



Tansley insight

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

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Summary

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Canopy temperature T_{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_{can} and forecasting canopy responses to weather extremes and climate change are difficult due to sparse measurements of T_{can} at appropriate spatial and temporal scales. Burgeoning observations of T_{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_{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_{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_{leaf} directly

influences a variety of cellular properties and processes, including membrane fluidity, enzyme reaction kinetics, and diffusion constants and dissolution of CO₂ 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 & Hiltbrunner, 2018). The temperature of any aboveground plant organ is strongly connected to air temperature T_{air} , but biological

and environmental variations can cause large deviations (*c.* 20°C) of T_{leaf} above and below T_{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_{air} .

Though controls on T_{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_{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_{can} are more established in the homogeneous canopy structures of crops, where T_{can} links directly to heat and water stress (Jackson *et al.*, 1981; Maes & Steppe, 2012; Ballester *et al.*, 2013). In natural ecosystems, however, T_{can} measurements can include multiple crowns with heterogeneous plant heights and diverse groupings of species and life forms. Wired contact sensors, like thermocouples, present multiple practical and methodological challenges for measuring T_{can} , from representativeness to durability (Kim *et al.*, 2018). Given these limitations, it becomes clear why our understanding of T_{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_{air} (Table 1). However, measuring T_{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_{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_{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; Heskell *et al.*, 2016; Gimenez *et al.*, 2019). For example, the catalytic

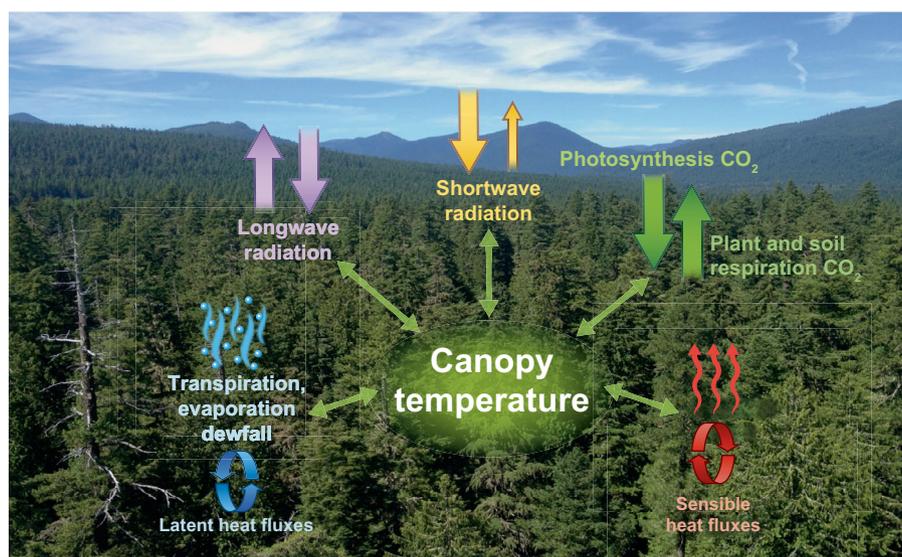


Fig. 1 Energy, water, and carbon fluxes influenced by and influencing canopy temperature T_{can} . Yellow and purple arrows represent shortwave and longwave radiation fluxes, respectively, to and from the canopy. Canopy latent heat symbols represent transpiration and evaporation from canopy surfaces, as well as condensation (dewfall) on canopy surfaces. Sensible heat arrows represent surface heating or cooling by the atmosphere. Photosynthesis and respiration CO₂ fluxes are represented by vertical green arrows. The relative sizes of radiation and CO₂ flux arrows represent different magnitudes.

Table 1 Correlation statistics for various daytime temperature measurements 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.

	T_{can}	T_{aero}	T_{LW}	LST
Wind River, WA				
T_{air}	$1.04x + 3.61$ $r = 0.99$	$1.0x + 3.11$ $r = 0.97$	$1.0x + 2.3$ $r = 0.99$	$1.04x + 1.78$ $r = 0.97$
T_{can}	1	$0.95x - 0.17$ $r = 0.96$	$0.96x - 1.09$ $r = 0.99$	$1.0x - 1.88$ $r = 0.98$
T_{aero}		1	$0.94x + 0.63$ $r = 0.97$	$0.99x - 0.05$ $r = 0.95$
T_{LW}			1	$1.04x - 0.47$ $r = 0.97$
LST				1
Metolius, OR				
T_{air}	$1.06x + 0.47$ $r = 0.99$	$1.04x + 4.64$ $r = 0.98$	$0.95x + 5.02$ $r = 0.99$	$0.89x + 9.57$ $r = 0.89$
T_{can}	1	$0.98x + 4.38$ $r = 0.97$	$0.89x + 4.76$ $r = 0.99$	$0.83 + 9.38$ $r = 0.89$
T_{aero}		1	$0.87x + 1.95$ $r = 0.97$	$0.82 + 6.47$ $r = 0.88$
T_{LW}			1	$0.95x + 4.67$ $r = 0.90$
LST				1
Barro Colorado Island, Panama				
T_{air}	$1.05x + 1.9$ $r = 0.91$	$1.1x - 1.95$ $r = 0.97$	—	$0.23 + 20.92$ $r = 0.16$
T_{can}	1	$0.92x + 0.18$ $r = 0.93$	—	$0.26 + 19.39$ $r = 0.20$
T_{aero}		1	—	$0.24 + 20.6$ $r = 0.18$
T_{LW}	—	—	—	—
LST				1

Relationships between each variable pair are based on ordinary least-squares linear regression. T_{can} , canopy temperature; T_{air} , air temperature; T_{aero} , aerodynamic temperature calculated from eddy covariance measurements of sensible heat flux, windspeed, and friction velocity using the R package BIGLEAF (Knauer *et al.*, 2018). T_{LW} , bulk surface radiometric temperature calculated from measurements of upwelling longwave radiation observed by radiometers mounted on the canopy tower (insufficient data available from Barro Colorado Island to calculate); LST, land surface temperature from NASA's Moderate Resolution Imaging Spectroradiometer. All data were screened to match the 10:30 h overpass time of the TERRA satellite.

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_{leaf} . Since leaves often reach temperatures 5–10°C higher than T_{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_{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_{leaf} to drive a leaf-level process model produced large increases in modeled photosynthesis and transpiration compared with using T_{air} as a driver.

Because of its role in metabolic processes, various measures of T_{air} are typically used as explanatory variables in ecosystem models. Ecosystem respiration is often modeled using T_{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_{can} was more strongly associated with afternoon net ecosystem C exchange than was T_{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_{can} than either T_{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_{leaf} relative to above-canopy T_{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_{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_{can} is strongly influenced by the relative proportions of sunlit and shaded foliage, which can be determined using multiangle 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,

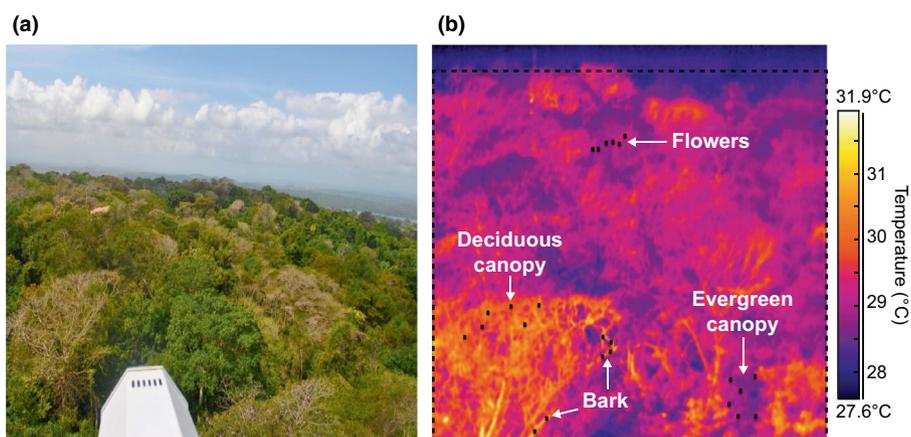


Fig. 2 Visible image of the forest canopy on Barro Colorado Island, Panama, during the dry season, with a thermal camera enclosure mounted on a 40 m tower in foreground (left). Corresponding thermal image of part of the same canopy (right). Black squares are regions of interest used to extract values for different canopy surfaces (deciduous leaves, evergreen leaves, flowers and bark). Both images captured on 17 February 2015. Reproduced with permission from Pau *et al.* (2018).

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_{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_{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_{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_{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_{can} varies with these factors across canopy types and landscape positions. If T_{can} equals T_{air} , then estimates of acclimation and adaptation of photosynthetic temperature response should scale linearly (Kumarathunge *et al.*, 2019). By contrast, if T_{can} changes at a different rate than T_{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_{leaf} are captured by energy budget theory (Jones, 2013), and these same drivers should influence T_{can} , their relative importance likely varies by vegetation type and season. We assessed environmental controls on T_{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_{can} and T_{air} across the growing season shows that the most important explanatory variable at Wind River is R_{net} , followed by VPD and soil moisture. Similarly, R_{net} dominates variable importance rankings at BCI. By contrast, the most important variable explaining the difference between T_{can} and T_{air} at Metolius is VPD, followed by wind speed (WS) and then R_{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

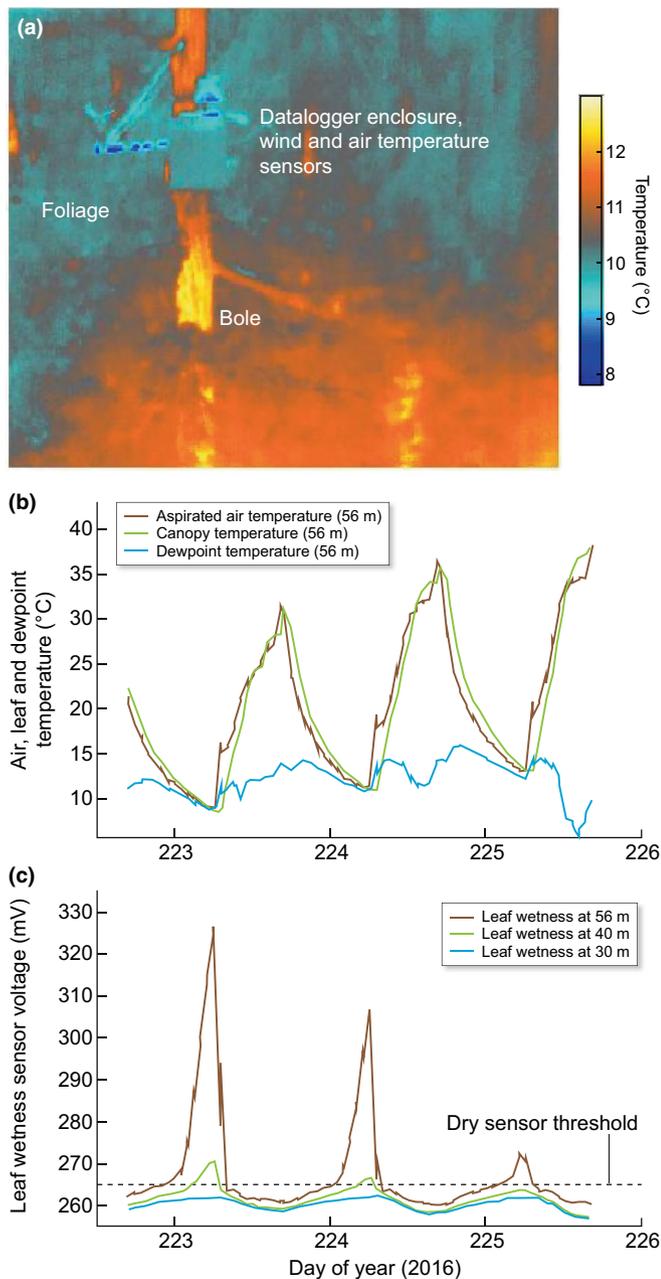


Fig. 3 Evidence for canopy cooling and resulting dewfall in an old-growth Douglas fir canopy at the HJ Andrews Experimental Forest near Blue River, OR, USA. (a) Canopy surface temperatures from thermal infrared imaging captured at 23:50 h on 6 August 2020. (b) Aspirated air temperature, mean canopy leaf temperature, and dewpoint temperature (all measured at *c.* 56 m) during a representative 3-d period in August 2016. (c) Condensation dynamics as measured by leaf wetness sensors at different canopy heights (30, 40 and 56 m) and used to infer dew formation.

denser canopies and higher leaf areas should be driven more by R_{net} and equilibrium evaporation (Jarvis & McNaughton, 1986; Jones, 2013). Particularly at the conifer sites, T_{can} should increase more rapidly than T_{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_{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_{can} and ecosystem function.

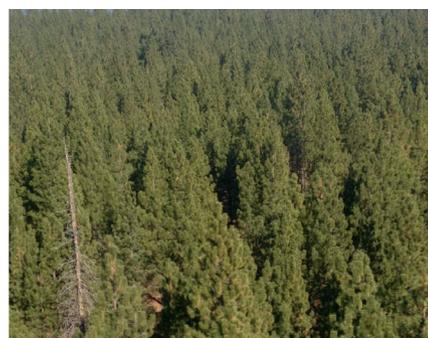
V. Future opportunities

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

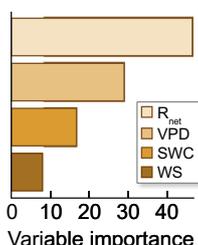
The improved accessibility of thermal imagers, in terms of cost, physical footprint, and power requirements, promises a rapid development of our understanding of leaf and canopy-scale function. In particular, the combination of fixed-mount, unmanned aerial-vehicle-based, and satellite remote sensing presents opportunities to understand variations in T_{can} at spatiotemporal scales that were previously unmeasurable. Fixed-mount imagers are already providing high spatial and temporal resolution data sets of T_{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_{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_{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_{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_{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_{can} observations can be used to help benchmark LSMs (Collier *et al.*, 2018) and test the accuracy of modeled T_{can} and its implications for temperature-dependent water and C cycling predictions.

**Metolius**

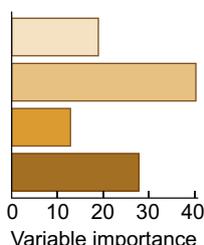
Semi-arid temperate second-growth conifer forest



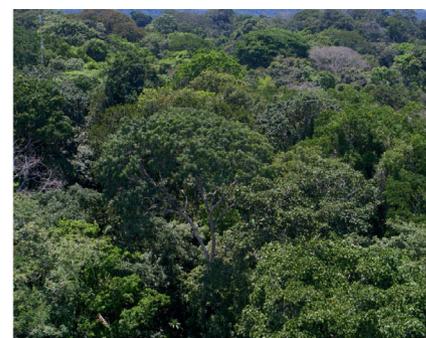
Location	44.45°N -121.55°E
Elevation	1253 m
MAT	6.3°C
MAP	523 mm
LAI	2.8
Mean tree height	18 m

**Wind River**

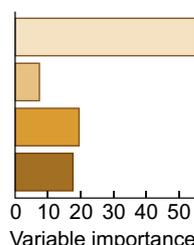
Moist temperate old-growth conifer forest



Location	45.82°N -121.95°E
Elevation	371 m
MAT	8.8°C
MAP	2200 mm
LAI	9.2
Mean tree height	50–60 m

**Barro Colorado Island (BCI)**

Tropical forest with deciduous and evergreen broadleaf trees



Location	9.15°N -79.84°E
Elevation	150 m
MAT	26°C
MAP	2640 mm
LAI	6
Mean tree height	25 m

Fig. 4 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 $T_{air} > 5^\circ\text{C}$ and downwelling shortwave radiation $> 25\text{ W m}^{-2}$ 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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