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Slope position influences vegetation-atmosphere interactions in a tropical montane cloud forest

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ABSTRACT

Throughout a single day, the microclimatic conditions in tropical montane cloud forests vary from strong solar radiation with simultaneous strong atmospheric water demand (high vapor pressure deficit, VPD, values), followed quickly by clouds and fog events drastically reducing both of these environmental variables. Due to the complex topography and weather patterns in these regions, microclimate, including fog events, can vary strongly across very small spatial scales as well, leading to a highly dynamic and compelling environment to examine how environmental variables influence tree water use across space and time. Due to this variation, the present study examines how environmental drivers of tree water use varies across three slope positions (upslope, midslope, low-slope) in a tropical montane cloud forest in Veracruz, Mexico. Measurements of sap flow using the heat ratio method were conducted on three dominant canopy species along with simultaneous measurements of microclimate within each site. To assess the relative importance of microclimatic variables in explaining tree water use across diurnal periods, data were separated into day and night periods and fog and clear events. Multiple regression models were conducted for each tree with input variables of VPD, solar radiation, air temperature, shallow soil moisture, deep soil moisture, and leaf wetness. We found that VPD explained a large majority of the variation in tree water use during daytime fog periods, particularly at the upslope and midslope sites. During nighttime periods, VPD was the dominant driver of water use variation during clear periods while a combination of VPD and leaf wetness explained variation during night, fog periods. Additionally, tree water use was more decoupled from environmental variables at the low-slope site. Finally, a separation of model components into fog and clear periods improved model outputs particularly at low flow conditions, highlighting the differential interactions between tree water use and environment during night and fog periods. Results from this study provide new insight into the importance of fog events, low VPD, and leaf surface wetting at controlling tree water use in cloud forests. The variation in drivers of water use across short spatial scales demonstrate the importance of considering individual and species level variation across fog and clear periods in predicting physiological responses of species to climate in cloud forests.

1. Introduction

The movement of water through plants is driven by gradients of water potential explained by the soil-plant-atmosphere continuum (SPAC) and constrained by plant functional anatomy (e.g. xylem vessel size, leaf area index) and management strategies (e.g. stomatal closure, altered rooting strategies and depths, leaf area index reduction). Typically, the drivers of this movement include solar radiation, vapor pressure deficit (VPD; or evaporative demand), temperature, and soil moisture availability with the importance of each varying across sites, species, and ecosystems. To further highlight this point, the classic Penman-Monteith equation for modeling evapotranspiration includes terms for temperature, solar radiation, and humidity and many studies have examined how these terms vary across additional abiotic parameters such as soil moisture and rainfall regimes (Monteith, 1973; Allen, 1986; e.g. Stape et al., 2004). However, the importance of each driver of tree water use has been shown to vary across species, times of year, and spatial locations demonstrating the importance of understanding

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variation across individuals. Loranty et al. (2008) found variation in plant transpiration across a climatic rainfall gradient between dryer upland forests and lower wetland forests. Additionally, Gazal et al. (2006) found that the sensitivity of transpiration rates to VPD also varied across two sites with differences in soil moisture. These are the few results that highlight how environmental variation at small spatial scales can influence tree water use, particularly in regions with complex terrain and climate patterns such as tropical montane cloud forests.

Tropical montane cloud forests (TMCF) are compelling environments to examine the effects of different environmental drivers on tree water use due to high variability in space and time. Because of their high elevation and proximity to the equator, TMCFs can receive high values of solar radiation with simultaneous strong atmospheric water demand (high VPD values), followed quickly by fog events, drastically reducing both of these variables (Bruijnzeel and Veneklaas, 1998). These periods also bring with them reduced temperatures and increased leaf wetness leading to even lower atmospheric demand on plant water balance. In the TMCFs of Veracruz, Mexico, there is also some seasonality in rainfall patterns leading to greatest soil water deficits in April and May (Muñoz-Villers et al., 2012). These quick, temporal changes in environment result in plant water management strategies that balance carbon gain and water loss across a wide array of environmental conditions. For example, in the temperate cloud forests of the southern Appalachian mountains in the USA, both carbon gain and water balance were more favorable on days with some fog due to greater afternoon carbon gain and higher water potentials (Berry and Smith, 2013). Another strategy that is particularly important in TMCFs is foliar water uptake, the direct utilization of water from leaf surfaces, which has been demonstrated in *Quercus lancifolia* (Gotsch et al., 2014). Foliar water uptake during fog events can alter water balance during both day and nighttime periods. In the TMCF of Veracruz, Mexico, nighttime transpiration accounted for 17.4% of the water lost during the dry season and foliar uptake (as measured by negative sap flow) accounted for a 9% recovery of this water (Gotsch et al., 2014). The same study also found a strong inverse relationship between reverse sap flow rates and the number of hours of leaf wetness suggesting that in these fog-inundated ecosystems, leaf wetness also plays a strong role in suppressing and reversing transpiration rates. An additional study examining tree water use in *Drimys brasiliensis*, a TMCF species in Brazil, found a similar role for leaf surface wetting events in suppressing transpiration rates and increasing foliar uptake during nighttime periods (Eller et al., 2015). Finally, there is also evidence that fog water can be absorbed through woody tissue as well further highlighting the importance of periods of atmospheric moisture (Earles et al., 2015). In TMCFs, where VPD is frequently low with high leaf wetness, these variables are likely to have strong influences on plant transpiration rates. Despite the growing knowledge that leaf wetness, low VPD, and foliar water uptake are critical for plant carbon and water balance in cloud forests, understanding the complex interactions of these variables and transpiration rates is still lacking.

Within steep, mountainous regions, topographic gradients of environmental variables arise over very short distances. Particularly, temperature, vapor pressure deficit, and soil moisture are likely to vary along slopes and have been shown to affect nutrient availability, water availability, and plant growth (Luizão et al., 2004; Tromp-van Meerveld and McDonnell, 2006; Kumagai et al., 2008). Across these gradients, drivers of plant transpiration rates can vary significantly. Kumagai et al. (2008) found that soil moisture did not limit evapotranspiration even at drier, upslope positions and that the relationship between transpiration and soil moisture varied across seasons. Contrary to this, Tromp-van Meerveld and McDonnell (2006) found a strong soil moisture limitation at upslope positions with shallower soils following moisture depletion during the growing season. While both of these studies provide some insight, they were conducted in temperate climates, a conifer plantation and a deciduous forest, respectively. Tropical cloud forests are likely to be more sensitive to variation in environmental parameters and thus may have unique responses to microclimate variation across hillslopes (Motzer et al., 2005; Gotsch et al., 2014). The high sensitivity of TMCF and evidence of site-to-site variation in evapotranspiration across slope positions in previous studies further underscores a need to understand variation in tree water use at the hillslope scale in habitually understudied TMCFs.

Another important consideration is that hillslope is often the main unit of measurement in hydrologic studies where transpiration measurements on a small number of trees are used to derive stand or catchment level evapotranspiration (e.g. Hatton et al., 1995; Santiago et al., 2000; Ewers et al., 2002). This assumption of spatial homogeneity of transpiration rates and species compositions can potentially have confounding affects during the scaling process and will alter outputs of modeling efforts (Seyfried and Wilcox, 1995). Loranty et al. (2008) found that transpiration rates varied strongly across the landscape within species and concluded that future work should focus on clarifying relationships with environmental drivers (particularly atmospheric vapor deficit) to improve modeling outputs.

In this study we examine how environmental drivers of tree water use varied across three slope positions in a tropical montane cloud forest. We utilized heat ratio method sap flow techniques on three dominant canopy tree species along with measurements of microclimate within each site to assess the influence of environmental parameters on tree water use. Additionally because of the potentially divergent and confounding responses during frequent fog periods we divided the analysis into four components encompassing fog and non-fog periods and day and night hours. Due to the role that low VPD and leaf wetness play in limiting plant transpiration in these ecosystems we expected these variables to explain variation in heat pulse velocities during fog and nighttime periods. During daytime clear periods, solar radiation, air temperature, and VPD were predicted to explain more variation. Across slope positions, we expected higher temperatures and VPD at the low-slope and midslope site due to less adiabatic cooling from lower elevations and less ventilation leading to greater heat storage during the day. Due to this expected difference in microclimate, we expected the low-slope and midslope sites to have increased atmospheric demand and reduced soil moisture leading to a greater proportion of variation in heat pulse velocities to be explained by air temperature, solar radiation, and soil moisture. During fog periods, sites with lower VPD and greater leaf wetness are likely to have a greater influence of these variables.

2. Materials and methods

2.1. Study region and site descriptions

This study was conducted in 2010 in a mature tropical montane cloud forest (TMCF) catchment located at an average elevation of 2170 m a.s.l. on the eastern slopes of Cofre de Perote volcano in central Veracruz, Mexico (19°29′N, 97°02′W). The climate of these TMCFs are defined as “temperate humid” by the Köppen classification modified by Garcia (1988) and characterized by average annual temperatures of $14.3 \pm 0.2\,^{\circ}$C and mean annual precipitation of 3011 ± 309 mm (F. Holwerda, unpublished data). The climate is seasonal with over 80% of rainfall occurring during the wet season from May to October and a dry season characterized by cold front intrusions that produce fog about 20% of the time (Holwerda et al., 2010). While fog is more frequent during the dry season, it can occur frequently throughout the year, particularly at higher elevations.

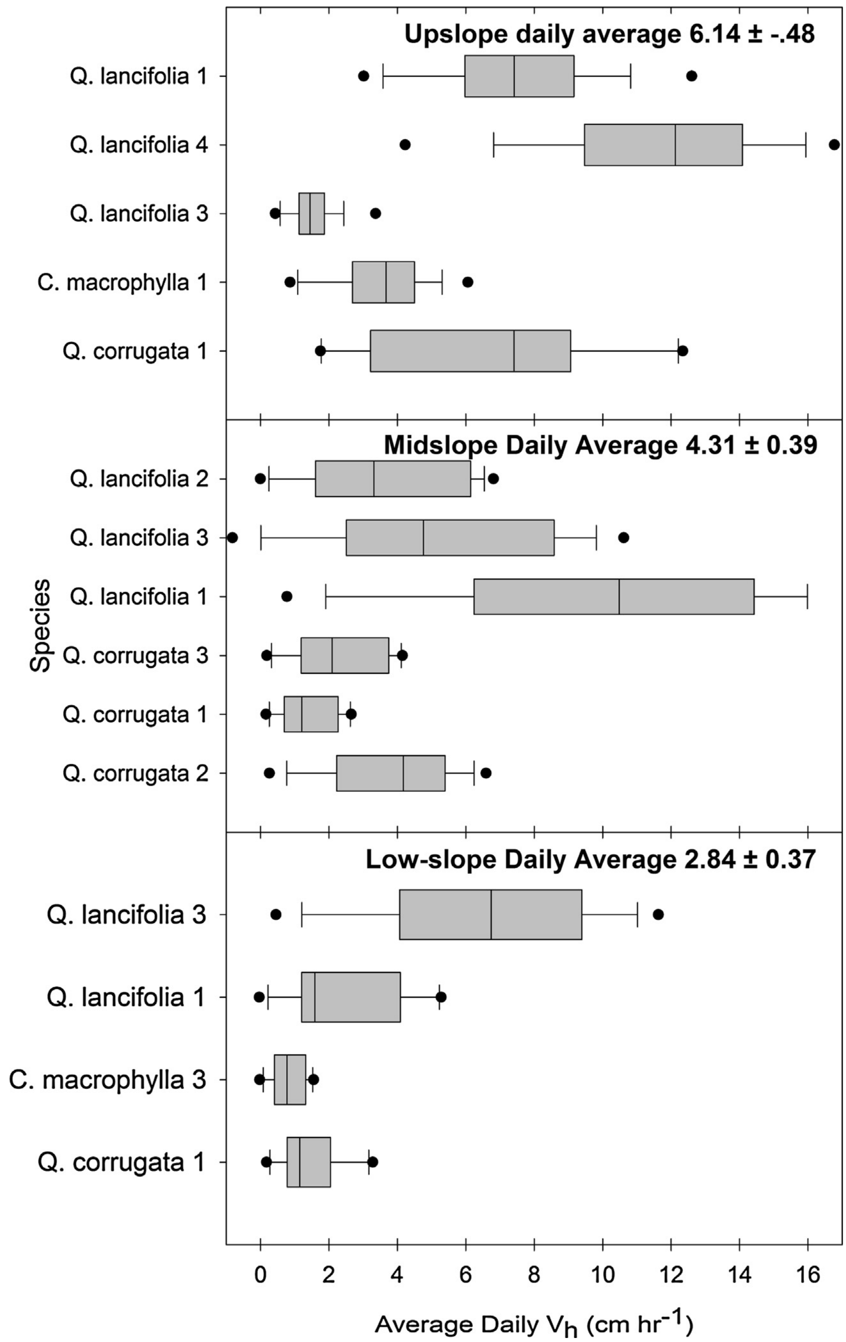

Fig. 1. Box plots of daily average heat pulse velocities (V_h) during the study period for each tree used in the analysis. Panels a, b, and c represent trees from the upslope, midslope, and low-slope positions, respectively. Boxes represent the 25th and 75th percentiles, the whiskers represent the 10th and 90th percentiles, and the line in each box represents the median. Points represent the maximum and minimum values. Site averages are included along with standard error.

The TMCF catchment is characterized by short, steep slopes drained by a first-order perennial stream (see Muñoz-Villers et al., 2012 or Muñoz-Villers and McDonnell, 2013 for more detailed site description). The soils of the region are Andosols (IUSS Working Group WRB 2006) and are characterized by deep profiles (up to 3 m), a loam texture, low bulk density (0.2–06 g cm^{-3}), and are nutrient-poor (Muñoz-Villers and McDonnell, 2013; Alvarado-Barrientos et al., 2015).

The TMCF is dominated by species from *Quercus, Clethra, Parathesis*, and *Alchornea* (García Franco et al., 2008). For this study, we focused on three of the more common canopy species, *Q. lancifolia, Quercus corrugata*, and *Clethra macrophylla*. To assess tree water use responses across different hillslope positions and associated variations in microclimate, three plots were established near the stream (low-slope), midway up the slope (midslope), and near the top of the slope (upslope) (Fig. 1). The entire slope was 123 m long with a mean slope of 33°; the study plots were approximately 40 m apart from each other. Within each plot, sap flow rates of four to six trees of varying sizes (Table 1) were measured using the heat-pulse ratio method (HRM). Simultaneously at each site, environmental variables were measured to examine the influence of each environmental parameter on sap flow velocity.

Table 1
Characteristics of each species used in this study including the number of each species (including the individual number for the up-, mid-, and low-slope sites, respectively), range of diameters sampled, range of basal areas for each species across plots sampled at the site, and the percent of total basal area.

	Quercus lancifolia	*Quercus corrugata*	*Clethra macrophylla*
# of individuals	8 (3, 3, 2)	5 (1, 2, 1)	2 (0, 1, 1)
DBH range (cm)	8.1–102.2	8.4–105.8	10.8–35.6
Basal area (m^2/ha)	2.57–4.66	1.38–3.67	0.88–1.16
Percent of total basal area (%)	9.3–17.6	6.3–13.3	4.0–4.3

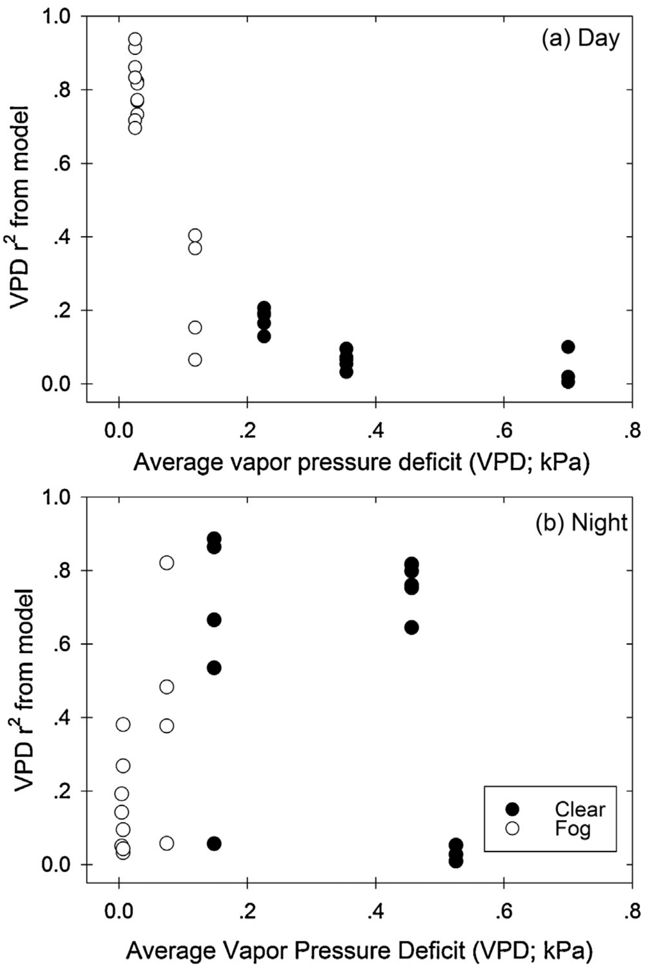

Fig. 2. Relationship between the goodness of fit (r^2) for VPD from each model with the average VPD value during that time period of analysis. During day periods (a) there is a strong negative non-linear relationship (r^2 = 0.81) with a greater influence on VPD on models at low VPD values. During night periods (b) there is not a strong relationship with VPD having high and low r^2 values throughout the range of VPD values measured. Open circles represent fog periods and closed circles represent clear periods.

2.2. Micro-meteorology

At each of the slope positions, canopy air temperature, relative humidity and leaf wetness were measured. Air temperature and relative humidity were measured using HOBO data loggers (U23 v2, Onset Computer Corporation; Bourne, MA, USA), while leaf wetness was measured using a dielectric leaf wetness sensor (LWS-L; Decagon Devices, Pullman, WA, USA) connected to a data logger (CR1000Campbell Scientific Inc, Logan, UT, USA). Air temperature, relative humidity and leaf wetness were logged every 10 min. Vapor pressure deficit (VPD) was calculated from relative humidity and temperature values using the associated saturation vapor pressure. All canopy sensors were installed within the canopy approximately 23 m off the ground with maximum canopy heights of 25 m.

Soil volumetric water content (VWC) was also measured at each of the sites using capacitance-based sensors and data logger and logged every 10 min (sensor 10HS and datalogger EM50; Decagon Devices Inc., USA). Soil moisture probes were installed horizontally at depths of 8 cm (hereafter “shallow soil moisture”) and 95 cm (“deep soil moisture”). Upon completion of the study, VWC probes were calibrated in the Soil Laboratory at the Instituto de Ecología A.C., Xalapa, Veracruz using undisturbed soil cores (diameter 10.4 cm, length 20 cm) extracted from the field (E. Hincapié et al., unpublished data) and following the calibration method of Starr and Palineanu (2002).

An automated weather station was installed near the upslope site in an open area with southeast exposure at 2128 m, a.s.l. At this weather station, solar radiation (CM3 pyranometer; Kipp and Zonen, Delft, The Netherlands), air temperature, actual vapor pressure (HMP45; Vaisala, Vantaa, Finland), wind speed (A100R cup anemometer; Vector Instruments, Denbighshire, UK), rainfall (ARG100 tipping bucket rain gauge; Environmental Measurements, Herefordshire, UK), and horizontal visibility (Mini Optical Fog Sensor; Optical Sensors, Gothenburg, Sweden) were logged as 10 min averages of measurements taken every 30 s on a CR1000 data logger. Solar radiation from this weather station was used for the analysis. In addition, if there were gaps in climate data from a particular site, data from this weather station was substituted for periods of analysis, which showed strong agreement across sites ($r^2 > 0.8$). Fog periods were defined as periods when visibility was <1000 m, which has been used previously in this region (Glickman, 2000; Gotsch et al., 2014).

2.3. Sap flow measurements

Heat ratio method (HRM) sap flow was conducted on trees across each of the three sites. In total, 15 trees were used for the analysis with four to six trees from each site (Table 1). Three species were included: *Q. lancifolia, Q. corrugata*, and *C. macrophylla*, which together encompass 19.6–35.2% of the basal area within the TMCF sites in this study. Trees were selected to span a range of size classes and to account for variability across sites. To minimize decoupling from the microclimate values measured, only canopy trees were used. This included canopy emergents with DBH values of ~8 cm to large canopy dominants with DBH values of ~100 cm (Table 1). There was no relationship between location within the canopy and the strength of the relationships with environmental variables and thus all trees were considered “canopy” trees for the analysis. All three sites included trees that spanned the range of size variation with ranges of 8.1–79.2 cm (upslope), 17.2–105.8 cm (midslope), and 8.4–102.7 cm (low-slope).

The HRM sap flow technique was used due to its ability to detect and quantify low and reverse flows more reliably during the cloud and foggy conditions often experienced in TMCF (Burgess et al., 2001). The HRM utilizes three sensors, one upstream and one downstream of a heater probe. Every thirty minutes, a heat pulse was sent to the heater probe and the ratio of increase in temperature between the upstream and downstream probes was calculated as the average of 60–100 s following the heat pulse. Each upstream and downstream temperature probe was positioned 0.6 cm from

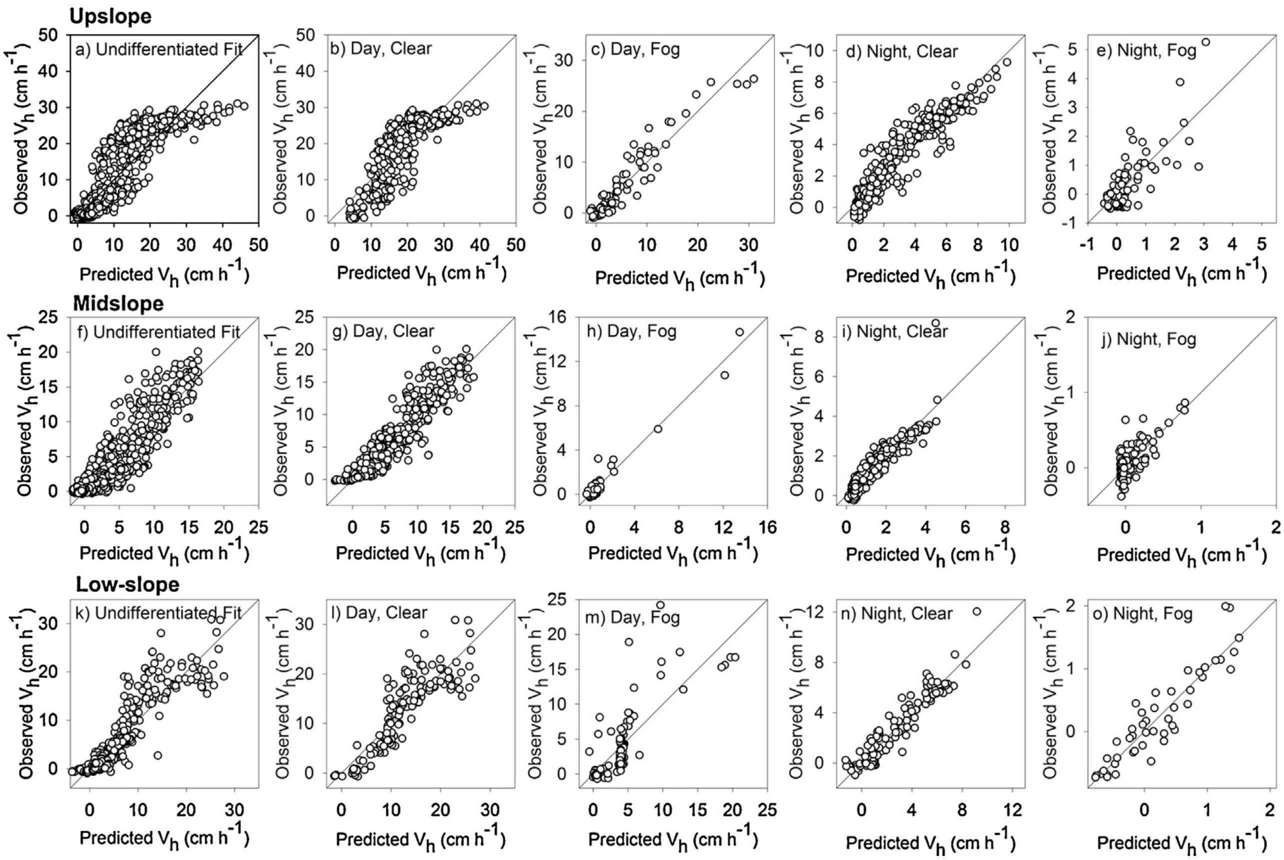

Fig. 3. Analysis of observed heat pulse velocities and predicted model performance outputs. Each far left panel (a,f,k) represents the analysis without consideration for time of day or fog occurrence (undifferentiated model) followed to the right by the subsets of data used for the separated analyses (fog differentiated model). This figure represents one example *Quercus lancifolia* at each slope positions, with all trees having similar agreements. The black diagonal lines represent the 1:1 reference line.

Table 2
Summary of vapor pressure deficit, air temperature, solar radiation, shallow soil moisture, and deep soil moisture (±SE) at the three slope positions in this study during four periods (day and clear, day and fog, night and clear, night and fog). Superscript letters (a, b, c, d) represent significant differences between the other time periods at the same site at the $p < 0.05$ level).

	Vapor pressure deficit (kPa)	Air temperature (°C)	Solar radiation (W m^{-2})	Shallow soil volumetric water content (%)	Deep soil volumetric water content (%)
UPSLOPE					
Day, Clear	0.23 ± 0.01^a	16.7 ± 0.1^a	368.2 ± 10.6^a	46.8 ± 0.2^a	61.3 ± 0.03^a
Day, Fog	0.03 ± 0.02^b	15.8 ± 0.2^b	155.0 ± 22.0^b	45.7 ± 0.3^a	61.1 ± 0.1^b
Night, Clear	0.15 ± 0.01^c	14.2 ± 0.1^c	-1.0 ± 11.0^c	47.9 ± 0.3^b	61.3 ± 0.03^a
Night, Fog	0.00 ± 0.02^b	15.0 ± 0.2^d	18.4 ± 33.0^c	49.9 ± 0.8^c	61.2 ± 0.1^{ab}
MIDSLOPE					
Day, Clear	0.35 ± 0.02^a	18.3 ± 0.1^a	423.8 ± 12.2^a	55.5 ± 0.2^a	32.1 ± 0.02^a
Day, Fog	0.03 ± 0.04^b	15.9 ± 0.2^b	187.7 ± 24.7^b	54.9 ± 0.6^a	32.1 ± 0.03^a
Night, Clear	0.46 ± 0.02^c	16.4 ± 0.1^b	1.3 ± 13.7^c	55.5 ± 0.3^a	32.2 ± 0.03^a
Night, Fog	0.01 ± 0.03^b	15.0 ± 0.2^c	4.7 ± 20.9^c	59.4 ± 0.5^b	32.2 ± 0.05^a
LOW-SLOPE					
Day, Clear	0.70 ± 0.03^a	18.9 ± 0.1^a	410.5 ± 12.3^a	59.7 ± 0.1^a	42.0 ± 0.01^a
Day, Fog	0.12 ± 0.05^b	16.5 ± 0.2^b	189.8 ± 24.1^b	58.5 ± 0.5^b	42.0 ± 0.01^a
Night, Clear	0.53 ± 0.03^c	16.3 ± 0.1^b	1.4 ± 13.5^c	60.3 ± 0.2^a	42.0 ± 0.01^a
Night, Fog	0.07 ± 0.05^b	15.1 ± 0.2^c	5.4 ± 21.5^c	60.4 ± 0.4^a	42.0 ± 0.01^a

the heater with thermocouples at three depths: 0.5, 1.7, and 3 cm from the outer surface of the sapwood. Sensors constructed in the Asbjornsen Lab at Iowa State University were installed 1.4 m from the ground on the north side of the primary trunk of each tree. For installation, bark was removed with a chisel until the edge of sapwood was reached. Using a calibrated guide with holes spaced 0.6 cm apart, sensors coated in petroleum jelly were installed perpendicular to the trunk. Molding clay and aluminum foil were placed over the sensors to avoid direct radiation and associated temperature fluxes. Probes were connected to a data logger and multiplexer (CR1000 and AM16/32; Campbell Scientific Inc, Logan, UT, USA) with 10 m extension cable powered by an external 12 v battery.

2.4. Data management and analysis

Using the methodology of Burgess et al. (2001), corrections for misalignment and wounding were conducted. To obtain a zero flow velocity for the correction calculation, meteorological periods were examined to find conditions likely to have zero or near zero flow (e.g. Ambrose et al., 2009; Gotsch et al., 2014). Since sensors were changed throughout the experiment, this method was preferable

Table 3
Upslope site model fits (r-squared values) derived from stepwise multiple linear regression models. Linear models were developed for each tree separated into clear and fog periods during both the day and night to assess how model fits from each variable changes in response to fog. If an r-squared value is included, it was a significant predictor variable in the model. If no value is included then that variable was not a significant predictor in that model. R-squared values greater than 0.10 are bolded.

Upslope Day	*Q. lancifolia* 1		*Q. lancifolia* 3		*Q. lancifolia* 4		*Q. corrugata*		*C. macrophylla*	
	Clear	Fog	Clear	Fog	Clear	Fog	Clear	Fog	Clear	Fog
Overall Fit	**0.82**	**0.92**	**0.85**	**0.88**	**0.67**	**0.90**	**0.64**	**0.92**	**0.86**	**0.91**
Vapor pressure deficit	**0.13**	**0.82**	**0.19**	**0.73**	**0.17**	**0.77**	**0.19**	**0.82**	**0.21**	**0.77**
Leaf wetness	0.00	0.02				0.02		0.05		0.09
Air temperature	**0.60**	0.07	**0.57**	**0.10**	**0.43**	0.08	0.03	0.02	0.06	
Solar radiation	0.08	0.02	0.08	0.03	0.06	0.03	**0.41**	0.03	**0.59**	0.02
Shallow soil moisture	0.00	0.00	0.01	0.01	0.01	0.01	0.01			
Deep soil moisture		0.00	0.00	0.02	0.01				0.01	0.03
Upslope Night										
Overall Fit	**0.88**	**0.62**	**0.67**	**0.69**	**0.90**	**0.59**	**0.72**	**0.71**	**0.60**	**0.49**
Vapor pressure deficit	**0.86**	**0.14**	**0.54**		**0.89**	**0.19**	**0.67**	0.05	0.06	
Leaf wetness	0.00		0.00	0.07	0.01		0.04	0.05	0.07	**0.37**
Air temperature	0.01	0.02	**0.11**	**0.60**	0.00	0.02	0.01	**0.43**	0.03	
Solar radiation		**0.42**				**0.35**		**0.18**		0.03
Shallow soil moisture		0.04	0.00			0.03	0.00			0.09
Deep soil moisture	0.01		0.02	0.02	0.00		0.01		**0.45**	

to xylem severing because we were able to find meteorological windows of "zero flow" throughout the study period and correct for errors in all installed sensors (Gotsch et al., 2014). Heat pulse velocities were then averaged across the three depths to obtain one value of corrected heat pulse velocity for each tree at each 10-min time point. We chose to conduct all analyses with these corrected heat pulse velocities because they are more likely to directly link to climate analyses.

To capture variation in climate, including completely clear and foggy days, data analysis focused on periods when a thorough data set was available between May 26 and July 2, the transition period from the dry to wet season. These data were part of a larger data set examining water balance in cloud forests conducted from December 2009 to July 2010. To assess the influence of multiple environmental variables on sap flow of each tree across different environmental conditions, we fit a stepwise multiple regression model to the data sets. Data from each slope position were divided into day and nighttime periods and clear and fog conditions, yielding four periods for each analysis. Daytime values were defined as when solar radiation increased above baseline values which typically occurred between 6 and 7 AM and ended between 6 and 7 PM. Fog conditions were defined as visibility less than 1000 m as measured from the visibility sensor at the weather station. This methodology has previously been calibrated in this region for defying fog events (e.g. Gotsch et al., 2014; Alvarado-Barrientos et al., 2015). Half hour measurements of corrected heat pulse velocity were used along with instantaneous measurements of calculated vapor pressure deficit, solar radiation, temperature, leaf wetness, shallow soil moisture, and deep soil moisture. Leaf wetness was converted to a percentage wetness of the sensor and then arcsine square root transformed to convert it to a continuous variable for analysis. Interactions between variables were included in initial models but were frequently not significant or only explained a very small portion of the variance and thus were removed from final analyses. Final models were selected using Akaike Information Criterion (AIC) to select the model with the best fit.

3. Results

3.1. Characterization of microclimate used for model analysis across slope positions and fog periods

Microclimate varied across all three slope positions (Table 2). Vapor pressure deficit (VPD) was generally highest during clear daytime periods at the low-slope site with a mean of 0.70 kPa compared to 0.35 kPa and 0.23 kPa at the midslope and upslope sites, respectively. Temperature followed a similar pattern with higher temperatures at the low-slope and mid-slope sites. Also, despite cooler air temperatures, VPD patterns during nighttime clear periods followed a similar pattern with means of 0.53, 0.46, and 0.15 kPa at the low-, mid-, and upslope sites, respectively. During foggy periods, VPD was very low during both day and night periods at all sites. Air temperatures were cooler during daytime fog periods than clear periods by a mean of 0.9–2.4 °C (Table 2). Additionally, temperatures were cooler during nighttime periods often producing similar temperatures during daytime fog periods and nighttime clear periods. As expected, solar radiation was highest during daytime clear periods, lower during daytime fog periods, and near zero during nighttime periods. Despite gaps that resulted in various windows of analysis across the six-week period, the microclimate trends were consistent across the specific windows of analysis and the entire study period. The variation in tree sizes resulted in wide ranges of heat pulse velocities with which to conduct the analyses. Trees ranged in average daily heat pulse velocities of less than 1 cm h^{-1} to greater than 10 cm h^{-1} (Fig. 1) and all three slope positions had trees with mean heat pulse velocities that spanned this range.

3.2. Modeling environmental drivers of heat pulse velocities

3.2.1. Upslope

The models derived for each slope position and period of analysis were statistically significant fits that explained a large portion of the variance with r^2 values ranging from 0.31 to 0.96 across all models (Tables 3, 4, and 5). At the upslope site, overall model fits were strong with r^2 values ranging from 0.49 to 0.92. Overall, vapor pressure deficit, air temperature, and solar radiation explained the majority of the variation. During clear day periods, variation in heat pulse velocities was explained predominantly by air temperature or solar radiation (r^2 from 0.413 to 0.600); less variation was explained by VPD (r^2 from 0.13 to 0.21; Table 3). During daytime fog periods, this relationship shifted with most of the variation in heat pulse velocities explained by VPD with r^2 values ranging from 0.77 to 0.82 and the overall model fits being slightly improved during these periods. While soil moisture and leaf wetness were often significant variables in the models, they rarely explained much of the variation (r^2 less than 0.1). At the same site during nighttime periods, VPD actually explained more of the variation in heat pulse velocities during clear periods than fog periods for the *Quercus* species.

Table 4
Midslope site model fits (r-squared values) derived from stepwise multiple linear regression models. Linear models were developed for each tree separated into clear and fog periods during both the day and night to assess how model fits from each variable changes in response to fog. If an r-squared value is included, it was a significant predictor variable in the model. If no value is included then that variable was not a significant predictor in that model. R-squared values greater than 0.10 are bolded.

Midslope Day	*Q. lancifolia* 1		*Q. lancifolia* 2		*Q. lancifolia* 3		*Q. corrugata* 1		*Q. corrugata* 2		*Q. corrugata* 3	
	Clear	Fog	Clear	Fog	Clear	Fog	Clear	Fog	Clear	Fog	Clear	Fog
Overall Fit	**0.78**	**0.87**	**0.85**	**0.96**	**0.85**	**0.92**	**0.86**	**0.96**	**0.79**	**0.86**	**0.90**	**0.92**
Vapor pressure deficit	0.07	**0.70**	0.05	**0.94**	0.03	**0.83**	0.07	**0.91**	0.09	**0.72**	**0.10**	**0.86**
Leaf wetness		**0.13**	0.00	0.01	0.00	0.00		0.04		0.03		
Air temperature	**0.61**		**0.70**	0.00	**0.78**	0.05	**0.72**	0.00	**0.61**		**0.75**	0.03
Solar radiation	0.07	0.04	0.09	0.00	0.03	0.01	0.06	0.01	0.07	**0.11**	0.05	0.01
Shallow soil moisture	0.02		0.00	0.00		0.02			0.01	0.01		0.01
Deep soil moisture	0.01		0.00		0.01	0.01	0.00	0.00	0.01		0.00	0.00
Midslope Night												
Overall Fit	**0.81**	**0.61**	**0.85**	**0.59**	**0.85**	**0.59**	**0.73**	**0.31**	**0.84**	**0.45**	**0.87**	**0.47**
Vapor pressure deficit	**0.75**	**0.38**	**0.82**	0.09	**0.76**		**0.65**	0.03	**0.80**	**0.27**	**0.82**	0.04
Leaf wetness	0.00	0.08	0.00	**0.48**		**0.42**	0.00	**0.20**	0.00	0.04		**0.29**
Air temperature	0.00	**0.12**		0.01	0.00		0.01	0.06	0.00	0.09	0.01	0.09
Solar radiation	0.04	0.01	0.03		0.07	0.01	0.07	0.02	0.03	0.03	0.05	0.03
Shallow soil moisture	0.01		0.00		0.01	**0.11**			0.00	0.02		0.01
Deep soil moisture	0.01	0.03			0.00	0.05			0.01	0.01		0.01

Table 5
Low-slope site model fits (r-squared values) derived from stepwise multiple linear regression models. Linear models were developed for each tree separated into clear and fog periods during both the day and night to assess how model fits from each variable changed in response to fog. If an r-squared value is included, it was a significant predictor variable in the model. If no value is included then that variable was not a significant predictor in that model. R-squared values greater than 0.10 are bolded.

Low-slope Day	*Q. lancifolia* 1		*Q. lancifolia* 3		*Q. corrugata*		*C. macrophylla*	
	Clear	Fog	Clear	Fog	Clear	Fog	Clear	Fog
Overall Fit	**0.82**	**0.67**	**0.75**	**0.63**	**0.67**	**0.51**	**0.69**	**0.43**
Vapor pressure deficit	**0.10**	**0.40**		**0.37**	0.02	**0.15**	0.01	0.07
Leaf wetness	0.01	**0.24**	0.02	**0.26**	0.04		0.04	**0.35**
Air temperature	**0.69**		0.09		**0.57**	**0.31**	**0.55**	0.02
Solar radiation			**0.63**		0.05		0.09	
Shallow soil moisture	0.02	0.02	0.01			0.05	0.01	
Deep soil moisture								
Low-slope Night								
Overall Fit	**0.81**	**0.45**	**0.91**	**0.85**	**0.67**	**0.64**	**0.66**	**0.53**
Vapor pressure deficit	0.05	**0.38**	0.03	**0.82**		**0.48**	0.01	0.06
Leaf wetness	0.05	0.03	0.05				0.02	**0.48**
Air temperature	**0.69**		**0.77**		**0.62**	0.03	**0.61**	
Solar radiation	0.02	0.05	0.03	0.02	0.04	**0.13**	0.02	
Shallow soil moisture	0.01		0.02				0.01	
Deep soil moisture			0.00	0.01	0.01			

Oddly, the heat pulse velocity of the one *Clethra* at this site was explained by deep soil moisture ($r^2 = 0.45$) despite stable isotope evidence that suggests that this species uses water from predominantly the first 40 cm of soil (Goldsmith et al., 2012). During fog periods, the variation in heat pulse velocities was reversed compared to daytime periods, where VPD explained much less of the variation than during clear night periods (Table 3).

3.2.2. *Midslope*

Overall, trees at the midslope site had very good model fits with r^2 values ranging from 0.31 to 0.96 and VPD, air temperature, and solar radiation explaining most of the variation. During daytime periods, trees followed similar patterns to the upslope site where air temperature explained the majority of the variation in sap flow velocities during clear periods and VPD explained most of this variation during fog periods (Table 4). Overall, VPD explained more of the variation in heat pulse velocities at this site with as much as 93.7% of the variation in heat pulse velocities explained by variation in VPD for one *Q. lancifolia*. Similar to the upslope site, heat pulse velocities during nighttime clear periods were largely explained by variation in VPD. However, unlike the upslope site, during nighttime fog periods, variation in heat pulse velocities was explained by a combination of leaf wetness and VPD. Leaf wetness explained as much as 48.1% of the variation in nighttime heat pulse velocities during fog periods (Table 4). Similar to the upslope site, soil moisture at the midslope site was often a significant factor in the models but rarely explained a large proportion of the variation.

3.2.3. *Low-slope*

Overall, the variables that best explained variation in heat pulse velocities were less consistent across individuals and had lower model fit r^2 values (0.43–0.90) at the low-slope site compared to the other slope positions. During daytime clear periods, air temperature and solar radiation explained the majority of the variation in heat pulse velocities while a combination of leaf wetness and VPD explained this variation during fog periods (Table 5). During nighttime periods, unlike the other two sites, VPD explained very little of the variation during clear periods (and was not significant in one model), while it explained from 5.7% to 82.1% of the variation in heat pulse velocities during fog periods further highlighting tree to tree variation. Leaf wetness played the strongest role at this site during daytime fog periods explaining 24–36% of three of the four trees studied. During nighttime periods, leaf wetness explained a large part of the variation in *C. macrophylla* only during fog periods

($r^2 = 0.48$). At this site, soil moisture was included in fewer models and never explained more than 4.9% of the variation in heat pulse velocities.

Assessing the relationship between the importance of VPD in explain variation in heat pulse velocities (r^2) and field VPD revealed contrasting responses during day and night periods. During day periods there was a strong logarithmic relationship with VPD explaining a lot of variation in heat pulse velocities at low VPD values (Fig. 2a; $r^2 = 0.81$). The predicted curve suggests that r^2 values of less than 0.2 are predicted for VPD values lower than 0.12 kPa. During night periods, this relationship falls apart with VPD explaining large and small components of the variation in the model throughout the range of VPD measured (Fig. 2b).

3.2. Assessment of model fit and model outputs

The importance of separating fog and clear days and daytime and nighttime periods can be seen in a comparison of the observed and predicted values from each model output (Fig. 3). Panels a, f, and k show the model output without the separated distinctions followed by each separated output for one *Q. lancifolia* at each site. Overall, models showed better fit during the separated models, particularly during daytime fog periods, and nighttime clear and fog periods. The midslope site had highest r^2 model fit values followed by the upslope and low-slope sites.

Predicted model outputs for heat pulse velocities varied widely across models used (Fig. 4). Specifically, the predicted response of heat pulse velocity was much steeper during daytime fog periods than the slopes of all other time periods signifying higher flow velocities at lower VPD values during fog periods (Fig. 4). As expected, predicted sap velocities during nighttime periods in the fog differentiated model were much lower than values predicted by the overall model but with a similar slope. The separated day type models were calculated together as an overall model (Fig. 5 "Fog Differentiated Model") and compared to the general overall model (Fig. 5 "Undifferentiated Model; not separated into fog and clear periods) and field data. This analysis revealed that sap flow velocities predicted by the Fog Differentiated model agree more closely with actual field measurements, particularly during low velocity periods (i.e. fog periods and nighttime; Fig. 5). At the upslope site, the Undifferentiated Model overestimated heat pulse velocities during nighttime and fog periods and underestimated maximum flows during clear daytime periods. Conversely, during a partly cloudy day with afternoon fog at the midslope site (Fig. 5, panel b), midday heat pulse velocity was overestimated by the Undifferentiated Model, while the Fog Differentiated model was highly consistent with the field measurements. Similar results were found at the low-slope site where the Fog Differentiated model predicted values similar to field data, particularly during low flow periods (Fig. 5, panel c). An assessment of the model outputs of the sum of daily heat pulse velocities per day with field data demonstrated that during nighttime periods, predicted heat pulse velocities of the Fog Differentiated model more closely estimated field-based measurements than the Undifferentiated Model, particularly at the upslope and midslope sites (Fig. 6).

4. Discussion

4.1. Variation in sap flow across landscape positions

This study examined the influence of environmental drivers on tree water use with on focus on how fog events, time of day, and slope position affected this relationship in a TMCF. Overall, our results demonstrate that the influence of VPD and solar radiation on tree water use varies strongly in response to fog across all three slope positions in the watershed. Vapor pressure deficit explains a large majority of the variation in tree water use during daytime fog periods, particularly at the upslope and midslope sites. During nighttime periods, VPD was the dominant driver of water use variation during clear periods while a combination of VPD and leaf wetness explained variation during night, fog periods. Overall, tree water use was more decoupled from environmental variables with greater variation between trees at the low-slope site relative to the upslope and midslope positions. Finally, the Fog Differentiated model that examined drivers of tree water use during fog and clear periods in both the day and night improved model outputs, particularly at low flow rates, i.e. during fog and night periods.

These data highlight that the influence of air temperature, solar radiation, and VPD in explaining tree water use can vary significantly across individuals and slope positions. In the primary study species, *Q. lancifolia*, air temperature explained the majority of the variation during day, clear periods with this effect particularly strong at midslope sites (r^2, 0.61–0.78). Vapor pressure deficit explained less than 20% of the variation during this period but was most important at the upslope sites than midslope and low-slope sites. However, during fog day and night periods, VPD became the dominant driver of tree water use, particularly at the upslope and midslope sites (Tables 3, 4, and 5). VPD explained as much as 81% of the variation at the upslope site, 93% of the variation at the midslope sites, and only 40% at the low-slope sites. Conversely, leaf wetness explained more of the variation at the midslope and low-slope sites, at times explaining as much as 47–48% of the variation across both sites. The varying influence of environmental variables is supported by other studies that demonstrated similar variability across slope positions (Tromp-van Meerveld and McDonnell, 2006; Kumagai et al., 2008). The poorer relationship between environmental drivers and tree water use at the low-slope site could be due to less water vapor transfer between the canopy and the atmosphere driven by lower wind speeds. As these data suggests, higher wind speeds at the upslope sites allow for greater transfer of water vapor and lead to a greater coupling between VPD and tree water use (Jarvis and McNaughton 1986). Another explanation could be that the higher temperatures measured at low-slope sites led to tighter stomatal regulation and closure, functionally reducing coupling between water use and the environment. Specifically, the relationship between tree water use and VPD was poorer at the low-slope site. During daytime periods there was a negative relationship between VPD and the r^2 of VPD in the model outputs highlighting the importance of this variable during low VPD periods (Fig. 2a). Thus, the lower relationship between VPD and tree water use at the low-slope site could be explained by more frequent conditions with higher VPD. Fig. 2 highlights this point and suggests that at VPDs greater than about 0.12, predicted r^2 of VPD to tree water use would be less than 0.2.

4.2. Tree water use in fog-affected ecosystems

The strong reliance on VPD during both fog day periods and night periods highlights the importance of the frequent fog events and leaf surface wetting that occur in TMCFs in driving tree water use patterns and maintaining carbon-water balance (Fig. 2, Tables, 3, 4, and 5). Multiple studies from fog-affected ecosystems around the world have demonstrated that fog periods can improve daily carbon gain, minimize water loss, improve seasonal water stress, and provide a direct moisture subsidy through soil drip (e.g. Dawson 1998; Berry et al., 2014; Gotsch et al., 2014). Low VPD values and leaf wetting are particularly important in TMCFs to provide a direct water source that is immediately and readily utilized by plant leaves, termed foliar water uptake. Within the three study species, foliar water uptake has been demonstrated in *Q. lancifolia* and *C. macrophylla* leading to a recovery of 9% of all dry season

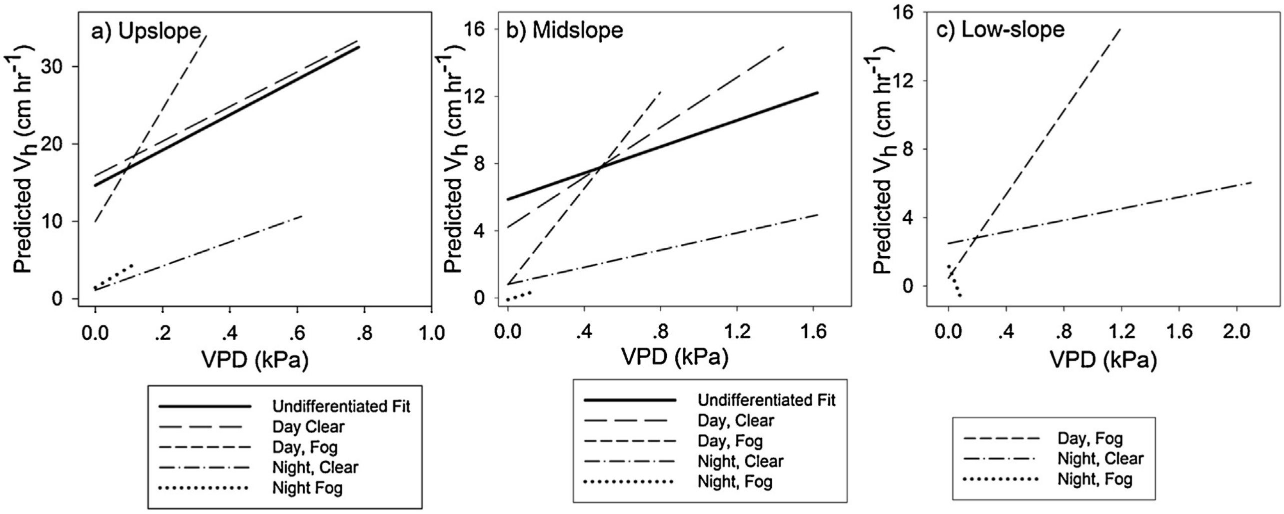

Fig. 4. Predicted effects of variation in vapor pressure deficit (VPD) on heat pulse velocities for one example *Quercus lancifolia* at each of the three slope positions. The model outputs not shown for other trees follow similar patterns. In each panel the response of predicted V_h to VPD is shown for the undifferentiated model (solid line) and each fog differentiated model (dotted lines). For each panel, temperature was held constant at 18 °C, leaf wetness at 5%, soil volumetric water content at 50%, and solar radiation at either 500 W m^{-2} (day) or 50 W m^{-2} (night). These values were chosen to represent relatively dry and clear conditions with median values of soil moisture and temperature.

water lost (Gotsch et al., 2014). Foliar water uptake has also been shown to directly improve plant water potentials (Berry and Smith 2013) and, in one study, directly improve branch hydraulic functioning (Laur and Hacke 2014). Foliar water uptake is also strongly associated with leaf wetting events and may serve as a critical functional plant response to this frequent inundation of fog (Gotsch et al., 2014). Foliar water uptake has been increasingly invoked to explain plant function and it is becoming clear that it serves as a critical water source and integral plant process in TMCFs.

Water use patterns and environmental drivers also varied across day and night periods. Previous research in the Mexican TMCFs of this study has demonstrated that nocturnal water use patterns are particularly important representing 16–26% of daytime transpiration rates (Alvarado-Barrientos et al., 2015). We found that the environmental drivers of tree water use in response to fog are different during day and night periods. During day periods, the importance of VPD increased dramatically during fog events while, during night periods, the importance of VPD typically decreased (Fig. 4, Tables 3, 4, and 5). During day periods, VPD was the primary driver only during very low VPD values, while, it was a strong driver across the range of VPD measured during nighttime periods (Fig. 2). The model prediction outputs (Fig. 4) demonstrate a much steeper response of tree water use to VPD during fog periods suggesting higher water use at lower VPD during fog periods, further highlighting the importance of assess water use across environmental periods. Currently, the TMCF literature demonstrates an understanding of the importance of VPD, leaf wetness, and fog, but the ecological significance and ability to model these effects in the future are lacking. Thus, we are at a unique moment where we can begin to improve these predictive efforts.

In this study there was very little influence of soil moisture on tree water use patterns across all sites, similar to Kumagai et al. (2008). Soil moisture parameters were often included in the best-fit models but rarely explained a large proportion of the variation in tree water use. This result contrasts with the study by Tromp-van Meerveld and McDonnell (2006), which found that transpiration rates were limited at upslope positions with shallower soils. There are potentially several reasons for the limited influence of soil moisture in the current study. It is possible that soil moisture was not limiting (e.g. Oren and Pataki, 2001) due to the both the ecosystem (TMCF), time period studied (wet season), and the particularly high rainfall during the wet season of the study year. These forests can receive up to 3200 mm of rainfall annually and a large proportion of this falls during the 'wetting up" period in this study (Holwerda et al., 2010). The scale of the data could have also contributed to a reduced significance of soil moisture. Data points were collected every 10 min revealing variable fluxes throughout even one day of the experiment. At this scale, environmental variables that fluctuate quickly (VPD, solar radiation, air temperature) are more likely to influence tree water use patterns than soil moisture, which fluctuates at slower time scales (Jipp et al., 1998). Finally, tree rooting depth could be deeper than both soil moisture depths measured in this study leading to a reliable water source with less variation. However, there is evidence that rooting depth in these TMCFs are relatively shallow with most water uptake coming from less than 60 cm of soil (Goldsmith et al., 2012).

4.3. Differentiating fog in modeled outputs

The Fog Differentiated model outputs provided a more accurate assessment of low flow periods than the non-separated model (Fig. 5). For example, in Fig. 5b, heat pulse velocities stay near zero the entire day, which is tracked closely by the outputs of the Fog Differentiated model whereas the general overall model predicts midday heat pulse velocities as high as 7 cm h^{-1}. An examination of the daily sums for day and nighttime periods (Fig. 6) demonstrate consistently low error for the Fog Differentiated model. For nighttime periods only (Fig. 6c), the difference between predicted and measured daily water use varied from 2 to 12% for the Fog Differentiated model and 7–86% from the overall model. For the total 24 h periods, the Fog Differentiated model performed better at the upslope and midslope sites producing differences of 0.22% and 0.66% difference from measured as compared to −0.27% and 1.1% for the overall model. This trend was reversed at the low-slope site where the overall model generally produced daily sums closer to measured field data. This is likely due to the strong variability and poorer fits in model outputs at the low-slope site.

The high variability in tree water use drivers between individual, species, and sites demonstrates the complex interactive mechanisms of environment, physiological mechanisms, and genetic variation in predicting water use patterns. To improve models of stand transpiration, future studies need to address the spatial patterns across the landscape within species. Mackay et al. (2010) found that to accurately scale transpiration rates to the stand scale

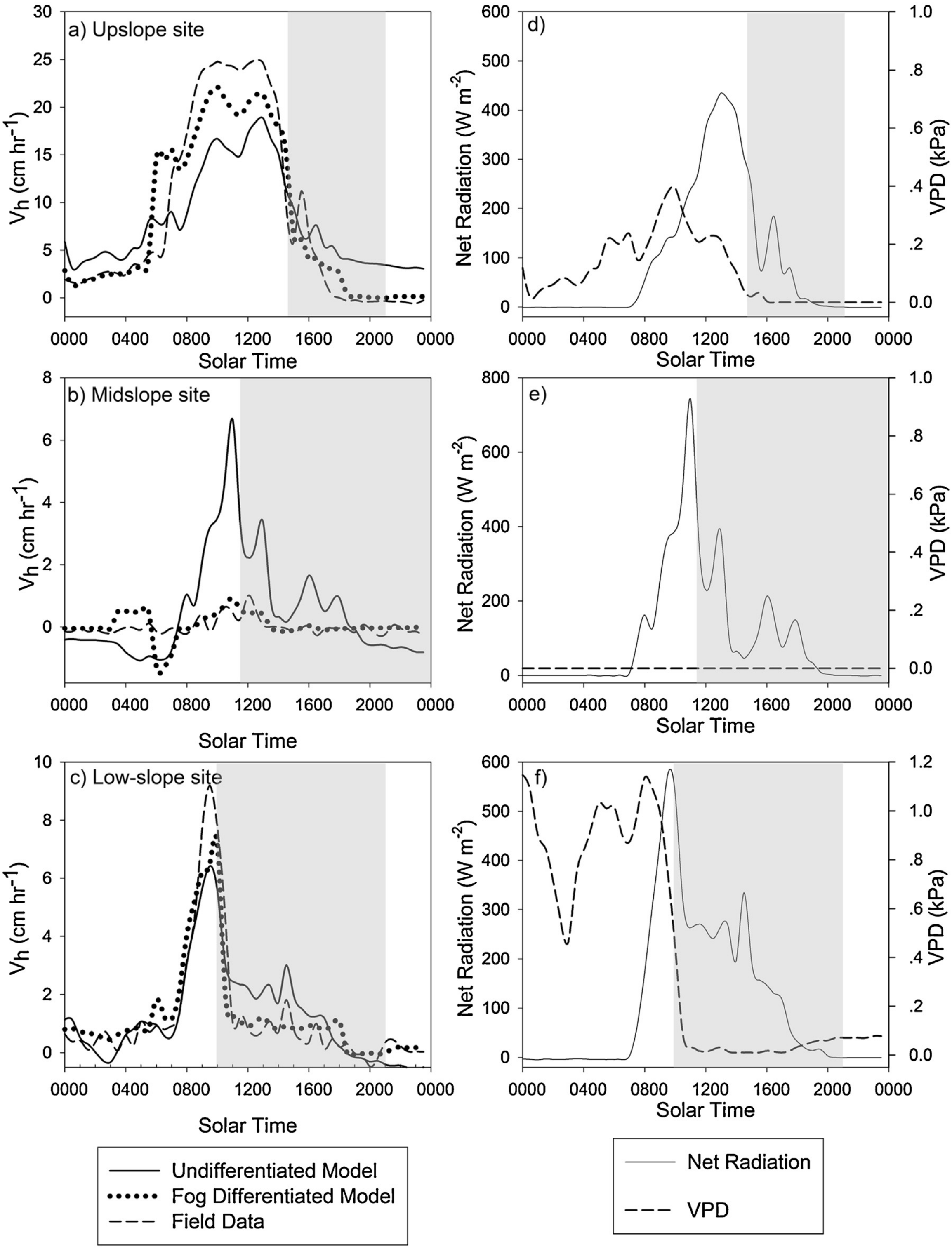

Fig. 5. Comparison of model outputs for one day that includes both a period of sun in the morning followed by fog in the afternoon. Panels a–c represent the prediction of the undifferentiated model (solid line), the fog differentiated model (dotted line), and the actual measured field data (dashed line) for the three slope positions. Panels d-f show net radiation (solid line) and VPD (dashed line) during the same period. Grey boxes represent fog periods.

required three plots spanning uplands to wetlands and included plots that reflected the spatial variation in leaf area index, canopy cover, and reference stomatal conductance. These data combined with accurate censuses of trees within a stand that include slope position and aspect will improve model outputs. Models of stand level transpiration rates should also focus on periods of low and negative sap flow rates such as during nighttime periods or fog events, as these are generally poorly modeled in many studies and have been shown to contribute significantly to the water cycle (Alvarado-Barrientos et al., 2015). Finally, microclimate (including leaf wetness and fog occurrence) within the experimental site should be studied if at all possible due to the strong variation in

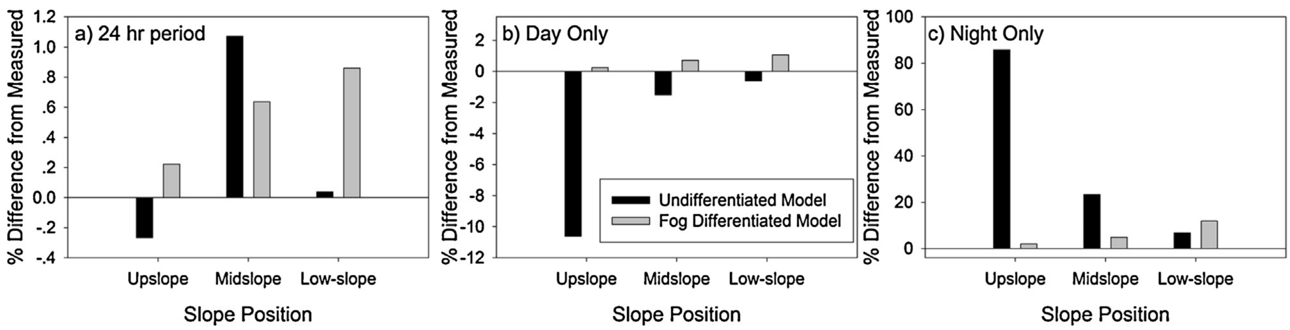

Fig. 6. The average percent difference in daily V_h between the two model outputs and measured V_h at three slope positions. Panel a represents a total 24 h period while b and c divide the same comparisons into daytime and night time periods. Black bars represent the undifferentiated model and grey bars represent the fog differentiated model.

climate variation across mountainous landscapes such as the one in this study.

4.4. Conclusions

In the present study, we examined the influence of environmental drivers on tree water use across three slope positions and different periods of the day and during fog events in a tropical montane cloud forest. The variation in environmental drivers of tree water use across short spatial scales varied across day/night and fog/clear analyses highlighting the complex interaction between microclimate and geospatial location in dictating water use. With increasing changes to climate likely leading to even greater variability in microclimate parameters within sites, further work is needed that examines variation in physiological responses to climate variation. Future studies that examine modeled tree water use in cloud forests should consider geographical and topographical variation as well as nighttime and fog periods as important factors when attempting to derive values for stand level transpiration over extended periods.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agrformet.2016.02.012.

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