VARIATION IN SPECIES AND STAND-LEVEL WATER USE FOR NATIVE FOREST AND NON-NATIVE TIMBER PLANTATION IN HŌNAUNAU, HAWAI'I

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We certify that we have read this thesis and that, in our opinion, it is satisfactory in scope and quality as a thesis for the degree of Master of Science in Botany (Ecology, Evolution, and Conservation Biology).

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CHAPTER 1

Introduction

This research was inspired by a desire to understand the dynamics of land use and vegetation change and their impacts on the water resources of Hawai'i. I carried out a case study of plant and stand water use in Hōnaunau Forest Reserve on the island of Hawai'i. The research focused on species and stand transpiration in native forest and non-native timber plantations growing under similar environmental conditions. I also modeled relationships of xylem sap flow and micrometeorological parameters to further explore species-specific variation in water use.

Ecohydrology: Considering the hydrological impacts of vegetation

In the last 50 years, humans have modified the global landscape at rates faster than in any other period in history. In the acquisition of food, water, fuel, timber, and fiber, human activities have negatively affected the ecosystem services sustaining the production of these very resources (DeFries et al. 2004, Foley et al. 2005, Millennium Ecosystem Assessment 2005). Water supplies, for example, have been affected by hydrological changes associated with changes in land use and vegetation cover (Huxman et al. 2005, Millennium Ecosystem Assessment 2005, Brauman et al. 2007). As demand for fresh water increases, it is increasingly critical that we understand the hydrological implications of different land uses.

To this end, the rapidly developing field of *ecohydrology* aims to characterize the dynamic role of vegetation in the land-based water cycle (see Baird and Wilby 1999, Eagleson 2002, Rodriguez-Iturbe and Porporato 2004, Eamus et al. 2006). Plants play an important role in not only local water balance but global atmospheric circulation by altering patterns of evaporation at the land-atmosphere interface (Sellers et al. 1997). Total evaporative losses are usually

referred to as evapotranspiration (ET); these include evaporation from the soil surface and vegetation-mediated evaporation: water intercepted by plant surfaces (interception) and water used by the plant directly as a consequence of stomata opening for photosynthesis (transpiration). Although the contribution of transpiration to ET varies depending on precipitation (frequency and intensity), microclimate, and the vegetation itself, transpiration is typically a large component of ET, 20-90% in different forested systems (Barbour et al. 2005).

Evidence of hydrological-ecological interactions can be found in various environments around the world where hydrological changes have followed vegetation change. Streamflow increases have followed deforestation (Bosch and Hewlett 1982) and conversely, streamflow decreases have followed the afforestation of grasslands (Farley et al. 2005). While this evidence supports the conclusion that vegetation types differ in hydrological impacts, Farley et al. (2005) demonstrated additionally that not all forests are equal. Different species can have varying effects on surface runoff; afforestation with eucalyptus, in particular, caused significantly larger decreases in annual surface runoff than afforestation with pines (-202 mm $year^{-1}$ and -167 mm $year^{-1}$, respectively).

These hydrologic changes are generally attributed to changes in transpiration rates as transpiration can vary strongly between different vegetation types (Roberts 2000). Even among forests of different species, transpiration estimates range from 151 mm $year^{-1}$ for oak to 427 mm $year^{-1}$ for scots pine (Baird and Wilby 1999); however, these stand-level values do not control for site environmental differences or stand age. Among forest stands of the same species but different age, studies in Australia and Europe indicate that younger stands transpire more than old stands (Roberts et al. 2001, Vertessy et al. 2001, Delzon and Loustau 2005) with a possible explanation being a decrease in plot sapwood area or leaf area index (LAI) with stand age.

A particular interest in the effects of invasive species on stand-level transpiration has driven comparative studies of species-level water use. This research on species water use has,

however, focused on only a few hydrologic systems—arid, semi-arid, riparian—and especially on certain taxa, including *Tamarix ramosissima* (e.g., Sala et al. 1996, Nagler et al. 2003), and vegetation types, such as grasslands or shrublands (e.g., Le Maitre et al. 1996, Cayrol et al. 2000). These studies have provided valuable ecohydrological insight: for a given leaf area, *Tamarix* water use varies little from other native species but is able to operate at lower leaf water potentials than native phreatophytes. Thus *Tamarix* is able to maintain high leaf area even under stressful conditions (Sala et al. 1996, Cleverly et al. 1997, Nagler et al. 2003) and use more water at stand-level.

Ecohydrology in Hawai'i: Do rates of native and alien transpiration differ?

The accurate quantification and modeling of forest evapotranspiration is especially important in small watershed systems as found in Hawai'i, where wet, montane forested areas of catchments capture orographic rainfall and recharge groundwater supplies for growing numbers of downstream users. The spatially-explicit quantification of water balance fluxes becomes even more important when we consider that the rapid spread of non-native trees and the current trend of afforestation to mitigate soil erosion in Hawai'i's watersheds may be affecting recharge in these high rainfall and recharge areas. However, there have been very few studies of plant- and stand-level water balance studies for Hawaiian forests (Santiago et al. 2000, Restom Gaskill 2004).

In my first study, I utilized thermal dissipation and heat balance sap flow technology to address whether native and non-native trees under similar wet climates transpire at different rates and whether stands dominated by these species differ in rates of ground area-based transpiration. In the second study, I used concurrent measurements of sap flow and micrometeorology to determine species-specific relationships between sap flow and environmental conditions and gain insight into species' ecophysiology.

Comparing species

Comparative leaf-level studies in Hawai'i of alien and native plants raise the possibility that alien species may often use more water than native species. While the differences have not always been significant (Cordell et al. 2002), past studies in Hawai'i show, on average, higher rates of net CO_2 assimilation and relative growth (RGR) for alien plants compared to native plants (Pattison et al. 1998, Baruch and Goldstein 1999, Baruch et al. 2000, Stratton and Goldstein 2001, Cordell et al. 2002, Funk and Vitousek 2007). These higher rates of photosynthesis for alien plants also suggest higher leaf-scaled rates of water use since photosynthesis and transpiration are simultaneously controlled by stomatal conductance. Based on these observations, I expected transpiration to be higher for individual trees of alien species compared to native when leaf area per individual was similar; in cases where leaf area is higher for an individual, whole plant water use should also be greater for the alien tree. This research, conducted in a wet forest system, will be useful for indicating how native and non-native species under non-water limiting conditions may vary in their water use due simply to intrinsic species differences.

Comparing stands

While alien forests in Hawai'i consist of relatively recent introductions, the forests of native species are usually unmanaged older forests resulting from natural succession and regeneration; there are likely differences of several hundred years in the ages of trees at the two forests. Stand transpiration is also affected by forest structure. While the alien-dominated forests are often characterized by a monotypic closed-canopy and little understory, in Hawai'i, the native forest is more open with a mid-canopy and thick understory layer of tree ferns, shrubs, and epiphytes. These differences in forest structure may lead to even transpiration, with the developed understory of the native forest compensating for decreased canopy transpiration. Or it is possible

that a denser understory might not fully compensate for decreased canopy as leaf area-based transpiration has been found to be lower for the understory than for the dominant canopy species {Vertessy, 2001 #107}.

For stand level estimates, when alien-dominated forest is younger than native forest as they are in our system, one would further expect the alien stands to have higher rates of transpiration. Thus I hypothesized that stands of native trees and alien trees will differ in their respective rates of stand transpiration with alien-dominated stands having higher transpiration due to higher individual plant water use and equal or higher tree density and sapwood area.

Comparing responses

Bulk sap flow methodologies, such as the methods employed here, facilitate the modeling of sap flow and stomatal conductance as a response to environmental variables at diurnal, daily and even seasonal and interannual timescales (Jarvis 1976, Meinzer et al. 1993, Sturm et al. 1998, Oren et al. 1999a, Oren et al. 1999b, Granier et al. 2000, Oren and Pataki 2001, Oren et al. 2001, Phillips and Oren 2001, Pataki and Oren 2003, Ford et al. 2005). This work has led to the development of empirical models describing relationships between sap flow or canopy conductance and environmental variables, including irradiance, temperature, and vapor pressure deficit on diurnal timescales. Species-specific coefficients may be obtained to allow estimation of sap flow from environmental conditions; however, there is not yet a standard simple model for characterizing this response. I used a model-selection approach to assess the suite of empirical and statistical models appropriate for each species studied. By fitting multiple models, I investigated differences among species' responses to environment.

CHAPTER 2

Does native forest conserve water relative to alien plantation? Species composition and stand structure influence water use in a Hawaiian wet forest

Abstract

Native forest trees have been claimed to use water conservatively and enhance groundwater recharge relative to faster-growing non-native species. This argument, if true, could increase the value of native forest preservation and restoration, especially where forests also play a role in mitigating soil erosion, as in watersheds in Hawai'i. Few studies have examined whether native and non-native plant water use differ at tree and stand level or to what extent species composition matters for stand level water use. We measured plant transpiration for over eight weeks in a continuous mosaic of native *Metrosideros polymorpha* forest and non-native *Eucalyptus saligna* or *Fraxinus uhdei* plantation in Hōnaunau, Hawai'i, for dominant tree species and dominant understory *Cibotium* tree ferns. Heat dissipation and heat balance sap flow methods were used to measure plant sap flow, and we estimated total stand water use by scaling up sap flow measurements by ground area-based sapwood and leaf area estimates from vegetation surveys. *M. polymorpha* had the lowest whole-tree daily water use (8 kg day^{-1} or 200 kg m^{-2} of sapwood day^{-1}), less than half that of the average *E. saligna* or *F. uhdei*; *M. polymorpha* also had the lowest maximum instantaneous transpiration rate. Stands dominated by *F. uhdei* had higher scaled-up water use than stands dominated by *M. polymorpha* due to 2.5-fold greater sapflow rates, five-fold greater sapwood allocation, and two-fold greater dominant tree density. In native stands dominated by *M. polymorpha*, *Cibotium* leaf area contributed to over 70% of water use, indicating the critical role of tree ferns in native wet forest water balance. Scaled-up forest water

use was influenced by various factors, including species composition, stem density, tree sizes, tree species' sapwood allocation, and understory *Cibotium* contribution. These findings highlight the importance of constituent species and tree sizes in forest water uptake and indicate the potential for substantially more conservative water use by native wet tropical forests.

Introduction

In the last 50 years, humans have modified the global landscape at rates faster than in any other period in history. In the acquisition of food, water, fuel, timber, and fiber, these activities have negatively affected the ecosystem services sustaining the production of these very resources (DeFries et al. 2004, Foley et al. 2005, Millennium Ecosystem Assessment 2005). For instance, changes in land use and vegetation cover have hydrological impacts that affect water supplies (Huxman et al. 2005, Millennium Ecosystem Assessment 2005, Brauman et al. 2007). As demand for fresh water increases, it becomes increasingly critical that we understand the hydrological implications of different land uses.

Recognition of the important and dynamic role of vegetation in shaping terrestrial water balance has grown tremendously with recent developments in the field of ecohydrology (see Baird and Wilby 1999, Eagleson 2002, Rodriguez-Iturbe and Porporato 2004). Plant transpiration, or water use, is a particularly important vegetation-controlled evaporative flux that removes precipitation otherwise contributing to streamflow or groundwater recharge. Numerous catchment-level studies highlight the effects of vegetation change on hydrology, where streamflow increases followed deforestation (Bosch and Hewlett 1982) and streamflow decreases followed the afforestation of grasslands, shrublands and croplands (Farley et al. 2005, Jackson et al. 2005). It is well established that vegetation types vary in water use; however, data on water use by assemblages of different species compositions within a given vegetation type (forest, shrubland, grassland) are scarce. We are far from having a predictive understanding of the current

and future impacts of land use and land cover change at a range of scales. A common hypothesis is that catchment-level water use should be influenced most strongly by climate and soil, not species traits, and similar rates of canopy water use would be expected for sites with similar rainfall and leaf area index (Hatton et al. 1998, Zeppel et al. 2006). However, stand-level differences in water use have been observed between young and older stands of eucalyptus (e.g., Roberts et al. 2001, Vertessy et al. 2001, Moore et al. 2004, Delzon and Loustau 2005), due to a greater tree density, sapwood-specific water uptake and/or leaf area index, and this evidence suggests we could find water use differences also among stands varying in species composition.

In Hawai'i, rainfall in upland areas feeds the ground- and surface waters that support all urban and agricultural activities. Thus, accurately quantifying the hydrological impacts of land management in these regions is critical for managing water supplies for a growing population. Of particular concern are the impacts of alien plant species on hydrology, as non-native species are an increasingly large percent of the islands' vegetated cover. As energy initiatives encourage the establishment of biofuel crops and tree plantations for local timber and carbon credits, the incentive for fast-growing alien crops with high invasive potential may create new problems for water management (Richardson 1998, Jackson et al. 2005). Physiological studies assessing alien plant water use in Hawai'i indicate higher leaf-level gas exchange rates for alien plants relative to co-occurring or phylogenetically related native plant species (Pattison et al. 1998, Baruch and Goldstein 1999, Baruch et al. 2000, Stratton and Goldstein 2001, Cordell et al. 2002, Funk and Vitousek 2007). As photosynthesis and transpiration are coordinated through stomatal conductance, this suggests alien species may use more water than native species at leaf level. However, few studies of alien species in Hawai'i focus on the whole plant and stand scales relevant to hydrology; data at these scales are available only for single species in different sites (Santiago et al. 2000), for alien species at a single site (Restom Gaskill 2004), or for irrigated agricultural crops (e.g., Ekern 1970).

We measured the water use in forest stands representing two forested land use types found across the Hawaiian Islands: native forest dominated by *Metrosideros polymorpha* and timber plantation dominated by alien trees *Fraxinus uhdei* and *Eucalyptus saligna*. Whether native and alien species differ in water use at the individual and stand levels has implications for land management, restoration, and conservation. Our study addressed, for a particular forest site in Hawai'i: 1) whether different tree species transpire at different rates, and 2) whether stands dominated by these different species would differ in rates of ground area-based transpiration. We expected transpiration might be higher for alien timber species compared to native tree species on a per-leaf area, on a per-sapwood area and on a whole-tree basis. We hypothesized that alien-dominated stands would differ from native-dominated stands in total water use. We hypothesized stand-level water use would be mediated by adjustments in tree sizes and stem densities, and contrasting abundances of understory tree ferns. We further determined the differences among species in daytime versus nocturnal water use and the degree to which water use per unit leaf area was consistent with other leaf functional traits.

Methods

Study site and species

The study was conducted at Hōnaunau Forest Reserve, a 4250-hectare patchwork of forest and tree plantations owned by native Hawaiian legacy trust Kamehameha Schools on the leeward slope of Mauna Loa, Hawai'i Island. Wild cattle populations had strongly impacted the forest by the time they were removed in the 1950s, and 350 ha were cleared and planted with 37 primarily nonnative timber species (Carlson and Bryan 1959). Since then, the area has been left largely unmanaged. We selected two sites to represent native and alien-dominated vegetation in the *ahupua'a* (land divisions) of Kahauloa (N 19.482°, W 155.869°) and Hōnaunau (N 19.435°, W 155.844°), respectively. The sites are 5 km apart, at 1000 m elevation on 750-1500 year old 'a'ā

lava flows (Lockwood 1995) of Puna-Udarent soil type (Soil Survey Staff , Niemeyer 2006). These sites were selected for their high substrate permeability and low slope which minimize horizontal fluxes; runoff occurs only in large storm events. At Kahauloa and Hōnaunau, mean annual precipitation is respectively 1520 and 1450 mm, mean annual temperature 17.5 and 17.3 °C, and relative humidity annual minimum/maximum 67.9/97.8% and 67.6/98.0% (Giambelluca and Cuo in prep).

In the native old-growth forest of Kahauloa, the study species were endemic canopy tree *Metrosideros polymorpha* Gaud. (Myrtaceae; common name *'ōhi'a*; Wagner et al. 1999) and endemic tree ferns *Cibotium glaucum* (Sm.) Hook. & Arn. and *Cibotium menziesii* Hook (Cibotiaceae; common name *hāpu'u pulu* and *hāpu'u 'i'i*; Palmer 2002, Smith et al. 2006). At the non-native tree plantation site in Hōnaunau, we studied *Eucalyptus saligna* Sm (Myrtaceae; Wagner et al. 1999) and *Fraxinus uhdei* (Wenzig) Lingelsh (Oleaceae; Wagner et al. 1999) in monotypic stands of approximately 2 ha and 25 ha respectively.

Sapflow measurements

Measuring sapflow for tree species

From August through September 2006, we monitored sapwood sap flux density for six individuals of each dominant tree species. All studied individuals of a given species were located within a 20x20m plot. We measured tree sapflow using modified Granier-style heat dissipation probes with 1 cm long sensor tips (James et al. 2002). To account for circumferential and radial variation in sapflow, two to five sensors were installed in each tree at 2-6 cm depth, positioned around the circumference at 1.3m height. The heated and reference probe tips of each sensor were positioned 10 cm apart vertically, and replicate sensors were installed at least 10 cm apart around the tree circumference to avoid heating the reference probes. We wrapped the trees with bubble wrap and aluminum foil to protect the sensors and reduce the effects of external thermal gradients

(Lu et al. 2004). The heated probe tips were supplied with continuous power via a voltage regulator circuit connected to 6V deep-cycle batteries (models T105 and T125, Trojan, Santa Fe Springs, CA, USA). We measured differential voltage between the two probe tips every minute and recorded averages every 10 minutes with AM16/32 multiplexers connected to CR1000 dataloggers (Campbell Scientific, Logan, UT) powered by 7Ah 12V sealed lead-acid batteries (Radio Shack, Fort Worth, TX).

We calculated sap flux density (v) for each interval using the calibration developed by Granier (1985) and recently validated for our modified probe design (McCulloh et al. 2007). Sap flux density can be estimated from the temperature difference between heated and reference probe tips (ΔT), which is proportional to the measured voltage difference between probes (ΔV; Lu et al. 2004):

$$v = 119 * \left(\frac{\Delta V_m - \Delta V}{\Delta V}\right)^{1.231} \quad (g \cdot m^{-2} \cdot s^{-1}) \quad \text{eqn 1}$$

where ΔV_m is the maximum voltage difference corresponding to the maximum temperature difference during (theoretical) zero flow each night, and ΔV is the voltage difference corresponding to the temperature difference at any point in time, which decreases as flow increases. While ΔV_m is usually assumed to be constant, we found that ΔV_m decreased over time as our deep cycle batteries discharged, so we used linear interpolation to estimate a ΔV_m value for each 10-minute interval between the measured ΔV_m values for successive nights.

To account for radial variation within the tree, we calculated whole-tree sap flux by weighting the measured sap flux density for each probe by an associated sapwood annulus (Hatton et al. 1990). We defined concentric annuli below the cambium as delimited by an outer and inner radius (r_i and r_{i-1}) midway between successive probe tips. Sap flux for each annulus was calculated by multiplying the measured sap flux density at a given depth (v_i) by the corresponding annulus area; these were summed for n probed depths to obtain whole-tree sapflow (Q):

$$Q = \sum_{i=1}^{n} \pi(r_i^2 - r_{i-1}^2)v_i \qquad (g \cdot s^{-1}) \quad \text{eqn 2}$$

We determined sapwood-area specific sapflow rates by dividing these whole tree flow rate values by tree sapwood area (see *Measuring tree sapwood area*) . The resulting data were used to plot diurnal curves for individual trees (Fig 1). We characterized daily parameters of these curves to compare sapflow between species (see *Water use parameters and statistical analysis*).

Measuring tree sapwood area

We determined cross-sectional sapwood area of the study trees from trunk cores extracted at the end of the study (to avoid any possible impacts of coring on sapflow patterns). For each tree, we measured diameter at 1.3m with a dbh tape and extracted cores of 5-15 cm length with a 4.3mm increment borer, noting outer bark and phloem depth.

We used several methods to determine sapwood depth, including staining of living parenchyma with triphenyl tetrazolium chloride in a phosphate buffer solution (Sigma-Aldrich; Spicer and Holbrook 2005), visual observation of vessel translucency, and projection from sapflow profiles of the depth at which flow was zero. *F. uhdei* had living parenchyma across the full extent of the cores, and sapflow measurements indicated that maximum flow did not significantly decrease with depth, so we assumed all of its sapwood was uniformly water-conducting. The *E. saligna* sapwood-heartwood boundary was determined by visually inspecting the point at which vessels were no longer translucent; sapflow depth profile data showed very low flow beyond this transition. Water-conducting sapwood in *M. polymorpha* was less distinct than in *E. saligna* but could be resolved similarly.

We calculated sapwood area as the difference between the area of the cross-sectional disc from the cambium inward and the area of the heartwood cross-section ($\pi r^2_{outer} - \pi r^2_{inner}$), where r_{outer}=dbh/2- (bark+phloem depth) and r_{inner} =dbh/2-(bark+phloem+sapwood depths).

Estimating tree leaf area

We estimated total leaf area for the trees measured for sapflow by multiplying by the number of tree branches by an average leaf area per branch, determined from branches sampled from three other similar trees for each species (using a LI-COR 3100C leaf area meter; LI-COR, Lincoln, NE, USA). For *E. saligna*, branches were inaccessible, and we used fallen branches. In cases where branch leaf area was very large, we estimated leaf area by dividing total branch leaf dry mass by leaf mass per area calculated from a subsample of 10 or more leaves on the branch, with dry mass determined after oven drying at 70°C for 48h. We estimated the number of branches on the sapflow trees by visual inspection of photographs (Santiago et al. 2000). While these estimates are subject to uncertainty, like those in previous studies that have estimated leaf area of tall canopy trees, they should allow robust comparisons of sapflow per leaf area across species (e.g., Meinzer et al. 1999, Santiago et al. 2000).

Measuring sapflow for tree ferns

From August through October 2006, we measured bulk sapflow for healthy fronds of seven individuals of dominant tree fern *Cibotium glaucum*. Although we measured sapflow for two *C. menziesii*, results are not reported here as low densities in the field did not allow sufficient replication. We took measurements every minute and recorded 15-min averages using a commercial stem heat balance collar system placed on frond stipes (Dynamax Flow32 system, Dynamax, Houston, TX, USA) powered by 12V deep-cycle batteries connected in parallel (model 30XHS Trojan, Santa Fe Springs, CA, USA; 85Ah Kirkland, Issaquah, WA, USA; 60 Ah Daleco,

Kailua-Kona, HI, USA). We calculated bulk sapflow from voltages of four thermocouples per collar using the manufacturer's calculation procedures (Sakuratani 1981, Baker and van Bavel 1987), and determined sapflow per frond area by dividing by frond area (minus that of the stipe) determined after the study using a LI-COR 3100C leaf area meter.

Measurements of leaf functional traits

We measured leaf functional traits for both tree and tree fern species using samples from branches and fronds collected for branch and frond area measurement. We determined specific leaf area (SLA, cm^2g^{-1}) as leaf area divided by mass after drying at 70°C for 48 hours. Leaves of three individuals per species were analyzed for nitrogen concentration per mass (N_{mass}, $g\ g^{-1}$) and carbon isotope composition ($\delta^{13}C$, ‰) using high temperature combustion in an elemental analyzer (Costech ECS 4010; Valencia, CA, USA), with effluent passed into a continuous flow isotope ratio mass spectrometer (CF-IRMS; ThermoFinnigan Delta V Advantage with a Conflo III interface; ThermoFisher Scientific; Waltham, MA, USA; (Fry et al. 1996). Samples were dry-ashed in glass vials (Miller 1998), dissolved in 1M hydrochloric acid and analyzed for phosphorus per mass (P_{mass}, $g\ g^{-1}$) using inductively-coupled plasma-optical emission spectrometry (ICP-OES; Varian Vista MPX Instrument, Varian Inc., Palo Alto, CA, USA; (Porder et al. 2005). Concentrations of nitrogen and phosphorus per area (N_{area} and P_{area}, $g\ m^{-2}$) were determined as N_{mass} and P_{mass} divided by SLA.

We measured stomatal traits from nail polish impressions of the undersides of tree leaves, imaged at 100-400x magnification under a light microscope and analyzed using ImageJ (http://rsb.info.nih.gov/ij); leaves of all species were hypostomatous (having stomata only on leaf undersides). For trees, we assessed average stomatal density and pore length for three fields of view for each impression, and averaged values for one impression for each of three leaves per branch sampled, and then averaged for three branches per individual tree, for three individuals per

species (except two individuals for *E. saligna*, as branches were too high to sample). For tree fern fronds, we made measurements on fronds from seven *C. glaucum* individuals. We calculated an index of stomatal pore area per leaf area (SPI) as the product of stomatal density and the square of pore length (Sack et al. 2003).

Scaling sapflow to the stand

Allometries for sapwood area and frond area

For our three study tree species, we scaled sapflow rates up to the stand level using sapwood area. We determined species-specific sapwood area versus dbh relationships by combining data from our six sapflow study trees per species with dbh and trunk core data for 9-24 additional trees of each species sampled along 100 m transects within each stand type. We calculated sapwood area for given trees (see *Measuring tree sapwood area*) and determined the coefficients of the least-squares linear regression of ln-transformed sapwood area against ln-transformed dbh (Supplementary Material, Table 2.S1).

For the tree fern, *C. glaucum*, we scaled sapflow rates to stand level using frond leaf area. We determined frond area for tree ferns using an allometry relating ln-transformed frond leaf area to ln-transformed frond length index (FLI), an easily-measured characteristic, the projected horizontal frond length from its base at caudex insertion to its distal tip (Arcand et al. *in press*). We used an allometric relationship based on ten mature fronds from our site, including our seven sapflow study fronds (see *Measuring sap flow for tree ferns*), and eight *C. glaucum* in a similar Hawaiian wet forest (Arcand et al. *in press*), since the allometric relationships were statistically similar in slopes and intercepts.

Estimating total stand water use

For each of the three stand types (*M. polymorpha*, *E. saligna*, and *F. uhdei*–dominated), we surveyed five to six 20m x 20m plots to determine total sapwood and *Cibotium* leaf area on a ground-area basis. In eight plots with high *Cibotium* densities, we surveyed these in a 10 m x 20 m plot within the larger plot. In each plot, we recorded species and dbh for every stem with dbh greater than 1 cm. For *Cibotium*, we recorded species (*C. glaucum* or *C. menziesii* Hook), number of live fronds, and FLI. From these data, we applied our species-specific allometries (Supplementary Material, Table 2.S1) to obtain estimates of plot sapwood area for each tree of our study species (SA_{plot}) and plot *Cibotium* frond area (FA_{plot}). For each plot with *n* trees and *m* *Cibotium*,

$$SA_{plot} = \sum_{i=1}^{n} e^{a} \cdot D_i^{b} \cdot c \qquad (\text{cm}^2) \quad \text{eqn 3}$$

$$FA_{plot} = \sum_{i=1}^{m} e^{a} \cdot L_i^{b} \cdot c \cdot j_i \quad \text{for } j \text{ fronds} \qquad (\text{m}^2) \quad \text{eqn 4}$$

where *D* and *L* are tree diameter and tree fern projected frond length, a and b are allometric coefficients, and c is the allometric correction coefficient (see Supplementary Material, Table 2.S1; Baskerville 1972, Sprugel 1983). We estimated total tree fern leaf area using the *C. glaucum* leaf area-FLI relationship as *C. glaucum* was the dominant tree fern species across stand types.

We estimated total sapflow for each plot by multiplying the daily-integrated sapflow for each study species by its stand sapwood area (for trees) or frond area (tree ferns). We summed these components to estimate combined canopy tree and understory *Cibotium* transpiration.

Water use parameters and statistical analysis

Comparing species

We extracted daily parameters from diurnal sapflow curves (Fig. 1) using R version 2.5.1 (R Core Development Team 2007; all scripts available on request). We determined integrated diurnal sapflow rate (E_{tot}, kg/day), daily maximum sapflow rate (E_{max}, g/s), time of maximum sapflow (t_{max}, hhmm), "peak" period of sapflow (defined as the period with >50% of maximum sapflow; Δt_{peak}, hours), and nocturnal sapflow as a proportion of total diurnal sapflow (with nocturnal flow defined as occurring between 1830 and 0630; E_n/E_{tot}, percent). Data for each parameter were averaged over the 2-month measuring period for each individual tree, and these individual means were ln-transformed to achieve better homogeneity of variance. These data were compared using a one-way analysis of variance, followed by Tukey's HSD comparisons with family-wise confidence level of 0.05 (using *aov* and *TukeyHSD* functions in R version 2.5.1; Zar 1999). We performed the same analyses for the parameters scaled by sapwood area and leaf area. To account for the importance of day-to-day variation in sapflow, we also compared species for each parameter in a repeated-measures analysis of variance, blocking by individual trees and tree ferns. The analyses were performed for the study periods during which data were collected simultaneously for every individual tree (19 days) and for individual trees and tree ferns combined (12 days).

Comparing stands

To determine stand-level sapflow, we utilized nonparametric bootstrapping methods that accounted for the multiple sources of error (Blukacz et al. 2005). For each of the 5-6 plots surveyed per stand type, we estimated sapwood area (or, for tree ferns, frond area) and sapflow for each measured individual and summed these for plot-level areas and rates. We repeated this procedure 2000 times, each time using a new set of allometric coefficients obtained by

resampling our dbh-SA and FLI-FA datasets with no replacement and calculating sapwood area or frond area for each individual tree or tree fern (see *Scaling sapflow to the stand*); we added a resampled allometry residual to account for variance of the estimate. We multiplied this corrected estimate of individual sapwood area or frond area by a resampled daily rate of sapflow per sapwood area (or frond area) for the appropriate species to determine an overall daily sap flow estimate for each individual in the plot. We then summed for all trees in a given plot to obtain stand sapwood area and tree sapflow; we summed across all tree ferns to obtain stand frond area and tree fern sapflow. We found the mean values of the 2000 bootstrap replicates and from these determined bias-corrected and accelerated confidence intervals for mean stand traits (Efron and Tibshirani 1993).

Our approach to estimating stand-level water uptake rates should be robust for resolving any substantial differences across stands of varying composition, as using sapwood to scale up sapflow rates by has been used previously to estimate stand water use in multi-species forests of Tennessee and the Pacific Northwest (e.g., Wullschleger et al. 2001, Moore et al. 2004). We note that our estimates of stand-level water use are conservative and include a level of uncertainty because they neglect on average 13% percent of stand basal area made up by species not measured for sapflow. Our estimates also assume the sapflow measurements and diameters of our study trees to be representative of their species for a wide range of individual sizes across the stand. We conducted additional calculations to ensure that these uncertainties would not have affected our findings of differences across stands in estimated sapflow.

Results

Species differences in water uptake

The mean maximum instantaneous sapflow per sapwood area varied four-fold from *M. polymorpha* (7.9 ±1.9 g $m^{-2}s^{-1}$, mean ± SE) to *F. uhdei* (31.1 ±4.8 g $m^{-2}s^{-1}$), with *E. saligna*

intermediate (16.0 ± 2.8 g $m^{-2}s^{-1}$; Fig. 2A). At whole-tree level, maximum sapflow rates varied seven-fold, with that of *M. polymorpha* (0.27 ±0.19 g s^{-1}) less than half that of *E. saligna* (1.08 ± 0.34 g s^{-1}) which in turn was half that of *F. uhdei* (2.03 ±0.46 g s^{-1}; Fig. 2A, inset).

Species also varied strongly in *total* daily sapflow, with *M. polymorpha* having less than 50% the sapwood area-specific sapflow of the other two species, 207 ± 53 kg m^{-2}, compared with 488 ± 80 kg m^{-2} and 513 ± 81 kg m^{-2} for *E. saligna* and *F. uhdei* respectively, which did not differ significantly (Fig. 2B). At the whole-plant level, *M. polymorpha* mean diurnal water use (7.6 ± 5.4 kg) was less than 30% that of *E. saligna* (33.3 ± 11.1 kg) and *F. uhdei* (33.8 ± 7.9 kg; Fig. 2B, inset).

Species showed strong variation in temporal sapflow patterns, quantified as the timing of maximum flow, the duration of peak flow, and the proportion of diurnal flow occurring outside of daylight hours (see Fig. 1). On average, *E. saligna* reached maximum flow at 0937 (±7 min), over an hour earlier than *M. polymorpha*, *F. uhdei* and *C. glaucum* (1048 ±8 min, 1052 ±3 min and 1105 ±6 min respectively) . The duration of peak flow was over 50% longer for *E. saligna* and *M. polymorpha* than for *F. uhdei* (6.9±0.5, 6.0±0.3, and 3.9±0.3 hours respectively); the duration of peak flow for *C. glaucum* was intermediate at 4.7±0.6 h. Both *E. saligna* and *M. polymorpha* exhibited strong nocturnal sapflow at 30 ± 3% and 24±4% of total sapflow respectively, while *F. uhdei* and *C. glaucum* showed relatively low rates of nocturnal sapflow (5± 2% and 4±1% respectively; Supplementary Material, Table 2.S2 and Figure 2.S1).

Leaf area-scaled sapflow varied strongly among tree species. *M. polymorpha* and *E. saligna* had maximum sapflow rates per leaf area of 2.05 ± 0.59 x10^{-3} g m^{-2} s^{-1} and 4.66 ± 0.79 x10^{-3} g m^{-2} s^{-1} respectively, while *F. uhdei* had a rate of 31.9 ± 4.6 x10^{-3} g m^{-2} s^{-1}. Understory *C. glaucum* leaf-area specific sapflow rates fell within the same range as for the tree species at 9.49 ± 1.10 x10^{-3} g m^{-2} s^{-1} (data not shown).

Tree species also varied strongly in several leaf functional traits (Supplementary Material, Table 2.S3). *M. polymorpha* had lowest N and P concentrations per-mass and per-area, and *E. saligna* highest N and P per mass and per area. SPI was lowest for *M. polymorpha* and highest for *F. uhdei*. Tree species were indistinguishable in their $\delta^{13}C$ discrimination and SLA. *C. glaucum* had higher SLA and SPI values, 1.5 to 2.5 times larger than the highest tree species values, and *C. glaucum* had N and P per mass values comparable to the highest tree species values.

Stand-level differences in water uptake

The three stand types studied were each dominated by one of the study tree species. In native old growth stands, *M. polymorpha* accounted for 87.7 ±5.0% of the total living tree basal area, with the remainder consisting largely of *Ilex anomala* (4.9%) and *Acacia koa* (2.3%; Supplementary Material, Table 2.S4). In the *E. saligna*- and *F. uhdei*-dominated timber plantations, *E. saligna* and *F. uhdei* accounted for 89.6 ±3.5% and 84.7 ±5.7% of the living basal area respectively, with the remainder consisting largely of remnant *M. polymorpha* (4.3 and 9.3%) and *Acacia koa* (1.6 and 6.0%).

The three stand types differed strongly in tree sizes and tree densities (Fig. 3A-C). The live stem density of the dominant species ranged two-fold from stands of *E. saligna* and *M. polymorpha* (415 ± 57 and 580 ± 106 stems ha^{-1} respectively) to stands of *F. uhdei* (1020 ± 99 stems ha^{-1}). Mean dominant tree species diameter (> 5cm dbh) also ranged two-fold, from *E. saligna* to *M. polymorpha* to *F. uhdei* (39.7 ±2.2 cm, 25.8 ±3.9 cm and 19.9 ±1.3 cm respectively). *F. uhdei* had highest sapwood allocation (see Supplementary Material, Table 2.S1). The variation in stem density, stem diameters, and sapwood allocation led to a four-fold variation in sapwood area per ground area among stands, (31.4 ±2.1, 12.2 ±3.5, and 8.7 ±2.6 $m^2 ha^{-1}$, for stands dominated by *F. uhdei*, *E. saligna* and *M. polymorpha* respectively; Fig. 3A-C).

Stand types also varied strongly in *Cibotium* abundance (Fig. 4D-F). Native stands dominated by *M. polymorpha* had especially dense *Cibotium* understory (2150±105 individuals ha^{-1}), twice that of timber stands dominated by *E. saligna* or *F. uhdei* (1580±190 ha^{-1} and 1060±150 ha^{-1} respectively). The number of fronds per tree fern did not vary among stand types; however the average estimated *Cibotium* frond was 50-65% larger in native forest stands dominated by *M. polymorpha* than in plantations dominated by *F. uhdei* or *E. saligna* (2.79±0.25 m^2, 1.99±0.09 m^2 and 1.69±0.14 m^2 respectively). Due to the larger fronds and more abundant tree ferns in *M. polymorpha*-dominated stands, estimated stand *Cibotium* frond area was two to three times higher than for *E. saligna* or *F. uhdei* plantations (33.0±2.8 10^3 m^2 ha^{-1}, 15.1±3.1 10^3 m^2 ha^{-1}, and 12.5±2.6 10^3 m^2 ha^{-1} respectively; Fig. 3D-F).

Estimated total stand water use varied 2.5-fold among stands (Fig. 3G). Stands dominated by *F.uhdei* used an estimated 1.78 ±0.09 mm day^{-1}, over twice the amount used by stands dominated by *E. saligna* or *M. polymorpha* (0.84 ±0.18 mm day^{-1} and 0.71 ±0.03 mm day^{-1} respectively). In native forest dominated by *M. polymorpha*, *Cibotium* water use was responsible for 75.3 ±6.7% of total stand water use. By contrast, for stands dominated by *F. uhdei* or *E. saligna*, the water use of *Cibotium* was secondary to that of the dominant tree species, though still substantial (11.8±2.6% and 32.2±5.6% respectively).

Discussion

The goal of this study was to compare water use of native forest vegetation with alien timber plantations to determine whether native tropical forest may be conservative in its water use. We used a well-drained, wet forest in Hawai'i as a case study. We found that tree species varied strongly in their water use even within forests facing similar climates, and that, when water use was scaled up, stands dominated by different species varied strongly in their water use. Water use at plant and stand level depended on several factors which varied independently and contributed

to total water uptake differences among species and among contrasting stands. Our findings provide the first strong evidence that Hawaiian native forest can be conservative of water relative to alien plantations. This finding extends previous work comparing leaf and whole plant traits in native and non-native species in Hawai'i (Pattison et al. 1998, Stratton 1998, Cordell et al. 2002, Daehler 2003, Funk and Vitousek 2007) and comparisons of native and non-native riparian tree water use in the southwestern U.S. that found trees did not vary in leaf area-scaled sap flow (Sala et al. 1996, Glenn et al. 1998) though high stand-level rates could be facilitated by high leaf area. While other studies in semi-arid areas of Australia and South Africa assessed native vegetation water use of fynbos or eucalyptus forest without comparing native vs. alien (e.g., Le Maitre et al. 1996, Calder and Dye 2001), our work for Hawai'i shows that contrasting water use can be as important in a wet forest system as has been expected for water limited or riparian systems.

Strong differences in water use among native and alien species

Hawaiian forest dominant species *M. polymorpha* exhibited the lowest rates of maximum sapflow on a sapwood-area, leaf-area, and whole-tree basis in our study, whereas *F. uhdei* had the highest rates. These differences would arise from intrinsic differences in wood and leaf properties. The higher maximum sapwood-area specific uptake rates of *F. uhdei* would arise from a higher canopy conductance, reflecting a higher whole-plant conductance and/or water potential gradient across the plant (Tyree and Zimmermann 2002). Large earlywood vessels in deciduous *F. uhdei* may contribute to a higher hydraulic conductance for *F. uhdei* relative to the two Myrtaceaous species.

The relationship among species' sapwood-scaled sapflow was maintained even when scaling up to the whole tree, as *F. uhdei* had high sapwood allocation relative to basal area compared to *E. saligna* and *M. polymorpha*. *F. uhdei* had greater maximum sapflow rates than *M. polymorpha* with *E. saligna* intermediate, but when accounting also for the large sizes of the *E.*

saligna trees, *F. uhdei* and *E. saligna* both had greater maximum whole-tree sapflow rates than *M. polymorpha*. Similar patterns were found for daily total water uptake with *M. polymorpha* having the lowest uptake. However, daily rates for *E. saligna* and *F. uhdei* were similar due to temporal variation in sapflow patterns among species. *F. uhdei* had short intervals of high flow rates whereas *E. saligna* had long periods of lower flow rates. Indeed, we noted a strong early peak of *E. saligna*, potentially due to open stomata, tall trees, or steep leaf angle facilitating light interception at low sun angles at dawn and dusk (King 1997). *M. polymorpha* also had long intervals of peak flow, but these were not enough to compensate for its very low flow rates. The understory *Cibotium* had even later sapflow peaks; it is likely that shading from canopy trees delays the onset of photosynthesis and transpiration in the morning.

We found substantial rates of nocturnal sapflow in our species, ranging from 4-30% of total sapflow. Higher proportions of nighttime flow in *E. saligna* and *M. polymorpha* may be due to tissue recharge and/or nocturnal transpiration. Nighttime sapflow has been documented for *M. polymorpha* (Dawson et al. 2007) and *Eucalyptus grandis* (Benyon 1999) and attributed to transpiration. Other studies have found nighttime percentages of total flow as large as 13-28% for trees in the Brazilian cerrado (Bucci et al. 2004) and 30-70% for *Drimys granadensis* in Costa Rican cloud forest (Feild and Holbrook 2000). Possible explanations for nocturnal transpiration include cuticular conductance or leakage from incomplete stomatal closure (Caird et al. 2007, Cavender-Bares et al. 2007). Possible functional roles include allowing carbon fixation to begin earlier in the day (Caird et al. 2007, Dawson et al. 2007), facilitating nutrient transport to the root surfaces in nutrient-limited systems (Scholz et al. 2007), improving oxygen supply in respiring sapwood (Gansert 2003), and/or preventing CO_2 buildup in the leaves due to nighttime respiration (Marks and Lechowicz 2007).

Leaf area-scaled rates indicating low water uptake for *M. polymorpha* and high uptake for *F. uhdei* parallel some of their leaf-level traits. In particular, high stomatal pore area per leaf area

(SPI) of *F. uhdei* relative to *M. polymorpha* suggests high leaf-level stomatal conductance (Sack et al. 2003), and the observed high leaf N and P concentrations of the high water-using alien species relative to that of *M. polymorpha* suggest higher relative growth rates (Niklas 2006), consistent with the paradigm of faster growing alien species with associated higher water uptake rates (Daehler 2003, Brauman et al. 2007). However, the degree to which differences in whole-plant traits are determined by leaf functional traits alone is contentious (Cordell et al. 2002, Poorter and Bongers 2006, Funk and Vitousek 2007). We note that sapflow per leaf area as determined in this study involved calculation based on estimated total canopy leaf area. Thus, while leaf-area specific rates will depend on the relative activity of transpiring leaves, they may also be decreased according to the amount of self-shaded, relatively inactive foliage. The structure of the tree crown may reduce wind and increase leaf boundary layers thus further reducing leaf-area specific transpiration rates (Larcher 2003).

We found *C. glaucum* to have an SPI much higher than that of tree species, suggesting a high leaf-level stomatal conductance, a potential adaptation for maximizing photosynthesis in the fluctuating light conditions of the understory (Hollinger 1987). While conductance may be higher for ferns than for trees, lower vapor pressure deficit in the understory means the tree ferns are not subjected to the same high atmospheric demand as at the canopy, and overall, understory *C.glaucum* had leaf area scaled transpiration rates similar to those of the canopy trees.

Strong differences in water use between native forest stands and alien timber plantations

Estimates of water use for forest stands varied according to differences in stand structure and composition. Stand types varied in structure, with *F. uhdei* stands characterized by a high stem density of relatively small trees, whereas *E. saligna* stands had lower densities of larger trees, and *M. polymorpha* had yet lower densities of trees that were on average slightly larger than those in *F. uhdei* stands. Although basal area per ground area tended to be highest in *E. saligna* stands,

when *F. uhdei*'s high sapwood allocation was taken into account, *F. uhdei* stands emerged as having the most sapwood area per hectare.

We found significant differences in water use among stand types, even when we accounted for other less-abundant species' sapwood and water use contributions. When we tested a scenario in which all other species contributed 100% of their basal area to sapwood, *F. uhdei* stands still had significantly higher sapwood area relative to the two other stand types. We also tested different sapflow rate scenarios to assess the robustness of the differences among stands. We accounted for sapflow in all trees other than the study species and found, even in the situations minimizing differences among stands (high rates for *M. polymorpha* non-study species and low rates for *F. uhdei* non-study species), that the same trend of high stand-level water use by *F. uhdei* stands versus either *M. polymorpha* or *E. saligna* stands was maintained. This further demonstrates native *M. polymorpha* has conservative water use relative to certain non-native timber covers and also that stand transpiration can vary among alien timber stands of similar age but different dominant species.

Another finding of our study is that site history affects stand water use. While native *M. polymorpha* stands at this site are the result of natural succession, the alien timber stands were planted in areas previously cleared of *M. polymorpha* forest during the 1950s (Carlson and Bryan 1963). As a result, these plantations consist of younger trees, and their respective sizes and densities are reflective of their growth rates and planting densities. *E. saligna* grows to larger sizes than *F. uhdei*; *M. polymorpha* can achieve large sizes, but has notably slow growth (Zimmerman et al. in press). The plantations' understory tree fern densities also reflect this disturbance history as old-growth *M. polymorpha* stands have had a longer period of time to develop high densities of tree ferns, and high fern frond cover is common in Hawaiian *M. polymorpha*-dominated wet forest (Drake and Mueller-Dombois 1993).

Even accounting for the high tree fern cover in *M. polymorpha* stands, stand-level water use differed strongly among stand types. Tree fern water use estimates obtained from high *Cibotium* frond area and sapflow rates more than doubled overall water use of *M. polymorpha*-dominated stands. Despite this, *F. uhdei* stands still used twice as much water as stands dominated by *M. polymorpha* and *E. saligna* on a daily basis. We tested different scenarios applying measured (but unpublished) *C. menziesii* flow rates (n=2) to all *C. menziesii* frond area or all *Cibotium* frond area to assess whether differences in overall stand water use were robust to variation in tree fern sapflow rates; the trends did not change.

In native *M. polymorpha*-dominated forest, understory tree ferns contribute significantly to overall stand transpiration. Understory components including bracken fern have previously been observed to strongly influence stand water use in studies assessing the partitioning of transpiration (Roberts et al. 1980, Hollinger 1987, Black et al. 1989, Kostner 2001). Vertessy et al. (2001) found that as overstory leaf area index (LAI) decreased with forest age, understory LAI increased, suggesting a corresponding increase in understory transpiration, which is consistent with our findings of high understory frond area in old-growth *M. polymorpha*-dominated forest versus the alien timber plantations. However, Vertessy et al. (2001) observed rates of leaf area-based transpiration that were only 63% that of the overstory on a leaf area basis, while our data indicate, in forests with more open canopy, tree ferns use water at rates comparable to or sometimes greater than those of the dominant canopy trees. It is clear that tree ferns are playing a significant role in the water balance of Hawai'i's native forests, and, on a leaf-for-leaf basis, ferns may be exerting more control over local water than the dominant canopy species, with implications for ecology and competitive interactions between dominant canopy species and tree ferns. Is it possible tree ferns are intercepting and transpiring water that would otherwise support more deeply-rooted tree species? While we did not investigate the depletion of soil water by our study species, tree ferns and trees are likely partitioning water resources as has been shown for

other ecosystems (e.g., Stratton et al. 2000). Thus, a forest's composition and site history (and resulting tree and understory cover) can contribute to major differences in stand water uptake and may influence ecological dynamics across sites.

Study limitations, future research needs, and implications for forest ecology and conservation

This study demonstrated strong species differences in sapflow within a given forest type, between native and alien tree species, and indicated that these scale up to whole-stand water use for contrasting forest compositions. However, logistical challenges limted our ability to determine the full water budget of the study forests. While our sites were chosen to have comparable soil and climate, an advantage of siting model forests in Hawai'i, a fully explicit quantification of the degree of variation *within* versus *across* stand types would require replication of sapflow and vegetation surveys across multiple sites. Further work should confirm the findings at a larger scale, with replication of native and alien plantation forests.

Because we were only able to measure *Cibotium* sapflow in the native *M. polymorpha* forest, we assumed for this study the measured *C. glaucum* sapflow rates were representative of all *Cibotium* in the *F. uhdei* and *E. saligna* stands. While ideally one would measure rates of *Cibotium* water use for all species in all sites, we expect that variation in rates between sites and species is minimal and thus would not change our conclusions on total stand water use; both *C. menziesii* and *C. glaucum*, the two native species found in our stands, co-occur in wet forest and have similar stomatal conductances in a range of environments (Durand and Goldstein 2001). Likewise, we also assumed our study trees were representative of all trees in a given stand type, though differences in site microclimate, soil water availability, and forest structure also may mean individuals in a stand are being subjected to different controls on transpiration. Further, differences in tree age may partially determine the findings of our species comparisons. However, our measured rates are useful for showing how such differences can indeed arise. Future

technological and methodological innovations will enable measurements on more trees to better allow quantification of variation within and among trees within given stands.

Another limitation of our study was the relatively short study length, covering only a period in which soil water was abundant, as is typical for this study system. Future work should consider water use by contrasting forest types across a whole year or multiple years. Such work would be particularly useful given that one of the stand-dominants, *F. uhdei*, is winter-deciduous, and remains leafless for up to four months. However, we expect that the *F. uhdei*-dominated stands are likely to have higher water uptake even if integrated over a year, all else being equal, as the 4-fold greater uptake rates during 8-9 months with leaves would not be obviated even if uptake was zero during the 3-4 months of the year without leaves. Future studies should also take into account seasonal variation and scale water use by leaf area to enable incorporation of remotely sensed LAI to model annual and interannual water use.

We note that our work focuses on one component of a forest water budget. Plant water use, i.e., sapflow, explains only a part of the evapotranspiration fluxes of the water balance. We did not assess potential differences in canopy interception and evaporation between sites, which would also reduce the plant available soil water and thus groundwater recharge. There is a strong need for work focusing simultaneously on all components of the water balance, including canopy interception, evaporation, stemflow, throughfall, infiltration, and soil water availability. Including species-specific water use with these measurements will create an interdisciplinary ecohydrology necessary for detailed forest water budgeting. The more complex structure of native stands may also have impacts on other aspects of the terrestrial water balance (increasing infiltration and decreasing runoff) and reducing wind speed (and thus transpiration) through the forest. However, the main principle shown by our study, that major differences in transpiration can arise among species in a given climate, and the conservative transpiration of a native forest, suggests the potential for higher recharge rates and water conservation through informed forest management.

We note that work on forest ecohydrology will eventually allow the elucidation of full forest water budgets, with implications for soil water availability to benefit forest plants, as well as groundwater recharge, as the interaction of forests and water has impacts on species-level biology to watershed hydrology. Future work on model ecohydrology systems can clarify these impacts at a wide range of scales.

Our findings indicate that water uptake of the contrasting forest species and stands should be assessed as a potentially critical factor in determining forest ecosystem services and informing land management decisions. In the case of Hōnaunau Forest, Hawaiian native wet forest has conservative water uptake, and further studies can determine whether the groundwater recharge enabled by the lower forest water uptake can contribute enough value to further motivate conservation and restoration of this forest type in appropriate areas. However, we caution against using these results in isolation, for example, to justify planting *E. saligna* or harvesting *Cibotium*. In all cases, the seeming benefits for water use must be considered together with other values and motivations, such as preservation of native habitat, biodiversity and ecological processes.

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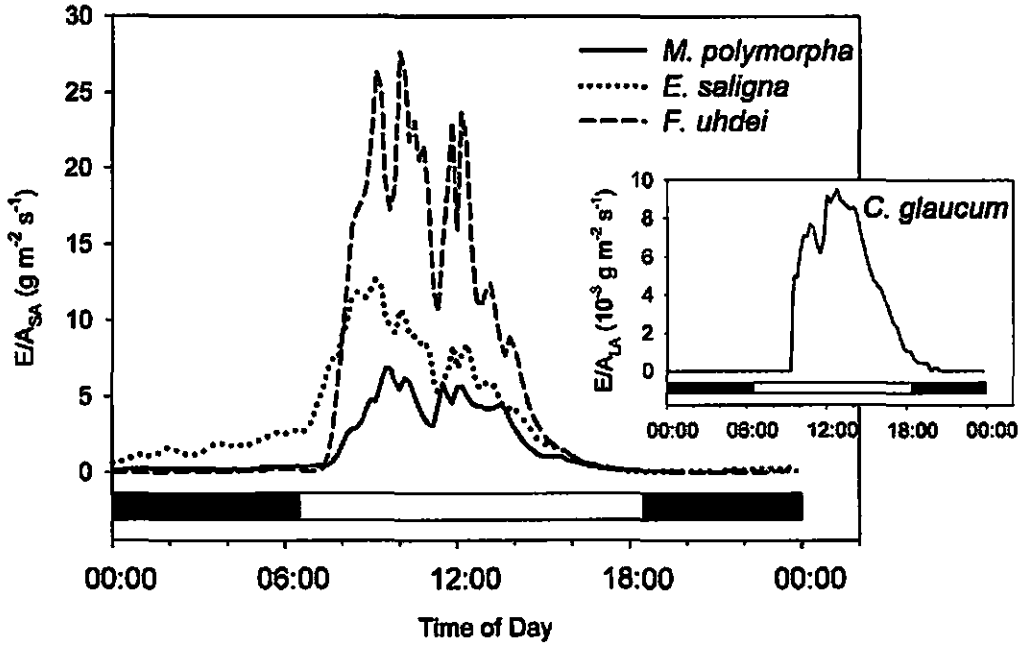

Figure 2.1. Sapflow per sapwood area (E/A_{SA}) on a representative day (30 August 2006) for *Metrosideros polymorpha* in native forest and for alien timber species *Eucalyptus saligna* and *Fraxinus uhdei* in adjacent plantations in Hōnaunau, Hawai'i Island. Inset: sapflow per frond area for understory dominant tree fern *Cibotium glaucum* in native forest. Day and night are indicated respectively on the *x*-axis with white and black bars.

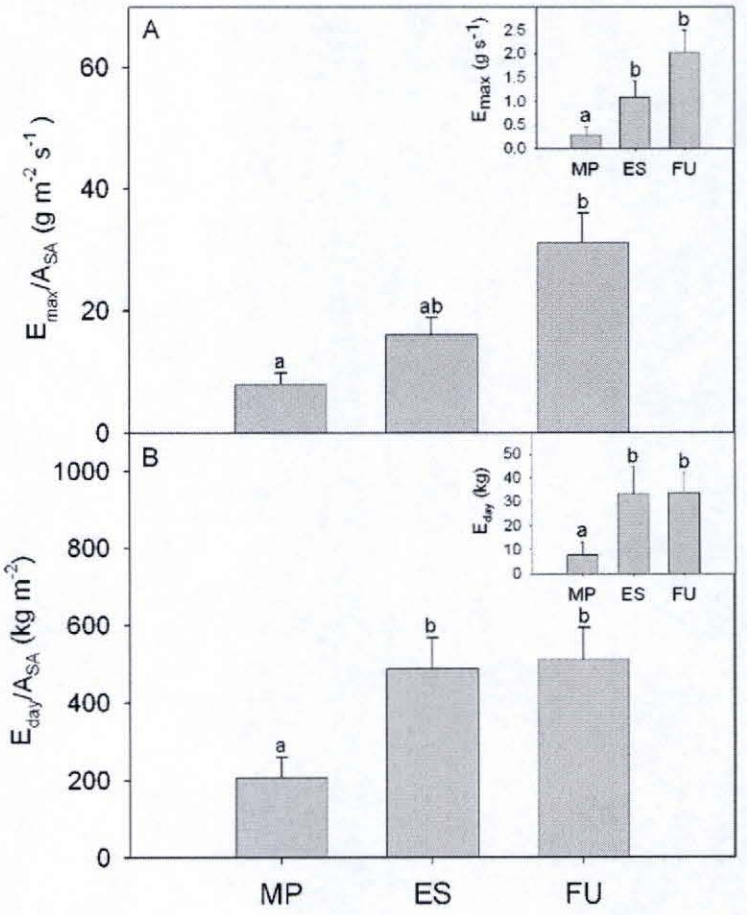

Figure 2.2. Sapflow parameters for native and alien tree species in Hōnaunau Forest, Hawai'i Island. (A) maximum instantaneous sapflow rate per sapwood area (E_{max}/A_{SA}), and per tree (E_{max}, inset), and (B) mean diurnal sap flow per sapwood area (E_{day}/A_{SA}), and for the whole plant (E_{day}, inset). Species abbreviations: MP, *Metrosideros polymorpha*; ES, *Eucalyptus saligna*; FU, *Fraxinus uhdei* (n = 6). Bars indicate means and standard errors, with same lower case letters indicating statistically indistinguishable means (at P = 0.05; post-hoc Tukey comparisons of ln-transformed data).

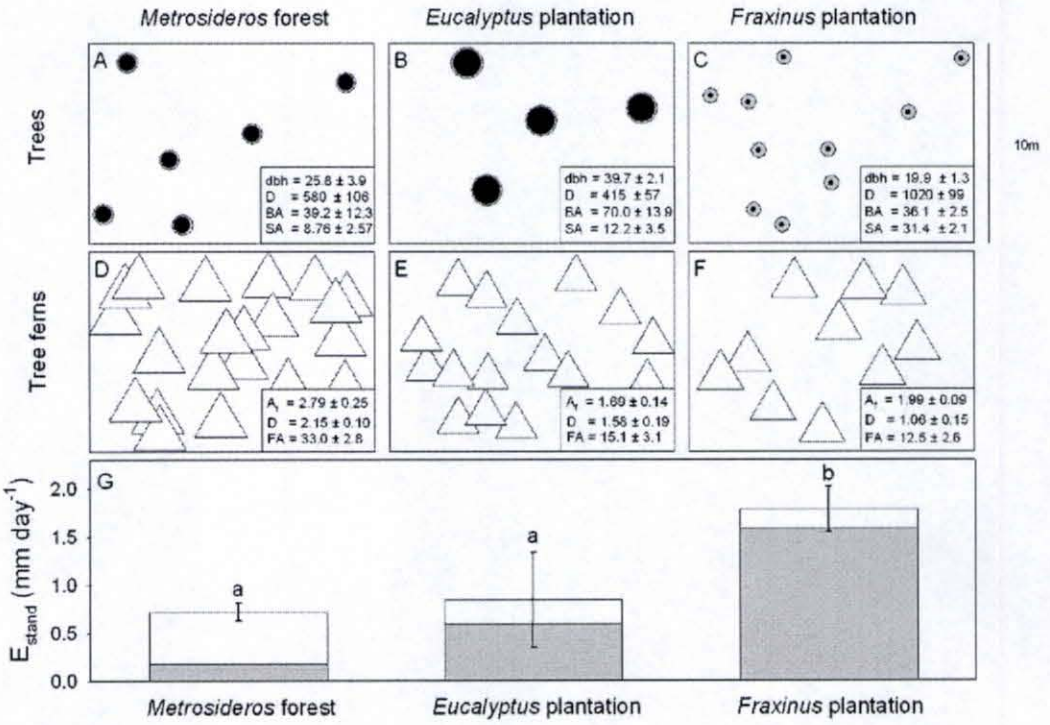

Figure 2.3. Stand structure and estimated stand-level water use for *Metrosideros polymorpha*-dominated native forest versus alien timber plantations dominated by *Eucalyptus saligna* and *Fraxinus uhdei* (n=5, 5 and 6 stands respectively). (A-C) Schematic of trees in a 10m x 10m plot for each stand type representing average values of the several factors important in determining stand-level water use: dominant tree densities, sizes, and sapwood allocation patterns (data provided in inset boxes: *dbh*, diameter at breast height, cm; *D*, density, stems ha^{-1}; *BA*, basal area, m^2 ha^{-1}; *SA*, sapwood area, m^2 ha^{-1}). In the schematic, tree dbh is indicated by outer circles, sapwood area by gray, and heartwood area in black; the scale line on the right represents distance along the ground in the plot. (D-F) Schematic of understory *Cibotium* in each stand type representing densities, with triangle sizes reflecting average total frond area per individual, i.e., frond area x number of fronds per individual (data provided in inset boxes: A_f, average area per frond, m^2; *D*, density, 10^3 caudices ha^{-1}; *FA*, stand-level frond area, 10^3 m^2 ha^{-1}). (G) Scaled-up mean stand diurnal sap flow as the sum of tree (gray) and tree fern (white) components. Error bars indicate 95% confidence intervals with lower case letters indicating statistically indistinguishable means according to post-hoc Tukey comparisons at $P = 0.05$.

CHAPTER 2 SUPPLEMENTARY MATERIAL

Table 2.S1. Mean traits of tree and tree fern species and sapwood and frond area allometric coefficients. Columns on the left indicate mean values: for tree species, diameter at 1.3m height (x, dbh) and sapwood area (y, SA), and for the tree fern species: frond length index (x, FLI; see text) and individual frond area (y, FA). Maximum heights in parentheses are those observed for the species. Columns on the right indicate coefficients a and b fitted to the relationship $\ln y = a + b \ln x$ with a dataset of sample size n. When applying the coefficients using the power-law $y = e^a * x^b$, the estimate is multiplied by a correction factor c to account for systematic bias arising from coefficients fitted to log-transformed data; c was calculated as $e^{\sigma^2/2}$ (Baskerville 1972, Sprugel 1983).

	x	y	*a*	*b*	*c*	*n*
x = dbh (cm), y = SA (cm^2)						
M. polymorpha (~30m max ht)	35.0 ± 8.5 (6)	261 ± 107 (6)	-0.779 ± 0.412	1.73 ± 0.12	1.02	15
E. saligna (~55m max ht)	73.3 ± 9.4 (6)	605 ± 158 (6)	-0.878 ± 0.417	1.68 ± 0.10	1.03	22
F. uhdei (~30m max ht)	30.0 ± 2.1 (6)	609 ± 84 (6)	-0.654 ± 0.034	2.07 ± 0.01	1.00	30
x = FLI (m), y = FA (m^2)						
C. glaucum (~7m max ht, median~1m)	2.43 ± 0.19 (7)	2.40 ± 0.25 (7)	-1.07 ± 0.21	2.13 ± 0.24	1.06	18

Table 2.S2. Mean squares (MS) of analyses of variance comparing water use parameters of tree species *Metrosideros polymorpha*, *Eucalyptus saligna*, and *Fraxinus uhdei*. We tested for differences among species' sapflow rates for integrated diurnal sapflow (E_{tot}, kg day^{-1}) and daily maximum sapflow (E_{max}, g s^{-1}) on a whole-tree basis (E_{tot}, kg day^{-1}; E_{max}, g s^{-1}), sapwood-scaled basis (E_{tot}/A_{SA}, E_{max}/A_{SA}), and leaf area-scaled basis (E_{tot}/A_{LA}, E_{max}/A_{LA}); we also compared parameters of temporal sapflow patterns, including time at maximum sapflow (t_{max}, hour), time duration at which sapflow was greater than 50% of maximum sapflow (Δt_{peak}, hours), and proportion of total sapflow occurring at night (1830-0630; E_n/E_{tot}, percent). The left columns contain the results of a one-way ANOVA, testing species differences for data for all species over the entire measurement period. The right columns contain the results of a repeated-measures ANOVA, testing species, day and species*day interaction for the 19 days that all individual trees were measured simultaneously. $Error_{indiv}$ refers to variation between individuals and $Error_{total}$ refers to overall variation from all observations. *$0.05>P\geq0.01$; ** $0.01>P\geq0.001$; ***$P<0.001$.

	One-way ANOVA		**Repeated-measures ANOVA**				
	Species df=2	**$Error_{indiv}$ df=15**	**Species df=2**	**$Error_{indiv}$ df=15**	**Day df=18**	**Species x Day df=36**	**$Error_{total}$ df=270**
Whole-tree							
$\ln(E_{tot})$	9.19**	1.37	203**	28.9	2.18***	0.466***	0.167
$\ln(E_{max})$	11.5 **	1.30	237**	28.6	0.932***	0.198**	0.108
Per sapwood area							
$\ln(E_{tot}/A_{SA})$	1.70*	0.339	45.1*	7.73	2.18***	0.466***	0.167
$\ln(E_{max}/A_{SA})$	3.04**	0.355	65.9**	8.60	0.932***	0.198**	0.108
Per leaf area							
$\ln(E_{tot}/A_{LA})$	8.20***	0.275	176***	6.48	2.18***	0.466***	0.167
$\ln(E_{max}/A_{LA})$	12.4***	0.259	247***	6.65	0.932***	0.198**	0.108
Temporal patterns							
t_{max}	2.975**	0.411	50.103*	10.798	12.51*	11.49**	6.74
Δt_{peak}	14.013***	0.808	225.05***	11.99	33.31***	5.86*	3.83
E_n/E_{tot}	0.09987***	0.00508	2.1331***	0.1217	0.05850***	0.02242**	0.01163

Table 2.S3. Leaf traits for tree and tree fern species measured for sapflow in Hōnaunau Forest, Hawai'i Island: specific leaf area (SLA), stomatal pore length (L_{pore}), stomatal density ($D_{stomata}$), stomatal pore index (SPI = L_{pore}^2 x $D_{stomata}$), nitrogen concentration per mass (N_{mass}) and per leaf area (N_{area}), phosphorus concentration per leaf mass (P_{mass}) and per leaf area (P_{area}), and carbon isotope discrimination ($\delta^{13}C$). Mean values ± standard errors are given; *n* ranged from 3-10 except for *E. saligna* (n=2). Tree species differed in all traits except for SLA and $\delta^{13}C$ (ANOVA, *0.05>*P*≥0.01; ** 0.01>*P*≥0.001; ***$P<0.001$). For each trait, lower-case letters indicate no significant difference between tree species according to post-hoc Tukey comparisons ($P=0.05$).

	SLA ($cm^2\ g^{-1}$)	L_{pore}*** (μm)	$D_{stomata}$** (mm^{-2})	SPI* ($mm^2 mm^{-2}$)	N_{mass}** (%)	N_{area}* ($g\ m^{-2}$)	P_{mass}** (%)	P_{area}* ($g\ m^{-2}$)	$\delta^{13}C$ (‰)
Tree species									
M. polymorpha	**61.6** ± 5.4 a	**17.3** ± 0.8 b	**195** ± 12 b	**0.0578** ± 0.0036 b	**0.778** ± 0.040 b	**1.28** ± 0.14 b	**0.041** ± 0.003 b	**0.068** ± 0.006 b	**-32.0** ± 0.3 a
E. saligna	**72.7** ± 4.8 a	**15.4** ± 0.7 b	**318** ± 20 a	**0.0748** ± 0.0032 ab	**1.66** ± 0.08 a	**2.29** ± 0.04 a	**0.091** ± 0.006 a	**0.126** ± 0.001 a	**-31.7** ± 0.1 a
F. uhdei	**99.8** ± 24.4 a	**24.5** ± 0.2 a	**137** ± 5 c	**0.0849** ± 0.0046 a	**1.28** ± 0.13 a	**1.37** ± 0.18 b	**0.075** ± 0.006 a	**0.082** ± 0.015 ab	**-32.2** ± 1.0 a
Tree fern species									
C. glaucum	**151** ± 11	**24.4** ± 0.8	**362** ± 30	**0.215** ± 0.019	**1.91** ± 0.14	**1.08** ± 0.17	**0.113** ± 0.015	**0.064** ± 0.013	**-30.3** ± 1.3

Table 2.S4. Percentages of basal area by component tree species as means ± standard error and total living tree basal area for each of the stand types represented in this study. Within each stand type, five to six plots were surveyed for all living stems greater than 1cm diameter at breast height; species are listed in order of decreasing abundance.

Metrosideros/Cibotium forest		*Eucalyptus saligna* plantation		*Fraxinus uhdei* plantation	
Metrosideros polymorpha	**87.7** ± 5.0	*Eucalyptus saligna*	**89.6** ± 3.5	*Fraxinus uhdei*	**84.7** ± 5.7
Ilex anomala	**4.9** ± 3.4	*Metrosideros polymorpha*	**4.3** ± 3.3	*Metrosideros polymorpha*	**9.3** ± 5.2
Acacia koa	**2.3** ± 2.3	*Acacia koa*	**1.6** ± 1.0	*Acacia koa*	**6.0** ± 1.7
Coprosma spp.	**1.3** ± 0.6	*Fraxinus uhdei*	**1.3** ± 1.3		
Toona ciliata	**1.2** ± 1.2	*Ilex anomala*	**1.2** ± 0.7		
Cheirodendron trigynum	**1.1** ± 1.0	*Perrottetia sandwicensis*	**0.8** ± 0.5		
Total basal area (m^2 ha^{-1})					
43.8 ± 12.3		79.0 ± 15.7		43.0 ± 2.6	

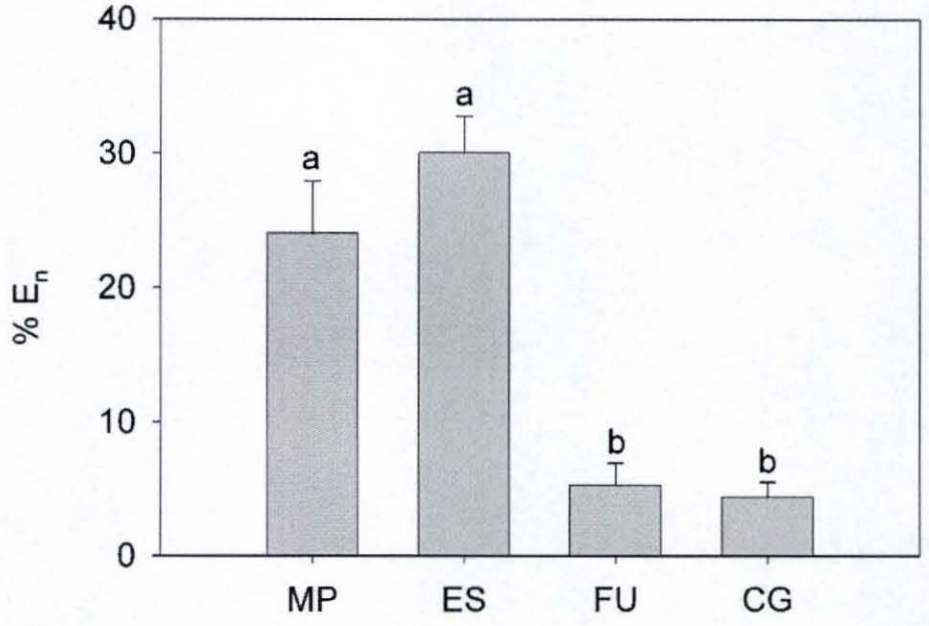

Figure 2.S1. Species differed in the percentage of total diurnal sap flow occurring at night (E_n; between 1830 and 0630 hours). Bars indicate means + standard error. Species abbreviations: MP, *Metrosideros polymorpha* (n=6); ES, *Eucalyptus saligna* (n=6); FU, *Fraxinus uhdei* (n=6); CG, *Cibotium glaucum* (n=7).

CHAPTER 3

Sap flow responses to microclimate:

Applying multi-model inference to assess variation among species

Introduction

Bulk sap flow methodologies have contributed significantly to the estimation of forest transpiration and studies of whole-plant physiology. Some examples from hydrology include the use of these methods to assess the water use of stands of different species compositions and ages (Barrett et al. 1996, Roberts et al. 2001, Delzon and Loustau 2005, Ewers et al. 2005) and the partitioning of vegetation water use into different flux components or vegetation components (Kelliher et al. 1992, Oren et al. 1998, Zeppel et al. 2006). Because sap flow methods allow continuous measurement of whole plant transpiration *in situ*, they have resulted in numerous studies on the response of transpiration and stomatal conductance to environmental variables at diurnal, daily, seasonal, and even interannual timescales (Jarvis 1976, Meinzer et al. 1993, Sturm et al. 1998, Oren et al. 1999a, Oren et al. 1999b, Granier et al. 2000, Oren and Pataki 2001, Oren et al. 2001, Phillips and Oren 2001, Pataki and Oren 2003, Ford et al. 2005).

Such studies have led to the development of empirical models describing relationships between transpiration or conductance and environmental variables, modeling these as responses to irradiance, temperature, and vapor pressure deficit on diurnal timescales. For daily, monthly, and seasonal timescales, soil moisture and leaf area components have been included in the models. One problem in the literature is that, among various studies, different environmental parameters are measured and different mathematical functions are fit to the sap flow or conductance data. Previous modeling efforts have focused primarily on fitting linear and nonlinear functions through a least-squares approach; these range from linear models with

multiple additive terms (Wullschleger et al. 2001) to nonlinear models of canopy conductance based on one or two environmental variables (Oren et al. 1999b, Ewers et al. 2005), usually vapor pressure deficit (VPD, kPa) or photosynthetically active radiation (PAR, μmol m^{-2} s^{-1}). Linear and nonlinear functions of single variables are often combined into multiplicative models as originally proposed by Jarvis (1976). Relatively recently, Ford et al (2005) put forth a strong argument for using time-series approaches to account for changing relationships of sap flow and environment in time, a more accurate approach to modeling sap flow, however, we will not consider these here.

In this paper, we assess the suite of empirical and statistical models presented in the literature, as well as some standard multiple regression forms, for characterizing the response of sap flow to PAR, temperature, and VPD for four different species in Hawai'i . We employ an information theoretic approach (based on likelihood and AIC) for selecting and comparing the relative success of different fitted models for each species. We then use the best AIC-selected models to explain differences among species' responses to environment. This approach provides additional insight into the control of sap flow by PAR, temperature, VPD, and combinations of these by showing which models of these variables best apply.

Methods

Study species and site

The study was conducted at Hōnaunau Forest Reserve, a 4250-hectare patchwork of forest and tree plantations owned by native Hawaiian legacy trust Kamehameha Schools on the leeward slope of Mauna Loa, Hawai'i Island. Within this forest, two sites were selected to represent native and alien-dominated vegetation in the *ahupua'a* (land divisions) of Kahauloa (N 19.482°, W 155.869°) and Hōnaunau (N 19.435°, W 155.844°), respectively. The sites are 5 km apart, at 1000 m elevation on 750-1500 year old 'a'ā lava flows (Lockwood 1995) of Puna-Udarent soil

type (Soil Survey Staff , Niemeyer 2006). At Kahauloa and Hōnaunau, mean annual precipitation is respectively 1520 and 1450 mm, mean annual temperature 17.5 and 17.3 °C, and relative humidity annual minimum/maximum 67.9/97.8% and 67.6/98.0% (Giambelluca and Cuo in prep). These sites were selected for their contrasting vegetation in conjunction with strong similarities in substrate and environment; in addition, the high substrate permeability and low slope of the area minimize horizontal fluxes of water thus simplifying water balance estimates.

We measured sap flow for individuals in four taxa representing both native and non-native plants; these included endemic canopy tree *Metrosideros polymorpha* Gaud. (Myrtaceae; common name *'ōhi'a*; Wagner et al. 1999) and endemic tree ferns *Cibotium glaucum* (Sm.) Hook. & Arn. and *Cibotium menziesii* Hook (Cibotiaceae; common name *hāpu'u pulu* and *hāpu'u 'i'i*; Palmer 2002, Smith et al. 2006) in the native old-growth forest of Kahauloa. At a non-native tree plantation site in Hōnaunau, we studied *Eucalyptus saligna* Sm (Myrtaceae; Wagner et al. 1999) and *Fraxinus uhdei* (Wenzig) Lingelsh (Oleaceae; Wagner et al. 1999) in monotypic stands of approximately 2 ha and 25 ha respectively.

Monitoring meteorological conditions

From August through September 2006 (wet season), we recorded meteorological data in forest gaps at both sites. Photosynthetically active radiation (PAR, μmol m^{-2} s^{-1}) was measured using LI-190 quantum sensors (LI-COR, Lincoln, Nebraska) at 30-second intervals, and we recorded 10-minute averages using a CR10X datalogger (Campbell Scientific, Logan, Utah). Power to the datalogger unit was supplied by a 7Ah 12V sealed lead-acid battery (Radio Shack, Fort Worth, TX). At each site, we also measured temperature (°C) and relative humidity (%) using the temperature and humidity sensors associated with a WS-2308 system (LaCrosse Technology, LaCrosse, Wisconsin). Due to memory constraints for these systems, we recorded average temperature, humidity, and rainfall data for the two sites only on an hourly basis. From the

measured temperature and humidity information, we calculated vapor pressure deficit (VPD, kPa) according to the Magnus equations using the coefficient values provided in Buck (1981).

Measuring sap flow in trees and tree ferns

From August 2006 through September 2006, we recorded sap flow for six individuals for each of the three tree study species. We measured tree sap flux density (J_s, g m^{-2} s^{-1}) using modified Granier-style heat dissipation probes with 1-cm long sensor tips (James et al. 2002). To calculate *J*s from sensor voltage output, we used the recently re-validated calibration of Granier (Granier 1985, McCulloh et al. 2007). Measurements of sap flux density were made every minute and recorded as 10-minute averages using a CR1000 datalogger from Campbell Scientific. Probes were heated continuously at 0.16W per heated sensor; power was supplied with 6V deep-cycle batteries and distributed using a self-built voltage regulating circuit. We installed two to five replicate probes in each tree at 1.3 m height at different depths in the sapwood and at different points around the tree's circumference. To estimate whole-plant sap flow, we scaled up probe measurements by assuming each probe measured flux through an annulus of sapwood. Sapwood was defined between the cambium and inner extent of sapwood determined for each species from increment cores (see Chapter 2), and within the sapwood, annuli were defined by the midpoints between successively deeper probes. We calculated total plant sap flow E (g s^{-1}) by summing the flux contributions from each annulus, effectively integrating across the cross-section of the tree trunk (Hatton et al. 1990).

We also recorded sap flow for fronds of nine individual tree ferns (seven *Cibotium glaucum*, two *Cibotium menziesii*, one frond per individual). We measured tree fern frond bulk sap flow (g s^{-1}) using a commercial stem heat balance collar system placed on frond stipes (Dynamax Flow32 system, Dynamax, Houston, Texas) powered by 12V deep-cycle batteries. We calculated bulk sap flow from voltages of four thermocouples per collar using the manufacturer's

calculation procedures (Sakuratani 1981, Baker and van Bavel 1987). Measurements were made every minute and recorded as 15-min averages using the Dynamax system.

Analysis of sap flow data: Correlations and modeling on PAR, temperature, and VPD

Prior to analysis, all data series were averaged to common hourly intervals. To facilitate fitting of species-specific models, we normalized sap flow data for individual trees and tree fern fronds as a new response variable, E_{norm}, calculated as E_t/E_{max}, where E_t is sap flow at any point in time and E_{max} is the overall maximum sap flow rate over the course of the study. These observations ranged from 0 to 1, which eliminated variation in sap flow magnitude among individuals and allowed us to conveniently pool data for a given species. We used the pooled normalized sap flow datasets for each species, which enabled us to compare model coefficients for different species. We compared hourly observations of E_{norm} and PAR, temperature, and VPD and focused our analysis on only daytime values (observations falling between the hours of 0600 and 1800). We performed a preliminary analysis by testing the strength of correlations of sap flow and environmental predictors of PAR, temperature, and VPD independently of each other. All analyses were performed in R version 2.6.2 (R Development Core Team 2008, scripts available upon request)

We constructed our candidate model set by collecting from the literature the various empirical and statistical models used to fit sap flow and stomatal conductance to predictors of PAR, temperature, and VPD (see Supplementary Material, Table 3.S1). The suite of models included nonlinear functions describing the saturating responses of sap flow and stomatal conductance to PAR and VPD (when considered independently) as well as multiplicative combinations of these functions (Jarvis 1976). For insight, we included multiple regression models of sap flow as 1) a linear response to PAR, temperature, and VPD and as 2) a linear

response to the natural log of these variables. These allowed us to explore the effects of including and excluding the interacting effects of PAR, temperature, and VPD on sap flow.

We then proceeded to fit models in R using least-squares methods for both the linear models and for the nonlinear models, using R's *lm* and *nls* functions; *nls* uses the Gauss-Newton algorithm to optimize parameters. All candidate models were fit independently for each species. When the model optimization procedure failed for some of the nonlinear models, we rejected the model as it was likely a poor model choice.

From the fitted models, we calculated the likelihood of the model given the data assuming a normal error structure. We used this calculated likelihood and the number of fitted model parameters (K) to obtain several test statistics: AIC, Akaike's information criterion; AIC_c, corrected AIC; Δ_i, AIC differences; w_i, Akaike weights (Burnham and Anderson 2002). To assess the goodness of fit for each model, we also calculated the slope of model predictions vs. observed data and the R^2 of the regression forced through the origin. For each species, we used the Akaike weights to assess the relative success of different models tested and ranked these in order of decreasing w_i, where the highest w_i indicates the best of the candidate models.

Results

Correlating E_{norm} and meteorological variables

Species differed with respect to magnitudes of whole-plant water use rates (shown in Chapter 2), thus normalizing sap flow allowed us to compare sap flow patterns of multiple species. Species varied in diurnal patterns of water use (Figure 3.1) with respect to both the timing of maximum flow and the duration of high flow rates over the course of the day. In particular, sap flow would begin earlier in the morning and would reach maximum rates earlier and for longer periods of time for trees than tree ferns. The detailed curves of Figure 3.1 indicate sap flow varies among species, for instance, major sap flow increases and maxima occur at different times of day for

different species. The sap flow rates of all species increase strongly at sunrise with increased PAR, temperature, and VPD, and decrease gradually in the afternoon. Smaller fluctuations in sap flow over the course of the day do not clearly follow any one single variable.

Normalized sap flow (E_{norm}) was strongly and positively correlated with all meteorological variables for all species (Figure 3.2, all *P*-values<0.001). Across all species, correlations were strongest between E_{norm} and VPD (Pearson correlation coefficient *r* ranged from 0.62-0.80) and E_{norm} and temperature (*r* ranged from 0.61-0.79). E_{norm} was also correlated with PAR to a lesser degree, with *r* ranging from 0.52-0.65. Between species, E_{norm} of *Fraxinus* and *Cibotium* were more strongly correlated with PAR, temperature, and VPD (*r* from 0.57-0.79 and 0.65-0.80 respectively). *Eucalyptus* and *Metrosideros* exhibited slightly weaker correlations with meteorological variables (*r* from 0.55-0.62 and 0.52-0.75).

The three measured meteorological variables were all highly inter-correlated, especially temperature and VPD, where at Kahauloa, r=0.90 and at Hōnaunau, r= 0.93. PAR and temperature are strongly correlated as were PAR and VPD (Kahauloa: r=0.71 and r=0.64; Hōnaunau: r=0.68 and r=0.65). Thus simple correlations do not allow conclusions that any one variable is more important than others in determining the sap flow rate of different species since increases in E_{norm} may be driven by increases in any of these three variables and their interacting effects.

Model selection and fitting

The models that best explained variation in sap flow for different species included all three variables (PAR, temperature, and VPD) as well as all two-way interactions (Table 3.1, Supplementary Table 3.S1). None of the single-variable models were in the top ten models for any species. The best two-variable models for *Metrosideros* and *Cibotium* tended to include temperature and vapor pressure deficit and not PAR. One of the top ten *Eucalyptus* models

included PAR and VPD only and not temperature. For *Metrosideros* and *Cibotium*, the best-supported model was a multiple linear regression model with all second-order interactions. For *Eucalyptus* and *Fraxinus*, the top three models with strongest support were identical for both species; these were multiple linear regression models describing sap flow as a linear response of additive and interacting log-transformed meteorological variables (Table 3.1). None of the Jarvis-type multiplicative models tested worked as well as these multiple linear-regression models that included interaction terms.

For *Metrosideros*, the best AIC-supported models had Akaike weights of w_1=0.631 and w_2=0.322 (see Table 3.1, models 1 and 2). These were both linear regressions including all main effects of PAR, temperature, and VPD as well as the two-way interactions of all of these (PAR:temperature, PAR:VPD, and temperature:VPD) and a third, three-way interaction term. The second-best model was similar in all aspects but did not include the three-way interaction. Because its Δ_i is less than 2, and it has one less parameter than the "best" model, it is the more parsimonious of the two and would be the preferred model. The most substantial and positive coefficients for the top two models (1 and 2) were associated with the VPD term and the PARxTemperature interaction.

For *Eucalyptus* and *Fraxinus*, the best AIC-supported model (model 4 in Table 3.1) was a linear regression of ln-transformed variables and all their interactions. For *Eucalyptus*, w_1 = 0.977 and for *Fraxinus*, w_1 =0.999, indicating this particular model was clearly much better than any other candidate model tested for both species (listed in Supplementary Material, Table 3.S1). For both *Eucalyptus* and Fraxinus, the interactions of VPD with both PAR and temperature were important and weighted positively.

Cibotium did not clearly fit to a single model; rather the top three models were weighted similarly (w_1=0.399, w_2=0.399, w_3=0.201) suggesting these three models are similarly supported, and the most parsimonious model (models 2 or 3) should be chosen. Across all three *Cibotium*

models, the most substantial and positive coefficients were for PAR, VPD, and PARxVPD interactions. The coefficient for the temperature term in model 3 was also relatively large.

The best-supported models for each species explained 40-65% of the variation in our data (Figure 3.3). We found that R^2 as an indicator of model goodness of fit was highest for *Fraxinus* (R^2=0.62) and *Metrosideros* (R^2=0.62) and lowest for *Eucalyptus* and *Cibotium* (R^2 values of 0.44 and 0.43 respectively). Slopes for model-predicted E_{norm} versus observed E_{norm} (fixed through the origin) ranged from 0.86 for *Eucalyptus*, 0.84 for *Fraxinus* and *Cibotium*, to 0.82 for *Metrosideros*.

Discussion

Correlating E_{norm} and meteorological variables

We found strong correlations of normalized sap flow with all meteorological variables, in particular, VPD and temperature. This is reasonable because transpiration is controlled by plant conductance and driven by atmospheric demand, characterized by VPD. VPD itself is calculated from temperature and relative humidity, which contributes to the intercorrelation of these two variables.

Among the four study species, we observed *Fraxinus* and *Cibotium* were more strongly correlated with all environmental variables, whereas *Eucalyptus* and *Metrosideros* were less responsive to these changes. One possible explanation is that the *Eucalyptus* and *Metrosideros* are larger and have higher capacitance; basal sap flow lags transpiration in these cases (Goldstein et al. 1998) and could result in weaker correlations. Another possible explanation is that sap flow of the more shallowly-rooted *Fraxinus* and *Cibotium* respond quickly to soil moisture deficits caused by drying of the upper soil layers; the more deeply-rooted Myrtaceous *Eucalyptus* and *Metrosideros* access deeper water supplies and sap flow responses would be more gradual (Crombie et al. 1988, Pataki et al. 2000, Oren and Pataki 2001).

Model selection and fitting

Model-fitting yielded two major insights: interactions are important in explaining sap flow as a response to meteorology and species do differ in their sap flow responses. We found linear models that included interaction terms performed better than the Jarvis-type multiplicative models established in the literature; this demonstrates the need to develop models accounting for interactions as was suggested originally by Jarvis (1976). The observation that the best-fitting models are not consistent across species provides support the argument that species differ in whole-plant sap flow responses to environmental conditions.

The best supported models for our study species explained some, but not all, of the variation in sap flow. One likely explanation for this is that we did not account for all important variables influencing sap flow. Lumping normalized data from multiple individuals would have added extra and unaccounted for variation to our datasets. In addition, we considered only PAR, temperature and VPD in modeling sap flow, and it is possible that other variables including soil moisture and wind speed are affecting sap flow rates. Bias in the modeled estimates (slopes of predicted vs. observed sap flow <1) indicate that our models are underestimating sap flow, primarily by failing to account for large high sap flow events Other studies using similar regression approaches varied in model-fitting success. While our models account for approximately half of the variation in our data, other studies using similar models have explained as little as 22% for a particular species (Oren and Pataki 2001) and as much as 82% (Ewers et al. 1999). The actual models used are not always consistent across studies, which make comparing studies, models, and species difficult: is the poor model fit due to model choice, or are the trees doing something different?

We observed that the best AIC-selected model was the same for *Eucalyptus* and *Fraxinus*, but did not explain the *Metrosideros* or *Cibotium* datasets well. Interestingly, the best models for *Metrosideros* and *Cibotium* were nearly identical. While better replication is needed,

we speculate that these differences might be explained by factors including native/nonnative status, stand age, unaccounted for site differences. While the best *Eucalyptus/Fraxinus* model is a function of the natural logs of the environmental variables, the best *Metrosideros/Cibotium* models are linear responses of the environmental variables. We speculate that low sap flow rates for *Metrosideros* might mean sap flow rates do not saturate while those of the nonnative *Eucalyptus* and *Fraxinus* trees, which have higher rates of sap flux density, do reach a maximum at high PAR, temperature, and VPD.

Study limitations and future research needs

Settling on a simple but complete model of sap flow response to environment would create a standard method for analyzing sap flow response to climate. The time series approach advocated by Ford et al (2005) properly accounts for changing relationships of environmental variables through time and provides an excellent starting point for this effort. Future work should be focused on developing a simple and rapid assessment of sap flow data using time series and potentially other types of models. This would facilitate comparison of sap flow models fit for different species, sites, and changing conditions. A standard sap flow modeling method would simplify the analysis and comparison of species' ecophysiological responses and may contribute to better integration of ecophysiology and ecohydrology. The use of information theoretic approaches and AIC in model selection is straightforward and promises to be useful in further standardization of sap flow methods.

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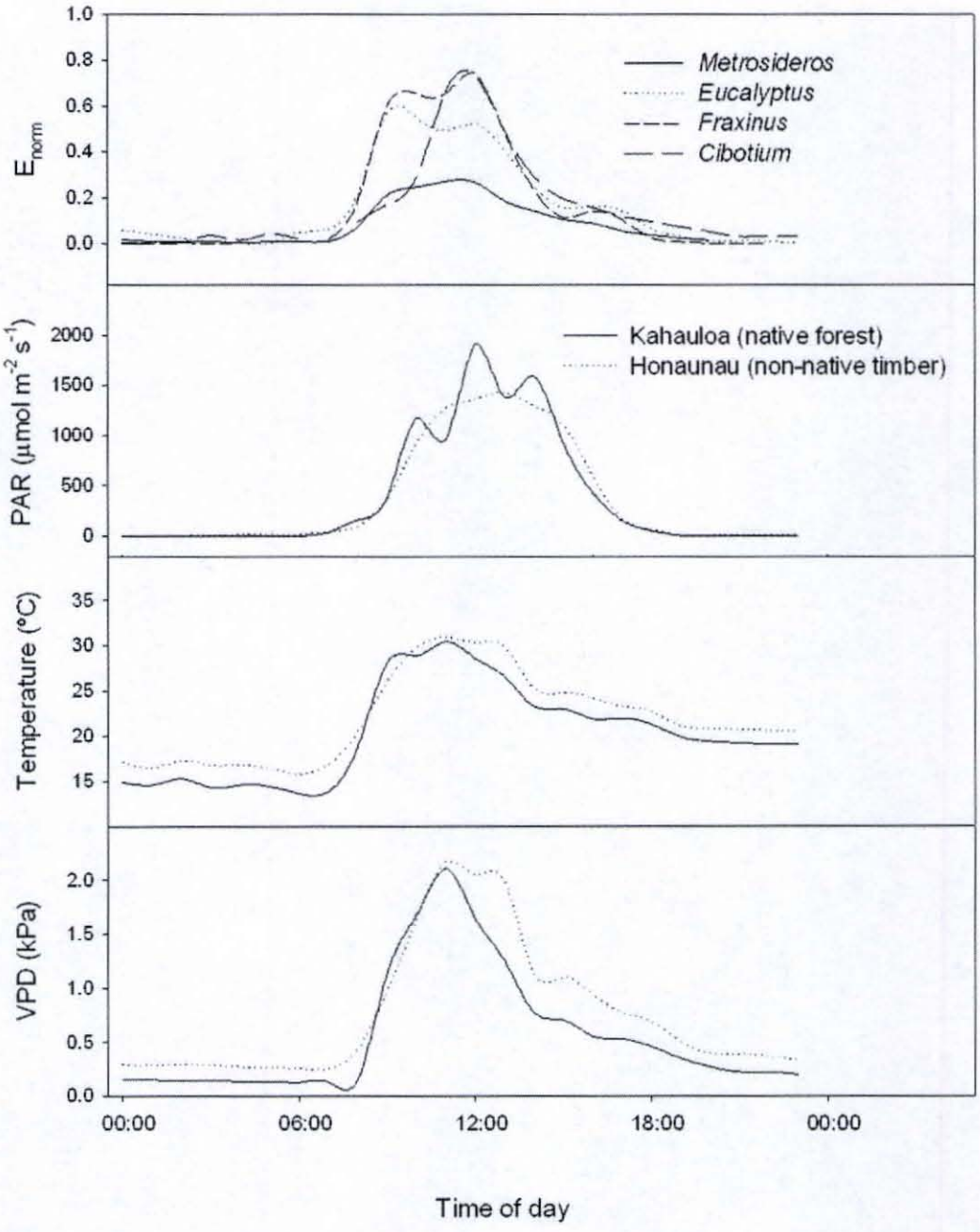


Figure 3.1. Diurnal patterns in sap flow and environmental conditions for representatives of four study species on a representative day, August 26, 2006. A) E_{norm}, normalized sap flow (unitless, ranging from 0-1) for representatives of each of the study taxa and B-D) PAR, temperature, and VPD measured in gaps near where sap flow study sites for native and non-native plant species.

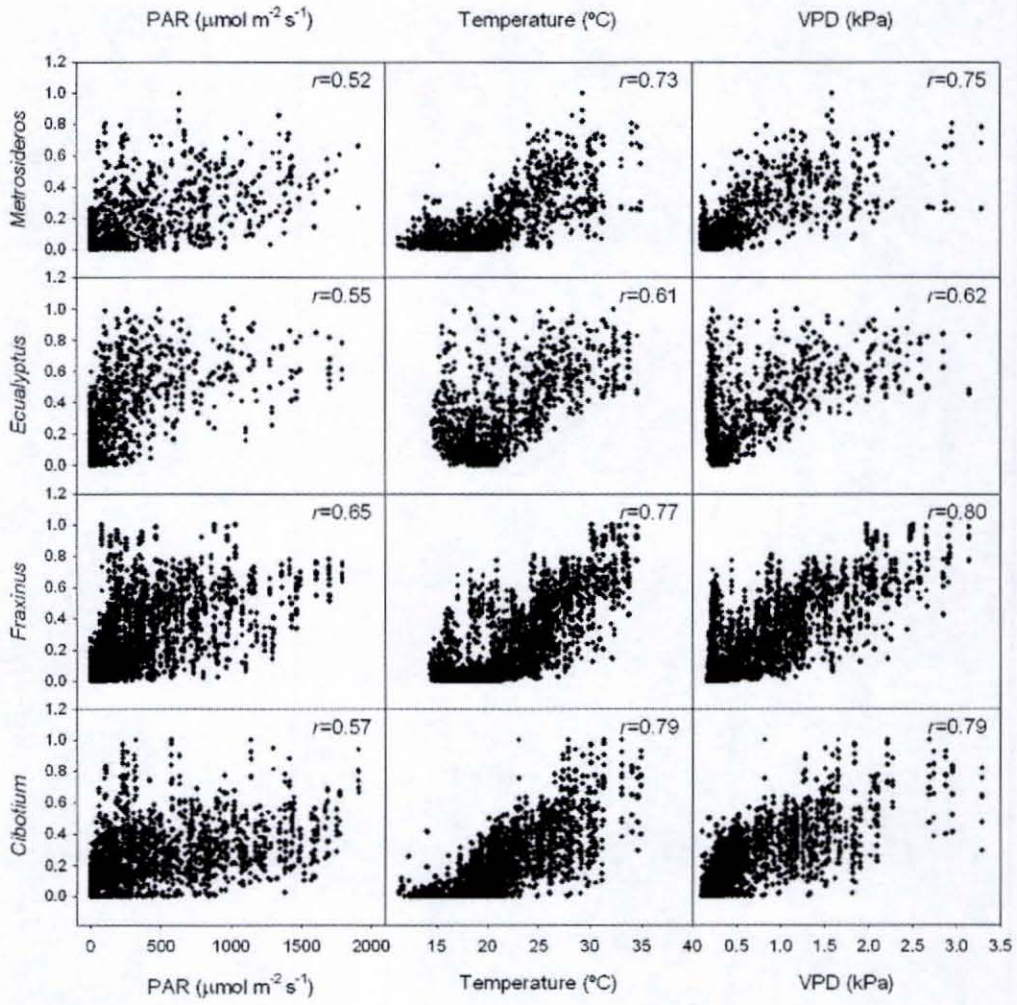
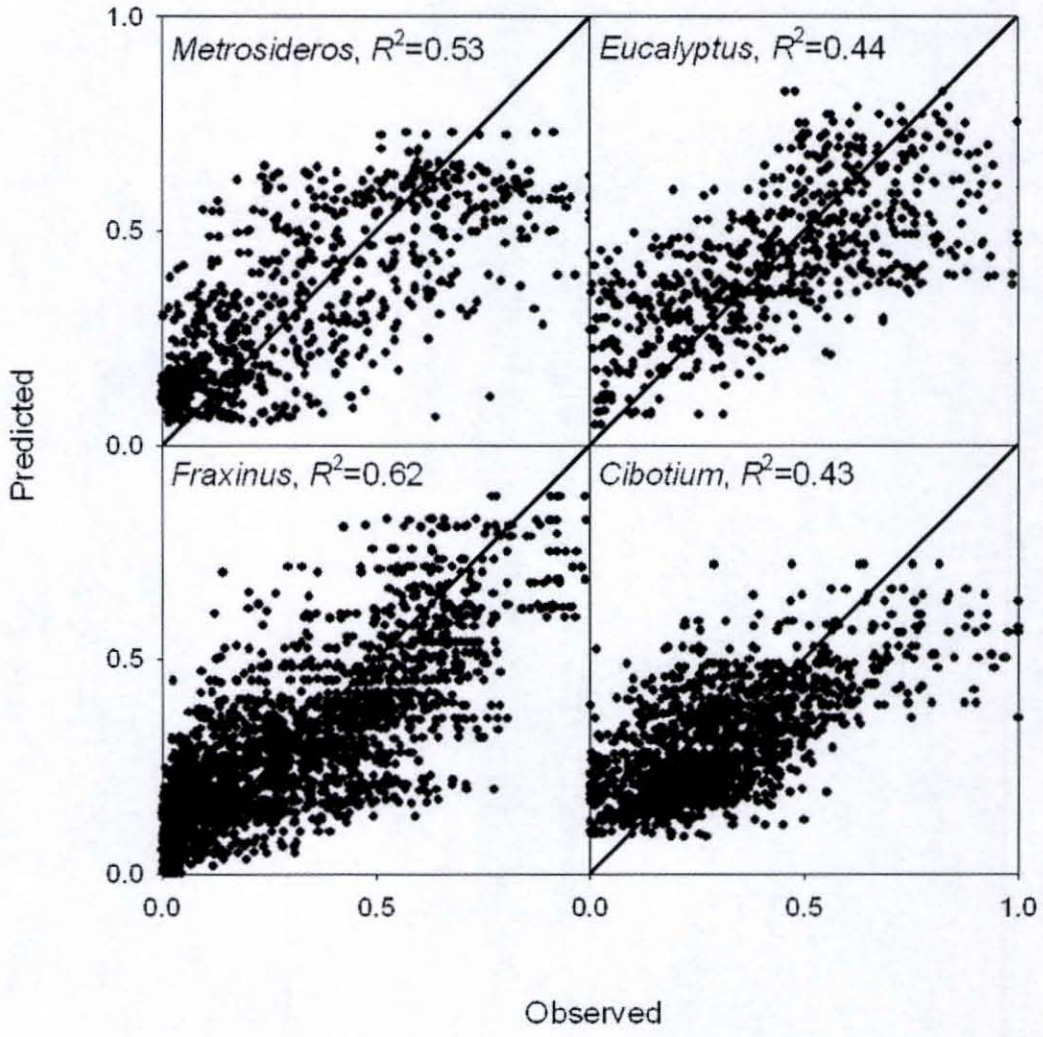


Figure 3.2. Normalized whole-plant sap flow (E_{norm}, calculated as E_t/E_{max}) for each of the four study taxa as a response to PAR, Temperature, and VPD. Pearson correlation coefficients I are provided for each relationship between E_{norm} and environmental variables, and all are significant at $P<0.001$.

Table 3.1. The best three models of sap flow vs. environmental variables for each species, selected using Akaike weights (w_i) from a set of candidate models listed in Supplementary Material, Table 3.S1. These describe the response of normalized sap flow (E_{norm}, unitless) to photosynthetically active radiation (PAR, Q, μmol m^{-2} s^{-1}), temperature (T, °C), and vapor pressure deficit (VPD, D, kPa) and log transformations of these. Data were pooled for all individuals and only daytime values were used (observations falling between 0600 and 1800). The same suite of models was tested for each species; the relative quality of the model fit is indicated by the w_i where values close to zero indicate a poor model and values close to 1 indicate an excellent fit. For the models selected, fitted coefficient values are indicated as means ± standard error.

	Model	n	K	ln-likelihood	R^2	Slope exp/obs	AIC_c	Δ_i	w_i	Fitted model coefficients
Metrosideros polymorpha										
(1)	$a + bQ + cT + dD + eQT + fQD + gTD + hQTD$	720	9	204	0.520	0.817	-389	0	0.565	**a**=0.268 ± 0.099; **b**=-9.98 ± 2.82 x10^{-4}; **c**=-1.58 ± 0.65 x10^{-2}; **d**=1.12 ± 0.20; **e**=5.08 ± 1.46 x10^{-5}; **f**=3.20 ± 3.87 x10^{-4}; **g**=-2.27 ± 0.52 x10^{-2}; **h**=-2.08 ± 1.13 x10^{-5}
(2)	$a + bQ + cT + dD + eQT + fQD + gTD$	720	8	202	0.518	0.816	-388	0.90	0.359	**a**=0.316 ± 0.096; **b**=-9.00 ± 2.80 x10^{-4}; **c**=-2.06 ± 0.60 x10^{-2}; **d**=1.38 ± 0.14; **e**=5.37 ± 1.46 x10^{-5}; **f**=-3.70 ± 0.94 x10^{-4}; **g**=-2.96 ± 0.36 x10^{-2}
(3)	$bQ + cT + dD + eQT + fQD + gTD + hQTD$	720	8	201	0.516	0.815	-385	4.26	0.067	**b**=-5.53 ± 2.37 x10^{-4}; **c**=1.37 ± 1.60 x10^{-3}; **d**=0.820 ± 0.168; **e**=-2.47 ± 1.11 x10^{-5}; **f**=7.54 ± 3.54 x10^{-4}; **g**=-1.71 ± 0.48 x10^{-2}; **h**=-2.88 ± 1.10 x10^{-3}
Eucalyptus saligna										
(4)	$a + b\,lnQ + c\,lnT + d\,lnD + e\,lnQ\,lnT + f\,lnQ\,lnD + g\,lnT\,lnD + h\,lnQ\,lnT\,lnD$	654	9	169	0.434	0.857	-321	0	0.970	**a**=7.26 ± 3.21; **b**=-1.89 ± 0.60; **c**=-2.32 ± 0.99; **d**=-3.89 ± 1.08; **e**=0.621 ± 0.184; **f**=0.346 ± 0.200; **g**=1.55 ± 0.31; **h**=-0.176 ± 0.059
(5)	$a + b\,lnQ + c\,lnT + d\,lnD + e\,lnQ\,lnT + f\,lnQ\,lnD + g\,lnT\,lnD$	654	8	165	0.426	0.855	-314	6.9	0.030	**a**=11.5 ± 2.9; **b**=-2.58 ± 0.55; **c**=-3.62 ± 0.90; **d**=-0.802 ± 0.329; **e**=0.829 ± 0.171; **f**=-0.241 ± 0.042; **g**=0.633 ± 0.067
(6)	$a + b\,lnQ + c\,lnT + d\,lnD + f\,lnQ\,lnD + g\,lnT\,lnD$	654	7	153	0.405	0.849	-292	28.1	~0	**a**=-2.31 ± 0.52; **b**=0.104 ± 0.011; **c**=0.656 ± 0.161; **d**=-2.16 ± 0.17; **f**=-0.0467 ± 0.0137; **g**=0.749 ± 0.064
Fraxinus uhdei										
(4)	$a + b\,lnQ + c\,lnT + d\,lnD + e\,lnQ\,lnT + f\,lnQ\,lnD + g\,lnT\,lnD + h\,lnQ\,lnT\,lnD$	2320	9	1160	0.623	0.844	-2300	0	~1	**a**=-2.17 ± 1.34; **b**=-0.082 ± 0.243; **c**=0.659 ± 0.413; **d**=-3.70 ± 0.46; **e**=0.045 ± 0.075; **f**=0.305 ± 0.083; **g**=1.30 ± 0.13; **h**=-0.118 ± 0.024
(5)	$a + b\,lnQ + c\,lnT + d\,lnD + e\,lnQ\,lnT + f\,lnQ\,lnD + g\,lnT\,lnD$	2320	8	1150	0.619	0.842	-2280	22.9	~0	**a**=1.43 ± 1.13; **b**=-0.676 ± 0.213; **c**=-0.442 ± 0.351; **d**=-1.52 ± 0.13; **e**=0.226 ± 0.066; **f**=-0.099 ± 0.017; **g**=0.667 ± 0.027
(6)	$a + b\,lnQ + c\,lnT + d\,lnD + f\,lnQ\,lnD + g\,lnT\,lnD$	2320	7	1140	0.617	0.841	-2270	32.7	~0	**a**=-2.39 ± 0.22; **b**=0.0549 ± 0.0045; **c**=0.738 ± 0.068; **d**=-1.89 ± 0.07; **f**=-0.0426 ± 0.0055; **g**=0.692 ± 0.026
Cibotium spp.										
(1)	$a + bQ + cT + dD + eQT + fQD + gTD + hQTD$	1478	9	827.181	0.461	0.846	-1640	0	0.399	**a**=-0.115 ± 0.081; **b**=12.4 ± 1.8 x10^{-4}; **c**=0.926 ± 0.479 x10^{-2}; **d**=0.443 ± 0.116; **e**=-6.54 ± 0.94 x10^{-5}; **f**=7.15 ± 2.18 x10^{-4}; **g**=-8.42 ± 2.99 x10^{-3}; **h**=-11.3 ± 6.1 x10^{-6}
(3)	$bQ + cT + dD + eQT + fQD + gTD + hQTD$	1478	8	826.168	0.460	0.846	-1640	~0	0.399	**b**=1.08 ± 0.14 x10^{-3}; **c**=2.61 ± 1.04 x10^{-3}; **d**=0.523 ± 0.101; **e**=-5.64 ± 0.69 x10^{-5}; **f**=6.03 ± 2.04 x10^{-4}; **g**=-9.59 ± 2.88 x10^{-3}; **h**=-9.58 ± 6.02 x10^{-6}
(2)	$a + bQ + cT + dD + eQT + fQD + gTD$	1478	8	825.483	0.460	0.846	-1630	1.37	0.201	**a**=-0.085 ± 0.079; **b**=1.25 ± 0.18 x10^{-3}; **c**=6.32 ± 4.52 x10^{-3}; **d**=0.595 ± 0.081; **e**=-6.21 ± 0.92 x10^{-5}; **f**=3.27 ± 0.58 x10^{-4}; **g**=-1.25 ± 0.20 x10^{-2}

Figure 3.3. Plots of predicted values vs. observed for the AIC-best model for each species, fitted using E_{norm} as a response to PAR, temperature, and VPD. See Table 3.1. for the species' models and fitted coefficients.



Chapter 3 Supplementary Material

Table 3.S1. Candidate models of sap flow as a function of PAR, temperature, and VPD. Columns indicate model rankings for each species coded as follows: *MP, Metrosideros polymorpha; ES, Eucalyptus saligna; FU, Fraxinus uhdei; C, Cibotium spp.*

Models	*MP*	*ES*	*FU*	*C*
Multiple linear regression models: response to log of meteorological variables				
a + b*lnQ* + c*lnT* + d*lnD* + e*lnQ lnT* + f*lnQ lnD* + g*lnT lnD* + h *lnQ lnT lnD*	17	1	1	11
a + b*lnQ* + c*lnT* + d*lnD* + e*lnQ lnT* + f*lnQ lnD* + g*lnT lnD*	16	2	2	13
a + b *lnQ* + c *lnT* + d *lnD* + e *lnQ lnT* + f *lnQ lnD*	27	7	49	40
a + b *lnQ* + c *lnT* + d *lnD* + e *lnQ lnT* + g *lnT lnD*	18	4	4	20
a + b *lnQ* + c *lnT* + d *lnD* + f *lnQ lnD* + g *lnT lnD*	12	3	3	24
a + b *lnQ* + c *lnT* + d *lnD* + e *lnQ lnT*	25	12	51	41
a + b *lnQ* + c *lnT* + d *lnD* + f *lnQ lnD*	23	22	54	42
a + b *lnQ* + c *lnT* + d *lnD* + g *lnT lnD*	19	5	5	29
a + b *lnQ* + c *lnT* + d *lnD*	35	42	60	39
a + b *lnQ* + c *lnT* + e *lnQ lnT*	58	14	52	60
a + b *lnQ* + c *lnT*	64	41	62	61
a + b *lnQ* + c *lnD* + f *lnQ lnD*	26	28	59	49
a + b *lnQ* + c *lnD*	45	45	61	48
a + b *lnT* + c *lnD* + g *lnT lnD*	20	24	32	30
a + b *lnT* + c *lnD*	32	67	63	38
a + b *lnQ*	79	48	81	77
a + b *lnT*	63	66	65	59
a + b *lnD*	42	71	67	43
a + e *lnQ lnT* + f *lnQ lnD* + g *lnT lnD*	28	32	53	31
a + e *lnQ lnT* + f *lnQ lnD* + g *lnT lnD* + h *lnQ lnT lnD*	14	6	6	21
Multiple linear regression models: linear response to meteorological variables				
a + b*Q* + c*T* + d*D* + e*QT* + f*QD* + g*TD* + h*QTD*	1	8	8	1
a + b*Q* + c*T* + d*D* + e*QT* + f*QD* + g*TD*	2	9	7	3
a + b*Q* + c*T* + d*D* + e*QT* + f*QD*	38	15	14	5
a + b*Q* + c*T* + d*D* + f*QD* + g*TD*	4	19	12	7
a + b*Q* + c*T* + d*D* + e*QT*	5	25	15	4
a + b*Q* + c*T* + d*D* + e*QT* + g*TD*	36	39	20	19
a + b*Q* + c*T* + d*D* +f*QD*	37	31	17	25
a + b*Q* + c*T* + d*D* + g*TD*	3	26	21	8
a + b*Q* + c*T* + d*D*	33	35	26	28
a + b*Q* + c*T* + e*QT*	55	47	47	58
a + b*Q* + c*T*	59	46	48	56
a + b*Q* + c*D* + f*QD*	34	29	18	26
a + b*Q* + c*D*	30	34	25	27
a + b*T* + c*D* + g*TD*	7	53	37	9
a + b*T* + c*D*	47	55	39	36
a + e*QT* + f*QD* + g*TD* + h*QTD*	24	13	11	12
a + e*QT* + f*QD* + g*TD*	54	18	10	51
a + d*QT*	77	65	77	75
a + d*QD*	74	64	75	74
a + d*TD*	61	54	44	52
a + b*Q*	80	70	85	78
a + b*T*	60	59	58	57
a + b*D*	50	56	41	33

Models *(cont'd)*	*MP*	*ES*	*FU*	*C*
Multiple linear regression models: linear response to variables, intercept fixed at 0				
$bQ + cT + dD + eQT + fQD + gTD + hQTD$	8	21	9	2
$bQ + cT + dD$	31	40	24	32
$bQ + cT + eQT$	62	43	66	67
$bQ + cT$	71	44	74	73
$bQ + dD + fQD$	49	76	19	53
$bQ + dD$	53	81	30	66
$cT + dD + gTD$	6	51	38	10
$cT + dD$	46	52	40	37
$eQT + cQD + gTD$	65	80	13	71
eQT	86	86	87	85
fQD	88	87	89	87
gTD	76	83	64	80
bQ	87	84	88	86
dD	66	82	50	72
Nonlinear multiplicative power models				
$a + bQ^d T^f D^k$	*	*	31	*
$a + bQ^d T^f$	*	16	28	*
$a + bQ^d D^k$	15	30	34	18
$a + bT^f D^k$	10	*	*	*
$a + bQ^d$	78	*	79	76
$bQ^d T^f$	57	17	27	55
$bQ^d D^k$	13	33	29	16
$bT^f D^k$	9	*	35	6
bD^k	29	62	45	15
$bQ^d + eD^k$	21	10	16	17
Linear models with sap flow as a response to inverse of meteorological variables				
$a + bQ^{-1} + cT^{-1} + dD^{-1}$	68	23	69	65
$a + bQ^{-1} + cT^{-1}$	67	63	71	63
$a + bQ^{-1} + dD^{-1}$	73	73	76	70
$a + cT^{-1} + dD^{-1}$	70	50	70	64
$a + bQ^{-1}$	83	69	86	81
$a + cT^{-1}$	69	74	72	62
$a + dD^{-1}$	72	79	83	69
Nonlinear models: saturating responses and combinations of these				
$Q/(a+Q)(1-dD)$	84	75	78	83
$Q/(b+Q)(d+e\ lnD)$	41	38	57	46
$Q/(a+Q)(d+e\ lnD)$	39	36	55	47
$aQ/(b+Q)(1-dD)$	44	11	23	22
$aQ/(b+Q)D^d$	22	27	33	14
$(aQ + dQ\ lnD)/(b+Q)$	40	37	56	45
$a(1-e^{-kQ})*(1-dD)$	48	20	22	23
$bQ/(d+Q)$	81	49	80	79
$a(1-e^{-kQ})$	82	60	82	82
$a*e^{b/T}$	56	61	36	54
$a-bD$	52	58	43	35
$aD/(b^D)$	11	78	46	50
e^{bD}	91	89	92	90
bD^{-1}	90	88	91	89
$bD^{-0.5}$	89	85	90	88
$(a-bD)^{-1}$	75	68	73	68
$Q/(a+Q)$	85	77	84	84
$a + b\ lnD$	43	72	68	44
$a + bD + cD^2$	51	57	42	34

CHAPTER 4

Conclusion

We found species varied significantly in rates of water use, even under different scaling scenarios. Species also varied in temporal patterns of water use, suggesting contrasting water use dynamics among the study species: ranging from high rates of water use over short periods by *Fraxinus* and *Cibotium* versus conservative water use by *Metrosideros*. When these species rates were combined with structural variation of stands dominated by the three study tree species, we found stands varied in estimated daily water use with *Fraxinus*, a deciduous species, used the most water as both a species and as a plantation stand. Native *Metrosideros*-dominated stands used less water, and we found most of this was contributed by the dominant understory tree ferns rather than the overstory tree species. These tree ferns play an important hydrological as well as ecological role deserving further investigation. When I analyzed relationships of sap flow with environmental variables PAR, temperature, and VPD, I found species differences suggesting a weaker relationship between sap flow and atmospheric conditions in the Myrtaceous species and a possible influence of stem water storage. No one empirical model best explained all species' relationships between sap flow and environmental variables. Overall, however, the best fitted models included interaction effects not accounted for in traditionally-used Jarvis multiplicative models, suggesting the need for further modeling method development. I propose alternative models be assessed and compared using information criteria, which are relatively easy to calculate and assess for inference.

These observations can be applied for forestry management purposes: the species differences shown here indicate certain species such as *Fraxinus* consume much more water during the summer wet season and annually (by our estimation) when compared to *Metrosideros*.

We can compare rates of *Fraxinus* uptake from our sites to *Fraxinus* rates at other sites and times to see how fixed or variable these rates are. From our stand water use scaling exercise, we see that if managing tree water use is a primary objective, stands of the species with high water use must be actively thinned and stand sapwood area controlled. Our observations that native stands use less water than stands of *Fraxinus* support conservation of existing native forest for hydrologic benefit. We did not expect to find the observed strong variation between stand water use of non-native timber species *Fraxinus* and *Eucalyptus*, but from the similarities in water use between the native and non-native Myrtaceae, we can conclude native/non-native status is not necessarily an indicator of low/high water use at whole plant and stand-level. Instead, species water use should be considered on a case-by-case basis as non-native timber species and stands of these can vary in their hydrological impacts. Forestry operations in Hawaii and beyond should consider the hydrologic impacts of species selection and long-term management practices as some non-native timber species will have fewer hydrological impacts than others. We note that ecological benefits (not studied here) should also be considered since planting native trees clearly also contribute to habitat preservation, ecosystem processes, and biodiversity.

We note that our study assessed only plant water use, or transpiration, and did not consider the other effects of vegetation on the terrestrial water balance. This leads to interesting future research: What water use differences among species and stands mean for groundwater recharge? Our observations can be interpreted in several ways: assuming precipitation is equal and canopy interception is equal, higher water use in *Fraxinus* vs. *Metrosideros* stands should result in higher groundwater recharge rates under *Metrosideros* cover (Precipitation=Interception+Transpiration+Recharge, $T_1+R_1=T_2+R_2$). However, if interception in different stands under the same environmental conditions is *not* equal, transpiration as well as recharge may be affected. Canopy interception is a critical piece of the puzzle that should be measured and considered in future comparative ecohydrological studies.

Modeling efforts and new computational tools will enable more careful analysis of large sap flow datasets. Inference made by comparing different models of sap flow and physiological regulation of water use provides a way to assess transpiration in a more ecologically-relevant way. By building a standard methodology for analyzing these large sap flow datasets, we can better integrate plant physiology, ecology, and hydrology. Generating species-specific coefficients for a single model can enable more explicit mapping of vegetation water use for watershed models, and along with climate data, can facilitate modeling of plant-water interactions in an ecological context. Integration with the powerful tools of remote sensing and eddy covariance provide a way to scale and validate sap flow estimates.

In general, the field of ecohydrology is rapidly advancing, and understanding when and how species differ can help bridge the gap between physiologists studying species traits and responses, ecologists studying patterns and interactions in space and time, and hydrologists assessing physical fluxes of water. Characterizing these dynamics is central to bridging the sciences of ecology and water resource management. Knowledge of the degree to which species differ in water use can be applied immediately in more informed forest and land management and the development of spatially explicit models of species and stand water use. Further research is necessary for understanding the other ways in which plants alter the local water balance through interception, infiltration, and soil water storage. These factors also affect ecology and dynamics of the landscape over a range of timescales. Understanding species and stand water use is thus also critical for anticipating the effects of global climate change as mediated through local hydrology.

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