is 0.79, and for BCI it is 0.85. MAT, mean annual temperature; MAP, mean annual precipitation; LAI, leaf area index.

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Author contributions

CJS, BR, GFMP, DMG, AS, MS, LH, SP, MD and BRH planned and designed the research and conducted fieldwork and analyzed data. CJS wrote the manuscript with contributions from all co-authors.

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