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Research paper

Water relations and microclimate around the upper limit of a cloud forest in Maui, Hawai'i

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The goal of this study was to determine the effects of atmospheric demand on both plant water relations and daily whole-tree water balance across the upper limit of a cloud forest at the mean base height of the trade wind inversion in the tropical trade wind belt. We measured the microclimate and water relations (sap flow, water potential, stomatal conductance, pressure–volume relations) of *Metrosideros polymorpha* Gaudich. var. *polymorpha* in three habitats bracketing the cloud forest's upper limit in Hawai'i to understand the role of water relations in determining ecotone position. The subalpine shrubland site, located 100 m above the cloud forest boundary, had the highest vapor pressure deficit, the least amount of rainfall and the highest levels of nighttime transpiration (E_N) of all three sites. In the shrubland site, on average, 29% of daily whole-tree transpiration occurred at night, while on the driest day of the study 50% of total daily transpiration occurred at night. While E_N occurred in the cloud forest habitat, the proportion of total daily transpiration that occurred at night was much lower (4%). The average leaf water potential (Ψ_{leaf}) was above the water potential at the turgor loss point (Ψ_{TLP}) on both sides of the ecotone due to strong stomatal regulation. While stomatal closure maintained a high Ψ_{leaf} , the minimum leaf water potential (Ψ_{leafmin}) was close to Ψ_{TLP} , indicating that drier conditions may cause drought stress in these habitats and may be an important driver of current landscape patterns in stand density.

Keywords: *Metrosideros polymorpha*, nighttime transpiration, 'ōhi'a, pressure–volume relations, sap flow, stomatal conductance, trade wind inversion, tropical montane cloud forest ecophysiology, water stress.

Introduction

Temperate forest lines, or timberlines, have been proposed to be controlled by temperature during the warmest part of the year (Jobbágy and Jackson 2000), suggesting potential for upward migration with future warming. Tropical and subtropical forest lines are less well studied, but may be controlled by moisture availability rather than temperature (e.g., Crausbay and Hotchkiss 2010). This may be particularly true within the

tropical trade wind belt, where the cloud forest's upper limit tends to co-occur with the mean base height of the trade wind inversion or TWI (Hawaiian Islands: Kitayama and Mueller-Dombois 1992; Canary Islands: Fernández-Palacios and de Nicolás 1995, Leuschner 2000, Crausbay and Hotchkiss 2010; Dominican Republic: Martin et al. 2007). The TWI is a subsidence inversion that limits atmospheric lifting and cloud development above its mean base height and, as a result, it

establishes a sharp decrease in relative humidity (RH) and rainfall across elevation (Cao et al. 2007). Thus, high evaporative demand above the TWI may increase potential transpiration rates and could lead to moisture stress and act as a mechanistic driver of cloud forest line position. Many authors have hypothesized that this dramatic elevational change in RH and rainfall near the TWI is the primary driver of the cloud forest's upper limit in these areas, rather than elevational trends in temperature (Kitayama and Mueller-Dombois 1992, Fernández-Palacios and de Nicolás 1995, Martin et al. 2007, 2010, Crausbay and Hotchkiss 2010, Crausbay et al. 2014). Therefore, studies of water relations around these upper cloud forest limits are needed to test this hypothesis.

We studied water relations around the upper cloud forest limit in Hawai'i, which occurs near the TWI mean base height of ~2100 m above sea level on the northeast slope of Haleakalā volcano on the island of Maui (Cao et al. 2007, Crausbay and Hotchkiss 2010). Immediately above the forest line and the mean TWI, Kitayama and Mueller-Dombois (1992) recognized two elevational zones—the frost-free zone from 1900 to 2400 m and the ground-frost zone at elevations >2700 m (Kitayama and Mueller-Dombois 1992). These microclimatic patterns show that the forest line is strongly associated with the TWI in a largely frost-free zone. In addition, because the TWI is a temperature inversion in which a warmer air mass sits atop a cooler air mass, the upper limit of cloud forest is on average warmer than some cloud forest habitat immediately below. Overall, these observations suggest that sharp gradients in moisture availability (Figure 1a) driven by the TWI likely drive this ecotone position.

Metrosideros polymorpha Gaudich. var. *polymorpha* occupies a number of broad biophysical gradients in Hawai'i including soil moisture availability, substrate age, precipitation and temperature (Cordell et al. 1998). Leaf polymorphism is common across these gradients in *M. polymorpha*, and biologists have investigated leaf functional traits and plasticity that correlate

with changes in environmental conditions. At higher elevations, *M. polymorpha* are generally shorter in stature with smaller and highly pubescent leaves, while individuals in lowland areas tend to be taller with larger and more glabrous leaves (Mueller-Dombois 1980, Stemmermann 1983, Dawson and Stemmermann 1990, Kitayama and Mueller-Dombois 1992, Drake and Mueller-Dombois 1993). *Metrosideros polymorpha* leaves along the same steep climatic gradient show heavier oxygen isotopic signatures with higher vapor pressure deficit (VPD), suggesting that moisture availability is likely an important driver of pubescence (Leuschner 2000, Kahmen et al. 2011). Decreases in boundary layer conductance due to pubescence may provide a mechanism to aid against water loss. While others have shown that these leaf traits also aid trees in freezing avoidance/tolerance (Cordell et al. 1998, Melcher et al. 2000), for the *M. polymorpha* populations in this study the most significant source of abiotic stress is atmospheric demand for water, as temperatures in these sites do not approach levels predicted to cause stress due to freezing (Kitayama and Mueller-Dombois 1992, S.D. Crausbay, unpublished data).

In this study, we investigated the microclimatic conditions and water relations of trees bracketing the forest line ecotone and the mean base height of the TWI in Hawai'i and asked (i) how do environmental drivers of transpiration vary across the cloud forest ecotone and (ii) do the water relations and daily whole-tree water balance of trees above and within the cloud forest differ?

Materials and methods

Site locations

The cloud forest in Hawai'i is largely dominated by *M. polymorpha* Gaudich ('ōhi'a), which occupies one of the broadest environmental ranges of any tree species, dominating from sea level to tree line (~2500 m) (Cordell et al. 1998, Cornwell et al. 2007). On Haleakalā, vegetation zonation is apparent, with a

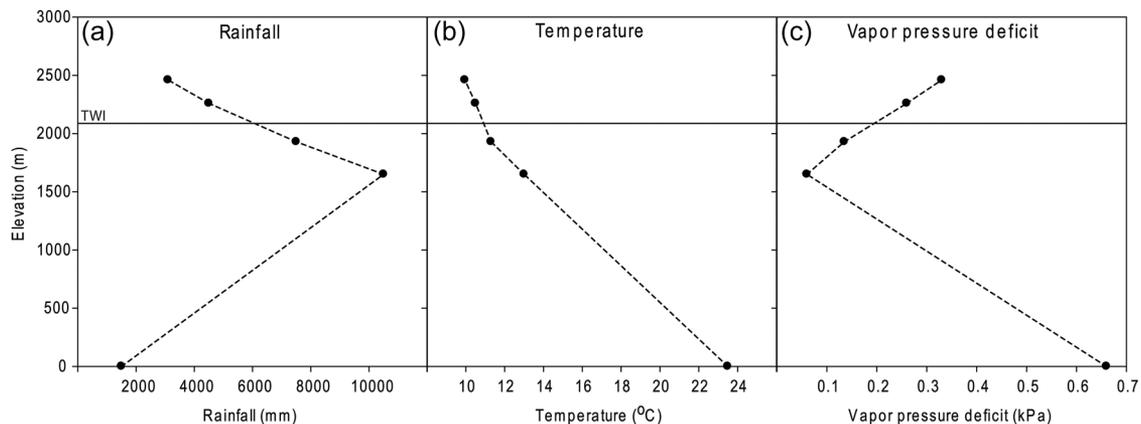


Figure 1. Long-term means for total annual rainfall (a), mean annual air temperature (b) and mean annual VPD (c), from the northeast windward Haleakalā, after Loope and Giambelluca (1998).

sharp upper limit of cloud forest coincident with the mean TWI between 1900 and 2200 m (Kitayama and Mueller-Dombois 1992, Crausbay and Hotchkiss 2010). The summit of Haleakalā volcano, East Maui rises to 3055 m above sea level and our study area from ~2100 to 2300 m brackets the cloud forest's upper limit at 2200 m on the windward, northeast slope. We established three sites in the study area: one above the forest line in the subalpine shrubland (2304 m, N°20 44.084', W°156 07.368'), one immediately below the forest line (2231 m) and one further below the forest line in the cloud forest (2109 m, N°20 44.094', W°156 07.183'; Figure 2). Microclimatic variation within the study area is heavily influenced by northeasterly trade winds, which bring high-humidity air masses, clouds and orographic rainfall to portions of the windward slope below the level of the TWI. Across the Hawaiian Islands, the TWI's mean base height occurs between 2076 and 2255 m (Cao et al. 2007). At this study site, mean annual rainfall ranges from ~3500 mm at the highest elevation to ~5000 mm at the lowest elevation (Giambelluca et al. 2011, 2013) and mean annual temperature ranges from 10.25 to 10.75 °C, respectively (S.D. Crausbay, unpublished data).

The upper forest line is abrupt and coincides with the upper limit of many species distributions on Haleakalā (Crausbay

and Hotchkiss 2010). The cloud forest is dominated by *M. polymorpha* trees and epiphytic bryophytes, ferns and lichens. Tree canopy heights in the upper cloud forest range from ~5 to 7 m and forest line position is defined by the sharp discontinuity arising when the >5-m height class dropped from >60% cover to <25% cover in successive elevational plots (Crausbay and Hotchkiss 2010). Above the cloud forest's upper limit, a subalpine shrubland is dominated by the shrub *Leptecophylla tameiameiae* (Cham. & Schldl.) C.M. Weiller, the tree fern *Sadleria cyatheoides* Kaulf. and the tussock grass *Deschampsia nubigena* Hillebr. In this subalpine shrubland, the most dominant height class of vegetation is ~2–3 m. The subalpine shrubland also contains scattered *M. polymorpha* trees that reach heights of ~3–5 m.

Haleakalā volcano is in its post-shield building stage, and the chemical composition of the basaltic parent material is fairly constant. However, the substrate age varies between 13,000 and 950,000 years and soils are derived from several rock types including ash deposits, vent deposits and lava flows (Sherrod et al. 2007).

Humans arrived in the Hawaiian Islands only ~1200 years ago (Kirch 2007) and, with no high-elevation agriculture, Hawaiians did not use these lands around the TWI extensively

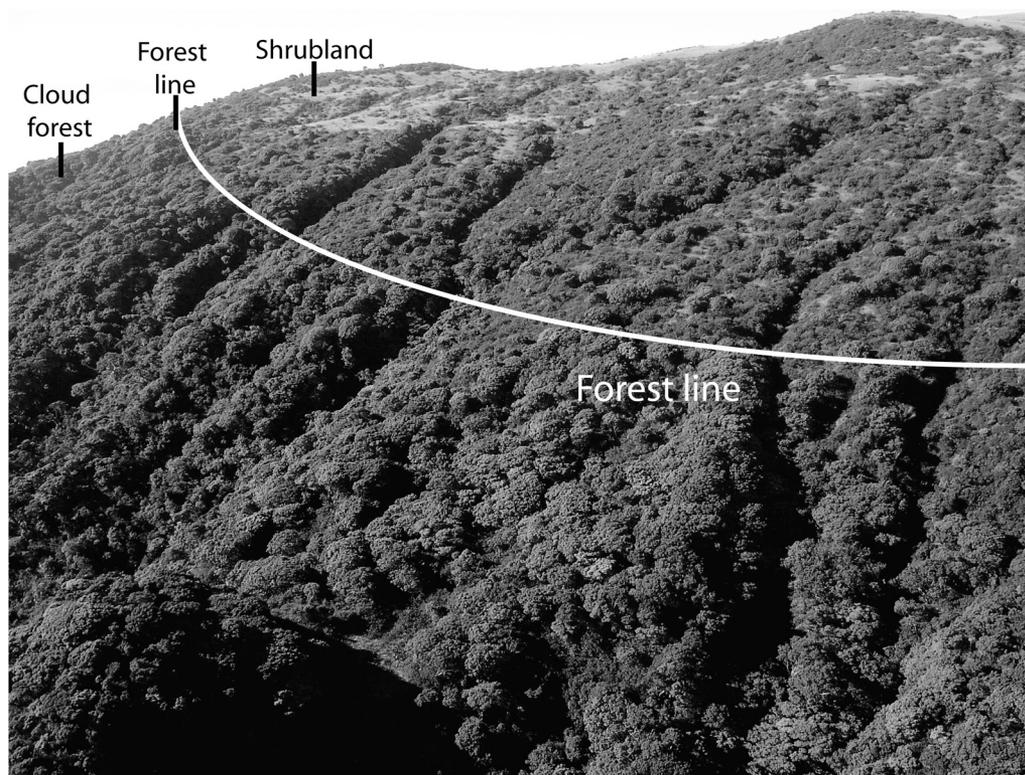


Figure 2. Aerial photograph of the windward slope of Haleakalā volcano in Maui, Hawai'i showing the study locations. This study takes place in three habitats close to the upper limit of the cloud forest: the subalpine shrubland, the cloud forest line and the cloud forest. One site was established in each of the three habitat types. In each site, we measured sap flow and diurnal courses of Ψ_{leaf} and stomatal conductance (on sunny days) and analyzed pressure–volume curves for individuals of the dominant tree species, *M. polymorpha*. In each site, we also measured air temperature, RH and rainfall. Photo courtesy of Gregor Schuurman.

(Burney et al. 1995). Today these ecosystems remain remote and, in the case of the windward Haleakalā study area, undeveloped. As a result, the study area has mostly escaped human impacts that most other tropical forest lines and tree lines have experienced (e.g., Miede and Miede 2000). However, from European contact until the 1980s the area was influenced by non-native ungulates (cattle, goats and pigs). Alpine grasslands and subalpine shrublands above the TWI experienced the greatest ungulate influence, and these landscapes are heavily invaded with Eurasian herbs. In contrast, the upper montane cloud forest largely resisted invasion by non-native plants (Loope et al. 1992).

This study took place over a 2-week period in late August 2010. Microclimate and sap flow were measured continuously for 11 days and leaf-level physiological measures were taken on 2 days without rainfall. The field site is within an area monitored under several related previous and ongoing studies including the HaleNet climate network established in 1992 (<http://climate.socialsciences.hawaii.edu/HaleNet>), microclimate, vegetation and paleoecological research focused on the forest-shrubland ecotone (Crausbay and Hotchkiss 2010, 2012, Crausbay et al. 2014), and a study of plant–soil–water interactions near the forest line (Menard 1999). All leaf-level and whole-plant water relation measures were taken on *M. polymorpha* var. *polymorpha*, which is a pubescent variety of this species.

Microclimate

We measured rainfall near each of the three sap flow sites with a HOBO® model RG2-M tipping-bucket rain gauge at 0.2-mm resolution and $\pm 1\%$ accuracy and logged rainfall measurements with a HOBO® model H21-002 Micro Station datalogger (Onset Computer Corp., Bourne, MA, USA). These three rainfall gauges occur at 2228, 2182 and 2143 m and are part of a larger 12-station network measuring microclimate within and beyond the sap flow study area.

Air temperature (T_{air}), RH and leaf wetness (LWS) were measured at the three study locations. A single HOBO® sensor (U23 pro v2, Onset Computer Corp.) and three LWS sensors (LWS-L, Decagon Devices, Pullman, WA, USA) were placed at canopy level throughout the sites. HOBO® sensors have an internal datalogger and battery, while the LWS sensors were connected to a datalogger (CR 1000, Campbell Scientific, Inc., Logan, UT, USA). All variables were sampled at 1-min intervals and recorded as a 10-min average value.

Sap flow

Sap flow was measured on eight *M. polymorpha* trees in each of the three sites. The heat-pulse ratio method (HRM) was employed because of its effectiveness in measuring the low flow rates associated with fog-dependent ecosystems (Burgess and Dawson 2004, Ambrose et al. 2010). The

procedures outlined by Burgess et al. (2001) were followed for sensor construction and wound damage correction. In the HRM, a pulse of heat is sent to the middle of three equally spaced sensors; following this pulse, the ratio of the increase in temperature in two sensors equidistant from the middle heater sensor is calculated. Heat-pulse velocity (V_h , cm h^{-1}) is calculated as (Marshall 1958)

$$V_h = k/x \ln(v1/v2) \times 3600,$$

where k is the thermal diffusivity of fresh wood, x is the distance between the middle (heater sensor) and the upstream and downstream thermocouple sensors (0.6 cm), and $v1$ and $v2$ are the increases in temperature at the upstream and downstream sensors due to the heat pulse. The thermal diffusivity was measured using a thermal properties probe (KD2 Pro, Decagon Devices) after severing the xylem at the end of the experiment.

Bark was removed from a small portion of the tree trunk prior to sensor installation. Small holes were drilled and a drill guide was used to ensure that the holes were made equidistant and unidirectional from the other sensors. Petroleum jelly was added to the sensors prior to insertion to aid in thermal conductance (Burgess et al. 2001). Following insertion, insulating materials were added around the sensors to minimize radiative heating of the sensors. The sensor sets were connected to a datalogger (CR 1000, Campbell Scientific) and multiplexer (Campbell Scientific AM 16/32) via 10-m-long cables. The sap flow stations were powered by 12-V batteries. Data were taken every 10 min throughout the study period.

After the experiment had concluded, we severed the xylem above and below the sensor sets to establish a reference zero-flow velocity. This reference velocity is used to correct for small errors due to probe misplacement. The stations continued to run (with severed xylem and no flow) for one complete clear day at the end of the experiment. The data for each sensor set were adjusted up or down based on the average sap flow value (cm s^{-1}) that was obtained when it was certain that no flow was occurring.

Sap flow velocity was multiplied by the sapwood area of each tree to represent sap flow volumetrically (F , l h^{-1}). The sapwood area (cm^2) for each tree was obtained using a previously published relationship between diameter at breast height (DBH) and sapwood area (Santiago et al. 2000). Santiago et al. (2000) studied three pairs of well-drained and water-logged sites and found that the sapwood/DBH relationships of *M. polymorpha* did not differ statistically; therefore, a single relationship was used.

Stomatal conductance

Stomatal conductance (g_s) was measured on three intact sun-exposed leaves of five individuals of *M. polymorpha* at the two

sites. Leaves were chosen near to the leaf used for leaf water potential (Ψ_{leaf}) measurement (see details below). Measurements of g_s were conducted at 10:00–11:00 am, 12:00–1:00 pm, 2:00–3:00 pm and 4:00–5:00 pm using a steady-state diffusion porometer (SC-1, Decagon Devices). Only two sites were included for measurements of g_s and Ψ_{leaf} (see below) because it would not have been possible to adequately sample three sites in 1 h. We chose to measure the two sites that were furthest apart since they likely experience the greatest differences in microclimate. On the first day of measurements (29 August), the leaves were wet throughout the morning; the first measurement on this day was not taken until noon. On the second day of measurements (30 August), the leaves were wet in the early morning and measurements were initiated at 10:00 am.

Leaf water potential

We measured Ψ_{leaf} and g_s on *M. polymorpha* trees on the 29th and 30th of August after a 3-day period with heavy rainfall. Only trees at the upper (shrubland) and lower (cloud forest) sites were measured. Ψ_{leaf} was measured on two sun-exposed leaves (different branches) of 10 trees at each site. To measure Ψ_{leaf} , damp plastic bags were placed over a leaf and the petiole was then cut with a sharp razor. The plastic bag was then sealed, placed in a styrofoam cooler and transported to the field laboratory where Ψ_{leaf} measurements were taken using a pressure chamber (Plant Moisture Systems, Corvallis, OR, USA). Measurements were made on leaves that were collected at predawn (6:00–6:30 am), mid-morning (8:30–9:00 am), noon (11:30 am–12:00 pm) and mid-afternoon (2:30–3:00 pm). We determined the minimum leaf water potential (Ψ_{leafmin}) by first identifying the absolute minimum Ψ during the study period in the shrubland and cloud forest sites. We then took the average Ψ of three leaves measured within that individual during the same time period in each site.

Pressure–volume curves

Pressure–volume curves were derived for 10 *M. polymorpha* trees in each site to determine a number of important ecophysiological parameters, including water potential at the turgor loss point. One branch was cut per tree. Cut branches were immediately placed in black plastic bags and transported to the field laboratory. Branches were re-cut under water; the stems were kept in water while the leaves were kept covered overnight to facilitate rehydration. The following morning, branchlets (with three to five leaves) were cut from the soaking branches and were immediately weighed, and their water potential was measured. Weight and water potential were determined repeatedly throughout the day (10–13 times) as the branchlets air-dried (Schulte and Hinckley 1985).

Data analysis

Volumetric sap flow (l day^{-1}) was analyzed using repeated-measures analysis of variance (ANOVA). The effects tested

in this analysis were 'site', 'day' and the interaction between these two effects. A one-way ANOVA was performed to test for the effect of 'site' on the daily percentage of total sap flow that occurred at night. Additional ANOVAs were performed to determine whether the sap velocity rates differed across the three sites both during the day and at night. The influence of VPD on sap velocity (cm h^{-1}) during the day and night was analyzed using a series of non-linear regressions for each site. In addition, we tested whether the slopes of these relationships differed significantly using an analysis of covariance (ANCOVA). All sap flow data were log-transformed prior to analysis to achieve normality.

Ψ_{leaf} and g_s were also log-transformed to achieve normality. For each variable, the overall effect of location was tested using a one-way ANOVA. The effect of location at each time step was tested with paired *t*-tests.

A pressure–volume plot was constructed for each sample showing the inverse water potential ($1/\Psi$) and the relative water content ($1 - \text{RWC}$). From this plot the following parameters were estimated based on calculations by Schulte and Hinckley (1985): osmotic potential at full saturation ($\Psi\pi_{\text{sat}}$), RWC at the turgor loss point (RWC_{TLP}), Ψ_{TLP} , maximum bulk modulus of elasticity (E_{max}) and RWC of apoplastic water (R_a^*). E_{max} was calculated as the maximum slope of the turgor pressure vs the RWC relationship minus the estimated R_a^* . The effects of site were tested with an ANOVA followed by additional post hoc tests when appropriate. All regression analyses in this study were performed using SigmaPlot (Version 12.2, Systat Software, Inc., San Jose, CA, USA) while the ANCOVA, ANOVAs and post hoc tests were performed in JMP (JMP, Version 7, SAS Institute, Inc., Cary, NC, USA).

Results

Microclimate

During the study period, the mean temperature at all three sites was 10 °C. Variation in air temperature was great among the three sites, especially during dry periods (Figure 3a). Maximum temperatures across sites ranged from 19.8 °C (shrubland) to 17.3 °C (cloud forest) and the minimum temperature ranged from 5.8 °C (shrubland) to 5.9 °C (cloud forest).

Relative humidity was generally high yet fluctuated considerably, especially in the absence of rain (Figure 3b). Relative humidity values <40% occurred on a number of occasions and values <20% occurred at the beginning of the study. During dry periods, the RH was generally lower at the shrubland site than at the other two sites (Figure 3b). Relative humidity at the forest line site was higher than at the shrubland site at the beginning of the study, but at other times the two sites had similar RH (Figure 3b). Large fluctuations in temperature and RH resulted in a wide range of VPDs throughout the study period. The VPD exceeded 0.8 kPa during dry periods

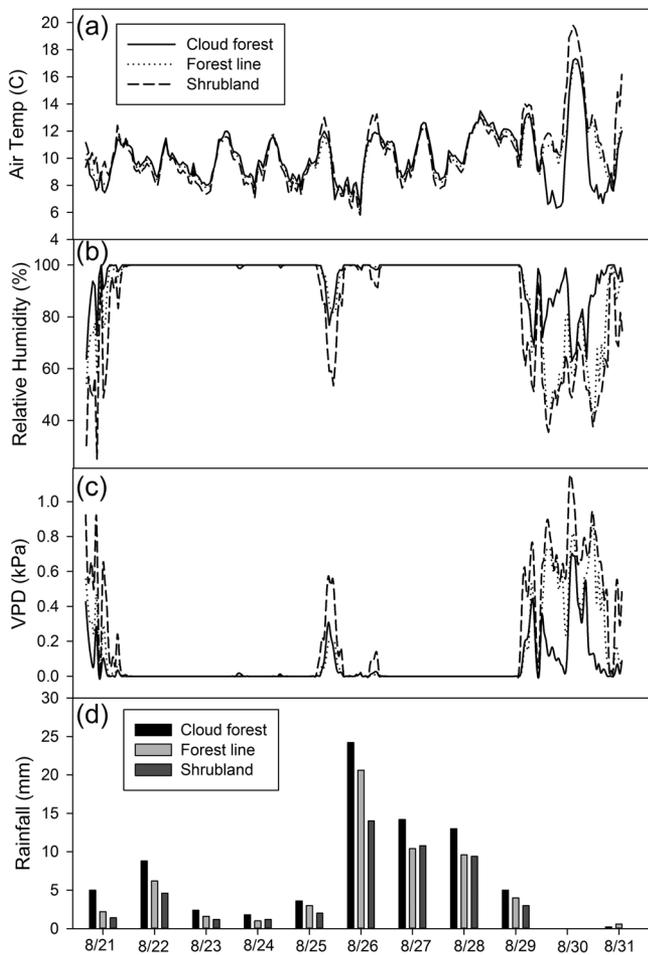


Figure 3. Air temperature (a), RH (b), VPD (c) and rainfall (d) in the shrubland, forest line and cloud forest sites during the study period in 2010.

and remained close to zero during rainy and foggy periods. Generally, VPD was higher in the shrubland site than in the cloud forest or forest line sites (Figure 3c).

Study-period rainfall totaled 48.4 mm (shrubland), 59.2 mm (forest line) and 78.6 mm (cloud forest). At each site, the majority of rainfall was received over a 3-day period (Figure 3d). While the conditions at all sites during the study could be characterized as 'wet', rainfall was <1 mm across all sites for the first 3 days and the final 4 days of this study. In general, however, rainfall for 2010 was lower than normal, with an annual sum of 3203.5 mm compared with an 18-year annual average sum of 4687.3 mm for HaleNet station 162 situated near the forest line. Total rainfall during the month of August 2010, when this study was carried out, was 159.8 mm and also was lower than the long-term August average sum of 269.5 mm.

Sap flow

There was significant daily and site variation in sap flow (Figure 4a). While the day of measurement had the largest influence on the data in the repeated-measures ANOVA

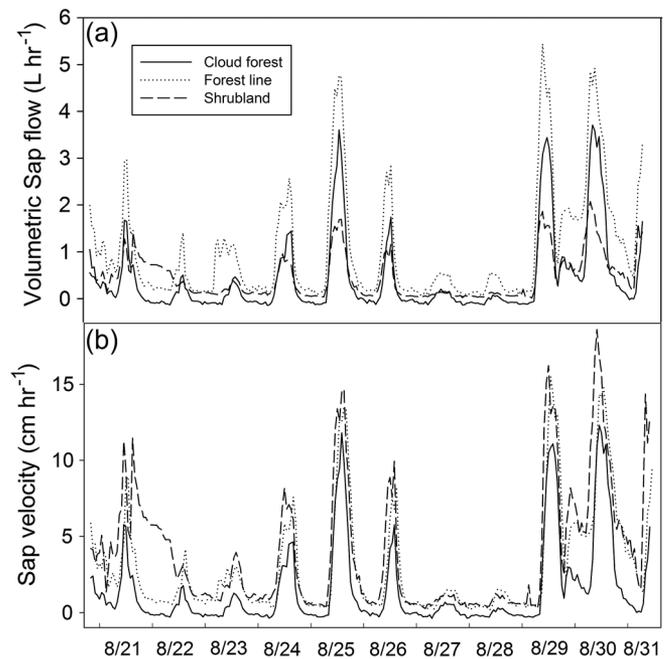


Figure 4. Hourly volumetric sap flow (a) and sap velocity (b) during the study period in the cloud forest, forest line and shrubland sites. Each line of sap flow data represents an average of eight trees in each site.

($F = 77.8$, $P < 0.0001$), the 'site' and 'site \times day' interaction were also significant ($F = 5.15$, $P = 0.02$ and $F = 9.19$, $P = 0.0006$, respectively). The highest rates of flow were measured on 25, 29 and 30 August during times of high evaporative demand. The greatest sap velocity values were generally found in the shrubland site (Figure 4b) while volumetric sap flow was always greatest at the forest line site (Table 1). The forest line site lies on the cloud forest ecotone; this site contains larger trees than the shrubland site and these trees are generally exposed to higher VPDs than the cloud forest site (Figure 3c). The combination of high evaporative demand and larger trees results in this site experiencing the greatest average water loss of the three sites.

During the study period, there were also a number of days when the driving force for transpiration (i.e., VPD) was at or near zero. Despite the fact that air temperature and RH sensors detected zero driving force for transpiration, we generally found positive, but low, rates of sap flow. During these periods, low-lying clouds were thin and conditions were rather sunny. We suspect that daytime sap flow during these relatively wet periods was due to surface heating of the leaves, which would have resulted in a leaf-level driving force for transpiration that we were unable to detect with the HOBO® sensors.

Nighttime transpiration (E_N) occurred in all sites. The percentage of daily volumetric sap flow that occurred at night was greatest during dry periods at the beginning and end of the study period (Table 1, Figure 5). The percentage of daily sap flow that occurred at night was significantly different across

Table 1. Daily mean F (l h^{-1}), total daily F (l h^{-1}), percentage of daily F that occurred at night and sap flow (cm s^{-1}) for each of the full days (date in August of 2010) of the experiment at the subalpine shrubland (SAS), forest line (FL) and cloud forest (CF) sites.

Date	Daily mean F (l h^{-1})			Total F (l h^{-1})			% of daily F (l h^{-1}) at night			Sap flow (cm s^{-1})		
	SAS	FL	CF	SAS	FL	CF	SAS	FL	CF	SAS	FL	CF
21	0.71	1.01	0.37	17.03	24.15	8.79	39.66	31.70	13.89	5.99	3.03	1.35
22	0.4	0.44	0.02	9.61	10.48	1.43	56.50	20.75	0	3.26	3.41	0.18
23	0.19	0.63	0.02	4.51	15.13	1.54	31.06	26.84	0	1.64	2.33	0.18
24	0.33	0.85	0.31	7.96	20.32	8.43	15.51	12.55	0	2.89	2.44	1.14
25	0.59	1.63	0.85	14.20	39.10	20.34	12.87	11.05	0.29	5.14	4.68	2.89
26	0.3	0.76	0.25	7.20	18.18	6.41	12.36	13.65	0	2.61	2.14	0.9
27	0.08	0.27	0	1.84	6.55	0.89	32.40	27.25	0	0.71	0.76	0.06
28	0.07	0.23	0	1.71	5.59	0.24	39.67	28.77	0	0.67	0.69	-0.09
29	0.7	1.89	1.05	16.75	45.27	25.09	20.35	19.44	10.62	6.15	5.52	3.50
30	1.03	2.63	1.44	24.67	63.12	34.52	31.54	32.26	16.68	9.15	7.89	4.71

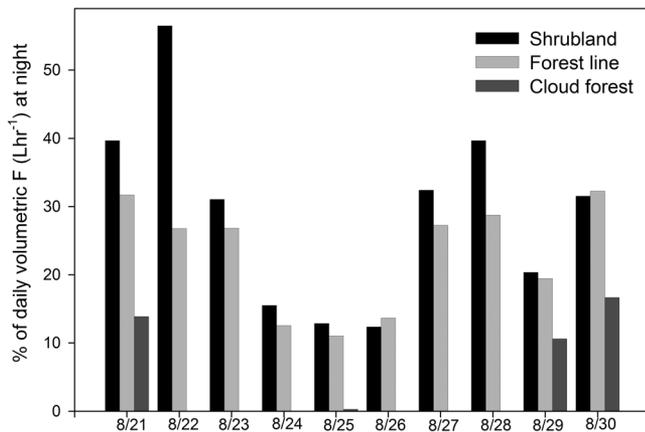


Figure 5. Percentage of the total daily sap flow (l h^{-1}) that occurs at night in the shrubland, forest line and cloud forest sites. Each bar represents the average of eight trees in each site. The x-axis represents the date of measurement and the y-axis represents the percentage of daily volumetric sap flow that occurred at night. Analysis of variance revealed significant differences in this variable across sites ($F = 16.2$, $P \leq 0.0001$).

sites ($F = 16.23$, $P \leq 0.001$). The average amount of sap flow that occurred at night was 29% at the shrubland site, 22% at the forest line site and 4% at the cloud forest site. On seven of the 10 days with complete sap flow data, there was little to no E_N in the cloud forest site, while rates were often $>15\%$ at the other two sites (Figure 5). In the shrubland site, E_N accounted for $\geq 30\%$ of the total volumetric sap flow on six of the 10 days studied. Recent findings have documented the importance of refilling as part of nighttime fluxes (Daley and Phillips 2006, Wang et al. 2012). While some of the flux in our study may also be due to xylem refilling, we suspect refilling is minimal due to the lack of correlation between periods of high daytime sap velocity and nighttime flow.

We found a significant relationship between sap velocity and VPD in all sites (Figures 6–8). This relationship was strongest at night ($P \leq 0.01$; day—forest line: $r^2 = 0.53$; shrubland: $r^2 = 0.38$; cloud forest: $r^2 = 0.68$; night—forest line: $r^2 = 0.79$;

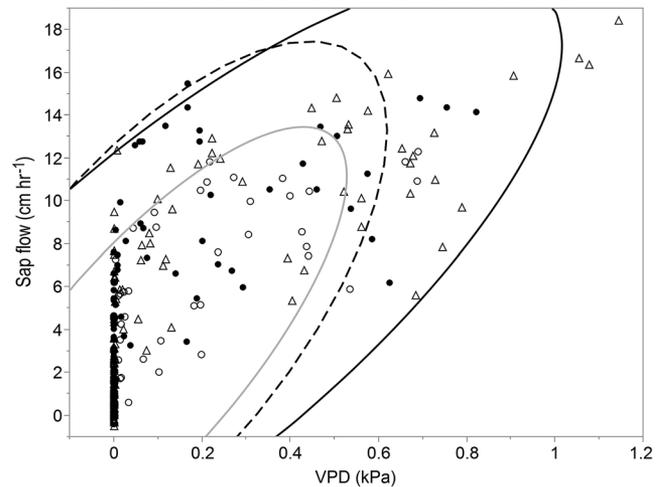


Figure 6. Relationships between mean VPD and daytime sap velocity (cm h^{-1}) in the cloud forest (open circle), forest line (shaded circle) and shrubland (triangle) sites. While the average sap velocity differed among sites ($F = 11.09$, $P < 0.0001$), the slopes of the relationships were not statistically different from one another (data not shown). Density ellipses represent the 99% confidence interval for each site and indicate that there is a high degree of overlap in daytime sap velocity across all sites.

shrubland: $r^2 = 0.58$; cloud forest: $r^2 = 0.87$; Figure 8). An ANCOVA indicated that the slopes of these relationships were not significantly different in the three sites (see overlap of relationships in Figures 6 and 7). While the slopes of these relationships did not differ, the range of sap velocity and VPD was much lower in the cloud forest than in the higher elevation sites (Figures 6–8).

Stomatal conductance

Stomatal conductance was significantly greater in the cloud forest than in the shrubland site (one-way ANOVA: F -ratio 6.6, $P = 0.01$). Although this study took place during a relatively wet period, we found differences in g_s rates over two consecutive days in these sites: the first and second clear days following 3 days of rain. On the first day, there was no clear diurnal pattern

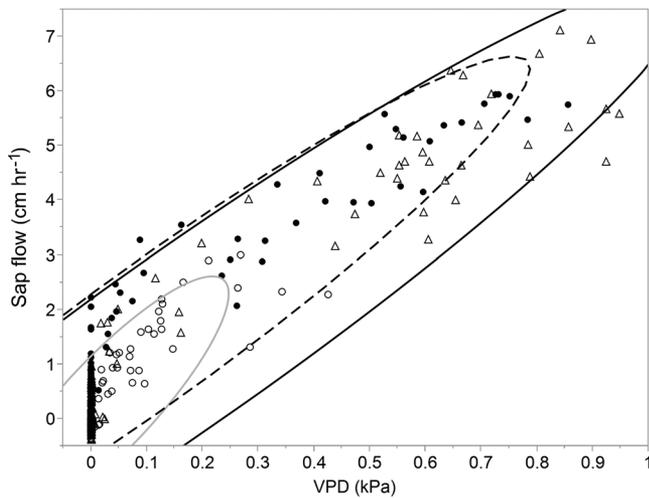


Figure 7. Relationships between mean VPD and nighttime sap velocity (cm h^{-1}) in the cloud forest (open circles), forest line (shaded circles) and shrubland (triangles) sites. While the average sap velocity differed among sites ($F = 26.86$, $P < 0.0001$), the slopes of the relationships were not statistically different (data not shown). Density ellipses represent the 99% confidence interval for each site and indicate that the range of sap velocity is greatly reduced in the cloud forest site when compared with the two drier sites.

in either site (Figure 9a and effect 'time' ns in ANOVA). However, on the second day, g_s rates decreased sharply at midday in the cloud forest site and then gradually increased throughout the afternoon (Figure 9b). On the second day in the shrubland site, midday rates decreased slightly at midday but were generally low throughout the day (Figure 9b). Pairwise t -tests at each time period revealed site differences at the following times: 10:00–11:00 am (Day 2 only), 2:00–3:00 pm (Day 1 only) and 4:00–5:00 pm (Days 1 and 2; see Figure 9).

Leaf water potential

The average Ψ_{leaf} was high in both sites, indicating that these trees did not generally undergo water stress during the study (Figure 10). The average Ψ_{leaf} in the cloud forest site was -0.55 , while in the shrubland site the average Ψ_{leaf} was -0.59 . Site differences were significant only on the second day of measurements ('site' significant in ANOVA: $F = 11.3$, $P = 0.0001$). Pairwise t -tests indicated that this variation was largely due to Ψ_{leaf} during mid-morning (t -tests: ns for all other times, Figure 10b). Ψ_{leaf} data exhibited statistically significant variation throughout the day ('time' significant factor in ANOVA: $F = 20.5$, $P < 0.0001$) although the amount of variation was small (-0.4 to -0.7 MPa).

Pressure–volume curves

Trees from different populations did not vary significantly in any pressure–volume parameters, except for the RWC at the turgor loss point (RWC_{TLP} ; see Figure S1 available as Supplementary Data at *Tree Physiology* Online). Cloud forest trees had an

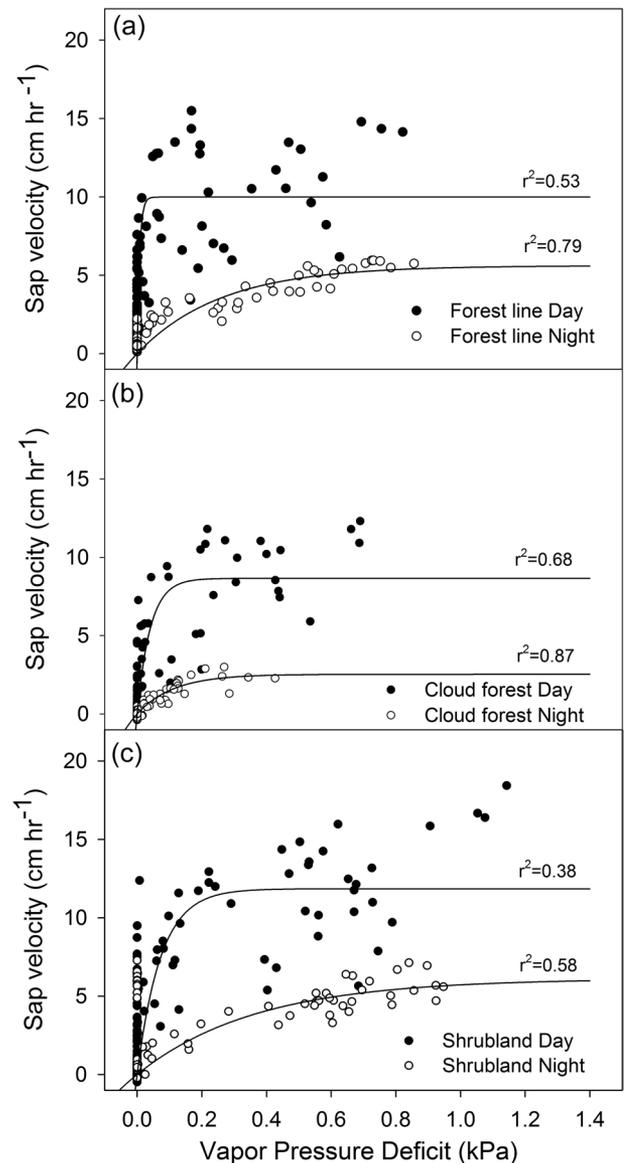


Figure 8. Relationships between observed and expected sap velocity and mean VPD during day and night periods for the forest line (a), cloud forest (b) and subalpine shrub (c) sites. All relationships were fitted with a non-linear line of best fit using SigmaPlot data analysis software, V12.2 (SAS Corp.). All relationships were significant at $P \leq 0.01$; r^2 values for each relationship are shown above the line of best fit.

average RWC_{TLP} of 75%, which was significantly lower than the RWC_{TLP} of forest line and shrubland trees (81 and 80%, respectively). The average Ψ_{TLP} was -1.8 MPa across all sites.

Discussion

We found clear differences in the water relations and the patterns of water use for *M. polymorpha* var. *polymorpha* trees growing above the cloud forest boundary and compared with those trees within the cloud forest habitat. Trees living above the forest line exhibited higher overall rates of sap velocity and

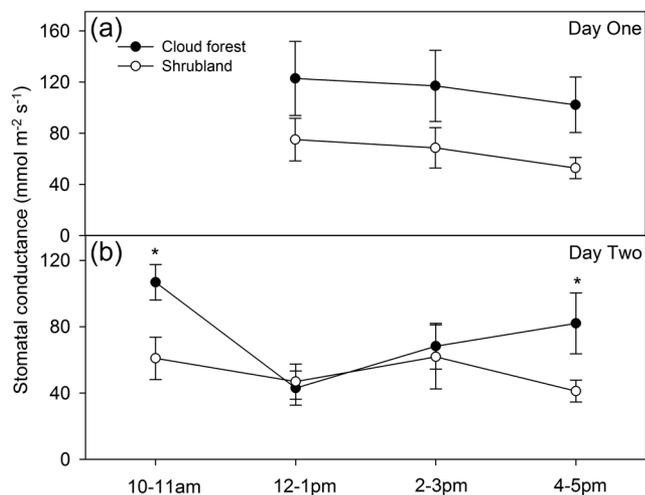


Figure 9. Stomatal conductance (g_s) on two consecutive sunny days following three full days with rain. Measurements were taken in the shrubland (open circle) and in the cloud forest (shaded circle) sites. Data in the top panel (a) were taken on the first clear day (29 August) while data in the bottom panel (b) were taken on the second clear day (30 August). Asterisks indicate times when the average g_s values are significantly different ($P \leq 0.05$) in the two sites.

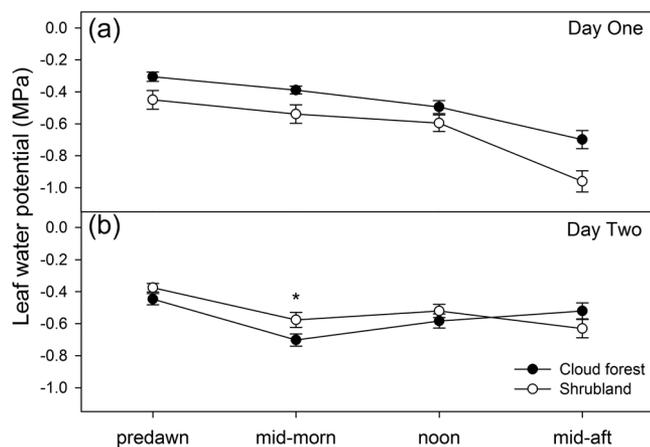


Figure 10. Ψ_{leaf} for trees in the shrubland (open circles) and cloud forest (shaded circles) sites on two consecutive sunny days in August 2010. Data in the first panel (a) were taken on the first sunny day (29 August) following a period of rain while the lower panel (b) shows data on the second clear day (30 August). Analysis of variance (not shown) revealed significant differences throughout the day (time significant factor in analysis, $F = 20.5$, $P < 0.0001$); site differences were only significant on the second clear day ($F = 11.3$, $P = 0.001$). Pairwise t -tests were also performed; the asterisk indicates a significant pairwise difference.

greater nighttime transpiration, but had lower rates of g_s when compared with trees in the cloud forest. Water relations in the shrubland site were significantly affected by VPD, which was consistently higher than in the cloud forest. Due to the small size of the shrubland trees, the lowest F ($l\ h^{-1}$) was observed in this site (Figure 4a). The largest trees in the shrubland site were ~ 20 cm in DBH, while the largest trees at the forest line and cloud forest sites were twice that diameter. Although rates

of sap flow ($\text{cm}\ h^{-1}$) were higher above the forest line (Figure 4b), the smaller tree size and lower density of trees ensure lower water loss at the whole tree and stand levels.

While F was lowest in the shrubland site, a much larger proportion of total transpiration was lost at night above the forest line. This study took place during a relatively wet period; nonetheless, E_N was common and often high in the shrubland site relative to values reported elsewhere. E_N accounted for $>30\%$ of the total daily sap flow on more than half of the days monitored in this study. While E_N has been shown to contribute significantly to daily water balance across a wide range of habitat types (Bucci et al. 2004, Dawson et al. 2007, Goldstein et al. 2008, Novick et al. 2009), the E_N rates observed here are higher than those previously documented for Hawai'i (Dawson et al. 2007). We are not able to conclusively explain our observations of non-zero E_N at the shrubland and forest line sites during times when measured VPD was zero. Dawson et al. (2007) also observed positive sap flow in *M. polymorpha* with VPD near zero at a wet forest site in Hawai'i. They attributed that finding to xylem refilling, i.e., sap flow but no transpiration, which might also be occurring in our case. Alternatively, small RH measurement errors, within the accuracy range for the U23 sensor, could also explain this result. If so, it suggests that a very low rate of transpiration is maintained at times when the sensor indicates saturation, but when a small VPD actually exists and windy conditions prevail. E_N has also been observed in similar circumstances, i.e., windy with very low VPD, in coastal redwood forests in California (Burgess and Dawson 2004).

Even under non-zero VPD conditions, a number of studies have found that a significant portion of nighttime flux may also be due to refilling of embolized vessels and rehydration of tissues in general (Snyder et al. 2003, Daley and Phillips 2006, Wang et al. 2012). While some of our volumetric E_N is likely due to refilling, we hypothesize that these processes contribute very little to the nighttime sap flow rates during our study period because we did not detect a relationship between high rates of daytime sap velocity and sap velocity on that night. If nighttime flux follows a daytime period with high transpiration, it then would follow that most flux detected at night would be due to rehydration rather than transpiration. We did however find a strong correlation between E_N and environmental conditions, indicating that most, if not all, of the nighttime flux measured in this study actually corresponded to transpired water.

Based on atmometer measurements on the leeward slope of Haleakalā reported by Giambelluca and Nullet (1992), nighttime evaporative demand increases with elevation in Hawai'i and averages $0.105\ \text{mm}\ h^{-1}$ (24% of mean daily demand if extrapolated to a 12-h nighttime period) at approximately the mean TWI base height. On the driest night of this study, rates of E_N exceeded 50% of the daily volumetric flow, which is higher than previously published values (Feild and Holbrook 2000, Dawson et al. 2007). This is surprising considering the copious

amounts of rainfall this site receives. However, high rates of E_N may be expected given that both high water availability and high atmospheric demand occur at this site. Given these data, it is likely that E_N contributes significantly to whole-tree water balance at this high-elevation site.

We found a strong correlation between nighttime VPD and rates of E_N at all three sites (Figures 7 and 8). The relationship between nighttime VPD and E_N has been documented across a number of temperate and tropical habitats, and is generally associated with species having poor stomatal regulation (Bucci et al. 2004, Motzer et al. 2005, Dawson et al. 2007). While the slope of the relationship between VPD and E_N was similar in the three sites, rates of E_N above and at the forest line were often twice that of the cloud forest site due to higher VPD above the TWI. Currently, nighttime temperatures are increasing across all elevations in Hawai'i, particularly >800 m, where steep increases in minimum temperatures, approaching 0.5 °C/decade, have been obvious since 1975 (Giambelluca et al. 2008). Increases in nighttime temperature may increase VPD, and according to these data will likely result in increased E_N across the ecotone.

The results of the plant water relation measures indicate that trees at the shrubland site experience greater rates of sap velocity when compared with cloud forest trees due to higher evaporative demand. These high rates of transpiration occurred in the shrubland site despite stomatal regulation. Stomatal conductance was low and was significantly lower than g_s at the cloud forest site even following a precipitation event (~80 vs ~120 mmol m⁻² s⁻¹ respectively, Figure 9a). Stomatal regulation at the shrubland site caused a relaxation in the xylem tension, which resulted in largely non-significant differences in Ψ_{leaf} in the shrubland and cloud forest sites (Figure 10). Our results indicate that trees in the shrubland site close their stomata as an adaptive behavior to buffer some of the effects of high evaporative demand. Water stress can be alleviated as stomata close and tension in the xylem decreases. While this immediate benefit is clear, stomatal regulation also limits carbon fixation and can have long-term consequences for plant health (Adams et al. 2009, Hartmann 2011). While stomatal regulation in the shrubland site is likely to confer some resistance to hydraulic failure, a further increase in evaporative demand is likely to further increase transpiration rates and may lead to drought stress. The degree to which stomatal regulation occurs in response to climatic variability throughout the year at our study sites is however unclear.

Despite evidence of stomatal regulation both above and below the forest line, Ψ_{leafmin} values were close to the turgor loss point (Ψ_{TLP}). High-elevation *M. polymorpha* trees tend to have smaller-diameter vessels (Fisher et al. 2007); however, this does not confer de facto resistance to cavitation (Hoffmann et al. 2011). While average Ψ_{leaf} values were high (−0.4 to −0.9 MPa) in the cloud forest and shrubland sites,

Ψ_{leafmin} at both sites was considerably lower (cloud forest: −1.55; shrubland: −1.8). Ψ_{leafmin} values for the study period were very close to the Ψ_{TLP} obtained from pressure–volume measurements (cloud forest: −1.76; shrubland: −1.89; see Figure S1 available as Supplementary Data at *Tree Physiology* Online). Previous work in the study area showed that Ψ_{leaf} approached or exceeded the theoretical permanent wilting point after a 17-day rainless period (Menard 1999). The clear proximity of Ψ_{leafmin} and Ψ_{TLP} at this site, during a relatively wet period, indicates a potential vulnerability of these populations to changes in moisture availability, particularly increases in the duration of periods with high VPD. Proximity of Ψ_{leafmin} and Ψ_{TLP} is common in plants that withstand lower water potentials. Many plants operate with a small margin of hydraulic safety, making them vulnerable to hydraulic failure under conditions of increased evaporative demand (McDowell et al. 2008). A greater understanding of the safety margin of populations of *M. polymorpha* in and above the cloud forest limit is needed to determine how vulnerable these populations are to changes in climate.

The soils in this region exhibit a rapid response to even a single day with little rainfall despite high annual precipitation; up to an ~15% decline in soil moisture by volume occurred during a rainless period that followed 3 days of high rainfall (S.D. Crausbay, unpublished data). Previous work has found that episodic soil drying occurs at this site, particularly after rainless periods, and that dry soils can induce wilting in *M. polymorpha* trees near the forest line (Menard 1999). Together these data indicate that soil water limitation is likely an important component in tree-level water balance and may be an important factor in determining the forest line under future climate scenarios. Therefore, future research should address the combined effects of VPD and soil water potential on stand water balance above and below the forest line.

Climate changes that could influence moisture availability are likely in Hawai'i. Projections of future rainfall suggest a 5–10% reduction in wet-season rainfall (Timm and Diaz 2009). Projections of the TWI mean base height are uncertain; however, recent trends show that in the past few decades, TWI frequency has increased, and during El Niño events the TWI base height is lower relative to base height position during non-El Niño events (Cao et al. 2007, Crausbay et al. 2014). If this trend in increased occurrence of the TWI continues, the mean VPD above the mean TWI level will likely increase (Cao et al. 2007). Perhaps most clear are the recent trends in increased nighttime temperatures (Giambelluca et al. 2008), which if continued, may also increase nighttime VPD. Although leaves at higher elevations are more tolerant to freezing temperatures (Melcher et al. 2000), at the upper cloud forest limit temperatures <0 °C are increasingly rare in Hawai'i (Giambelluca et al. 2008, Diaz et al. 2011). Our findings indicate that patterns of water relations and water cycling along the cloud forest

line ecotone in Maui are significantly affected by evaporative demand. Increases in temperature or decreases in RH, rainfall and the cloud base of the TWI are likely to affect future water balance and cloud forest distribution.

Conclusions

In this study, we found clear differences in microclimate and water relations of the dominant tree species in three sites that bracket the cloud forest boundary. Our results indicate that high and variable VPDs affect stomatal conductance and transpiration above the cloud forest boundary and that E_N is likely an important component of whole-tree water balance in the shrubland site. Greater atmospheric demand above the TWI causes water loss despite stomatal regulation and is likely a contributing factor in stand density in the shrubland habitat, and thus ecotone position. Further studies are needed to determine how a shift in the TWI would affect stand-level water balance and water stress in cloud forest trees. Recent climate changes at high elevation in Hawai'i that influence VPD, including increased nighttime temperatures (Giambelluca et al. 2008), increased TWI frequency (Cao et al. 2007) and potentially reduced cloud cover (Giambelluca et al. 2008), suggest that this ecotone is vulnerable to climate change impacts. It is likely that a decrease in TWI base height or other changes in moisture availability may have detrimental effects on the water relations of cloud forest trees as well as on stand-level water balance.

Supplementary data

Supplementary data are available at *Tree Physiology* online.

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Conflict of interest

None declared.

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