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Title

Canopy skin temperature variations in relation to climate, soil temperature, and carbon flux at a ponderosa pine forest in central Oregon

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Abstract

Thermal infrared (TIR) techniques to collect thermal imagery have been useful for recording quasi-continuous plant surface temperatures. In this study, we applied a thermal camera to measure canopy skin temperatures in a mature ponderosa pine forest in central Oregon over one growing season from May to September 2014. This study had the following objectives: (1) to examine spatial and temporal variations of canopy temperature; (2) to explore the effects of climate and soil conditions on canopy temperature; and (3) to quantify the relationships of canopy temperatures to forest-atmosphere heat and carbon fluxes. The temporal variation of 30-min mean canopy temperature was large, and leaf temperatures ranged from -2.1 to 33.6 °C during the study period. The temperature difference was small between the whole canopy and leaf regions, while tree stems had warmer temperatures than leaves, especially during the afternoon (12:00 to 19:59 hr). The canopy thermal regime was largely controlled by climatic conditions and related to the soil thermal states. Air temperature, relative humidity, longwave radiation, and soil temperature at 2-cm depth were tightly correlated with 30-min and daily/sub-daily mean canopy leaf temperatures ($r \geq 0.6$ or ≤ -0.6 , $p < 0.01$). The daily/sub-daily mean canopy temperatures contained stronger relationships with the climatic and soil variables than the 30-min mean temperatures. During the afternoon, the mean leaf temperature was more closely related to net ecosystem exchange ($r^2 = 0.69$) than air temperature, driven by the strong relationship between tissue temperature and photosynthesis and respiration. Our results show that canopy thermal conditions can be monitored almost continuously for extended time periods to better characterize how canopies respond to environmental conditions. Finally, thermal measurements show great promise for quantifying linkages to carbon exchange in forest ecosystems.

Keywords

Thermographic imaging techniques, canopy temperature, coniferous forest, climate, soil temperature, carbon dioxide flux

1. Introduction

Temperature is an important environmental variable that strongly affects the physiology of plants and a variety of biogeochemical mechanisms in forest ecosystems (Harley et al. 1996, Medlyn et al. 2002, Scott-Denton et al. 2003, Tierney et al. 2003). Air temperature has been typically used as a thermal metric to study the enzymatic and organismal response of forest canopies to changes in climate and environment (Ball et al. 1994, Tanja et al. 2003). However, forest canopies can be uncoupled from their surroundings (Jarvis and McNaughton 1986), with substantial deviations between leaf and air temperature. Measurement of leaf and branch surface temperatures should be more directly related to biophysical and physiological reactions and states of forest canopies (Amani et al. 1996, Leinonen and Jones 2004). The deviation of canopy temperature from air temperature can vary by meteorological and environmental conditions of the forests, resulting from the physiological response in trees. The temperature deviations have been frequently used as an index of drought and water-related stress in agricultural studies (e.g., West et al. 1988, Sepulcre-Cantó et al. 2006), while this has been explored far less in the forest ecosystems. Canopy temperature measurements thus represent a promising approach for interpreting and integrating biochemical, physiological, hydrological, and biogeochemical processes in forests.

It is particularly important to understand how canopy leaf temperatures vary due to abiotic climatic and environmental conditions as well as leaf size and canopy position. For example, canopy temperature and various ecosystem functions (e.g., evapotranspiration and

photosynthesis) are strongly interrelated with each other, and are non-linearly related to temperature. As global warming increasingly affects forest ecosystems (Bonan 2008), measurements of canopy temperature should be useful for analyzing how climate change influences ecosystem functions. Longer temporal records of canopy temperature data are required for understanding variation in physiological and biogeochemical processes in forests. To our knowledge, no study has made based on quasi-continuous *in-situ* measurements of forest canopy temperatures over the growing season or year. A primary reason is limited technical capability, but recent advances have produced compact, reliable, and durable instruments for the temperature measurement.

The advance of thermal infrared (TIR) imaging enables us to measure organismal surface temperatures more broadly and frequently (e.g., Jones 2004, McCafferty 2007, Hristov et al. 2008). TIR techniques using thermal cameras to collect imagery have been applied to record plant surface temperatures of temperate forests for 2–3 days (Leuzinger and Körner 2007, Scherrer et al. 2011) and alpine landscapes for periods of four days to several weeks (Scherrer and Körner 2010, Scherrer and Körner 2011). The analyses showed clear differences in surface temperature due to topographical variation (Scherrer and Körner 2010), distribution of tree species and plant functional types, i.e., coniferous vs. deciduous trees (Leuzinger and Körner 2007), as well as the surrounding environment (e.g., urban vs. rural surroundings) (Leuzinger et al. 2010). Maes et al. (2011) suggested that plant-water relations and water deficits were affected by leaf angle and size as key characteristics of plant species. TIR measurements by Scherrer et al. (2011) revealed that drier areas, resulting from topographical variation, are more likely to experience dryness and thus additional warming in the future. However, determining how

climate variability and extreme climate events, such as heat waves, droughts, and frosts, influence the variability of forest canopy temperatures has not been addressed previously.

To date, monitoring of canopy temperatures using TIR imaging has been used primarily to examine the status and regulation of stomatal conductance and its influence on water vapor (H_2O) and carbon dioxide (CO_2) exchanges (Collatz et al. 1990, Fischer et al. 1998, Jones et al. 2009). During the last several decades, a variety of such short-term TIR studies on stomatal conductance have been conducted in agricultural fields (e.g., Jackson et al. 1981, Cohen et al. 2005, Möller et al. 2007), with a goal of assisting water management of croplands through optimized irrigation and water stress reduction. Similar TIR monitoring of forest ecosystems would enhance understanding of relations among forest canopy temperature, stomatal conductance, and energy, water, and carbon exchanges.

At the scale of individual leaves, temperature variations result from physical and biological interactions that are affected by leaf morphology and albedo, canopy position, radiation, wind, and stomatal response to the environment (Jones 2004, Leuzinger and Körner 2007). These interactions always vary in time and space, so the temporal and spatial scales must be defined to delineate biotic and abiotic processes. In order to describe details of diurnal or seasonal patterns of canopy temperatures and their relationships with environmental variables in ecosystems, continuous TIR monitoring over several months or a year from the same location is required. Moreover, TIR monitoring allows us to measure temperatures across a large forest canopy, thus extending the spatial scale in comparison to traditional measurements of leaf temperatures using thermocouple arrays. By applying TIR imaging, research into the composition of forest canopies (e.g., leaves and trunks) and the spatial variability of canopy temperature can be pursued. This work thus focuses on quantifying the spatial and temporal

changes in thermal regimes from a forest canopy across a fairly long time period that spans most of one growing seasons.

In this study, we used TIR imagery to measure canopy temperatures in a mature ponderosa pine forest in the Pacific Northwest of the USA. This site provided an opportunity to explore correlations among canopy temperature, climatic and soil variables, as well as energy (sensible and latent heat) and carbon fluxes. The objectives of this study were: (1) to examine spatial and temporal variations of canopy temperature in a mature coniferous forest; (2) to investigate the effects of climatic and soil factors on spatial and temporal variations of canopy temperature; and (3) to interpret the relationships of canopy temperatures to heat and carbon fluxes from this forest. We hypothesized that: (1) there would be considerable temporal and spatial variability in canopy temperatures, as they are strongly affected by multiple climatic and soil variables, such as insolation, air temperature, humidity, and soil moisture; and (2) significant correlations between canopy temperatures and heat and carbon fluxes would be revealed. To our knowledge, this study is the first attempt to measure multi-day canopy surface temperatures using near-surface TIR approaches from a coniferous forest with simultaneous eddy covariance measurements.

2. Methods and materials

2.1. Study site

This study was conducted in a mature coniferous forest in central Oregon that is located within the Cascade Mountains near the city of Sisters at an elevation of 1253 m (44.45°N, 121.56°W) (Figure 1). The study forest has been privately owned and well protected after harvest in the early 20th century. This forest is named the Metolius mature ponderosa pine forest and was

designated as a core research site in the AMERIFLUX network (<http://ameriflux.lbl.gov>, site US-Me2) where microclimate and eddy covariance flux measurements are collected from a flux tower. The overstory consists of ponderosa pine trees (*Pinus ponderosa* Dougl. Ex P. Laws) with scattered cover from a few incense cedars (*Calocedrus decurrens* (Torr.) Florin). Mean stand age is 65 years in 2015, and the oldest 10% of trees are 100 years. Trees are homogeneously distributed and a typical leaf area index (LAI) is $2.8 \text{ m}^2 \text{ m}^{-2}$. Average tree height and density is 22 m and $325 \text{ trees ha}^{-1}$, respectively (Irvine et al. 2008, Thomas et al. 2009). The understory is sparse and primarily composed of antelope bitterbrush (*Purshia tridentata* (Pursh) DC.) and greenleaf manzanita (*Arctostaphylos patula* Greene). LAI of the understory is $0.2 \text{ m}^2 \text{ m}^{-2}$ (Thomas et al. 2009). Soils are ultic haploxeralfs, freely draining sandy loam derived from volcanic ash (69/24/7% sand/silt/clay at 0 to 0.2 m), and soil depth is approximately 1.5 m (Schwarz et al. 2004, Irvine et al. 2008). The forest is nearly homogenous in all directions to a few kilometers, except an area to the north within an 1 km from the flux tower that was logged in 2005 (Thomas et al. 2009). The climate is semi-arid, with warm/dry summers and cool/wet winters. Most precipitation at the site falls as snow or rain during the winter and spring (between November and April). Annual mean air temperature ranged from 6.7 to 8.0 °C, and mean annual total precipitation varied from 194 to 728 mm in the period from 2002 to 2012. Additional descriptions of the study site are found in Law et al. (2001) and Anthoni et al. (2002).

A 34-m scaffold flux tower was constructed in 2001 for climate and flux observation, and physiological measurements were initiated in the same year (Schwarz et al. 2004, Irvine et al. 2008, Thomas et al. 2009). Numerous climatic variables, fluxes, and concentrations of water vapor (H_2O) and carbon dioxide (CO_2) have been continuously measured from the flux tower at various heights from near the surface to the top of the tower. Among the measured variables, this

study used measurements from the top of the tower which include sensible and latent heat fluxes and net ecosystem exchange (NEE) and the climatic variables of wind speed and direction, air temperature, humidity, shortwave and long wave radiation fluxes, and rainfall (Table 1). Flux measurements were taken from the top of the tower using an eddy covariance system consisting of a sonic anemometer and temperature sensor (CSAT-3, Campbell Sci., Logan, UT, USA) and an infrared gas analyzer for CO₂ and H₂O concentration variations (Li-7500, Li-Cor, Lincoln, NE, USA). The sampling rate of the eddy covariance system is 20 Hz, and fluxes were aggregated into 30-min means. The sampling rate of climate is 10 seconds, and all climatic data were processed into 30-min means or totals using standard approaches. A solar power system provides power for all instruments. Additional information about instrumentation and methodology for meteorology and flux observations is provided by Thomas et al. (2009).

Soil temperature (ST) and soil water content (SWC) were also used (Table 1), which were measured in a patch 150-m south of the flux tower (within the flux footprint). ST was measurements at 2 and 64-cm depth at two locations (ST2 and ST64), while SWC was monitored data at 10 and 160-cm depth using three EnviroSmart soil water content profile probes (Campbell Sci., Logan, UT, USA). The mean values of multiple probes were used in this study. The temporal interval of soil variables is 30 minutes, the same as the other climatic and flux sampling.

We calculated a bulk canopy temperature using the observed upwelling longwave radiation (R_{lu}) over the period of climatic measurement. This version of canopy temperature is called ‘R_{lu}-based canopy temperature’ hereafter. This estimation was based on the Stefan-Boltzmann Law ($W = \varepsilon \times \sigma \times T^4$, W : total emitted radiation from an object (W m^{-2}); ε : emissivity of an object (0 to 1); σ : Stefan-Boltzmann constant ($5.67 \times 10^{-8} \text{ W m}^{-2} \text{ K}^{-4}$); and T : surface

temperature of the object (K)), and an emissivity of 0.95, the same value for the thermal camera measurements, was applied. These estimates were used to compare to canopy temperatures measured by the thermal camera.

2.2. Instrumentation of field measurement

A thermal camera (FLIR A325sc, FLIR System Inc., Wilsonville, OR, USA) was used to capture TIR images from the study forest. The pixel resolution of this camera is 360×240 (pixel numbers: 76800); a FLIR IR 30-mm lens (focal length: 30.38 mm; field of view: $15^\circ \times 11.25^\circ$) was used for image collection. Note that distances to canopy points from the camera are provided below. Within the field of view, spot sizes of a single pixel are 0.083 cm from 1 m, 0.83 cm from 10 m, and 8.3 cm from 100 m in a single pixel. This camera uses an uncooled microbolometer detector to scan the longwave spectra ranging from 7.5 to 13.0 μm . The maximum frame rate for recording is 60 Hz, and the external air temperature operating range for the camera is -20 to 120°C . A personal computer (PC) is required to control the camera and collect images. Gigabit Ethernet is the data streaming protocol for connection between the camera and PC. A software package of FLIR ResearchIR 3.4 SP2 was used in this study.

Measured TIR temperatures (uncorrected temperatures) are accurate within error ranges of $\pm 2^\circ\text{C}$ or $\pm 2\%$ of the temperature recording, according to the manufacturer (<http://www.flir.com>). These errors are due to the fixed parameters (e.g., emissivity, reflected apparent temperature, and atmospheric temperatures) and calibrating processes in the camera and software. The response of an object's thermal status to the outside environment (e.g., microclimate) should be almost consistent within the same canopy area, and therefore, our measurement sufficiently accounted for the heterogeneity of canopy temperatures. The TIR

camera is precise in regard to differences among measurement pixels within a single image when pixels lie within a similar distance from the camera (Faye et al. 2016). If several objects by vegetation type and structure are measured, and their distances from the camera is almost same within an image, the information on relative temperature differences is accurate compared to that on their absolute temperatures (D. Scherrer, personal communications, 2014). Since the same error in the estimation of absolute temperature persists for all parts of image, our purpose of exploring temporal and spatial variations of canopy temperature can be established using uncorrected TIR temperatures.

The camera was housed in a FLIR F-Series waterproof enclosure to protect it from ambient moisture and precipitation (rain and snow at the site). We used a fanless PC which was stored in a 25.4×30.5 cm standard environmental enclosure (Campbell Sci., Logan, UT, USA). These instruments were combined in a TIR system that was installed on the 32-m platform of the flux tower. The camera faced N-NW (20° west of due north in azimuth angle), and this orientation avoided direct sunlight to the camera. The camera was mounted at a tilt angle of 8° down from the horizontal, which allowed it to capture the largest view in the study forest without imaging part of the sky. Using a laser rangefinder, distances from the camera to the lowermost (southernmost) and to the uppermost (northernmost) part in the images were measured respectively at ~ 70 and ~ 300 m; the long dimension in the monitored rectangular area was calculated at 236 m. Distances from the camera on tower to the rightmost (easternmost) and leftmost (westernmost) trees in the image rectangle were measured at ~ 70 and ~ 80 m, respectively; the short dimension in the monitored rectangular area was 39 m. The forest area captured in the images was therefore approximately 0.92 ha.

The TIR system was deployed on the tower in May 2014. The measurement interval was fixed at 5 minutes throughout the study period, creating 288 images per day. However, due to power failures and glitches in the camera's software, continuous 5-min collections could not be acquired throughout the deployment period in 2014. In the end, canopy temperatures were monitored for a total of 84 days. The time-series measurements including most of the 2014 growing season spanned four time slices: May 29 to June 21 (day of year, DOY, 149 to 172), June 24 to July 12 (DOY 175 to 193), July 28 to August 14 (DOY 209 to 226), and August 29 to September 24 (DOY 241 to 267). In total, 24153 TIR images were retrieved.

2.3. Data processing

Measured climatic and soil variables and fluxes for the periods of TIR collection were used in this study (Table 1). Climatic observation from the tower top (34 m) were used to represent the canopy-level (22 m) microclimate in our analysis, as it was shown that in most situations, the vertical gradient of climate (e.g., air temperature, humidity, and radiation) from the forest canopy to ~10 m above the canopy was not significant (Tajchman 1981). The tower measurements included a vertical profile of eight thermistors (non-aspirated) at the level of 1 to 32.1 m, so we compared them with the tower-top air temperatures to determine the strength of the gradient from the tower top to just above and within the canopy. The differences between tower-top air temperatures and 20.2-m thermistor measurements (canopy-top temperatures), canopy minus tower top, were small with 0.1 ± 0.7 °C (mean $\pm$ standard deviation) for the study period. Larger temperature gradients occurred within the canopy, as the mean difference between canopy-top and mid-canopy (10.5-m) air temperatures (mid canopy minus canopy top) was -1.2 ± 2.3 °C.

TIR images were collected as FLIR's data format, 'fff', which was converted to 'csv' files using batch file processing in a separate FLIR software package (ThermaCAM Researcher Professional 2.10). Due to distance from camera, pixel resolution, and size of the needles, imaging of individual leaf clusters was not feasible as it was for trunk, deadwood, and exposed soil regions in the entire image. Instead, the collected canopy images were a mixture of leaves and trunks, where leaves were predominant and exposed trunk areas were small and randomly distributed especially in the half of image near the flux tower. Selecting and clipping each region of interest (ROI) for leaves (L) and trunks (T) from all images was completed using IDL (Exelis Inc., McLean, VA, USA). To the extent possible, ROI selections with even distribution across the lower half image (southern part) were used to avoid biases as a result of sun/shade effects and geographical locations (e.g., distance from the camera) as well as the potential errors due to the different pixel size by varying distance from the camera to the objects (Faye et al. 2016). These selections were carried out by referring to the same image (Figure 2).

For ROIs from leaves, three rectangles of areas, aligned horizontally, were picked up from the left to right in an image, and two sets of the horizontal selections were made to sample leaf areas vertically from the bottom to center in an image. Six leaf ROIs (L1 to L6) were thus retrieved from a single TIR image (Figure 2), comprising pixel totals of 231 (11×21) to 735 (21×35). All pixels in the L1 to L6 ROIs were summed to 2083 (2.7% of all pixels). For trunk ROIs, four regions (T1 to T4) were selected in the image (Figure 2), where trunk structures were clearly visible. Pixel sums in trunk ROIs spanned from 5 (1×5) to 27 (1×27); the combined trunk ROIs summed to 69 pixels (~0.1% of all pixels). The half image from the bottom (320×120 pixels), containing the leaf and trunk ROIs, were selected as the canopy ROI to represent the temperature from the whole forest canopy. The same ROI selections were processed for all files.

2.4. Data analysis

Uncorrected pixel temperatures in each of the leaf, trunk, and canopy ROIs in a TIR image were averaged to define the temperatures for each region as time-series datasets from May to September. The half-hour (30-min) interval was designated as a finest temporal scale for the data analysis, since climate, soil, and flux measurements were reported every 30 minutes. Therefore, we calculated half-hour averages in TIR temperatures and focused on half-hour variations to examine temporal changes. The half-hour averages in each type of ROI were produced when all six temperature measurements were available. In this study, the period of the measurements were indicated by the earliest time of the 30-min window (e.g., data at 1:00 hr include the period from 1:00 to 1:29 hr). All half-hour averages were then calculated as means per day (entire day, 0:00 to 23:59 hr) and means for each of the three 8-hour time periods: morning (4:00 to 11:59 hr), afternoon (12:00 to 19:59 hr), and night (0:00 to 3:59 and 20:00 to 23:59 hr). All measured variables from the flux tower and forest soils were also processed as daily and sub-daily means to allow comparisons between TIR temperatures and tower or soil observations. As there were some gaps in TIR and tower/soil measurements for the study period, datasets during the gap periods were discarded in both measurements and then daily and sub-daily means were calculated. The daily/sub-daily means determined using most of the half-hour datasets within a time period (entire day: $n \geq 44$; morning, afternoon, and night: $n \geq 14$) were only used in our analysis. TIR temperature differentials (TIR temperature minus air temperature) were then estimated for 30-min averages and daily/sub-daily averages in all four time slices.

Overall *F*-tests were used to quantify differences in TIR temperatures and the temperature differentials between the leaf and trunk ROIs. The tests were completed using

daily/sub-daily means in every ROI (six for leaves; four for trunks). The ROI's means were averaged across the whole measurement time period for four separate time slices (entire day, morning, afternoon, and night).

Correlations of TIR temperatures or their differentials in leaf and trunk ROIs to climatic, soil, and flux variables were calculated using 30-min average data. These correlations were based on simultaneous data collection. The other set of 30-min average correlations was analyzed to examine the possibility of a half-hourly lagged response of canopy fluxes (i.e. sensible and latent heat and NEE) to thermal variations. The flux measurements which are 30 min later than TIR temperatures were applied in this analysis (e.g. TIR temperature of 1:00 to 1:29 hr vs. flux of 1:30 to 1:59 hr). Correlation tests between daily/sub-daily mean variables (including all four time slices) were conducted. Moreover, a correlation test between the canopy ROI temperatures and Rlu-based canopy temperatures was conducted using 30-min averages. The statistical package of R version 3.0.2 (R Development Core Team 2011) was used, and the statistically significant level was denoted at $p \leq 0.05$.

3. Results

3.1. Temporal variations of TIR temperatures

Means of the 30-min average TIR temperatures ($n = 3999$) were 15.6 ± 7.5 °C (range of -2.2 to 33.8 °C) in canopy ROI (Figure 3a), 15.6 ± 7.4 °C (range of -2.1 to 33.6 °C) in leaf ROIs, and 16.1 ± 7.5 °C (range of -2.1 to 33.5 °C) in trunk ROIs. Minimum temperatures in all ROIs occurred on DOY 168 (June 17). Maximum temperatures varied by ROI, appearing on DOY 212 (July 31) for whole canopy and leaves, and DOY 210 (July 29) for trunks. The minima occurred during a cloudy and rainy day and maxima did during sunny and dry days. The temperature

difference was small between the canopy ROI and leaf ROIs, while trunks exhibited warmer temperature than these two ROIs.

Means of the 30-min average temperature differentials ($n = 3941$) were -0.7 ± 2.5 °C (range of -9.1 to 8.5 °C) in canopy ROI (Figure 3b), -0.7 ± 2.5 °C (range of -9.1 to 8.4 °C) in leaf ROIs, and -0.2 ± 2.5 °C (range of -8.2 to 8.7 °C) in trunk ROIs. Minimum differentials in all three ROIs occurred on DOY 155 (June 3). Maximum differentials for all ROIs appeared on DOY 211 (July 29). Both of the minima and maxima occurred during sunny and dry days. The trunk ROIs had the largest differentials among the three ROIs, and the difference between the canopy and leaf ROIs was small.

The calculated daily means showed that TIR temperatures and their differentials varied in similar ranges among ROIs (Figure 3). During the study period, temperatures fluctuated from minimum of $2-3$ °C to maximum of ~ 25 °C, and the differentials spanned from minimum of -2 to -1 °C to maximum of ~ 1 °C.

3.2. Spatial variations of TIR temperatures

According to our F -tests (all time slices: $n = 10$), TIR temperatures and their differentials in ROIs were significantly different between leaves and trunks for three time slices (F -statistic: $5.43-9.20$ on 1 and 8 DF; $p \leq 0.05$) except for night (F -statistic: $1.80-1.85$ on 1 and 8 DF; $p = 0.21-0.22$) (Figure 4). Temperatures and their differentials of the three canopy regions varied from each other, and their trunk values were higher than other two for all time slices (Figure 4). Canopy TIR temperatures and their differentials were higher than the leaf temperatures and differentials in all time slices except night hours (Figure 4).

3.3. Correlation of TIR temperatures to climatic, soil, and flux variables

For each of leaf and trunk ROIs, we calculated 22 and 19 correlation tests respectively with 30-min and daily/sub-daily means of TIR temperatures and the temperature differentials. Various numbers of 30-min datasets (entire day: $n = 3279\text{--}3999$; morning: $n = 1183\text{--}1320$; afternoon: $n = 1212\text{--}1342$; night: $884\text{--}1337$) and daily/sub-daily datasets (entire day: $n = 37\text{--}77$; morning: $n = 60\text{--}81$; afternoon: $n = 62\text{--}81$; night: $37\text{--}79$) were used in our tests.

Wavelet coherence analysis (see Torrence and Webster 1999 and Grinsted et al. 2004) was used to examine which time period of climatic and soil datasets, 30-min vs. daily means, generates better regressions with TIR temperatures. Half-hour mean data without gaps (DOY 177 to 190: June 26 to July 9, $n = 672$) were used for this analysis. The results of wavelet coherence analysis, using T_{air} , RH, Rld, Rlu, ST2, and ST64 (Figure S1), showed that daily relationships (period of 1) were consistently stronger than 30-min relationships (period of 0.02) throughout the two weeks.

The results of 30-min or daily/sub-daily mean temperatures are reported as correlation coefficients in Figure 5. Most of the individual tests with TIR temperatures and their differentials, especially from 30-min data, showed significant correlations ($p \leq 0.05$) between any two factors (Figure 5), except 30-min Rain and daily/sub-daily LE, Rsd, Rsu, Rnet, and Rain. Correlation coefficients for entire day and afternoon hours were highest in 30-min climate variables (Figures 5a and b) and daily/sub-daily NEE (TIR temperatures; Figure 5e), while morning or night hours included the highest coefficients in 30-min soil variables (Figures 5c and d). In general, correlation coefficients with 30-min flux data were lower during the night (data not shown), since an inversion near the surface prevails when the temperature gradient is large, and energy and CO_2 are stored within the canopy. The profile air temperature measurements showed that the

differences between mid-canopy and canopy-top air temperatures were largest during the night: -2.5 ± 2.3 °C of averaged mid-canopy minus canopy-top temperatures as compared with -1.4 ± 2.5 °C during the morning and 0.2 ± 0.6 °C during the afternoon. The differences between the canopy-top and tower-top temperatures were small in all sub-daily periods (≤ 0.6 °C of averages), so gradients were not predominant within the layer between the canopy and tower top.

3.3.1. Correlation with climatic and soil variables

Correlations among TIR temperatures and T_{air} , RH, Rld, and Rlu were strongest ($r \geq 0.6$ or $r \leq -0.6$, arbitrarily defined in this study) in both 30-min analyses (Figure 5a) and daily/sub-daily analyses (data not shown). Although the correlations between temperature differentials and Rlu were strongest, the correlations with the differentials were generally less strong than those with TIR temperature (Figure 5b). All climatic variables except RH showed a positive relationship, and their coefficients were large in all time slices. The 30-min and daily/sub-daily analyses of soil variables exhibited strong positive correlations between soil temperatures at 2-cm depth and either TIR temperatures or the temperature differentials (Figures 5c and d). Negative correlations were found with soil water content, and these relationships were weaker.

3.3.2. Correlation with flux variables

For TIR temperatures and their differentials, r with H and LE (Figures 5c and d) was higher than that with NEE (temperatures: -0.09 to 0.29 ; temperature differentials: -0.40 to 0.59) in 30-min datasets, while NEE exhibited higher r than either heat flux in daily/sub-daily datasets (Figures 5e and f). No clear difference was found in correlations between the same-time and lagged-time 30-min analyses (data not shown). Morning hours exhibited the highest r in the 30-min mean

analyses, whereas afternoon or night hours included the highest r from the daily/sub-daily mean analyses for NEE (Figures 5e and f).

3.3.3. Comparison between leaves and trunks

Correlation coefficients between TIR temperatures (or differentials) and climatic and soil variables were almost same for leaves and trunks in 30-min and daily/sub-daily datasets (Figures 5a to d). For the flux variables, small differences in coefficients existed between leaves and trunks in 30-min datasets (Figures 5c to f). However, the correlation between leaf ROI and NEE was higher than that between trunk ROI and NEE, especially in the daily/sub-daily datasets (Figure 5f).

In the following sections, we will discuss further regression analyses between TIR temperatures and the variables with strongest correlations (≥ 0.6 or ≤ -0.6) such as T_{air} , RH, longwave radiation, soil temperature, and NEE for leaf and trunk ROIs.

3.4. Relationships with climatic variables

For the entire day, the regressions between 30-min mean climate and TIR temperatures showed that the variation of leaf and trunk temperatures were similarly explained well by T_{air} and R_{lu} ($r^2 = 0.91\text{--}0.92$, $n = 3941$) (Figure S2). The next closest relationships were between TIR temperatures and RH and R_{ld} . The relationship between TIR temperatures and R_{lu} should be closest as the TIR measurement is a related measurement of longwave radiations emitted from the canopy. Compared to the entire-day period, morning or afternoon hours had high r^2 in T_{air} and RH, and morning or night hours had high r^2 in R_{ld} and R_{lu} . In general, r^2 from the daily/sub-daily mean analyses (0.30 to 1.00) was slightly larger than the 30-min analyses, and the leaf

relationships were stronger than the trunk ones in longwave radiation but less strong in T_{air} and RH.

Additional analyses were conducted by partitioning the entire-day 30-min datasets into sunny hours ($\geq 100 \text{ W m}^{-2}$ of net radiation) and cloudy hours ($0\text{--}100 \text{ W m}^{-2}$ of net radiation) (defined in Ryszkowski and Kędziora 1993). Sunny relationships for leaves and trunks ($r^2 = 0.34\text{--}0.96$, $n = 1697$) were tighter than the cloudy ones ($r^2 = 0.22\text{--}0.97$, $n = 279$) except for R_{lu} .

3.5. Relationships with soil temperatures

Soil temperatures near the surface showed a tighter positive link with TIR temperatures ($r^2 = 0.81\text{--}0.82$ at 2 cm vs. $r^2 = 0.26\text{--}0.27$ at 64 cm, $n = 3991$) for the entire day (Figure S2). The results of the same-time and lagged-time analyses with soil temperatures were same at the surface and deep soil depth (data not shown). Morning or night hours produced the highest r^2 with soil temperatures among the four time slices, and the daily /sub-daily mean soil temperatures resulted in higher r^2 (0.26 to 0.90) than the 30-min means. The leaf relationships were tighter than the trunk ones from both of the 30-min and daily/sub-daily analyses.

The analyses with sunny and cloudy-hour means for the entire day showed stronger relationships during cloudy hours ($r^2 = 0.34\text{--}0.94$, $n = 279$) than sunny hours ($r^2 = 0.26\text{--}0.76$, $n = 1747$), which was not the case for climatic variables. The leaf and trunk relationships were similar in both soil temperatures.

3.6. Relationships with carbon fluxes

For the entire day, half-hour means of leaf and trunk temperatures showed stronger relationships with NEE during sunny hours ($r^2 = 0.34\text{--}0.35$, $n = 1629$) than cloudy hours ($r^2 = 0.18\text{--}0.19$, $n =$

229) and the whole hours ($r^2 = 0.01$, $n = 3279$). Daily/sub-daily leaf TIR temperatures were significantly related to NEE for the time slices except for night hours (leaf temperatures in Figure 6; $r^2 = 0.62$ – 0.69 , $n = 37$ – 62). Afternoon-hour TIR temperatures were correlated with the NEE variations better than other periods (Figure 6), and leaf temperatures explained NEE variation slightly better than trunk temperatures.

Excluding night-hour average leaf ROI, temperatures ranging from 0 to ~ 20 °C were correlated with negative NEE (carbon uptake by the forest), and this uptake rate was highest between 5 and 15 °C, especially for afternoon hours (Figure 6). Temperatures over 30 °C were associated with positive NEE (carbon release from the forest) for afternoon hours. By comparison, the regressions between daily/sub-daily mean T_{air} and NEE indicated weaker relationships than those with leaf and trunk temperatures (entire day: $r^2 = 0.53$, $n = 54$; morning: $r^2 = 0.52$, $n = 92$; afternoon: $r^2 = 0.65$, $n = 90$; and night: $r^2 = 0.00$, $n = 51$).

3.7. Comparison of TIR temperatures to another dataset

The changing patterns in daily means of TIR and Rlu-based canopy temperatures were similar, and 30-min means of the two temperatures were highly correlated each other ($r^2 = 0.93$, $n = 3941$) (Figure 7). The Rlu-based temperatures were consistently higher than the TIR temperatures by up to 9.5 °C from the comparison of 30-min means (3.5 ± 2.0 °C of mean difference). Although both 30-min averages were highly related, the TIR temperatures were smaller than the Rlu-based bulk estimates (Figure 7b).

4. Discussion

This study was based on near-continuous monitoring of canopy temperatures for extended periods, with a focus on investigating temporal and spatial variations of TIR-derived canopy temperature and the relationships among canopy temperatures and climate, soil factors, and fluxes from a mature ponderosa pine forest. We showed that canopy temperatures of coniferous forests can be well retrieved using a thermal camera, and thus represent the various forest thermal regimes in space and time. Correlation of TIR temperatures in the leaves and trunks to the climatic, soil, and flux variables helps to understand how these variables affect or are related to canopy temperatures.

The result of *F*-tests and the means for the study period (Figures 3 and 4) support the first objective of assessing spatial and temporal variations of canopy temperatures and the temperature differentials. The analyses revealed temperature difference between leaves and trunks. As most of the canopy was composed of leaves, the temperature difference between the selected canopy and leaf ROIs could be small. The high temperatures in trunks compared to leaves principally result from a lack of transpirational cooling, with lesser contributions from albedo and sensible heat differences. Other studies with thermal cameras (Merlot et al. 2002, Möller et al. 2007) and thermal sensors (Lu et al. 1994) also identified cooler temperatures in leaves, and this is associated with variations in stomatal conductance and transpiration. This is consistent in comparing the temperature differentials between leaves and trunks (Figure 4): lower temperature differentials in leaves would be due to greater cooling from leaf transpiration.

The hourly fluctuation are accompanied by radiative heating and cooling during the afternoon and morning/night (Jones 2004), while daily fluctuations could originate from weather conditions like rain leading to a drop of canopy temperatures (Figure 3a). There was rain in the

middle of June (DOY 167), the end of June (DOY 178), and the middle of August (DOY 225). Lower afternoon temperatures corresponded to these rain events. Hence, fluctuations of forest canopy temperatures represent canopy responses to changes in micrometeorological and environmental conditions in the forest. The deviation of canopy temperature from air temperature is largely positively related to longwave radiation on the canopy layer and negatively related to afternoon-hour soil water content (Figures 5b and d), supporting other findings that water stress in deciduous and coniferous trees (demanding more water) increases in response to higher radiation (Hunt and Rock 1989, Riggs and Running 1991).

As T_{air} , RH, R_{ld} , and R_{lu} accounted for the strongest correlation with the leaf and trunk temperatures (Figure 5a), this study supports the hypothesis that microclimate considerably affects the variations of canopy temperatures. Previous studies showed that climatic conditions largely influenced the thermal status of forest and grassland canopies (Idso et al. 1986, Scherrer et al. 2011). The primary factors controlling the dynamics of canopy temperatures were T_{air} , water vapor, and longwave radiation, according to this study (Figure 5a). Higher T_{air} and longwave radiation were correlated with increasing temperature of the canopy, while more water vapor in the atmosphere (i.e., higher RH and lower VPD, vapor pressure deficit) led to decreasing the temperature, likely due to greater cloud cover and lower irradiance at times of high RH and lower VPD (Leuzinger and Körner 2007). While lower water vapor increases VPD and might increase evapotranspiration, there is a chance that lower water vapor led to fast transpirational cooling in the forests. According to the relationships between 30-min mean VPD (estimated by Anderson 1936) and LE for the whole day, lower water vapor is somewhat related to greater evapotranspiration from the forest surface ($r^2 = 0.11$, $n = 5175$). It is thought that multiple variables affect the variations of canopy temperatures, and thus no single factor would

fully describe the temperature changes in canopies. For example, a linear regression between 30-min averaged leaf temperatures and both T_{air} and R_{lu} for the entire-day measurement period resulted in r^2 of 0.96 ($n = 3940$), which is a stronger relationship than individual correlations with either T_{air} or R_{lu} .

Soil temperature near the forest floor were revealed as an important factor (Figure 5c), supporting the hypothesis that canopy temperatures were closely related to soil thermal states. However, the direct effect of soil temperatures on canopy temperatures is unclear in the study forest. Although soil heat fluxes transport thermal energy to the trees (Heilman et al. 1994, Ogée et al. 2001), this effect is rare when forest trees are tall (> 20 m). At the least, our analysis with soil temperatures suggests that canopy and soil temperature are highly correlated. Unlike relationships between air and canopy temperatures, soil surface temperature was more strongly correlated to canopy temperature during cloudy periods. We assume that the correlation of soil to canopy temperature varies by incoming radiation on the surface. More radiative heating during sunny hours leads to fast changes in canopy temperatures, while small changes exist in soil temperature as soils are rarely exposed with radiative heating under the thick canopies.

Our correlation tests do not fully support the hypothesis of tight relationships between canopy temperatures and heat and carbon fluxes in the forest. The stronger correlations of daily mean NEE to leaf temperatures (Figures 5e and 6) suggest that the measured temperatures influence photosynthesis and leaf respiration especially in the afternoon, as long as there is sufficient water for canopy and soil processes (Law et al. 1999, Irvine et al. 2008). Canopy temperatures over 30°C tended to release carbon to the atmosphere, presumably because such higher temperatures strongly stress these trees (Atkin and Tjoelker 2003; King et al. 2006). This stress, caused by water shortage, is shown in canopy temperature differentials, as the higher

differential likely represents more water stress (3.1 °C if ≥ 30 °C of canopy temperature vs. -0.8 °C if < 30 °C of canopy temperature). By contrast, canopy temperature from ~8 to ~20 °C is an optimal range for carbon uptake during the afternoon (Figure 6). This range is similar to the findings of Niu et al. (2012) in which optimum temperature for NEE in deciduous and coniferous forests were found to range from 9.6 to 23.2 °C. Less carbon uptake during the night (Figure 6) is attributed to the limit of sunlight in the nighttime that cannot raise photosynthesis. Our analysis for both sunny and cloudy periods clarifies that more carbon uptake occurs when canopy temperature is below 25 °C under non-limiting light conditions during the morning and afternoon (Figure 6). The highest uptake rates appear when temperatures are below 15 °C. The temporal variation of forest NEE has been explained by climatic factors in many studies (e.g., Greco and Baldocchi 1996, Law et al. 2001, Barr et al. 2007, Piao et al. 2008). As daily/sub-daily leaf and trunk temperatures were found to be more related to NEE (Figure 6) than T_{air} was, the measured canopy temperatures will be very useful in predicting the NEE variability of the study forest.

The correlations between canopy temperature and H and LE were weaker than for NEE, however, the relationships in 30-min means were positive for both variables. We assume that more energy transfer and evapotranspiration occur from the forest cover to the atmosphere when the canopy gets warmer. The measured fluxes changed rapidly over a short time and were largely distributed in a day, resulted in less correlation with canopy temperatures. The complexity of canopy architecture (e.g., leaf shape and size and canopy density) and boundary layer resistance might account for the lower correlation, although canopy temperature is a resultant of the energy balance as determined by heat and vapor fluxes (Leuzinger and Körner 2007, Scherrer et al. 2011). This is supported by further correlations between 30-min mean canopy temperature and H and LE for the entire day in two groups using the averaged wind speed (i.e. ≤ 2.8 or $> 2.8 \text{ m s}^{-2}$

of wind speed). Better correlations are present in the group with low wind speed ($r = 0.46$ with H; $r = 0.43$ with LE), compared to the group with high wind speed ($r = 0.29$ with H; $r = 0.28$ with LE) and all 30-min data ($r = 0.38$ with H; $r = 0.36$ with LE). It is thus difficult to generalize the relation of canopy thermal states to heat fluxes for the entire study period due to the various meteorological conditions. Vining and Blad (1992) determined heat fluxes of grasslands using TIR canopy temperatures and found that the heat fluxes changed with wind speed. We rarely address that the flux changes corresponded to earlier canopy temperature changes in the study forest, since correlations with the 30-min later and same-time fluxes were similar.

Compared to the correlations of canopy temperatures to heat fluxes, the correlations of the temperature differentials are high (especially 30-min means; H and LE in Figure 5d), and therefore, energy exchanges in the forest are more relevant to the deviation of canopy thermal states from the atmosphere. The temperature differentials should represent more the physiological changes (e.g., due to drought and water stress) in trees in response to the heat fluxes.

The comparisons between the TIR temperatures and another method of canopy temperatures extend our insights into the principle and reliability of measured canopy temperatures. The calculation of Rlu-based temperatures relies on a simple function and measurement of radiative longwave radiation (4–40 μm) from the forest, while TIR wavelengths detected by the FLIR camera are from 7.5 to 13 μm . The longwave estimation compares well with the TIR estimation (Figure 7). The larger Rlu-based temperatures would be derived from more radiative energy for the temperature calculation. In addition, different field of view between the sensors of TIR and Rlu-based temperature would cause the temperature difference,

as the Rlu sensor, based on hemispheric measurement, captures all of the canopy element plus bare soils and even part of the flux tower.

A number of ecological studies have applied the TIR imaging technique for the interpretation of variability in organismic surface temperatures in plants (e.g., Leuzinger et al. 2010, Maes and Steppe 2012, Janka et al. 2013) and animals (e.g., Hristov et al. 2008, Briscoe et al. 2014). However, caution is needed when the precision of temperature measurement is a research priority. The significant variations between leaf and trunk ROIs (Figure 4a) imply that our data processing approach addressed the heterogeneity of canopy temperature. However, there exist potential errors when retrieving a series of TIR temperatures from a specific ROI. These errors were related to the chances of moving tree branches and leaves when strong winds blew. At this time, selected pixels of ROIs would differ from previous selections.

This work highlights spatial and temporal variability of canopy skin temperatures, as well as the relationships among canopy temperatures and climatic, soil environmental, and flux factors. Our results demonstrate that spatial variations in temperature were significant between leaf and trunk regions, and that there were also large temporal variations in the forest. Canopy temperatures were highly correlated with climatic factors such as air temperature, relative humidity, and longwave radiation, as well as soil temperature at the shallowest depth. This demonstrates that the canopy thermal regime is strongly controlled by climatic conditions and correlated to the soil thermal states. During the afternoon, canopy thermal status was strongly related to variation of NEE, which suggests that canopy temperatures strongly affect the mechanisms determining forest carbon exchange. Our analysis with canopy temperature differentials indicates that water stress of the canopy is linked to the climatic variables like longwave radiation. The major implications of this study are: (1) TIR imaging is useful for

investigating the thermal characteristics of forest canopies and their linkages to environmental variation and carbon exchange; and (2) future work, based on the TIR imaging, can further examine biophysical, physiological, and hydrological functions and mechanism of forest ecosystems which are being affected by climate change. Subsequent analyses that explore how canopy temperatures relate to GPP (gross primary production), ER (ecosystem respiration), and sapflow from individual trees will bolster these findings.

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Figure captions

Figure 1. Description of the study area. (a) Map of the US Pacific Northwest region; (b) location of the study forest (red square: Metolius Mature Pine Forest) near the city of Sisters in Oregon; and (c) view of the forest stand from the 32-m level of the eddy covariance flux tower where the thermal camera was installed (image taken on July 28, 2014). The rectangular part of the forest stand contained within the camera image is marked with a white rectangle (white dashed line).

Figure 2. Selected regions of interest (ROI) in thermal infrared (TIR) images collected from the forest. Three types of ROI were chosen to denote specific regions: L (L1 to 6) for leaves, T (T1 to 4) for trunks, and Canopy for the entire canopy. A TIR image taken on May 6, 2014 at 12:00 hr was used for the selections of all images. Scales on the right of the images indicate the temperature range (°C).

Figure 3. Temporal changes in thermal infrared (TIR) and air temperatures from DOY 149 (May 29) to 267 (September 24) in 2014. TIR temperatures (T_{canopy}), air temperatures (T_{air}), the deviation of T_{canopy} from T_{air} ($T_{\text{canopy}} - T_{\text{air}}$) are daily mean, maximum, and minimum from the datasets of 30-min means. (a) Comparison between T_{canopy} and T_{air} ; and (b) comparison between $T_{\text{canopy}} - T_{\text{air}}$ and T_{air} . ' $T_{\text{canopy}} = T_{\text{air}}$ ' indicates the line at which T_{canopy} and T_{air} are equal.

Figure 4. Box plots of (a) 30-min thermal infrared (TIR) temperatures and (b) the deviations of TIR temperature from air temperature for the comparisons among the averages of study period in canopy ROI, region of interest (Canopy), leaf ROIs (Leaf), and trunk ROIs (Trunk) about four time slices including whole day (0:00–23:59 hr: Entire-day); (b) morning hours (4:00–11:59 hr: Morning); (c) afternoon hours (12:00–19:59 hr: Afternoon); and (d) night hours (0:00–3:59 and 20:00–23:59 hr: Night). The boxes include upper quartile of 25% greater data (upper line), median data (middle black line) and lower quartile of 75% great data (lower line), and upper and lower error bars respectively indicate the greatest and least values except for outliers. Red lines in the boxes are the averages of all data, and 5 and 95% greater data are marked with gray dots upper and lower error bars, respectively. Different letters above the upper error bars indicate significant difference ($p \leq 0.05$) between the means of leaf and trunk temperatures or the deviations of leaf and trunk temperatures.

Figure 5. Correlation coefficients (r , ranging from -1 to 1) resulting from the correlation tests between thermal infrared (TIR) temperatures (left column) or their deviations from air temperatures (right column) and climatic, soil, and flux variables from the study area during the four daily time slices including whole day (0:00–23:59 hr: Entire-day), morning hours (4:00–11:59 hr: Morning), afternoon hours (12:00–19:59 hr: Afternoon), and night hours (0:00–3:59 and 20:00–23:59 hr: Night). (a and b) The coefficients with climatic variables (T_{air} , RH, Rld, and Rlu: details are in Table 1); (c and d) the coefficients with soil and flux variables (ST2, ST64, SWC10, SWC160, H, and LE: details are in Table 1), and (e and f) correlation coefficients with flux variables (H, LE, and NEE: details are in Table 1). TIR temperatures in leaf ROIs, region of

interest (L) and trunk ROIs (T) were acquired. A pair of correlation factors is expressed as ‘variable-ROI’ in X-axis (e.g., the correlation between H and leaf ROI: H-L). Data used in the correlation tests are averages of the 30-min period (**a** to **d**) and the daily/sub-daily period (**e** and **f**). The symbol of ‘N’ above or below the bars denotes no significant level ($p > 0.05$). Otherwise, correlation coefficients are significant at $p \leq 0.05$.

Figure 6. Relationships between daily/sub-daily mean thermal infrared (TIR) temperatures from leaf ROIs (region of interest) and net ecosystem exchange in the four time slices including the entire day (0:00–23:59 hr: Entire-day), morning hours (4:00–11:59 hr: Morning), afternoon hours (12:00–19:59 hr: Afternoon), and night hours (0:00–3:59 and 20:00–23:59 hr: Night).

Figure 7. (a) Temporal patterns of daily mean, maximum, and minimum of Rlu-based temperatures (estimation using upwelling longwave radiation) and thermal infrared (TIR) canopy temperatures; and **(b)** a scatter plot between 30-min means of the Rlu-based and TIR temperatures. The red dashed line in figure **b** indicates the 1:1 line.

Tables and Figures

Table 1. Description of climatic, soil environmental, and flux variables used in this study. All variables were directly measured from the eddy covariance flux tower (climatic and flux variables) or in the forest stand (soil variables) near the flux tower.

Type	Variable	Unit	Description
Climate	WS	m s^{-1}	Wind speed
	WD	°	Wind direction
	T _{air}	°C	Air temperature
	RH	%	Relative humidity
	PAR	$\mu\text{mol m}^{-2} \text{s}^{-1}$	Photosynthetically active radiation
	Rsd	W m^{-2}	Downwelling shortwave radiation
	Rsu	W m^{-2}	Upwelling shortwave radiation
	Rld	W m^{-2}	Downwelling longwave radiation
	Rlu	W m^{-2}	Upwelling longwave radiation
	Rnet	W m^{-2}	Net radiation
	Rain	mm	Rainfall
Soil	ST2	°C	Soil temperature (ST) at 2-cm depth
	ST64	°C	ST at 64-cm depth
	SWC10	%	Soil water content (SWC) at 10-cm depth
	SWC160	%	SWC at 160-cm depth
Flux	H	W m^{-2}	Sensible heat flux
	LE	W m^{-2}	Latent heat flux
	NEE	$\mu\text{mol m}^{-2} \text{s}^{-1}$	Net ecosystem exchange of carbon dioxide

Figure 1

Figure 2

Figure 3

Figure 4

Figure 5

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Figure 7