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Spatiotemporal dynamics of leaf transpiration quantified with time-series thermal imaging

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ABSTRACT

Accurately capturing the spatiotemporal dynamics of transpiration from sub-leaf to ecosystem scales remains a key challenge in eco-physiology and hydrology as typical methods face a trade-off between spatial coverage and temporal resolution. Here, we developed a new scalable, semi-automated method to produce highly precise estimates of water and energy fluxes and applied it to single leaves. High-resolution thermal infrared (TIR) images and paired colour photographs of excised soybean leaves were captured at 15 s intervals until wilting, automatically registered and segmented, and used as input for transient energy balance models to estimate latent heat flux (transpiration) at a temporal resolution of one second. Three approaches to estimating leaf boundary layer conductance to heat (g_{Ha}) and sensible heat flux were compared, two of which did not require the use of any dry or wet reference surface. The accuracy of water loss modeled using average leaf temperature was also compared to models retaining pixel-scale temperature heterogeneity at a spatial resolution of 0.326 mm^2. Cumulative leaf water-losses modeled using average leaf temperature closely matched gravimetric measurements (r^2 = 0.95) and pixel-scale models identified striking spatiotemporal patterns of water loss at the sub-leaf scale. Different methods of estimating g_{Ha} did not significantly alter model results. Use of leaf energy balance models with time series thermal images to quantify transient transpiration fluxes was able to accurately resolve 1-s time-varying leaf water loss in outdoor conditions, did not require any reference surfaces, and also produced data on the characteristic length scales of heterogeneous sub-leaf response. Given the ability to omit reference surfaces and retain accuracy, this approach also has the potential to be scaled-up to quantify energy fluxes in more complex plant canopies.

1. Introduction

Although 80–90% of the flux of water from the land to the atmosphere occurs via transpiration (Jasechko et al., 2013), our ability to accurately capture its spatial and temporal dynamics at scales ranging from leaves to ecosystems and seconds to years has been limited. The dynamics of transpiration vary by climate zone (Wang et al., 2014) and season (Dubbert et al., 2014), while the spatial distribution of transpiration varies according to vegetation structure and composition (Holdo and Nippert, 2015). Transpiration is also variable within plant canopies, with exposed leaves on the outer edges transpiring at higher rates than the inner canopy (Buckley et al., 2014) and leaf-scale transpiration dynamically responding to brief changes in microclimate and illumination (e.g., sunflecks) (Schymanski et al., 2013; Chazdon, 1988). Traditional site- and ecosystem-scale approaches, including eddy covariance, are capable of measuring transpiration at a resolution of seconds to months over a varying footprint area (Goulden et al., 1996) but lack the ability to identify species-specific or location-specific contributions (Soubie et al., 2016). Alternatively, point-based measures of transpiration, including sap-flux and leaf-chamber gas exchange or porometer measurements, can provide highly detailed measurements of water fluxes from individual plants and plant organs but with low spatial coverage and high labour costs. Therefore, development of methodological approaches that can span the gap between point-based measurements and spatially and temporally integrated flux measurements is needed.

Thermography, also called thermal infrared (TIR) photography, has the potential to bridge the large gap between leaf- and ecosystem-scale approaches to estimating transpiration by spanning a variety of spatial and temporal scales (Maes and Steppe, 2012; Costa et al., 2013). The advantage of using thermography in place of point-based measurements is the collection of thousands of simultaneous and spatially-distributed

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measurements of leaf temperature (Aubrecht et al., 2016), allowing rapid determination of the leaf-to-air temperature gradient ($T_l - T_a$) over a wide area (Kim et al., 2016). Leaf temperature crucially affects physiological performance (Berry and Bjorkman, 1980) and the leaf-to-air temperature gradient is central to the exchange of water and energy between plants and the atmosphere (Jarvis and McNaughton, 1986). Consequently, thermography is proving useful for spatiotemporal mapping of evapotraspiration (ET) in natural ecosystems at a scale of centimetres (Moffett and Gorelick, 2012) to metres (e.g., Loheide and Gorelick, 2005). In contrast, approaches that quantitatively model leaf transpiration at leaf and sub-leaf scales remain largely restricted to controlled and laboratory environments (Osama and Croxdale, 1992; Jones, 1999b; McAusland et al., 2013). Therefore, further development of thermography based leaf and sub-leaf scale transpiration models will improve our ability to examine the dynamics of leaf transpiration under more natural conditions and extend our capacity to model natural ET fluxes at increasingly finer scales.

Transpiration can be modeled using thermographic measurements of T_l by manipulating the leaf energy balance equation (Eq. (1)). A change in leaf temperature with time (dT_l/dt, °C s^{-1}) is a product of the balance between incoming and outgoing energy fluxes, moderated by the heat capacity of the leaf per unit area (c_{lA}, J K^{-1} m^{-2}, Eq. (2)). The latent heat flux (λE, W m^{-2}) can therefore be modeled as the residual of the leaf energy balance after measuring or estimating the terms for net absorbed radiation (R_{abs}, W m^{-2}), emitted long-wave radiation (L_{oe}, W m^{-2}), and sensible heat flux (H, W m^{-2}):

$$c_{\mathrm{lA}}\frac{\mathrm{dT}_l}{\mathrm{dt}} = R_{\mathrm{abs}} - L_{\mathrm{oe}} - H - \lambda E \tag{1}$$

Latent heat flux (λE, W m^{-2}) is then converted to transpiration mass flux (E, kg m^{-2} s^{-1}) by dividing by the latent heat of vapourization, $\lambda = 2.265 \times 10^5$ J kg^{-1}. Definitions of all variables are provided in Table 1.

The leaf heat capacity per unit area c_{lA} is predominately determined by the leaf water mass per unit area (mass density, m_{wA}, kg m^{-2} H_2O m^{-2}) scaled by the specific heat capacity of water at constant pressure, $c_w = 4182$ J kg^{-1} °C^{-1} (Eq. (2)). The mass density of water in the leaf (m_{wA}) can also be represented as the water fraction (w_f, kg H_2O/kg leaf) of the total leaf mass (m_l, kg) given the total one-sided leaf area (A_l, m^2). Note m_{wA}, w_f, and m_l will vary according to the leaf water balance:

$$c_{\mathrm{lA}} = m_{\mathrm{wA}} c_w = \left(\frac{w_f m_l}{A_l}\right) c_w \tag{2}$$

For the latent heat flux to be determined as the residual of the energy balance, the absorbed and emitted radiation and the sensible heat flux must be measured or estimated. The sensible heat flux term (H) is driven by the leaf-to-air temperature gradient $T_l - T_a$, which is provided by thermography and air temperature data; however, calculating the flux is complicated by requiring additional assumptions to characterize the leaf boundary layer. The thickness of the leaf surface boundary layer determines the rate of diffusion (conductance) of heat and water vapour to and from the leaf surface (Schuepp, 1993). The dynamic behaviour of the boundary layer in response to environmental conditions (e.g., wind speed and humidity) along with leaf characteristics (e.g., size, shape, distribution and activity of stomata) and the boundary layer's very small size make its measurement impractical (Defraeye et al., 2013). Therefore, boundary layer conductance of heat (g_{Ha}, mol m^{-2} s^{-1}) is typically estimated using empirical approximations (Schuepp, 1993). For example, the simplest and most common method only estimates the forced convection of heat energy (advection by wind) and requires only wind speed (u) and the characteristic leaf length (d) ($g_{\mathrm{Ha}} = 1.4 \times 0.135\sqrt{u/d}$, mol m^{-2} s^{-1}, Campbell and Norman, 1998). More detailed empirical approaches can also account for free (buoyancy-driven) convection, although it is debatable to what extent these methods improve the accuracy of sensible heat flux estimates (Buckley et al., 2014). Alternatively, boundary layer conductance to heat can be directly estimated by measurement of the energy balance and $T_l - T_a$ gradient for a non-transpiring leaf (the so-called 'dry reference', cf. Thorpe and Butler, 1977). Although the empirical approximations of g_{Ha} are frequently applied in experiments using the leaf energy balance equation (Defraeye et al., 2013; Schymanski et al., 2013; Schymanski and Or, 2015), it remains unclear how different approaches impact the accuracy of transpiration predictions.

In this study we used a time-series of high-resolution thermal images to calculate the energy and water balances of excised leaves and to quantify the spatio-temporal heterogeneity of transpiration across the leaf surface in an uncontrolled outdoor environment. We tested three different methods for quantifying the boundary layer resistance to sensible heat flux and also made use of the spatially-rich thermal

Table 1
Parameters and units referred to in this paper.

Parameter	Units	Description [Standard Value]
A_l	m^2	One-sided leaf area
α_l	–	Longwave absorptivity of leaf
α_s	–	Shortwave absorptivity of leaf
A_{pix}	m^2	Pixel area
C_l	W m^{-2}	Conductive heat flux
c_{lA}	J K^{-1} m^{-2}	Leaf heat capacity per area
c_{pa}	J mol^{-1} K^{-1}	Heat capacity of air at constant pressure [29.3]
c_w	J kg^{-1} K^{-1}	Specific heat capacity of water at constant pressure [4182]
d	m	Characteristic leaf length (0.72*length in the direction of the wind)
ε	–	Leaf emissivity
E_i	kg m^{-2} s^{-1}	Instantaneous transpiration mass flux
F_a	–	Atmospheric view factor
F_g	–	Ground view factor
g_{Ha}	mol m^{-2} s^{-1}	Boundary layer conductance to heat
g_r	mol m^{-2} s^{-1}	Radiative conductance in the boundary layer
H	W m^{-2}	Sensible heat flux
h_c	W K^{-1} m^{-2}	Average 1-sided convective heat transfer coeffcient
k_a	W K^{-1} m^{-1}	Thermal conductivity of air in the boundary layer
L_a	W m^{-2}	Downwelling longwave radiation
λ	J kg^{-1}	Latent heat of vaporization of water [2.265×10^5]
λE	W m^{-2}	Latent heat flux
$\lambda E_{j,i}$	W m^{-2}	Latent heat flux at time i, pixel j
$\overline{\lambda E_j}\vert_i$	W m^{-2}	Average pixel latent heat flux at time i
L_g	W m^{-2}	Upwelling longwave radiation
L_{oe}	W m^{-2}	Emitted longwave radiation
m_l	kg	Leaf mass
$m_{l,0}$	kg	Initial leaf mass at time t = 0 for leaf l
$m_{l,d}$	kg	Dry leaf mass for leaf l
$m_{l,f}$	kg	Final leaf mass at time of wilting for leaf l
m_{wA}	kg m^{-2}	Leaf water mass per area
$m_{w,pix}$	kg	Sum of cumulative mass of transpired water from all pixels
m_w	kg	Cumulative modeled water mass loss using average leaf temperature
$m_{w,j}$	kg	Cumulative modeled water mass loss from pixel j
$m_{w,\ scl}$	kg	$m_{w,pix}$ scaled to full leaf area
m_{wg}	kg	Cumulative gravimetric leaf mass loss
n_l	–	Number of pixels in leaf image for leaf l
Nu	–	Nusselt number
P_r	–	Prandtl number
R_{abs}	W m^{-2}	Net absorbed radiation
Re_c	–	Critical Reynold's number
R_e	–	Reynold's number
σ	W m^{-2} K^{-4}	Stefan-Boltzmann constant [5.67×10^{-8}]
T_a	K	Air temperature
T_b	K	Mean boundary layer temperature
T_l	K	Leaf temperature
$T_{l,j,i}$	K	Pixel temperature of leaf l, time i, pixel j
T_{ref}	K	Dry reference leaf temperature
u	m s^{-1}	Wind speed
ν_a	m^2 s^{-1}	Kinematic viscosity of air
w_f	–	Leaf water fraction