

Hawaiian native forest conserves water relative to timber plantation: Species and stand traits influence water use

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Abstract. Tropical forests are becoming increasingly alien-dominated through the establishment of timber plantations and secondary forests. Despite widespread recognition that afforestation results in increased evapotranspiration and lower catchment yields, little is known of the impacts of timber plantations on water balance relative to native forest. Native forest trees have been claimed to use water conservatively and enhance groundwater recharge relative to faster-growing alien species, and this argument should motivate native forest preservation and restoration. However, data have been available primarily for leaf-level gas exchange rather than for whole-plant and stand levels. We measured sap flow of dominant tree and tree fern species over eight weeks in native *Metrosideros polymorpha* forest and adjacent alien timber plantations on the island of Hawai'i and estimated total stand transpiration. *Metrosideros polymorpha* had the lowest values of sap flux density and whole-tree water use (200 kg·m⁻² sapwood·d⁻¹, or 8 kg/d for trees of 35 cm mean diameter at breast height, *D*), substantially less than timber species *Eucalyptus saligna* or *Fraxinus uhdei* (33 and 34 kg/d for trees of 73 and 30 cm mean *D*, respectively). At the stand level, *E. saligna* and *F. uhdei* trees had three- and ninefold higher water use, respectively, than native *M. polymorpha* trees. Understory *Cibotium* tree ferns were most abundant in *M. polymorpha*-dominated forest where they accounted for 70% of water use. Overall, *F. uhdei* plantation had the highest water use at 1.8 mm/d, more than twice that of either *E. saligna* plantation or *M. polymorpha* forest. Forest water use was influenced by species composition, stem density, tree size, sapwood allocation, and understory contributions. Transpiration varied strongly among forest types even within the same wet tropical climate, and in this case, native forest had strikingly conservative water use. Comparisons of vegetation cover in water use should provide additional resolution to ecosystem valuation and land management decisions.

Key words: ecohydrology; ecosystem services; forest water budget; hāpu'u; Hawaii, USA; heat balance collar; heat dissipation sensor; 'ōhi'a; sap flow; scaling; tropical forest; watershed.

INTRODUCTION

In the last century, humans have modified the global landscape at rates faster than in any other period in history, with direct and indirect impacts on water resources. Tropical forests are becoming increasingly alien-dominated through the establishment of high-productivity alien timber plantations and invaded secondary forest (Fine 2002, Lugo and Helmer 2004, Wright 2005). While these forested systems are valued for fiber, fuel, and carbon sequestration, monotypic timber plantations often consist of species chosen for fast growth, high yield, and tolerance to a wide range of

conditions; these traits often enable these plants to spread beyond their planted range and become invasive (Richardson 1998). Such substantial changes in vegetation may significantly decrease water supplies (Le Maitre et al. 2002, Huxman et al. 2005); thus, as demand for freshwater increases, there is a critical need to understand the hydrological implications of different land uses. In Hawaii and elsewhere, rainfall in forested upland areas feeds the groundwater and surface water resources serving human activities and natural ecological functions. Quantifying the hydrological impacts of land use and vegetative cover has critical implications for ecology, land and water management, and restoration.

The rapidly expanding field of ecohydrology attests to the increased recognition of the important and dynamic role of vegetation in shaping the terrestrial water balance (Baird and Wilby 1999, Eagleson 2002, Rodriguez-Iturbe and Porporato 2004). Vegetation water use (transpiration) makes up the bulk of evapotranspiration

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(ET), which removes precipitation from the ecosystem that would otherwise contribute to streamflow or groundwater recharge. Catchment-level studies show that following deforestation, ET decreases and consequently streamflow increases (Bosch and Hewlett 1982, Brown et al. 2005); following the afforestation of grasslands, shrublands, and croplands, ET increases and streamflow decreases (Le Maitre et al. 2002, Farley et al. 2005, Huxman et al. 2005, Jackson et al. 2005). However, there are few available data showing differences in plant water use for native and plantation forest stands of contrasting species composition in a given climate.

We examined the degree to which stand transpiration can differ between native Hawaiian old-growth forest and the alien timber plantations to which it is often converted, and we quantified the factors that contribute to differences. Several previous studies of native temperate forests have suggested that stand water use can depend on species composition as well as stand structure (e.g., Vertessy et al. 2001, Ewers et al. 2002). The rapid growth that characterizes alien plantation trees suggests these species are also high water users. Physiological studies in Hawaii have indicated higher stomatal conductance and 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). All else being equal, higher stomatal conductance for alien species would predict higher whole-plant transpiration rates of alien species vs. native species.

There exist very few comparative studies of native and alien species' water use at the whole-plant and stand scales relevant to hydrology. In Hawaii, there have been no previous studies to our knowledge; transpiration data for whole trees are available only for native species at contrasting sites (Santiago et al. 2000) or stand densities (Meinzer et al. 1996) or for alien species at a single site (Barnard and Ryan 2003, Hubbard et al. 2004, Restom Gaskill 2004). Whole-plant transpiration depends on site conditions and on species traits. The sap flow per sapwood area (sap flux density), a frequently used measure of sap flux capacity standardized by tree size, depends upon anatomical and functional properties including hydraulic conductance, capacitance, and resistance to cavitation; these properties can vary strongly among trees of given species and across species (see Meinzer et al. 2003, Melcher et al. 2003). Another way to express rates of sap flow is per leaf area, which is equivalent to the product of sap flow per sapwood area and the sapwood area:leaf area ratio; this ratio varies among trees of given species, in particular tending to increase with tree size and age, and also varies strongly across species (McDowell et al. 2002). Stand-level transpiration additionally depends on stand-level traits, including tree sizes and ages, and stand densities, as well as understory development (Hatton and Wu 1995,

Vertessy et al. 2001). For example, young, mature stands typically transpire more than old stands due to a greater stand density and sapwood area, greater sapwood-specific transpiration, and/or greater overstory leaf area index (Richardson 1998, Roberts et al. 2001, Vertessy et al. 2001, Moore et al. 2004, Delzon and Loustau 2005, Wright 2005). Notably, alien-dominated forests in Hawaii consist of relatively recent introductions, with a monotypic closed canopy and little understory, and thus differ in many aspects of stand structure from naturally regenerating, native-dominated forest.

We focused on old-growth forest vs. alien timber plantation and aimed to measure water use for several dominant tree species found across the Hawaiian Islands and to scale up to stand level. We measured plant water use in native forest dominated by *Metrosideros polymorpha* and timber plantation dominated by the alien trees *Eucalyptus saligna* and *Fraxinus uhdei*. Our study addressed, for a wet forest site on the island of Hawai'i: (1) whether different tree species transpire at different rates and (2) whether stands dominated by these different species differ in rates of ground-area-based transpiration. We hypothesized that transpiration would be higher for alien timber species compared to native species on a leaf, sapwood area, and whole-tree basis. We further determined the degree to which species differed in their temporal partitioning of water use. We also hypothesized that stand-level water use would be higher for timber plantations, with intrinsic species water use differences further mediated by adjustments in tree sizes and stem densities and by understory development.

METHODS

Study sites and species

The study was conducted at Hōnaunau Forest Reserve on the leeward slope of Mauna Loa, Hawai'i Island (Fig. 1). The reserve is a 4250-ha mosaic of native forest and alien tree plantations owned by native Hawaiian legacy trust Kamehameha Schools. From 1956 to 1962, 340 ha were cleared and planted in various alien timber species (Carlson and Bryan 1959, 1963). Since then, the area has been left largely unmanaged. The Hōnaunau Forest was chosen for its continuous native and alien-dominated stands and for its simple hydrology; due to the high substrate permeability and low slope that minimize horizontal fluxes, runoff occurs only in large storm events.

Within the forest reserve, we selected two sites 5 km apart representing native and alien-dominated vegetation in the *ahupua'a* (land divisions) of Kahauloa (19.482° N, 155.869° W) and Hōnaunau (19.435° N, 155.844° W). The sites were selected to isolate the effects of forest type on stand transpiration; both were at 1000 m elevation on 750–1500-yr-old basaltic 'a'ā lava flows (Lockwood 1995) of Puna-Udarent soil type with gradual slopes of <20% (P. Niemeyer, *personal commu-*

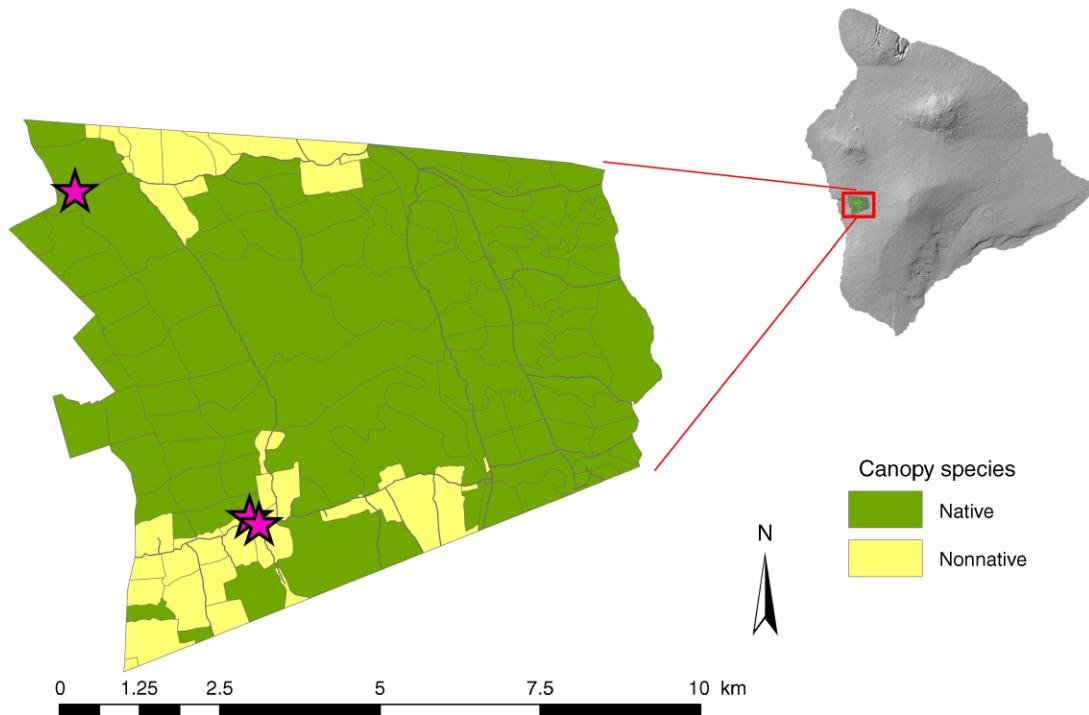


FIG. 1. Native and alien-dominated timber stands in Hōnaunau Forest, Hawaii, USA. Study sites were located 5 km apart within the same continuous patchwork of native forest and alien timber plantation. The study stands are represented by stars: from north to south, native old-growth forest dominated by *Metrosideros polymorpha* (Kahauloa) and timber plantations dominated by *Eucalyptus saligna* and *Fraxinus uhdei* (Hōnaunau), respectively.

nication). At Kahauloa and Hōnaunau, mean annual precipitation is 1520 and 1450 mm, respectively, with >65% occurring during the wet summer months of April–October (T. Giambelluca, unpublished data), while estimated annual pan evaporation is between 760 and 1020 mm (Ekern and Chang 1985). Soil moisture measurements for one year prior to the study showed minimal variation in the upper 15 cm, with soil water content always >64% of that at field capacity, with a median of 71–83% (CS-616 water content reflectometers; Campbell Scientific, Logan, Utah, USA). During this study, measurements of photosynthetically active radiation (PAR), temperature, and vapor pressure deficit (VPD) were made in nearby forest gaps (WS-2308 system; LaCrosse Technology, LaCrosse, Wisconsin, USA). Values across the study period for daily maximum and mean PAR (considered 06:00 to 18:00) were 981 and 404 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, respectively; values for 24-h minimum, mean, and maximum temperature were 15.2°, 19.9°, and 28.2°C, respectively; and values for VPD were 0.16, 0.47 (0.72, if considered 06:00 to 18:00), and 1.52 kPa.

In the native old-growth forest of Kahauloa (Fig. 2A), we measured the water use of the dominant endemic canopy tree *Metrosideros polymorpha* (Myrtaceae; common name 'ōhi'a; Wagner et al. 1999) and the endemic understory tree fern *Cibotium glaucum* (Cibotiaceae; common name *hāpu'u pulu*; Palmer 2002, Smith et al.

2006). At the alien tree plantation site in Hōnaunau (Fig. 2B, C), we measured sap flow for *Eucalyptus saligna* (Myrtaceae; Wagner et al. 1999) and *Fraxinus uhdei* (Oleaceae; Wagner et al. 1999) occurring in monotypic stands of 2 ha and 25 ha, respectively, also with tree-fern-dominated understory.

Measuring and characterizing tree sap flow

From August through September 2006 (wet season), we measured whole-plant transpiration for six individuals of each dominant tree species. Tree sap flow was determined 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 sap flow, two to five sensors were installed in each tree at 2–6 cm depth, positioned around the circumference at 1.3 m 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. To protect the sensors and reduce the effects of external thermal gradients (Lu et al. 2004) we insulated the tree trunk with bubble wrap and aluminum foil. The heated probe tips were supplied with continuous power via a voltage regulator circuit connected to 6-V deep-cycle batteries (models T105 and T125; Trojan, Santa Fe Springs, California, USA). These batteries were replaced with recharged batteries each week. We

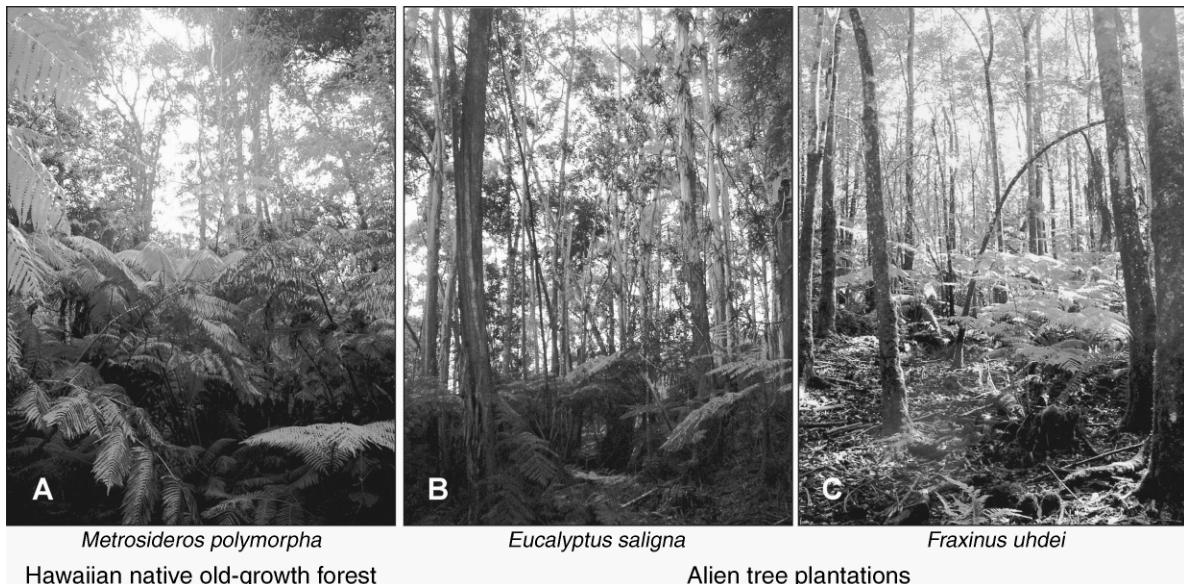


FIG. 2. Stands typical of the forest types studied: (A) native old-growth *Metrosideros polymorpha* forest with dense *Cibotium* tree fern understory, and alien timber stands of (B) *Eucalyptus saligna* and (C) *Fraxinus uhdei*.

measured differential voltage between the two probe tips every minute and recorded means every 10 min with AM16/32 multiplexers connected to CR1000 dataloggers (Campbell Scientific, Logan, Utah, USA) powered by 7-Ah 12-V sealed lead-acid batteries (Radio Shack, Fort Worth, Texas, USA).

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 (in grams per square meter per second) 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)

$$v = 119 \times \left(\frac{\Delta V_m - \Delta V}{\Delta V} \right)^{1.231} \quad (1)$$

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 by 10–20% during the weekly discharge of our deep-cycle batteries. To prevent an overestimation of sap flow, linear interpolation was used to estimate a ΔV_m value for each 10-min interval between the measured ΔV_m values for successive nights.

To account for radial variation of sap flux density within the tree, we calculated whole-tree sap flow by weighting the measured sap flux density for each probe by an associated sapwood annulus (Hatton et al. 1990). Concentric annuli were defined below the cambium as delimited by an outer and inner radius (r_i and r_{i-1})

midway between successive probe tips. Sap flow 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 sap flow (Q , in grams per second):

$$Q = \sum_{i=1}^n \pi(r_i^2 - r_{i-1}^2)v_i. \quad (2)$$

We determined sapwood-area- and leaf-area-specific sap flow rates by dividing these whole-tree flow rate values by estimated sapwood and leaf area for the study individuals. The resulting data were used to plot diurnal curves for individual trees (Fig. 3) that were then characterized on a daily basis to allow comparison of sap flow patterns among species.

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 sap flow patterns. For each tree, we measured diameter at 1.3 m height (D) and extracted cores of 5–15 cm length with a 4.3-mm increment borer, noting the depth of outer bark (d_{bk}) and phloem (d_{ph}).

Several methods were used to determine sapwood depth (d_{sw}), including staining of living parenchyma with triphenyl tetrazolium chloride in a phosphate buffer solution (Sigma-Aldrich, St. Louis, Missouri, USA; Spicer and Holbrook 2005), visual observation of vessel translucency, and projection from sap flow profiles of the depth at which flow was zero. *Fraxinus uhdei* had living parenchyma across the full extent of the cores, and sap flow measurements indicated that maximum flow did not significantly decrease with depth, so we assumed all of its

wood was uniformly water conducting. The *E. saligna* sapwood–heartwood boundary was determined by visually inspecting the point at which vessels were no longer translucent; sap flow 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.

Sapwood area (A_S , in square centimeters) was calculated as the difference between the area of the cross-sectional disc from the cambium inward and the area of the heartwood cross-section:

$$A_S = \pi \times r_{\text{outer}}^2 - \pi \times r_{\text{inner}}^2 \quad (3)$$

where

$$r_{\text{outer}} = \frac{D}{2} - (d_{\text{bk}} + d_{\text{ph}}) \quad (4)$$

$$r_{\text{inner}} = \frac{D}{2} - (d_{\text{bk}} + d_{\text{ph}} + d_{\text{sw}}) \quad (5)$$

and the radius is in centimeters.

Estimating tree leaf area

We estimated total leaf area for the study trees by multiplying the number of tree branches by an average leaf area per branch, determined from branches sampled from three other similar trees for *M. polymorpha* and *F. uhdei* (using a LI-COR 3100C leaf area meter; LI-COR, Lincoln, Nebraska, USA). In cases in which 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 48 h. For *E. saligna*, branches were inaccessible; to obtain mean leaf area per branch, we assessed mean area per leaf from fallen branches and multiplied this value by the number of leaves counted in digital photographs of sample branches in the canopy. The number of branches on the sap flow trees was estimated by visual inspection of photographs (Santiago et al. 2000). These estimates of leaf area for tall canopy trees are relatively coarse, but they should allow robust comparisons of sap flow per leaf area across species (e.g., Meinzer et al. 1999, Santiago et al. 2000).

Measuring tree fern sap flow

From August through October 2006, we measured bulk sap flow for healthy fronds of seven individuals of the dominant tree fern *Cibotium glaucum*. We took measurements every minute and recorded 15-min averages using a stem heat balance collar system placed on frond stipes (Dynamax Flow32 system; Dynamax, Houston, Texas, USA) powered by 12-V deep-cycle batteries connected in parallel (model 30XHS Trojan; 85 Ah, Kirkland, Issaquah, Washington, USA; 60 Ah, Daleco, Kailua-Kona, Hawaii, USA). We calculated bulk sap flow from voltages of four thermocouples per collar using the manufacturer's calculation procedures

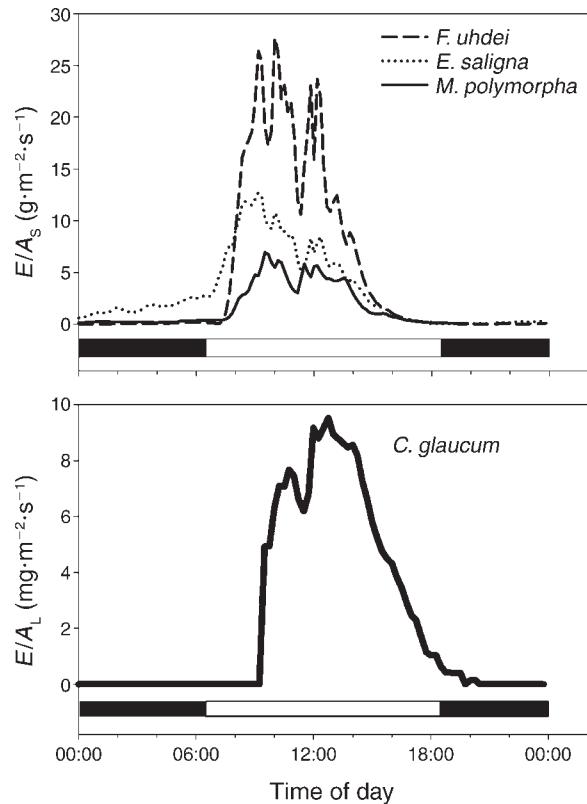


FIG. 3. (Top) Sap flow per sapwood area (E/A_S) on a representative day (30 August 2006) for *Metrosideros polymorpha* in native forest and for *Eucalyptus saligna* and *Fraxinus uhdei* in adjacent alien timber plantations. (Bottom) Sap flow per frond area (E/A_L) for the tree fern *Cibotium glaucum* in native forest. Day and night are indicated on the x-axis by white and black bars.

(Sakuratani 1981, Baker and van Bavel 1987) and determined sap flow 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.

Water use parameters and statistical analyses for comparing species

We extracted daily parameters from diurnal sap flow data (all statistics calculated using R version 2.5.1; R Development Core Team 2007). We determined diurnal sap flow rate (E_{tot} , in kilograms per day), daily maximum sap flow rate (E_{max} , in grams per second), time of maximum sap flow (t_{max}), daily period with >50% of maximum sap flow (Δt_{peak} , in hours), and proportion of nocturnal sap flow, with nocturnal flow defined as occurring between 18:30 and 06:30 (E_n/E_{tot} , in percentages). Data for each parameter were averaged over two months for each individual tree or tree fern. These individual means were ln-transformed to improve homogeneity of variance and compared using one-way ANOVA, followed by Tukey's hsd comparisons with a family-wise confidence level of 0.05 (Zar 1999). We performed the same analyses for the parameters

TABLE 1. Mean traits for tree and tree fern species and allometric coefficients for sapwood and frond area in native and alien-dominated timber stands in Hōnaunau Forest, Hawaii, USA.

Species	Approximate maximum height (m)	Mean trait values			
		<i>D</i> (cm)	<i>A_S</i> (cm ²)	<i>L</i> (m)	<i>A_L</i> (m ²)
<i>Metrosideros polymorpha</i>	30	35.0 ± 8.5 (6)	261 ± 107 (6)		
<i>Eucalyptus saligna</i>	55	73.3 ± 9.4 (6)	605 ± 158 (6)		
<i>Fraxinus uhdei</i>	30	30.0 ± 2.1 (6)	609 ± 84 (6)		
<i>Cibotium glaucum</i>	7			2.43 ± 0.19 (7)	2.40 ± 0.25 (7)

Notes: Mean trait values for tree species include tree diameter at 1.3 m height (*D*) and sapwood area (*A_S*) and, for the tree fern species, frond length index (*L*) and individual frond area (*A_L*). Allometric coefficients *a* and *b* were fitted for $\ln(A_S) = a + b \ln(D)$ for trees and $\ln(A_L) = a + b \ln(L)$ for tree ferns with a data set of sample size *n*. These allometries were applied as $A_S = e^a \times D^b \times c$ and $A_L = e^a \times L^b \times c$, respectively; the correction factor *c*, calculated as $e^{\sigma^2/2}$, accounts for systematic bias in fitting coefficients to ln-transformed data (Baskerville 1972, Sprugel 1983).

scaled by sapwood area and leaf area. To account for the importance of day-to-day variation in sap flow, we also compared species' parameters in repeated-measures ANOVAs 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), blocking by individual trees and tree ferns.

Sapwood and frond area allometries for scaling transpiration to the stand

For each of the three study tree species, we determined sapwood area vs. *D* relationships by combining data from our six study trees per species with *D* and trunk core data for 9–24 additional trees of each species sampled along 100-m transects within each stand type. We calculated *A_S* for trees and fitted coefficients for the least-squares linear regression of ln-transformed *A_S* against ln-transformed *D*.

For *C. glaucum* tree ferns, we developed an allometry relating ln-transformed individual frond leaf area (*A_L*) to ln-transformed frond length index (*L*), an easily-measured characteristic, the projected horizontal frond length from its base at caudex (stem) insertion to its distal tip (Arcand et al. 2008). We used an allometric relationship based on 10 mature fronds from our site, including our seven sap flow study fronds, and eight other *C. glaucum* individuals in a similar Hawaiian wet forest (Arcand et al. 2008), as the allometric relationships were statistically similar in slopes and intercepts.

Scaling transpiration to the stand

For each of three stand types (*M. polymorpha*-, *E. saligna*-, and *F. uhdei*-dominated), we surveyed five to six 20 × 20 m plots to determine total sapwood and *Cibotium* leaf area on a ground area basis. In each plot, we recorded species and *D* for every stem (*D* > 1 cm). For each individual of *Cibotium*, we recorded the number of live fronds and representative *L*. In eight plots with high *Cibotium* densities, we surveyed these in a 10 × 20 m plot within the larger plot. We applied our species-specific allometries (Table 1) to the data to

obtain estimates of plot sapwood area (*A_{S,pl}*, in square centimeters) and plot *Cibotium* frond area (*A_{L,pl}*, in square meters). For each plot with *n* trees and *m* *Cibotium*,

$$A_{S,pl} = \sum_{i=1}^n e^a \times D_i^b \times c \quad \text{for each tree species} \quad (6)$$

$$A_{L,pl} = \sum_{i=1}^m e^a \times L_i^b \times c \times j_i \quad \text{for each tree fern species} \quad (7)$$

where *a* and *b* are species-specific allometric coefficients, *c* is a species-specific allometric correction coefficient, and *j* is the number of fronds per tree fern caudex (Table 1; Baskerville 1972, Sprugel 1983). We estimated total tree fern leaf area using a *C. glaucum* leaf area–frond length index relationship as *C. glaucum* was the dominant tree fern species across stand types.

For each plot, we estimated daily plot transpiration (*E_{pl}*, in millimeters per day) by multiplying the daily sap flow rates for each study species (\bar{E}_S , \bar{E}_L) by its corresponding stand sapwood area (*A_{S,pl}*) for trees or frond area (*A_{L,pl}*) for tree ferns. We summed the contributions from each tree species (*i* from 1 through *k*) and the understory *Cibotium* and divided these by the plot ground area (*A_{pl}*, typically 400 m²):

$$E_{pl} = \frac{\sum_{i=1}^k (A_{S,pl} \times \bar{E}_S)_i}{A_{pl}} + \frac{A_{L,pl} \times \bar{E}_{L,CG}}{A_{pl}} \quad (8)$$

Statistical analyses for comparing stands

We compared stand structure and transpiration using one-way ANOVA and post hoc Tukey comparisons. Our estimates assumed the sap flow measurements of the study trees and their scaling with tree size to be representative of their species across the stand.

To account for the propagation of error from multiple sources in our estimates, we performed the same one-way ANOVA on stand transpiration data simulated

TABLE 1. Extended.

Allometric coefficients			
<i>a</i>	<i>b</i>	<i>c</i>	<i>n</i>
-0.779 ± 0.412	1.73 ± 0.12	1.02	15
-0.878 ± 0.417	1.68 ± 0.10	1.03	22
-0.654 ± 0.034	2.07 ± 0.01	1.00	30
-1.07 ± 0.21	2.13 ± 0.24	1.06	18

using nonparametric bootstrap methods (Blukacz et al. 2005). For each of the five to six plots surveyed per stand type, we generated 2000 bootstrap replicates to estimate stand sapwood area, frond area, and transpiration rates, using our vegetation survey data, allometry data, and sap flow data. For each bootstrap replicate, we generated new allometric coefficients obtained by resampling, with replacement, pairs of data from our allometry data sets. To estimate sapwood area and frond area of each individual surveyed, we applied these new coefficients to tree *D* and tree fern *L* data, adding a resampled residual each time. Each sapwood or frond area estimate was then multiplied by a resampled mean daily transpiration rate for the appropriate species, and these were summed over the stand. While the 2000 bootstrap replicates enabled determination of confidence intervals (bias-corrected and accelerated; Efron and Tibshirani 1993) for mean stand traits and transpiration, we used only the bootstrap means for ANOVAs and post hoc analyses to compare the effect of stand type on stand transpiration. Because estimates of stand-level water use neglected the sap flow from non-study species, we additionally tested different scaling scenarios to estimate their contribution to overall stand rates.

RESULTS

Species differences in tree size, sapwood allocation, and water use

The study trees varied in sizes and in sapwood allocation (Table 1). Trees of *E. saligna* were much larger than those of *M. polymorpha* and *F. uhdei* (means for *D* of 73, 35, and 30 cm, respectively). Despite the difference in sizes, tree sapwood area was similar for *F. uhdei* and *E. saligna* because of high allocation to sapwood in *F. uhdei* relative to *M. polymorpha* and *E. saligna* (84%, 23%, and 14% of basal area, respectively). Of all the study trees, *M. polymorpha* had the lowest sapwood area per individual.

Across the study period, the temporal dynamics of sap flow for each tree species correlated well with environmental drivers. Sap flow rates calculated at hourly intervals correlated strongly with PAR, temperature, and VPD during the daytime (06:00 to 18:00; Pearson correlation coefficients range = 0.2–0.8; $P < 0.001$). Testing a range of models for prediction of sap flow from combined environmental drivers indicated that the species differed in which models fitted best and thus

showed different responses to given and combined environmental factors (A. Kagawa, L. Sack, K. Duarte, and S. James, *unpublished manuscript*). Species also differed strongly in their realized overall sap flow rates. Daily maximum sapwood area-specific sap flow rates (sap flux density) varied fourfold from *M. polymorpha* to *F. uhdei*, with *E. saligna* intermediate (Figs. 3 and 4A). Maximum whole-tree sap flow rates varied sevenfold across species, from *M. polymorpha* to *F. uhdei*, with *E. saligna* intermediate (Fig. 4A, inset). Species also varied strongly in total daily water use, with *M. polymorpha* having <50% of the sapwood area-specific sap flow of *E. saligna* and *F. uhdei* (Fig. 4B), and whole-tree daily water use of *M. polymorpha* was <30% that of *E. saligna* and *F. uhdei* (Fig. 4B, inset). Sap flow scaled by leaf area also varied strongly among tree species (Table 2). *Metrosideros polymorpha*, *E. saligna*, and *F. uhdei* had maximum sap flow rates per leaf area of 2.05 ± 0.59 $\text{mg}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, 4.66 ± 0.79 $\text{mg}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and 31.9 ± 4.6 $\text{mg}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. The leaf-area-specific sap flow rate of understory *C. glaucum* was 9.49 ± 1.10 $\text{mg}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, intermediate between the alien tree species' rates.

Species showed strong variation in diurnal sap flow patterns (Fig. 3, Table 2). On average, *E. saligna* reached maximum flow at 09:37 (± 7 min), >1 h earlier than *M. polymorpha*, *F. uhdei*, and *C. glaucum* (10:48 ± 8 min, 10:52 ± 3 min, and 11:05 ± 6 min [mean \pm SE], respectively). The duration of peak flow was >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 h, 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 sap flow at 30% $\pm 3\%$ and 24% $\pm 4\%$ of total sap flow, respectively, while *F. uhdei* and *C. glaucum* showed relatively low nocturnal rates (5% $\pm 2\%$ and 4% $\pm 1\%$, respectively; Fig. 5).

Stand-level differences in structure and water use

The three stand types were each characterized by a different dominant canopy tree species and a fern understory. In native old-growth stands, *M. polymorpha* accounted for 87.7% $\pm 5.0\%$ of the total living tree basal area, with the remainder consisting largely of *Ilex anomala* and *Acacia koa* (Table 3). In the *E. saligna*- and *F. uhdei*-dominated timber plantations, *E. saligna* and *F. uhdei* accounted for 89.6% $\pm 3.5\%$ and 84.7% $\pm 5.7\%$ of the living basal area, respectively, with the remainder consisting largely of remnant *M. polymorpha* and *A. koa*.

The three stand types varied strongly in tree sizes and tree densities (Fig. 6A–C). The live stem density (*N*) in stands of *F. uhdei* was twice that for stands of *E. saligna* and *M. polymorpha*. By contrast, *D* for *E. saligna* was nearly twice that *F. uhdei*, contributing to high stand basal area. Overall, the variation in stem density and diameter in conjunction with species-specific sapwood allocation patterns resulted in *F. uhdei* stands having the

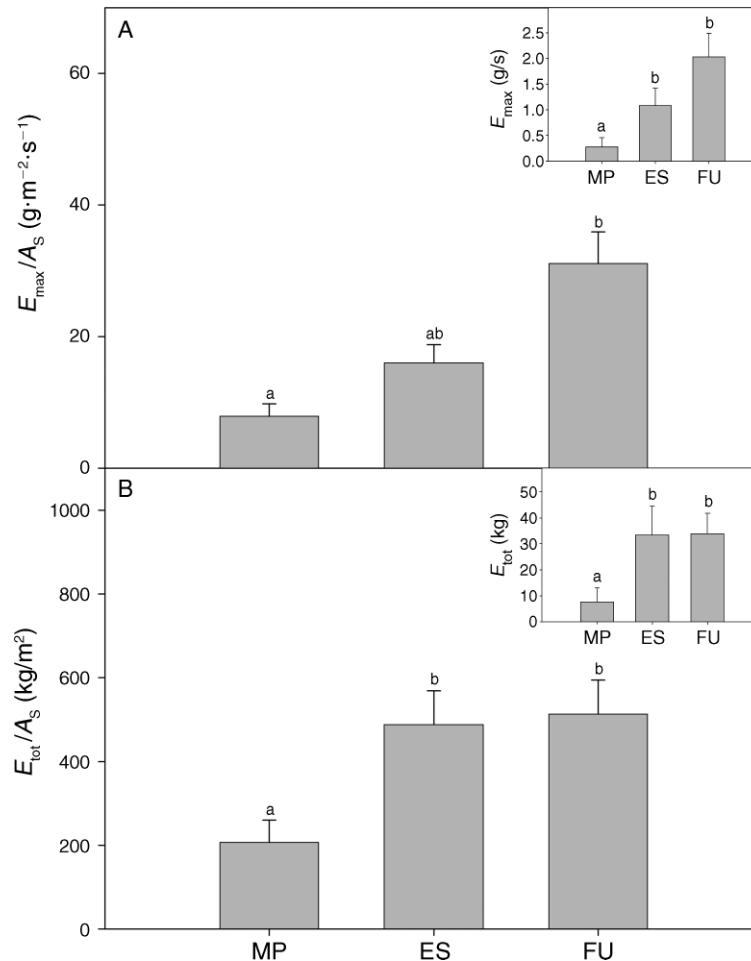


FIG. 4. Mean sap flow rates of tree species in Hōnaunau Forest: (A) mean diurnal maximum sap flow rate per sapwood area (E_{\max}/A_S) and per tree (E_{\max} , inset) and (B) mean diurnal sap flow per sapwood area (E_{tot}/A_S) and for the whole plant (E_{tot} , inset). Species abbreviations: MP, *Metrosideros polymorpha*; ES, *Eucalyptus saligna*; FU, *Fraxinus uhdei* ($n = 6$ individuals per species). Bars show mean + SE, with the same lowercase letters indicating no statistically significant difference ($P = 0.05$; post hoc Tukey comparisons of ln-transformed data).

highest total stand sapwood area, nearly four times greater than that of *M. polymorpha*-dominated stands (Fig. 6A–C).

Stand types also varied strongly in *Cibotium* abundance (Fig. 6D–F). Native stands dominated by *M. polymorpha* had especially dense *Cibotium* understory, twice the fern density found in *E. saligna* or *F. uhdei* timber stands. While the average *Cibotium* frond was 50–65% larger in native *M. polymorpha* stands, the number of fronds per tree fern was statistically similar across stand types. Overall, stand *Cibotium* frond area estimates were two to three times higher for native stands than for the timber stands (Fig. 6D–F).

The estimated total stand water use varied 2.5-fold across stand types (Fig. 6G). With both high transpiration rates and high sapwood area, stands dominated by *F. uhdei* used more than twice as much water as stands dominated by *E. saligna* or *M. polymorpha*. In native forest dominated by *M. polymorpha*, *Cibotium* transpi-

ration accounted for $75.3\% \pm 6.7\%$ of stand water use. By contrast, for alien timber stands dominated by *F. uhdei* or *E. saligna*, *Cibotium* transpiration, while still substantial, was secondary to that of the dominant tree species ($11.8\% \pm 2.6\%$ and $32.2\% \pm 5.6\%$, respectively).

Stand types still varied strongly in water use even after accounting for contributions from the other less-abundant species that were not measured in our study. In a scenario in which all other species contributed 100% of their basal area to sapwood, *F. uhdei* stands still had at least 75% higher sapwood area than the two other stand types. We tested different sap flow rate scenarios, and we arrived at the same overall finding. For instance, when, as the most conservative case, we used the highest rates (i.e., *F. uhdei* rates) for the non-study species in *M. polymorpha* stands and the lowest rates (*M. polymorpha* rates) for the non-study species in *F. uhdei* stands, *F. uhdei* stands had 60% higher daily transpiration.

TABLE 2. Mean squares for ANOVA for water use parameters of the tree species *Metrosideros polymorpha*, *Eucalyptus saligna*, and *Fraxinus uhdei*.

Parameter	One-way ANOVA		Repeated-measures ANOVA				
	Species df = 2	Error _{ind} df = 15	Species df = 2	Error _{ind} df = 15	Day df = 18	Species × day df = 36	Error _{tot} df = 270
Whole-tree							
E_{tot} (kg/d)	9.19**	1.37	203**	28.9	2.18***	0.466***	0.167
E_{max} (g/s)	11.5 **	1.30	237**	28.6	0.932***	0.198**	0.108
Per sapwood area							
E_{tot}/A_S	1.70*	0.339	45.1*	7.73	2.18***	0.466***	0.167
E_{max}/A_S	3.04**	0.355	65.9**	8.60	0.932***	0.198**	0.108
Per leaf area							
E_{tot}/A_L	8.20***	0.275	176***	6.48	2.18***	0.466***	0.167
E_{max}/A_L	12.4***	0.259	247***	6.65	0.932***	0.198**	0.108
Temporal patterns							
t_{max} (h)	2.975**	0.411	50.103*	10.798	12.51*	11.49**	6.74
Δt_{peak} (h)	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

Notes: Results are shown for integrated diurnal sap flow and daily maximum sap flow rate on a whole-tree basis (E_{tot} ; E_{max}), and scaled by sapwood area (E_{tot}/A_S , E_{max}/A_S), and leaf area (E_{tot}/A_L , E_{max}/A_L); and for time at maximum sap flow (t_{max}), time duration at which sap flow exceeded 50% of maximum (Δt_{peak}), and percentage of sap flow occurring at night (18:30–06:30; E_n/E_{tot}). One-way ANOVAs tested species differences, including all data over the eight-week measurement period; repeated-measures ANOVAs tested differences among species, days, and the interaction for 19 days that all study trees were measured simultaneously. Error_{ind} refers to variation among individual trees, and Error_{tot} to overall variation.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

DISCUSSION

Strong differences in water use among native and alien species

Metrosideros polymorpha exhibited the lowest rates of mean maximum sap flow on a whole-plant, sapwood area, and leaf area basis relative to the two alien tree species in our study, whereas *F. uhdei* had the highest rates and *E. saligna* was intermediate. The relative water use rates of these species parallel their differences in

growth rates, and especially the slow growth of *M. polymorpha* (Zimmerman et al. 2008).

Our measured transpiration rates were broadly consistent with values reported in the literature for the individual species considered separately in largely

TABLE 3. Stand compositions for the native forests and timber plantations.

Species	Percentage of TBA
<i>Metrosideros/Cibotium</i> forest (TBA 43.8 ± 12.3 m ² /ha)	
<i>Metrosideros polymorpha</i>	87.7 ± 5.0
<i>Ilex anomala</i>	4.9 ± 3.4
<i>Acacia koa</i>	2.3 ± 2.3
<i>Coprosma</i> spp.	1.3 ± 0.6
<i>Toona ciliata</i>	1.2 ± 1.2
<i>Cheirodendron trigynum</i>	1.1 ± 1.0
<i>Eucalyptus saligna</i> plantation (TBA 79.0 ± 15.7 m ² /ha ²)	
<i>Eucalyptus saligna</i>	89.6 ± 3.5
<i>Metrosideros polymorpha</i>	4.3 ± 3.3
<i>Acacia koa</i>	1.6 ± 1.0
<i>Fraxinus uhdei</i>	1.3 ± 1.3
<i>Ilex anomala</i>	1.2 ± 0.7
<i>Perrottetia sandwicensis</i>	0.8 ± 0.5
<i>Fraxinus uhdei</i> plantation (TBA 43.0 ± 2.6 m ² /ha ²)	
<i>Fraxinus uhdei</i>	84.7 ± 5.7
<i>Metrosideros polymorpha</i>	9.3 ± 5.2
<i>Acacia koa</i>	6.0 ± 1.7

Note: Included are the percentages of total living tree basal area (TBA) accounted for by component tree species (means ± SE), in order of decreasing abundance and TBA for each of the stand types.

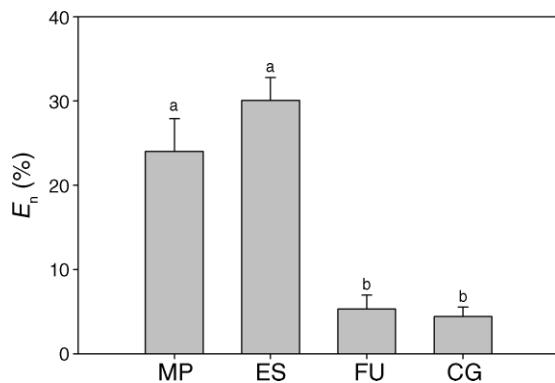


FIG. 5. Nocturnal sap flow of study species calculated as a percentage of total diurnal sap flow occurring at night (E_n ; between 18:30 and 06:30 hours). Bars show means + SE, with the same lowercase letters indicating no statistically significant difference ($P = 0.05$; post hoc Tukey comparisons of ln-transformed data). Species abbreviations: MP, *Metrosideros polymorpha* ($n = 6$ trees); ES, *Eucalyptus saligna* ($n = 6$); FU, *Fraxinus uhdei* ($n = 6$); CG, *Cibotium glaucum* ($n = 7$).

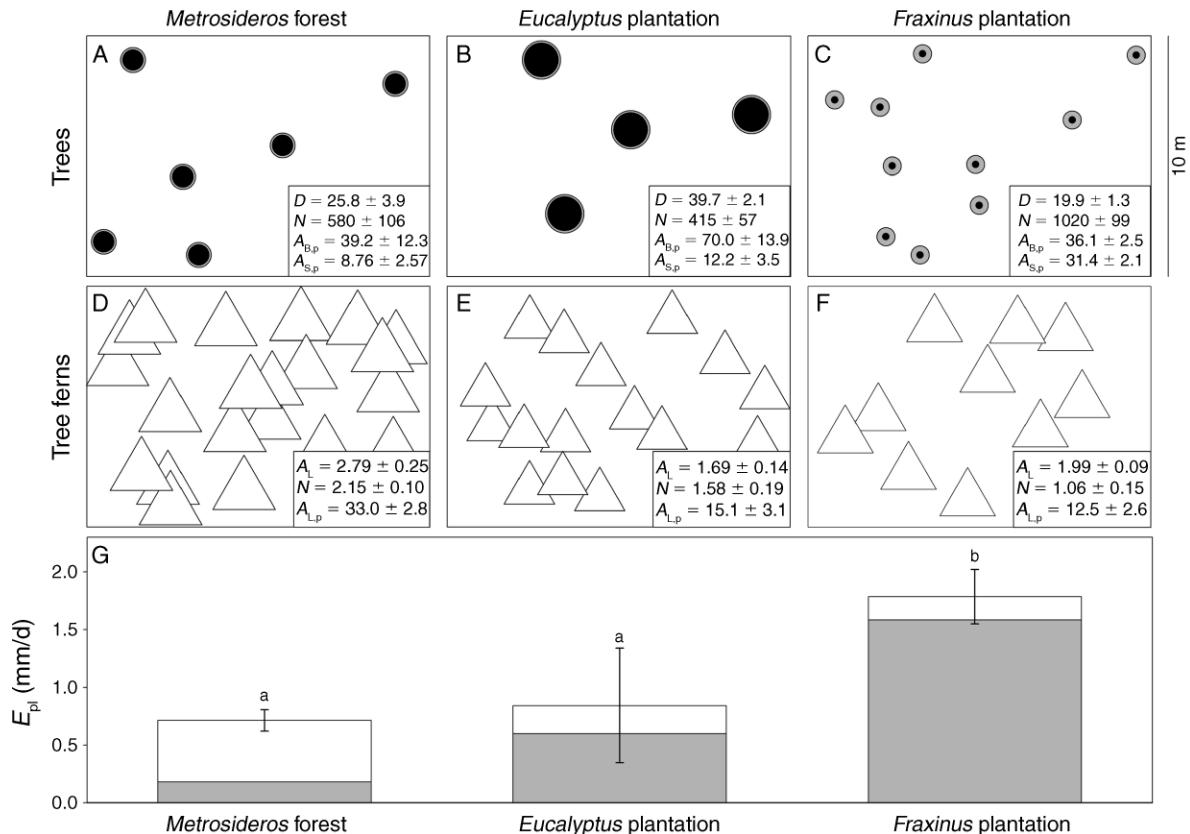


FIG. 6. Stand structure and estimated stand-level water use for native forest dominated by *Metrosideros polymorpha* and alien timber plantations dominated by *Eucalyptus saligna* and *Fraxinus uhdei* ($n = 5, 5,$ and 6 stands, respectively). Panels (A)–(F) show schematics of trees and tree ferns in 10×10 m plots for each stand type, indicating mean values for the factors important in determining stand water use. (A–C) Circles indicate dominant tree species cross-sectional area at breast height, with sapwood area in gray and heartwood area in black. (A–C insets) Diameter at breast height (D , cm), density (N , stems/ha), basal area at the plot scale ($A_{B,pl}$, m^2/ha), and sapwood area at the plot scale ($A_{S,p}$, m^2/ha). (D–F) Triangles indicate *Cibotium* tree fern mean frond area per individual (frond area \times number of fronds per plant). (D–F insets) Frond area (A_L , m^2), density (N , 10^3 caudices/ha), and frond area at the plot scale ($A_{L,p}$, $10^3 m^2/ha$). (G) Scaled-up mean stand diurnal sap flow (E_{pi}), the sum of tree (gray) and tree fern (open) components. Error bars indicate 95% confidence intervals, and the same lowercase letters indicate statistically indistinguishable means ($P \geq 0.05$; post hoc Tukey comparisons).

monotypic stands. Trees of individual species can show substantial ranges in sap flow rates depending on their ages, sizes, and sites with different climates and histories. Our values for *M. polymorpha* were low to moderate in the range reported by Santiago et al. (2000) for a much wetter site at 1200 m elevation on the island of Maui (5000 mm annual rainfall). In that study, the whole-plant daily transpiration rates were 3–44 kg/d and rates scaled by leaf area were 0.07 – 0.48 $kg \cdot d^{-1} \cdot m^{-2}$ for trees of unspecified size by comparison with our rates of 0.4 – 34.5 kg/d and 0.03 – 0.14 $kg \cdot d^{-1} \cdot m^{-2}$, respectively. We note that the rates in our study were for averages over two months, while those reported by Santiago et al. (2000) were for five measurement days with the highest evaporative demand.

While we found that the tree and stand transpiration rates of *E. saligna* were relatively low, especially relative to *F. uhdei*, we note that this species has been widely regarded as a rapid water user based on high transpira-

tion rates per sapwood area under different conditions. The mean diurnal maximum sap flow rate per sapwood area for *E. saligna* (16 $g \cdot m^{-2} \cdot s^{-1}$) in our study was approximately half of the 35 $g \cdot m^{-2} \cdot s^{-1}$ reported for much younger 5-yr-old plantation trees with D of 21 cm and height of 26 m, grown at 350 m elevation in Hāmākua, Hawaii (Barnard and Ryan 2003). The trees of *E. saligna* at our site were over 50 years old, with D of 70 cm on average and height of 50–60 m. The lower rates observed for trees at our site were consistent with previous observation of a decline in sap flow rates per sapwood area with increasing tree age and size (McDowell et al. 2002); in the Hāmākua study, maximum sap flow decreased 40% between 1-yr-old and 5-yr-old trees (Barnard and Ryan 2003). In addition, environmental conditions differed between these studies; although similar in VPD range, the Hāmākua site had a greater mean annual precipitation (MAP) by 2500 mm, a deep ash substrate in contrast to the shallow soil at our sites,

and likely windier conditions associated with its lower elevation on the island's windward side. Soil nutrient availability may also influence sap flow differences among sites; a study at the Hāmākua site showed that fertilization increased sapwood-scaled sap flow by 43% (Hubbard et al. 2004). Finally, we note that a study of closely related congener *Eucalyptus grandis* in South Africa also found high daily water use for 9-yr-old trees, $70 \text{ kg}\cdot\text{d}^{-1}\cdot\text{tree}^{-1}$ (Dye 1996), in contrast with the 33 kg/d found for *E. saligna* in this study. That study reported that trees exploited deep water sources, which would have been highly unlikely at our site given the exceedingly high permeability of the lava substrate; the shallowest groundwater sources would have been at least 300 m below the ground surface (Bauer 2003). By contrast, our mean value for the whole-tree sap flow rate of *F. uhdei* was 34 kg/d , similar to that for *E. saligna*, higher than the $2.6\text{--}17.3 \text{ kg/d}$ reported for *F. uhdei* trees in a stand at 460 m elevation on the island of O'ahu, for trees with D of $10\text{--}45 \text{ cm}$ (Restom Gaskill 2004); that site was drier, with mean annual rainfall of $540\text{--}750 \text{ mm}$. These differences in sap flow rates for the trees in this study relative to the mean values published for trees of the same species or genus at other sites further confirm the degree to which transpiration can be plastic within species. These comparisons highlight the ongoing need to determine species' relative water use for specific tree sizes and ages and for the soil and atmospheric conditions at specific sites.

Notably, the leaf-level transpiration rates for understory *C. glaucum* ($9.49 \pm 1.10 \text{ mg}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) were within the range of the canopy tree species with higher irradiance and evaporative demand. Previous work reported that the stomatal conductance of *C. glaucum* as measured by porometry ranged up to $180 \text{ mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for plants at sites of a range of elevation and exposures (Durand and Goldstein 2001), a moderate value relative to the range for woody angiosperms (Jones 1992). To our knowledge, there are no previously published studies of sap flow in tree ferns, and thus, further study of tree fern water use is needed, especially in systems in which they are abundant and play a potentially major role in forest water use, as shown in this study.

The substantial differences in transpiration on a sapwood and whole-tree basis observed among the coexisting species at our study sites may arise from variation in the microclimate at leaf level (e.g., light, temperature, and wind) and/or at the root level (e.g., due to contrasting rooting depth). Species differences may also arise from variation in root, wood, and leaf properties, contributing to differences in hydraulic, stomatal, and canopy conductances (Tyree and Zimmermann 2002). Differences at the whole-tree level can also be explained by lower sapwood allocation, and thus lower sapwood area per tree, which contributed to the low maximum sap flow rates for *M. polymorpha*. Differences among species in daily rates also corresponded to differences in temporal partitioning of water use. The

high daily rates for *F. uhdei* and *E. saligna* were driven by short intervals of high sap flow for *F. uhdei* vs. long periods of relatively lower flow for *E. saligna*; *M. polymorpha* also sustained its low peak rates for long periods. The early sap flow peak of *E. saligna* could arise from its greater height or steep leaf angle facilitating light interception at low sun angles (King 1997) or nocturnal tissue recharge, while late maxima for understory *Cibotium* are most likely due to shading from canopy trees delaying the onset of photosynthesis and transpiration in the morning. We found substantial nocturnal sap flow and that this varied across species; further, the rates of nocturnal sap flow may have been underestimated to some degree due to our assumption of zero sap flow at night (Dawson et al. 2007). Substantial nocturnal sap flow in *E. saligna* and *M. polymorpha* may arise from tissue recharge and/or nocturnal transpiration; nocturnal transpiration has been documented previously for *M. polymorpha* and *Eucalyptus grandis* (Benyon 1999, Dawson et al. 2007) and attributed to stomatal leakiness or to partially open stomata (Marks and Lechowicz 2007). The variation among species in sap flow rates and their temporal dynamics highlights the importance of further work, e.g., to model the response of stomatal conductance and transpiration to climate variables and to elucidate the specific internal and external control mechanisms. Such work should allow prediction of species-specific transpiration rates across a range of climatic conditions (Oren et al. 1999, Oren and Pataki 2001, Pataki and Oren 2003, Ford et al. 2005, Ewers et al. 2007).

Strong differences in water use among native forest and alien timber plantations

Our finding of strong variation among stands in transpiration demonstrates that individual tree species' traits (sap flow, as well as sapwood allocation) can strongly influence stand-level transpiration in native vs. alien-dominated wet tropical forests. These findings are consistent with previous work in temperate and boreal forests in which species composition was responsible for variation in stand-level transpiration even given similar leaf area index and soil type (Ewers et al. 2002, 2005). In a study of 40- vs. 450-yr-old temperate riparian forests, higher stand-level transpiration in the younger forest was associated with greater numbers of young trees of species with high sap flux densities and higher stand-level sapwood area (Moore et al. 2004). Thus, differences in species composition can affect stand-level transpiration, and stand transpiration is further affected by stand structure and age.

Stand structure reflects differences in site history, including planting densities, and species' growth rates. The 1.7-fold higher stem density for *F. uhdei* than for *M. polymorpha*, along with its sixfold higher sapwood allocation, resulted in over threefold higher total sapwood area for *F. uhdei*; this difference, combined with the fourfold higher sap flux density of *F. uhdei*,

resulted in a nearly ninefold higher stand-level transpiration rate than for *M. polymorpha* trees. The conservative stand-level transpiration of native *M. polymorpha*-dominated stands was associated with not only low sapwood area-specific transpiration for *M. polymorpha* and low sapwood allocation, but also to lower stem densities, the result of natural recruitment and centuries of forest establishment and regeneration (Drake and Mueller-Dombois 1993). By contrast, the alien timber stands had higher densities of younger trees with lower understory tree fern development. The importance of stem density and total sapwood area has been shown by previous studies of plantations; high-density stands had higher transpiration rates under non-limiting soil moisture conditions (Meinzer et al. 1996, Cienciala et al. 2000) and higher sapwood area correlated with greater stand water use (Dunn and Connor 1993, Vertessy et al. 2001).

Transpiration from the understory was especially important in native *M. polymorpha*-dominated stands, where water use by the abundant tree ferns more than doubled the water use contributed by the trees alone. This result is striking, yet consistent with estimates of high contributions to forest water use of understories of bracken fern (Roberts et al. 1980) and the evergreen ericaceous shrub salal (Black et al. 1989). A strong understory contribution may be common especially when canopies are relatively open and/or for old-growth stands; as overstory leaf area index (LAI) declines with stand age, understory LAI and transpiration increase in importance even though the rates of transpiration per leaf area for the understory would be less than that of the overstory (Vertessy et al. 2001, Eamus et al. 2006). We highlight the need to consider understory plants, and especially fern-dominated understories, as significant water users. More broadly, this finding further demonstrates that species composition influences stand water balance as high frequencies of relatively low water-using species can exert strong effect on comparative stand water use. Because tree ferns were much more abundant in the *M. polymorpha* forest, the ninefold difference in transpiration between *F. uhdei*- and *M. polymorpha*-dominated stands was reduced to a 2.5-fold difference when tree fern water use was included. While understory contributions did compensate for differences among tree contributions, leading to narrower variation among stands in transpiration, the remaining 2.5-fold difference provides a case against the contention that transpiration is always conservative across different forests (Roberts 1983, 2000).

We measured native and alien timber transpiration for two months in the peak growing season, but our findings are indicative for annual differences in transpiration. We note that the highest water user studied here, *F. uhdei*, is winter-deciduous and remains partially or completely leafless for one month (Harrington and Ewel 1997). However, we expect that annual transpiration for *F. uhdei* would be highest even if that of evergreen

species *M. polymorpha* and *E. saligna* remained the same during the remainder of the year. Even three to four months of zero sap flow for *F. uhdei* should not obviate its fourfold greater transpiration rates during the wet summer season, especially as the transpiration rates of the evergreen species might also decrease for part of the year, e.g., during the typically drier winter (see Hubbard et al. [2004] for evidence of decreased sap flow during a dry summer). We note that transpiration is typically considered the most important determinant of stand evapotranspiration (which also includes the evaporation of intercepted rainfall), especially in the tropics (Calder 2001). Future work should elucidate the full water balance of contrasting forest types by including canopy and understory interception, stem flow, and seasonal changes in soil water availability and leaf area. This study, by showing significant variation across stand types in transpiration, points to strong and dynamic variation in overall water balance.

Implications for forest and water resources conservation

Our finding that alien timber stands can use much more water than native forest has significant implications for the management of forested areas for hydrologic services in addition to other ecological services and objectives. In cases in which alien vegetation contributes to higher evapotranspiration, the economic costs of the lost water resources should inform land use and land management decisions. We note that the economic and ecological importance of vegetation water use may be strong not only when considering timber plantations and forest, but also in cases of rapid vegetation change, such as during the spread of invasive species such as *F. uhdei*, which is known to displace native trees in Hawaii following disturbance (Friday et al. 2008), or as would occur with pest-induced mortality of hydrologically important species (e.g., mortality of eastern hemlock caused by hemlock woolly adelgid; Ford and Vose 2007). The observed strong differences in stand transpiration between *E. saligna* and *F. uhdei* in this study further highlight the importance of considering hydrologic services in assessing the costs against benefits of alternative commercial timber production designs at specific sites.

The findings of this study also point to a strong need to characterize the water uses of different vegetation covers at a range of scales. While effective water resources management depends on understanding processes at the catchment scale, the land use decisions affecting water resources tend to be made at smaller spatial scales by landowners and local municipalities (Agrawal et al. 2008). At those scales, timber plantations are currently considered to be of higher market value than native old-growth forests, but a broader valuation of hydrological services may change the bases upon which land management decisions are made (e.g., Kremen et al. 2000, Kaiser and Roumasset 2002, Brauman et al. 2007). A wide range of forest types have

often been estimated to have similar hydrological value based on their prevention of runoff and erosion (Bruijnzeel 2004, Scott 2005). However, an additional resolution in calculation of hydrologic costs and services, by incorporating differences among vegetation types in transpiration rates, could contribute to higher valuation of old-growth native forest relative to commercial plantations. Given the increasing recognition of the value of forests for carbon sequestration, there is a strong need for detailed assessment of the ecohydrological costs and benefits of alternative forest covers for appropriate land use decisions.

CONCLUSIONS

Our study demonstrated that old-growth native *M. polymorpha* forest can have conservative water use relative to certain alien timber plantations, despite similar climate and soil. Even accounting for the strong understory contributions in native forest, *F. uhdei* stands used water at twice the rate of stands dominated by native *M. polymorpha* or alien *E. saligna* on a daily basis. Our study also found strong differences in stand-level transpiration even among similarly aged alien timber stands with different dominant species, *E. saligna* and *F. uhdei*. This study provides an example of how major variation in stand-level water use can arise through differences in species' sap flow rates, size, and structure, and in stand history and organization. These findings point to the importance of considering species differences and stand structure in the valuation of forests for hydrologic services.

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