

Hydrological effects of tree invasion on a dry coastal Hawaiian ecosystem

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ARTICLE INFO

Keywords:

LiDAR
Transpiration
Groundwater
Remote sensing
Isoscape
Riparian

ABSTRACT

In ecosystems invaded by non-native plants invasion effects are often spatially variable, and this variability is difficult to capture via plot-scale sampling. We used airborne high-resolution LiDAR (Light Detection and Ranging) to generate spatially explicit and contiguous information on hydrological effects of invasive trees (*Prosopis pallida* (Humb. & Bonpl. ex Willd.) Kunth). We developed regression relationships between LiDAR metrics (i.e., ground elevation and tree canopy height) and plot-scale measurements of vegetation stem water $\delta^{18}\text{O}$, to assess groundwater use, and transpiration rates. We used electrical resistivity imaging to assess subsurface geology and hydrology and their relationships to *P. pallida* stand structure. *P. pallida* biomass and transpiration varied greatly across the study area; both were controlled by depth to groundwater. Stem water $\delta^{18}\text{O}$ values (-8.6 to 3.7‰) indicated a threshold ground elevation of ca. 15 m above sea level, above which *P. pallida* could not access groundwater; this threshold corresponded to declines in tree biomass and height. Transpiration modelled across the study area was $0.034 \pm 0.017 \text{ mm day}^{-1}$, but over 98% of transpiration came from the ca. 25% of the total study area where groundwater depths were less than 15 m. Our combination of methods offers a new way to incorporate fine-scale spatial variation into estimation of plant invasion effects on hydrology, increase our understanding of interactions of geology, hydrology, and biology in such invasions, and prioritise areas for control in well-advanced invasions.

1. Introduction

In arid and semi-arid (dryland) environments, geological and climatic controls of water availability typically determine distributions of organisms and ecosystem dynamics (Noy-Meir 1973, Austin et al. 2004). In turn, biota often exert powerful feedbacks on the hydrologic processes of these dry environments (Huxman et al. 2005). Because these processes are inextricably linked, multidisciplinary approaches are needed to examine controls of biological invasions in drylands (Newman et al. 2006, Jackson et al. 2009). The need to understand relationships between invasive plants and their hydrologic setting will become still more pressing as climate change alters these dryland systems through time. Such knowledge may aid preparation for, and reduction of, ecological and socioeconomic impacts that follow ecosystem change (Clark et al. 2001).

Transpiration by phreatophytic vegetation (deep-rooted plants that obtain much of their water from the phreatic zone and its capillary fringe) can remove considerable quantities of water from aquifers (Thorburn et al. 1993, Naumburg et al. 2005). Changes in phreatophyte abundance - such as introductions of invasive phreatophyte species or removal of large trees in place of shallow-rooted crops - may profoundly affect regional hydrology and soil chemistry. Increased groundwater transpiration by phreatophytes may reduce base flow (Le Maitre et al. 2000, Dahm et al. 2002) to the detriment of aquatic communities (Dewson et al. 2007). In contrast, reduced groundwater table depth following deforestation of native phreatophytes has contributed to widespread and costly salination of croplands across many of Australia's dryland regions (White et al. 2002, Hatton et al. 2003, Rengasamy 2006). Methodological challenges exist in quantifying the effects of phreatophytes when vegetation density varies across large

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spatial scales (Le Maitre et al. 2000). Process-based understanding of such spatial variation is increasingly acknowledged as critical to comprehensive understanding of biogeochemical impacts in invaded ecosystems (Hultine et al. 2006, Rascher et al. 2012, Hughes et al. 2014).

On leeward coasts of the Hawaiian Islands, groundwater plays an important role in the structure and function of terrestrial, estuarine, and marine ecosystems. The bulk of leeward rainfall falls in high elevation cloud forests, while coastal environments receive substantially less rainfall (~270 mm; Giambelluca et al. 2013). The highly fractured and porous nature of basalt lava flows of the region coupled with low amounts of rainfall on leeward sides of the Hawaiian Islands results in upslope groundwater flow being the major hydrologic connection of land to sea and the major freshwater input to coastal marine systems on leeward sides of islands (Lau and Mink 2006, Johnson et al. 2008, Peterson et al. 2009). This groundwater flow to the coast as submarine groundwater discharge (SGD) provides cool, nutrient rich freshwater that sustains the productivity of communities in nearshore environments, including keystone marine species such as Hawai'i's indigenous marine algae (Peterson et al. 2009, Duarte et al. 2010). Because it is derived from high-altitude recharge, groundwater in this area is isotopically distinct from most low-altitude rainfall events, allowing it to be traced through lowland ecosystems (Scholl et al. 1996, Dudley et al. 2014).

The impacts of *Prosopis pallida* (Humb. & Bonpl. ex Willd.) Kunth, a phreatophytic invader to Hawai'i, have been shown to be heavily influenced by spatial patterns of groundwater availability. Dudley et al. (2014) documented groundwater-dependent differences in tree physiology, stand structure and soil chemistry in coastal forests of *P. pallida*. Trees in areas where stem water $\delta^{18}\text{O}$ values indicated uptake of groundwater (less than ca. 15 m above sea level) showed physiological evidence of greater water availability, including higher stem water potential, higher pre-dawn photosynthetic yield, and lower water use efficiency than trees nearby for which stem water $\delta^{18}\text{O}$ values indicated a reliance on local rainfall. Productivity, nitrogen (N) fixation rates, soil N, carbon (C) and phosphorus (P) content were all substantially greater in areas where *P. pallida* had access to groundwater compared to where it did not. While *P. pallida* is adapted to survive in very dry conditions without available groundwater, in areas where groundwater was present within the rooting zone it forms tall, dense and often monospecific stands (Miyazawa et al. 2016). Since the introduction of *P. pallida* to Hawai'i in 1828, *Prosopis*-dominated dry forest and shrubland has spread to cover approximately 3.5% of the total land area of the Hawaiian archipelago (ca. 59,000 ha), predominantly along lowland, arid leeward coasts (Gallaher and Merlin 2010). Young lava substrates along these coasts tend to be devoid of deep-rooted vegetation, and *P. pallida* stand establishment widely represents afforestation rather than competitive displacement of other tree species. Rates of transpiration of groundwater by dense stands of *Prosopis* spp. in the southeastern United States have been previously estimated to range from 374 to 750 mm yr⁻¹ (Scott et al. 2000, Scott et al. 2004, Scott et al. 2008), although transpiration on the lava of leeward Hawai'i may be lower, particularly during periods of drought (Miyazawa et al. 2016). Such flow rates may diminish both groundwater availability for human use and flows of groundwater to near-shore marine environments. An understanding of spatial patterns of transpiration rates in these phreatophytic plant communities will inform assessments of their impacts to groundwater resources as well as spatial patterns of their impacts to soils and ecosystem function.

In this study, our aims were to accurately incorporate the heterogeneity of these forests in assessment of transpiration during a drought period and identify areas where impacts of the invasion were likely to be greatest. This latter aim would inform on the potential to focus biological control of this species in areas of greatest impact.

For this, we collected biomass, stem water $\delta^{18}\text{O}$, and transpiration data from ground measurements during a drought period and scaled-up these measurements to the entire area of interest by developing

relationships between them and airborne LiDAR metrics (canopy height and elevation). We used electrical resistivity imaging of subsurface geology to identify depth to water table and substrate heterogeneity along multiple coastal-to-upland transects within this coastal riparian stand of *P. pallida*. We also related depth-to-water to tree height along transects and along the entirety of Kiholo Bay coastal area using wall-to-wall inventories of tree height obtained from LiDAR data.

We hypothesized firstly that a ground elevation could be identified above which *P. pallida* in this area can no longer access groundwater, due to physiological limitations of the tree's hydraulic system. Secondly, we hypothesized that *P. pallida* biomass and transpiration rates – and thus influence on groundwater discharge – below this elevation would be significantly higher than the average across the stand.

2. Methods

2.1. Study system

The study was conducted along the coastline within the boundaries of Kiholo State Park on the western, leeward coast of Hawai'i Island (lat. 19.84°, lon. –155.93°). Mean annual precipitation of the area over the 30 years prior to the study was ca. 270 mm (Giambelluca et al. 2013) and mean annual temperature of the area between September 30, 2010 and September 30, 2012 was ca. 24 °C. Rainfall typically occurs as sporadic small events in summer months and larger events between October and March (Giambelluca et al. 1986).

During dry periods, the area consists of monospecific *P. pallida* stands which have established and proliferated from individuals planted in leeward Hawai'i in the latter 19th century and early 20th century (Maly and Maly 2011). The invasive spread of this species away from planted stands occurred rapidly, largely due to dispersal of seeds by goats or cattle (Gallaher and Merlin 2010). These stands are augmented by an ephemeral understory cover of native herbs, *Sida fallax* Walp. ('Ilima) and *Waltheria indica* L. ('Uhaloa) following large rain events. The geology is comprised of contiguous pāhoehoe and 'ā'ā basalt bedrock that is derived from lava flows ca. 3,000 – 10,000 ybp (Wolfe and Morris 1996). Soil in the area typically occurs as a thin (i.e., depth ca. 4 cm) discontinuous layer over this flow (Dudley et al. 2014). Lava flows originated from Hualālai Volcano, and their morphology includes groundwater-bearing subsurface channels (Bauer 2003). Aerial thermal infrared imaging of the coastline (Adams et al. 1971, Johnson et al. 2008), aerial magnetotelluric and electrical resistivity reconnaissance (Adams et al., 1971), and surveys for geochemical tracers of groundwater (Street et al. 2008, Peterson et al. 2009, Knee et al. 2010) indicate that groundwater flow is limited to a basal aquifer connected to the ocean, with water exiting from the coastal region of the site via subsurface lava tubes and voids between layers of lava flows.

Within this area we established ten transects for measurement of $\delta^{18}\text{O}$ of stem water (T1-T10), two further sets of five 20 m-radius reference plots (L1-L5, U1-U5) to measure $\delta^{18}\text{O}$ of stem water, four transects to measure depth to ground water (A-D), and LiDAR over the whole site to measure elevation, and tree canopy height. Rainfall $\delta^{18}\text{O}$ and sapflow were measured at reference plots L1 and U1. Tree density and stem diameters were measured in all plots within three of the ten stem water transects, and all reference plots (Fig. 1).

2.2. Determination of belowground structure and depth to groundwater

We used electric resistivity tomography to identify heterogeneity in subsurface geologic structures and to locate groundwater along established transects. Ground resistivity is related to mineral content, porosity, and water saturation of the rock. Hence, this technique allows for a differentiation of low-resistivity groundwater-saturated layers from higher-resistivity unsaturated lava flows, fractures and voids. We recorded bulk apparent resistivity (Ohm-m) of the geologic substrate using an electrode array. The apparent resistivity cross sections were

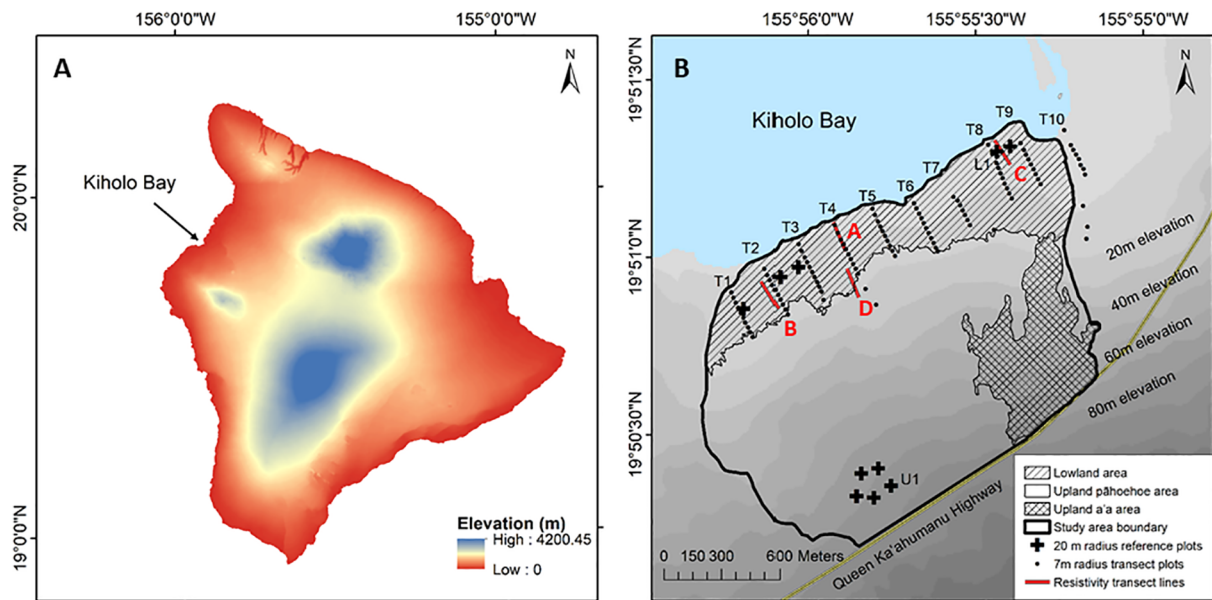


Fig. 1. A) Location of the study site, which lies west of the central peaks of Hawai'i Island and in their rain-shadow during predominant easterly trade winds; B) Locations of plots and transects along which we examined spatial patterns of tree water use, vegetation biomass, and presence of groundwater. LiDAR data covers the study area and extends beyond the boundaries of panel B. Resistivity transects are identified with upper case letters A-D. Sapflow was measured within reference sites L1, where groundwater was at around 5 m depth, and U1, where groundwater was expected to be at over 60 m depth. Areas compared within the larger study area are the 'lowland' area below 15 m ground elevation (diagonal lines), and two 'upland' areas with differing surface rock types shown by cross-hatched lines ('a'a lava) and no cross-hatched lines (pāhoehoe lava).

then inverted to determine a model of the true subsurface resistivity distribution. A SuperSting R8/IP unit (Advanced Geosciences Inc., AGI, Austin, TX, USA) with an 8-channel receiver, connected via an external switch box to a 168 m streamer (56 electrodes, spaced 3 m apart) was used to obtain resistivity readings of the subsurface. Electrodes along the resistivity cable were covered with water saturated bentonite to assure good current penetration into the basalt. We used a dipole-dipole configuration of the electrodes, which allows for mapping of vertical structures such as cavities; this approach has been shown to perform well in the Kiholo Bay geologic setting (Dimova et al. 2012). All resistivity surveys were performed in October 2012. Any systematic errors due to poor ground contact and random errors resulting in bad data points were removed before converting apparent resistivity values to a true resistivity model. Data were filtered using criteria of 20% root mean square error (RMSE) based on departure of modeled from measured apparent resistivity values and L2-norm statistic values below 10. Apparent resistivity values were converted to true resistivity values using the AGI Earth Imager 2D resistivity and IP inversion software. We used the Smooth Model to execute the inversion; this model is based on Occam's inversion (Constable et al. 1987).

2.3. LiDAR imagery and determination of spatial patterns of plant water use

We inventoried tree canopy height of all trees in the study area using airborne LiDAR data acquired by the Global Airborne Observatory (GAO; formerly Carnegie Airborne Observatory; (Asner et al. 2007)). This system can detect the various components of forest structure at a sub-meter resolution, including ground, sub-canopy, and canopy layers (Asner et al. 2012). The LiDAR data were collected with the GAO from Jan 29-30th in 2007, from a flying altitude of 3000 m above ground level (a.g.l.), with a flight speed of 58 kts (30 m s⁻¹) and LiDAR instrument settings set to 33 kHz pulse frequency and 12 Hz scan frequency with a 38-degree field of view, yielding an average of 0.93 laser pulses per square meter of ground area. Ground returns were identified in the LiDAR data using TerraScan software (Terrasolid, Ltd; Helsinki, Finland) using a maximum building size of 30 m, an iteration angle of 5° and an iteration distance of 1.5 m. To make a ground surface

model, the elevation of the lowest ground point in each 1.5 m × 1.5 m pixel was retained, and missing pixels were interpolated using a Triangle Irregular Network (TIN) interpolation. Similarly, the maximum elevation of all ground or vegetation points within each pixel was used to create a model of the top of the vegetation surface. The difference between these two maps was used to compute a model of the top-of-canopy height (TCH) above ground.

From these data, the Mean Canopy Profile Height (MCH) was calculated as the weighted height of the LiDAR point cloud in each 3 × 3 m kernel (Lefsky et al. 2002), and maximum value from the TCH map in each 3 × 3 kernel. Above ground biomass was estimated from relationships derived previously where MCH values predicted the dependent variable of above ground biomass across the study area at a 9-m² pixel resolution (Asner et al. 2012, Hughes et al. 2018).

To calculate groundwater use across the stand we measured stem water $\delta^{18}\text{O}$ in ten 20 m radius plots at the lowland and upland extremities of the stand used by Dudley et al. (2014), and in 102 additional 7 m² plots in 10 transects beginning at the seaward limit of the stand and extending past the estimated limit of groundwater access by trees (112 plots in total; Fig. 1). Transect lengths ranged from 200 to 600 m. Initial estimates of groundwater access were based on the density, height and vigor of trees at the upper limit of transects. Trees at the upper limits of each transect and beyond showed evidence of water stress (i.e., leaf yellowing, leaf loss and branch cavitation). We used Garmin 76Cx global positioning system receivers (Garmin Ltd., Olathe, KS, USA) to locate all field plots within the LiDAR data. We collected stem water samples from *P. pallida* trees located within each plot on October 5, 2012. This date was selected based on two criteria. Firstly, regular collections of rain and soil water samples over the previous two years indicated that precipitation was at its most ^{18}O -enriched during late summer, and therefore best separated from the $\delta^{18}\text{O}$ values of groundwater which were consistently low (i.e., ^{18}O -depleted) over this time. Secondly, this date occurred during a drought period in which only 36 mm of rain fell in the six months prior to stem sample collection. This resulted in leaf loss and stem sacrifice across much of the *P. pallida* stands. We collected one fully-suberized *P. pallida* stem segment ca. 5 cm in length, taken from around head height from each of 5 trees

selected haphazardly within a 7 m radius around each plot center point. Stem segments from each site were placed together in 20 mL glass vials with screw-top lids and sealed with Parafilm (Bemis Flexible Packaging, Neenah, Wisconsin, USA) to create a composite sample. Samples were kept on ice during transport and frozen until analyzed. Stem water extraction and $\delta^{18}\text{O}$ analysis of all water samples were conducted at the Stable Isotope Ratio Facility for Environmental Research (SIRFER) at the University of Utah (Salt Lake City, UT, USA). Stem water extraction was performed following West et al. (2006). $\delta^{18}\text{O}$ values were measured by isotope ratio infrared spectroscopy (IRIS) on a wavelength-scanned cavity ring-down spectrometer (WS-CRDS) model L1102-i water analyzer (Picarro, Sunnyvale, CA, USA). Samples were analyzed against three lab reference materials calibrated to Vienna Standard Mean Ocean Water (VSMOW). Instrument precision for $\delta^{18}\text{O}$ values was $\pm 0.2\text{‰}$. To map stem water $\delta^{18}\text{O}$ values, we generated an inventory of $\delta^{18}\text{O}$ data within the study area by applying a LiDAR/stem- $\delta^{18}\text{O}$ regression equation to each 9-m^2 pixel, where elevation and MaxTCH were the independent variables, and $\delta^{18}\text{O}$ was the dependent variable.

Water sources for trees were determined at the landscape scale using the resulting inventory of stem water $\delta^{18}\text{O}$ values. We calculated relative contributions of water sources at each 9-m^2 pixel throughout the stand using a two-source mixing model, and variances for these estimates according to Phillips and Gregg (2001). Groundwater $\delta^{18}\text{O}$ values were taken from collections from two water-filled lava tube caves within the study area on eight separate dates between December 2010 and September 2012 (Dudley et al. 2014). These sites were at around 110 m and 330 m from the seaward limit of *P. pallida* and had salinities of around 2 (using the Practical Salinity Scale). Based on the results of Dudley et al. (2014), and assuming a marine water $\delta^{18}\text{O}$ value of 0‰ , groundwater $\delta^{18}\text{O}$ values would become enriched by around 0.2‰ for each additional salinity unit. Based on previous measurements of groundwater salinity near the seaward limit of *P. pallida* at this site (Peterson et al. 2009) we assume salinity to be stable throughout the stand. We estimated the $\delta^{18}\text{O}$ values of plant-available soil water based on precipitation samples taken weekly from sites U1 and L1 during the six months prior to the collection of stem samples, weighted by rainfall amount. We used precipitation samples rather than soil samples to estimate $\delta^{18}\text{O}$ values of available soil water for several reasons. Firstly, we were unable to sample soil water at depths greater than ca. 10 cm depth due to the presence of shallow, poorly weathered pāhoehoe bedrock across the Kīholo site. Secondly, during drought periods the shallow soils at the site (discontinuous patches that average 3–4 cm depth over the bedrock) regularly contain $< 5\%$ water content (Dudley et al. 2014). Under these conditions, cryogenic extraction of water from silty loam soils gives an unacceptably poor representation of soil water isotope values (Orlowski et al. 2016) and at such low water content it was also unlikely that these surface soils were a major source of water for *P. pallida*. Thirdly, in areas of the site where groundwater is not accessible $\delta^{18}\text{O}$ values in time-series of precipitation and *P. pallida* stem water are closely matched, indicating that $\delta^{18}\text{O}$ values of plant-available soil water follow of $\delta^{18}\text{O}$ values of recent rainfall (Dudley et al. 2014). In semi-arid environments water may persist through dry periods in deeper soils and cracks in bedrock (Zwieniecki and Newton 1995, Rempe and Dietrich 2018). A study of soil water $\delta^{18}\text{O}$ values in nearby (ca. 25 km) and climatically similar Kohala shows that deeper soils (50–90 cm) hold water for some time after rain events in this area, and that the $\delta^{18}\text{O}$ values of this soil water depended primarily on $\delta^{18}\text{O}$ values of recent recharge (Hsieh et al. 1998). However shallow, and to a lesser degree deeper soil water $\delta^{18}\text{O}$ values also depend on evaporation rates of soil water (Hsieh et al. 1998), and so inferring groundwater use from stem water $\delta^{18}\text{O}$ values relies on similar climate across the extent of our study site. Mean annual vapor-pressure deficit (VPD; the difference between actual and saturation water vapor pressure at a given temperature) decreases from around 0.92 to 0.84 kPa in a gradient from the coastal (L1 – 1 m elevation) to upslope (U1 – 70 m elevation) stations, while temperature decreases from 23.7 °C to 23.3 °C

(Giambelluca et al. 2014).

To generate spatially continuous datasets of transpiration for trees across the stand, transpiration calculated for a subset of transect plots within the stand were related to LiDAR MaxTCH and DEM data for each plot. Plot-level transpiration rates were calculated from *P. pallida* stem metrics measured in thirty-two 7 m-radius plots established along transects 1, 4 and 8, as well as the five previously established 20 m radius plots within the upland *P. pallida* stands that lacked groundwater access, and in each of the five previously established 20 m radius plots in the coastal *P. pallida* stands with groundwater access (Fig. 1; Dudley et al. 2014). We estimated sapwood area within each plot from a regression relationship that predicted sap wood area from stem diameter derived from image analysis of 72 *P. pallida* stem cross sections ranging in diameter from 2.9 to 59 cm and harvested at 2.5 m above the ground within both upland and coastal zones of the study area (Miyazawa et al. 2016). Stem area of *P. pallida* was calculated from the measured diameter of all stems larger than 1.5 cm diameter at 2.5 m above ground level within each plot. We note that this measurement height – selected to match the installation height of sapflow sensors – may result in a slight underestimate of transpiration at a stand level by ignoring the contributions of trees < 2.5 m in height. Meteorological data were acquired from a weather station in an open area adjacent to the lowland reference site L1. Sensors included a photosynthetically active radiation (PAR) sensor (LI-190SB, LI-COR, Lincoln, NE, USA), a tipping-bucket rain gauge (TE525, Texas Electronics, Dallas, TX, USA), and air temperature–humidity sensors (HMP45C, Vaisala, Vantaa, Finland). To capture any differences in rainfall across the study site, a further tipping bucket rain gauge was established in an open area adjacent to the upland reference site U1. Sap flux (J_s ; $\text{g m}^{-2} \text{s}^{-1}$) was estimated within each transect plot from data obtained from reference sites U1 (without groundwater access) and site L1 (with readily accessible groundwater) between 10 October 2012 and 20 October 2012 (Fig. 1). Within these plots, J_s was monitored continuously using Granier-type sap flux sensors (Granier 1987, James et al. 2002). We installed sensors in 17 trees near the most seaward point of transect 8 (site L1; lat. 19.8550°, long. –155.9246°), where trees obtained the great majority of their stem water from groundwater, and in 10 trees in an area of the stand at an elevation of ca. 70 m above sea level (site U1; lat. 19.8382°, long. –155.9300°) where trees could not access groundwater (Dudley et al. 2014). Each sensor consisted of a pair of probes 10 mm in length (heated probe and reference probe) inserted into the stem. The heated probe emitted heat of a known power (0.15 W) (James et al. 2002). A thermocouple measured the temperature difference between the heated probe and a reference probe inserted 15–20 cm below the heated probe (ΔT ; °C). Each sensor was shielded by an aluminum cover and heat insulator to avoid the effects of solar radiation on temperature measurements. Two sensor pairs were installed in each tree to monitor the circumferential variation in sap flux. Because the sapwood area was narrow and less than 30 mm in depth from the bark, we assumed that each sensor (10 mm in length) covered the whole range of sapwood along the radial profile of the stem. Sap flow sensors were installed at 2.5 m to avoid equipment damage by feral goats that frequent the study area. We note that goats were present throughout the study area and we assume that their browsing habits were similar across the elevation gradient of the stand. Sensors were checked periodically for damage and replaced as needed. A data logger (CR1000, Campbell Scientific) attached to a multiplexer (AM16/32, Campbell Scientific) scanned ΔT at 30-s intervals, and the average was recorded at 10-min intervals. The ΔT was monitored and used to calculate sap flux (J_s ; $\text{g m}^{-2} \text{s}^{-1}$) following (Kumagai et al. 2007):

$$J_s = \frac{\sum_{i=1}^n A_{si} F_{di}}{\sum_{i=1}^n A_{si}} \quad (1)$$

where A_{si} and F_{di} represent the sapwood area (m^2) and the mean sap flux ($g\ m^{-2}\ s^{-1}$) of tree i .

Recent studies have reported underestimation of sap flux using Granier's probe (Bush et al. 2010) when using the original coefficients of Granier et al. (1987). This is likely to result in an overall underestimate of transpiration flux in this study, but because calculation procedures were the same in both sapflow measurement plots any error would tend to be systematic and should not affect our estimates of spatial patterns of transpiration. As VPD was > 0.3 – 0.5 kPa even at night, we suspected that nighttime transpiration may have influenced our F_d calculation, which assumes zero predawn sap flux (Zeppel et al. 2014). However, previously published predawn leaf gas exchange rates (Miyazawa et al. 2016) showed leaf-level transpiration rates only 1–4% of daytime peaks. Therefore, we assumed that influences by nighttime transpiration on our F_d calculation were negligible. Nocturnal sap flux is thought to reduce ΔT_{max} with this effect becoming greater with increasing nighttime VPD (Meinzer et al. 2013). In our study sites, however, the relationship between ΔT_{max} and nighttime VPD was not significant for most sensors despite large variations in VPD, further suggesting that calculated F_d was not greatly influenced by nocturnal sap flux.

We calculated sapflow in each transect plot in which it was not directly measured using:

$$GJ_{si} = J_{sU1} + \left[(J_{sL1} - J_{sU1}) \cdot \left(\frac{P_{gU1} - P_{gi}}{P_{gU1} - P_{gL1}} \right) \right] \quad (2)$$

Where GJ_{si} is the sapflow ($g\ m^{-2}\ s^{-1}$) in transect plot i , J_{sU1} and J_{sL1} are the measured sapflow rates in plots U1 and L1, P_{gi} is the proportion of stem water derived from groundwater in the i th transect plot, and P_{gU1} and P_{gL1} are the proportions of stem water derived from groundwater in plots U1 and L1. Transpiration in each plot located along each transect was calculated as a function of plot sapwood area and calculated sapflow during the 10-day study period. Notably, the use of P_{gw} as a predictor of changes in sapflow rates at each transect location assumed a linear relationship between J_s and P_{gw} across the gradient of groundwater availability during the period of study. Covariance of J_s and P_{gw} across the stand is supported by data showing early stomatal closure of sun-exposed leaves in lowland areas of the stand with the highest groundwater access (Miyazawa et al. 2016), indicating that even in these lowland areas *P. pallida* has to control stomatal conductance to low levels at midday in order to avoid excessive transpiration. Hence, during this lengthy dry period transpiration rates were a) dependent on groundwater access and b) unlikely to be saturated by the availability of groundwater over the vertical gradient of the stand.

The LiDAR/plot level transpiration relationship was applied to each 9-m² pixel across the entirety of LiDAR coverage acquired for the parcels within the study area to create an inventory of transpiration data.

We used maps of lava flow age to characterize and distinguish among lava flows in order to establish study area boundaries (Wolfe and Morris 1996). Inside these boundaries, we compared water sources, above ground biomass and transpiration across lava type (pāhoehoe or 'a'ā). Previous work has shown substantial differences in plant biomass between these two lava types when flows are similar in age (Hughes et al. 2014). We also compared water source, above ground biomass, and transpiration above and below 15 m above sea level to establish whether depth to groundwater was the primary determinant of differences in stand structure. We note that for these comparisons we assumed that the relationships developed between LiDAR metrics and measurements within plots held across all study areas.

2.4. Statistical analyses

Our objectives were to discern patterns in forest biomass, transpiration, and water sources with respect to groundwater depth and

geology. We first quantified the relationships between individual variables; elevation and stem water $\delta^{18}O$ values, and between tree height (MaxTCH) and stem water $\delta^{18}O$ values using linear regression. Because we expected a logarithmic relationship between stem water $\delta^{18}O$ values and elevation we log-transformed elevation data prior to this analysis. We then conducted pairwise comparisons of biomass, transpiration, and groundwater contribution to transpiration between sections of the study area above and below our estimate of the maximum ground elevation where groundwater was accessible to *P. pallida* (> 15 m and < 15 m) and across surface lava type (i.e., 'a'ā or pāhoehoe). Areas compared are shown in Fig. 1. Differences between areas were assessed using Games-Howell tests, which consider unequal variances. Estimates and standard errors for these tests were calculated directly from our regression and variance equations, following Hughes et al. (2018). Within our selected areas we would expect differences in tree growth due to underlying lava distribution, and surface lava structure not explained by our pāhoehoe vs 'a'ā grouping. Our analysis is distinctive to some degree in that it represents a complete inventory of the entire study area, rather than just a sampling within the area. Therefore, in comparing given parameters, we were able to employ the totality of pixels that contribute to those parameters within each section of the study area. Values of biomass (Mg/ha), transpiration (mm), and proportion of transpiration derived from groundwater (%) were obtained for 324,578 pixels on a 3-m² grid split among the three study area sections. We treated these pixels as representing the complete population of interest, rather than merely a sample. The study area was divided into a varying number of polygons classified by elevation (i.e., > 15 m 241,907 pixels, and < 15 m, 82,672 pixels), and the area above 15 m elevation was further divided by lava type (i.e., 'a'ā, 39,661 pixels and pāhoehoe, 202,246 pixels). Values of biomass, transpiration and groundwater use within each section of the study area were derived from the collection of pixels of each parameter and represent the mean value of the entire population. While TCH and elevation values are a complete census of polygons within the area, mean values for biomass, transpiration and stem water $\delta^{18}O$ values have error values associated with the regressions used to derive them. We note that uncertainty for these means values tends to decrease as spatial scale increases. For example, uncertainty in MCH-biomass predictions propagates close to the inverse of the square root of the pixel size (Mascaro et al. 2011). For this calculation, on individual 9-m² pixels, uncertainty was high, but at a 1-ha resolution it declines to $\sim 10\%$ of the predicted biomass value. Given the sizes of the areas considered within this study, we have confidence that comparisons among them are robust. Calculation of standard errors for coefficients of regressions, and 95% confidence intervals bracketing mean values are covered in detail in Appendix S1. Statistical and spatial analyses were performed using the software 'R' (R Core and Team, 2018).

3. Results

3.1. Belowground structure

The model of the true resistivity distribution of the four investigated transects exhibit values that range broadly from < 1 to 5,000 Ohm-m (Fig. 2). In all four transects the upper part of the images depict more resistive layers (50–5,000 Ohm-m), while on sections A, B, and C there is a sharp decrease into a lower resistivity layer (< 50 Ohm-m) a few meters below the surface. This is consistent with the presence of unweathered basalt flows for which the published values for resistivity range from 1,000 Ohm-m for wet to as much as 10^7 Ohm-m for dry substrates (Loke et al. 2013). Fresh groundwater and seawater saturated basalt resistivities are less than few hundred Ohm-m (Zohdy and Jackson 1969). In the context of aquifer composition, we interpret the high resistivity layer as the unsaturated zone of the aquifer and the low resistivity area represents basalt saturated by groundwater. Groundwater is clearly identified by the sharp transition from high to low

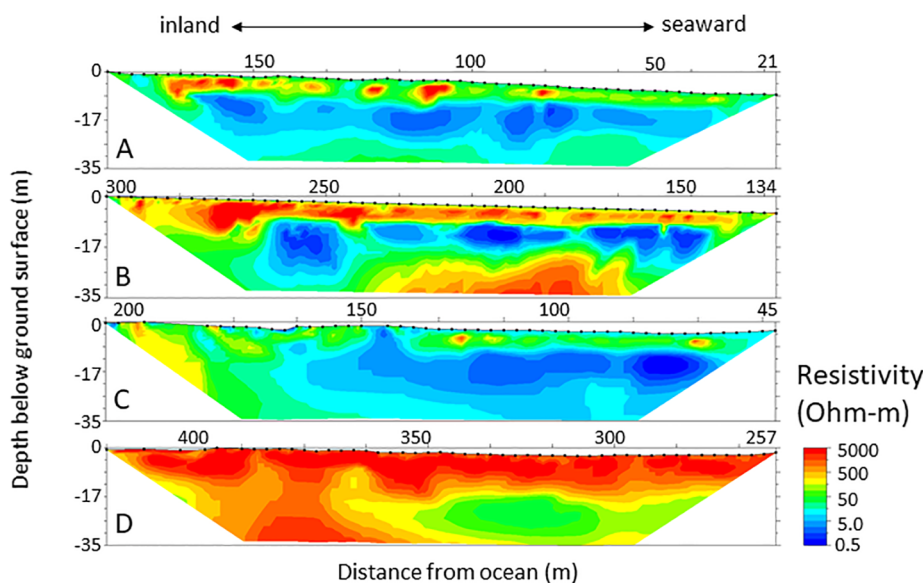


Fig. 2. Modelled true resistivity of the subsurface at selected transects used to confirm the presence of groundwater and below-ground geological heterogeneity. A relatively flat groundwater level is clearly identified by sharp upper boundaries between hotter (high resistivity) and cooler (low resistivity) colours along profiles A, B, C. Groundwater is expected to be at sea level. Line D is the continuation upslope of line A (see Fig. 1).

Table 1

Environmental conditions (PAR, VPD and rainfall), sapflow and transpiration measured during the study period – 8 October 2012 to 20 October 2012 at an upland site within the study area (U1; ~70 m asl), and a site near sea level where the trees have groundwater access (L1; ~7 m asl). Sapwood area data from the two sites are derived from equations from Miyazawa et al. (2016).

Mean daily PAR ($\text{mol m}^{-2} \text{ day}^{-1}$). (L1)	Mean daily VPD (kPa). (L1)	Site	Sum of rainfall (mm)	Mean daily sapflow ($\text{m}^3 \text{ m}^{-2} \text{ day}^{-1}$)	Sapwood area ($\text{m}^2 \text{ ha}^{-1}$)	Transpiration (mm day^{-1})
27.36 ± 5.50	1.16 ± 0.12	Lowland (L1)	0	1.64 ± 0.12 (n = 11)	5.47	0.90 ± 0.07
		Upland (U1)	0	0.10 ± 0.04 (n = 11)	0.82	0.01 ± 0.00

resistivity along profiles that extended below sea level (A, B, C). In the model of the true resistivity most groundwater-saturated areas have a resistivity of $< 5 \text{ Ohm-m}$ in contrast to $> 500 \text{ Ohm-m}$ of dry basalt. The shape of the upper boundary of the low resistivity area suggests a flat groundwater level most likely at sea level as suggested by hydrological models and field observations.

In addition, on line B resistivity in the high-conductivity layer progressively decreases towards the coastline, probably due to seawater intrusion into the aquifer creating a salinity gradient. This is consistent with the presence of brackish groundwater of salinity ~ 2 at 200 m from the coast (Dudley et al. 2017) and salinity 5 at the coastline (Dimova et al., 2012).

Additional relevant information is that there is no evidence for the presence of perched water at depths above the groundwater level during the study. This however does not exclude the possibility of water being present in the vadose zone after rain events. There is a low resistivity outcrop on line B at a distance of 70 m. This line runs along a drainage channel and unconsolidated rock material that may be the reason for the change in resistivity values.

On a finer scale, areas of variable resistivity are present in the unsaturated zone in the upper few meters of the section profiles. On lines A, B, and C resistivity in the unsaturated zone varies from a few tens to thousands of Ohm-m. These could be a result of air-filled void spaces between horizontal layers of lava flows and fractures.

3.2. Relationships between depth to groundwater, stem water $\delta^{18}\text{O}$ values, and tree height

Based on the data from resistivity transects, we assumed groundwater to be at a height close to that of sea level throughout the stand, and hereafter use elevation as a proxy for depth to groundwater. The relationship between elevation and stem water $\delta^{18}\text{O}$ values was logarithmic, with a horizontal asymptote at around 15 m elevation. Linear

regression with log-transformed site elevations showed a significant ($F = 115.3$, $1,110 \text{ df}$; $P \ll 0.001$) relationship that explained 51% of the variation in measured stem water $\delta^{18}\text{O}$ values across all sites. Linear regression between stem water $\delta^{18}\text{O}$ values and maxTCH at each transect site showed a significant ($F = 54.41$, $1,110 \text{ df}$; $P \ll 0.001$) relationship that explained 33% of the variation in maxTCH values across all sites.

3.3. Distribution of above ground biomass

Above-ground biomass of *P. pallida* estimated across the 292.25 ha study area totaled 4.38 Gg (1 Gg = 109 g) and averaged 15 Mg ha^{-1} (Table 1; Fig. 3). This was distributed between Lowland ($3,019 \pm 148 \text{ Mg}$), Upland pāhoehoe ($1,357 \pm 80 \text{ Mg}$), and Upland 'a'ā ($7.4 \pm 0.6 \text{ Mg}$). Average biomass on an area basis was greatest in the lowland area ($40.51 \pm 1.99 \text{ Mg ha}^{-1}$), substantially lower in upland pāhoehoe area ($7.46 \pm 0.44 \text{ Mg ha}^{-1}$), and lower still in the upland 'a'ā area ($0.21 \pm 0.02 \text{ Mg ha}^{-1}$).

3.4. Transpiration

The LiDAR/ plot level transpiration relationship for the study area was

$$(10T_{\text{point}})^{0.5} = (0.005779 \times \text{elev}) + (0.3688771 \times \text{MaxTCH}) - 0.0111547 \times \text{MaxTCH}^2 - 0.3773366 \quad [1]$$

where T_{point} is the transpiration (mm day^{-1}) in each 9-m^2 pixel, $n = 42$, adjusted $r^2 = 0.63$, and RMSE = $0.1958 \text{ (mm day}^{-1}\text{)}$.

Modelled transpiration across the entire study area was at $0.03 \pm 0.02 \text{ mm day}^{-1}$, totaling $98 \pm 50 \text{ m}^3 \text{ day}^{-1}$. Nearly all (over 98%) of this total was transpired in the lowland area (i.e. coastal

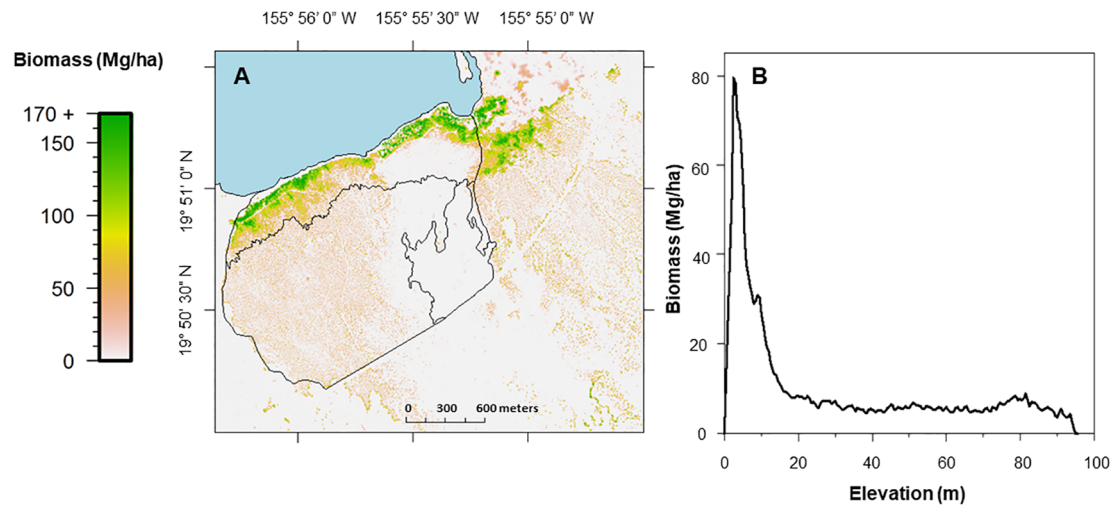


Fig. 3. A. Above ground biomass (AGB) within the study area, calculated from LiDAR data collected from the Global Airborne Observatory, and allometric equations linking canopy height of *P. pallida* to AGB from Hughes et al. (2014). Black lines within the study area separate the 'lowland' area below 15 m ground elevation (northern, seaward section) from those 'upland' areas with 'a'a' (southeastern section) and pāhoehoe (southwestern section) surface rock types. B. Relationship between elevation above sea (and groundwater) level and *P. pallida* biomass across the study area. Both plots show greatest biomass in low lying areas where groundwater is shallow.

areas < 15 m above sea level) (Table 2). There was considerable spatial variability in transpiration rates within the lowland area, and daily transpiration rates over the lowland area were approximately 14% of transpiration rates measured at the lowland reference site L1 (Tables 1 and 2; Fig. 4).

Sap flux rates of *P. pallida* over the duration of the study period at the lowland reference site L1 were $1.64 \pm 0.12 \text{ m}^3 \text{ m}^{-2} \text{ day}^{-1}$ ($n = 11$), an order of magnitude higher than that recorded at upland reference site U1 ($0.10 \pm 0.04 \text{ m}^3 \text{ m}^{-2} \text{ day}^{-1}$ ($n = 11$)). Sapwood area of the upland reference site was less than 15% of that of the lowland reference site; trees in lowland areas were larger and more closely spaced than trees in upland areas (Table 1). The multiplicative effects of higher sap flux rates, and greater sapwood area per unit of land area at the lowland site relative to the upland site resulted in transpiration nearly 100 times greater at lowland stand L1 than upland stand U1 during the study period (Table 1).

3.5. Plant water sources

Rainwater was enriched in ^{18}O ($1.12 \pm 0.36\%$; $n = 10$) relative to groundwater ($-7.21 \pm 0.01\%$; $n = 8$) during the six months prior to stem sample collection. *P. pallida* stem water tended to be ^{18}O -depleted in low-elevation areas nearer to the coast, and this indicated increased access to groundwater (see supplementary material for raw transect data). Groundwater contributions to stem water in transect plots calculated from mixing equations ranged from 0 to 100%.

The LiDAR/stem- $\delta^{18}\text{O}$ regression equation was:

$$\delta^{18}\text{O}_{\text{point}} = (0.351390 \times \text{elev}) - 0.003478 \times \text{elev}^2 - (0.633620 \times \text{MaxTCH}) + (0.025774 \times \text{MaxTCH}^2) - (0.004199 \times \text{elev} \times \text{MaxTCH}) - 4.444407 \quad [2]$$

with $n = 112$, adjusted $r^2 = 0.61$, and RMSE = 1.745‰

The relationships among $\delta^{18}\text{O}$ values of stem water, Max(TCH), and elevation ($P < 0.001$) suggested that groundwater was not easily accessible upslope where trees were smaller; this relationship explained 61% of the variability in stem water $\delta^{18}\text{O}$ values observed (Fig. 5, and Appendix S2). When inventories of $\delta^{18}\text{O}$ values across the study area were converted to groundwater contributions to stem water as described above, the percentage of transpiration by *P. pallida* derived from groundwater was estimated at $42.57 \pm 3.49\%$ for pixels within the

lowland area, $3.78 \pm 7.01\%$ for pixels on upland pāhoehoe and $0.88 \pm 9.75\%$ for pixels within upland a'a areas (Table 2).

4. Discussion

Our results demonstrate that the distribution of hydrological change resulting from *P. pallida* invasion is influenced by interactions between geology, hydrology, and vegetation structure and function across the invaded landscape. Our resistivity transects showed that groundwater was near sea level, and that ground elevation appears a good proxy for depth to groundwater during drought periods. While *P. pallida* is found throughout the elevation gradient of the site, 69% of the biomass and over 98% of the transpiration is occurring within 15 m elevation of the coastline, such that this species influence on SGD is largely driven by proximity to the coastline where groundwater is accessible. Importantly, our approach was able to resolve spatial heterogeneity in ecosystem function apparently linked to spatial patterns of geological features that tend to be missed by approaches based on plot sampling alone. This approach can be performed over scales that would be prohibitively expensive to assess by plot scale sampling (Asner et al. 2011), and may prove useful in prioritizing areas to control widespread, well-advanced invasive species to reduce hydrologic impacts.

Our first hypothesis was supported by the data; stem water stable isotope values showed an increase from values close to those of local precipitation above an elevation of approximately 15 m above sea level to values near those of groundwater in low-elevation areas near the coast. This pattern could not be explained by differences in climate across the stand; VPD and air temperature are slightly lower in higher elevation areas of the stand (Giambelluca et al. 2014), which could cause slightly greater isotopic enrichment of soil water in lowland sites (Hsieh et al. 1998). The opposite pattern was present in *P. pallida* stem water, and trees at low elevations had stem water $\delta^{18}\text{O}$ that was depleted by > 8‰ relative to recent precipitation. This pattern was, however, not entirely consistent across the stand, with an apparently lower elevation limit to groundwater access in central and north-eastern areas of the study area (Fig. 5). This may be attributable to geological variation identified in resistivity transects. The best regression model of stem water stable isotope values used both canopy height and elevation as predictors. In arid climates rooting depth tends to be much greater in larger trees (Schenk and Jackson 2002), and the relationship between canopy height and stem water $\delta^{18}\text{O}$ likely also

Table 2
Biomass, transpiration by the invasive tree *P. pallida* and percentage of transpiration derived from groundwater for three regions of the study site: area < 15 m, Pāhoehoe lava > 15 m, and 'a'ā lava > 15 m, where groundwater is at or near sea level. (Means in a column with the same letters are not significantly different at the 5% level using the Games-Howell multiple comparison test).

Location	Area (ha)	Pixels (n)	Biomass (Mg)		Biomass (Mg/ha)		Transpiration (mm day ⁻¹)		Transpiration (m ³ day ⁻¹)		Mean pixel groundwater contribution to transpiration (%)	
			Total	SE	Mean	SE	Mean	SE	Total	SE	Mean	SE
Lowland (Below 15 m elevation)	74.40	82,672	3,019.25 a	148.52	40.51 a	1.99	0.1298a	0.0518	96.79a	38.61	40.87a	4.17
Upland pāhoehoe (Above 15 m elevation)	182.02	202,246	1,357.23b	80.18	7.46b	0.44	0.0007b	0.0060	1.32b	10.82	3.62b	7.67
Upland 'a'ā (Above 15 m elevation)	35.69	39,661	7.47c	0.59	0.21c	0.02	0.0000b	0.0004	0.01b	0.13	0.37b	9.33
Kīholo total area	292.25	324,578	4,383.95	219.84	14.99	0.75	0.0335	0.0170	97.99	49.64	12.71	6.23

reflects geological influences on root penetration down to groundwater, and hence the potential for trees to grow. We also found stark differences in biomass between stands occurring on pāhoehoe flows as opposed to 'a'ā flows. Pāhoehoe flows above 15 m above sea level had much greater biomass than 'a'ā flows at the same elevation. A study of biomass accumulation on lava flows in the Puna region of windward Hawai'i Island showed that native forests occurring on 'a'ā flows exhibited much greater biomass compared to native forest counterparts on comparably aged pāhoehoe lava flows (Hughes et al. 2014). Previous authors have documented similar results (Raich et al. 1996, Aplet et al. 1998), and attributed this pattern to the greater surface area of 'a'ā lavas relative to pāhoehoe lavas that results in increased rates of rock weathering and subsequent increased nutrient availability in wet environments on Hawai'i Island. In dry environments of Hawai'i, however, the opposite pattern was demonstrated by Aplet et al. (1998) whereby vegetation development was more rapid on pāhoehoe lavas relative to 'a'ā lavas of comparable age. These authors attribute this to concentration of resources (i.e., water and organic matter) in cracks of pāhoehoe lavas found in arid environments; such pockets provide suitable sites for seed germination and seedling recruitment. Due to their diffuse structure, 'a'ā lavas provide few such resource pockets, and vegetation development is highly constrained as a result. This phenomenon explains the patterns of greater *P. pallida* biomass on pāhoehoe lavas relative to 'a'ā lavas across the Kīholo Bay region. Incorporation of both elevation above sea level and LiDAR derived *P. pallida* canopy height variables into our regression models (equations 3 and 4) effectively reveals the influences of this fine scale geological variation – both at the surface and below ground – on plant growth and water relations.

Secondly, we hypothesized that both *P. pallida* biomass and transpiration in this arid environment are tightly controlled by access to groundwater, and that both would decrease to low levels at elevations above sea level where groundwater is no longer accessible. Our isotope results indicated major reductions in groundwater access with elevation; during our study period sap flux rates in upland areas were considerably lower than those recorded in trees that were able to access groundwater. Mean pre-dawn stem water potentials at upland sites were between -40 and -50 MPa in June and September 2012 (Dudley et al. 2014), and corresponding reductions in leaf mass per area suggest that plants in upland areas were under considerable water stress over this time. Reductions in stem density and size with increasing elevation are very likely driven by reductions in photosynthetic rates during drought periods and mortality of *P. pallida* individuals in areas with little or no groundwater access (Allen et al. 2010, Dudley et al. 2014). As such, drought periods ultimately determine spatial patterns of tree biomass in the area above elevations of practical groundwater access (Fig. 6).

Stand-level mean transpiration across the entire study area during this dry period was 0.0335 ± 0.016 mm day⁻¹, substantially lower than that recorded at the lowland reference site (0.897 ± 0.067 mm day⁻¹), but nearly double that recorded at the upland reference site (0.0085 ± 0.0034 mm day⁻¹). These results are near or below annual estimates for portions of the study region with groundwater access (0.843 mm day⁻¹; Miyazawa et al. 2016), and values previously documented for riparian stands of *Prosopis* in continental U.S. systems (1.02 to 2.05 mm day⁻¹) (Scott et al. 2000, Scott et al. 2004, Scott et al. 2008). We note that constraints to groundwater uptake during extreme drought in lowland areas seem sufficient to limit LAI (Miyazawa et al. 2016), and we suspect that lowland geology (i.e., relatively young basalt beneath discontinuous soil patches) contributes to the low transpiration rates exhibited by lowland stands relative to rates determined elsewhere (Scott et al. 2000, Scott et al. 2004, Scott et al. 2008). Our results clearly indicate that during periods of low rainfall the vast majority of total transpiration within the study area is derived from groundwater. Dry periods occur seasonally in this area and the sap flux rates of trees during the study period were within the

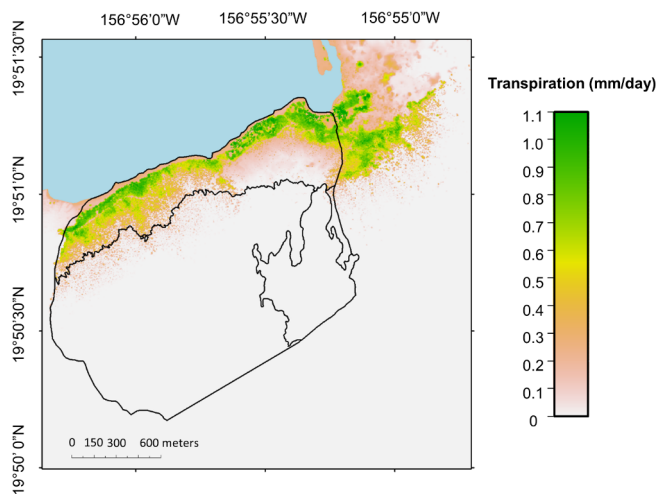


Fig. 4. Transpiration within the study area, derived from relationships between on-the-ground measurements of sapflow, sapwood area and groundwater access, and LiDAR measurements of elevation and tree canopy height. The standard error of prediction is 0.1958 with an adjusted r-squared of 0.627. Transpiration is highest in low elevation areas of the stand which have the greatest groundwater access, tree height, and biomass. Black lines within the study area separate the 'lowland' area below 15 m ground elevation (northern, seaward section) from those 'upland' areas with 'a'ā (southeastern section) and pāhoehoe (southwestern section) surface rock types.

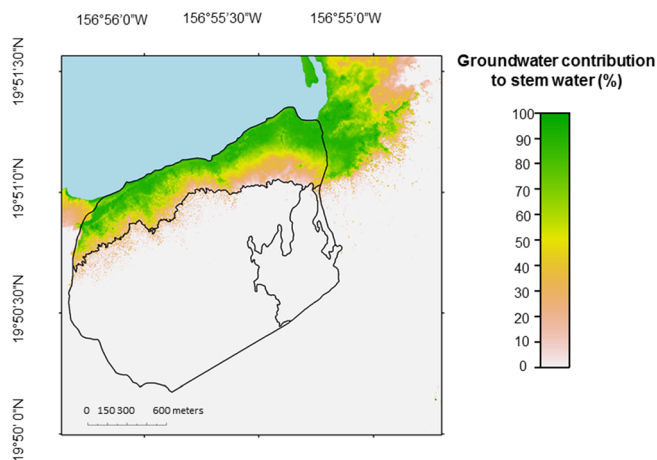


Fig. 5. Modelled groundwater contribution to stem water within the study area, derived from relationships between transect stem sampling stem water $\delta^{18}\text{O}$ values and LiDAR measurements of elevation and tree canopy height. The standard error of prediction is 1.75 with an adjusted r-squared of 0.61. Groundwater is at or near sea level within the study area. Black lines within the study area separate the 'lowland' area below 15 m ground elevation (northern, seaward section) from those 'upland' areas with 'a'ā (southeastern section) and pāhoehoe (southwestern section) surface rock types.

range of those from other dry periods between 2010 and 2012 (Miyazawa et al. unpublished data). We suggest that transpiration rates observed during our study period are typical for these dry periods, but not annual average rates for the area.

The presence of *P. pallida* has a negative impact on available groundwater in dryland areas of Hawai'i. Young pāhoehoe and 'a'ā substrates such as those within the study area are found along the leeward Hawai'i coast and tend to be devoid of deep-rooted vegetation. While the native tree, *Thespesia populnea* (L.) Sol. ex Corrêa (aka, Milo) is a common component of leeward coastal communities (Nelson-Kaula et al. 2016) its distribution tends to be limited by surface water availability. This is true for other native and non-native woody species as well (Warshauer et al. 2009). *P. pallida* stand establishment and growth

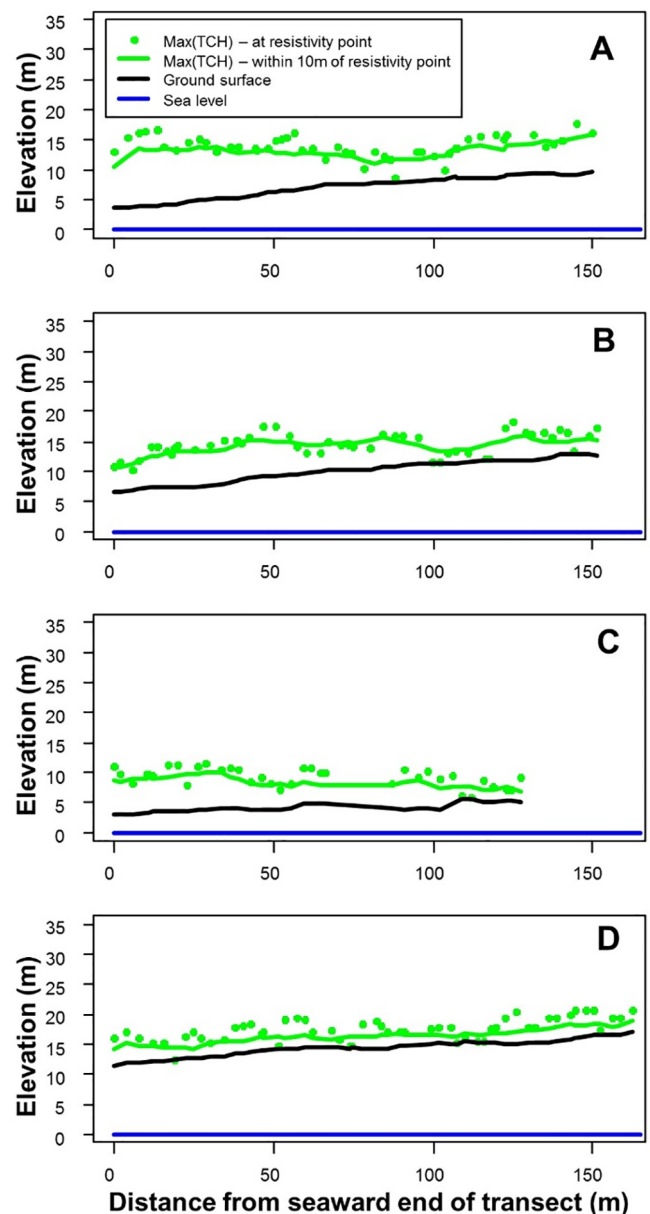


Fig. 6. Maximum tree canopy height (Max(TCH)) along the length of the four resistivity transects, derived from LiDAR data. The solid green Max(TCH) line gives the average maximum canopy height for all points in a 10 m circular area around each transect point. The dotted green line 'Max(TCH)-point' gives Max (TCH) for the pixel closest to each transect point. The black line gives ground elevation from the same LiDAR dataset. The blue line at sea level gives the estimated groundwater level. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

along arid coastal environments of leeward Hawai'i is thus best characterized as afforestation rather than competitive displacement of other species. As well as increases in transpiration, we would expect afforestation to increase evaporation via interception but reduce evaporation from surface soils (Farley et al. 2005). However, in dry lowland areas we would expect the major hydrologic influence of *P. pallida* to be via direct transpiration of groundwater; infiltration and leaching rates are very low at this site with or without canopy cover, especially during low-rainfall periods (Dudley et al. 2014). Daily transpiration by *P. pallida* stands located within lowland areas represented ca. 1.4% of the mean $7,100 \text{ m}^3 \text{ day}^{-1}$ of fresh submarine groundwater discharge through Kīholo calculated by Peterson et al. (2009). Groundwater discharge through Kīholo is high when compared to other stretches of

Hawai'i's leeward coastlines; transpiration impacts may be proportionally higher in areas where *P. pallida* is present but through which only diffuse groundwater discharge occurs (Johnson et al. 2008, Peterson et al. 2009). Other pressures on the coastal aquifer from which *P. pallida* draws water are increasing; Frazier and Giambelluca (2017) documented significant long-term declines in annual and dry season rainfall across the leeward portions of Hawai'i Island between 1920 and 2012, and these trends coincide with long-term declines in base flow (Bassiouni and Oki 2013). As patterns and effects of global warming continue, further declines in regional precipitation should be expected, and such declines will very likely result in reductions to SGD as well. Additionally, population growth and concomitant development along the leeward coast of Hawai'i Island is estimated to increase water demand by 300,000 m³ d⁻¹ by 2030 (Hawai'i Community Foundation 2015). Such increased demand will also likely significantly decrease SGD delivery to marine communities. Unfortunately, anticipated declines in SGD due to declining precipitation and increased groundwater extraction will occur at a time when nearshore marine communities will likely need SGD the most. Emerging research has documented the deleterious impacts of ocean water warming events on coral health (i.e., coral bleaching), and such events are expected to increase in severity and duration as our oceans continue to warm (West and Salm 2003). As such, sustaining adequate supplies of cool freshwater SGD to thermally stressed nearshore marine communities may prove critical to their continued survival (West and Salm 2003), and management actions to reduce declines in SGD are both prudent and warranted. Our results are revealing and unequivocal for managers and policy makers concerned about sustaining adequate SGD rates. Virtually all groundwater withdrawal from *P. pallida* stand transpiration occurred exclusively from large individuals occupying lowland areas located < 15 m in elevation from the high-water line. *P. pallida* transpiration above that 15 m elevation accounted for only 1% of the total, and isotope results indicated that almost none of that small amount was drawn from groundwater. As such, when considering *P. pallida* removal activities to help maintain levels of SGD into nearshore environments of Kiholo Bay, managers should prioritize those large stands occurring at elevations low enough to allow for groundwater access; *P. pallida* stands above that elevation have virtually no effect on SGD.

At a global scale, similar ecosystems are common, as indicated by the distribution of such plants that can maintain biomass and grow during summer droughts, and by desert plants transpiring in excess of local precipitation for long periods (Canadell et al. 1996). Our approach appears best suited:

1. for vegetation that gains a sizable portion of its water from groundwater where this is within its rooting depth
2. when transpiration rates are limited by access to groundwater
3. where, and when groundwater isotope values are well separated from those of water in surface soils and precipitation.
4. where periodic droughts limit plant height, growth and retention of biomass, creating a strong relationship between tree stand structure and transpiration.

Within our study area, the first three of conditions were best met during summer drought conditions and our results are applicable to these dry periods. This site is particularly suited to the use of our stable water isotope techniques because high altitude mountains in the groundwater watershed give large differences between soil and groundwater $\delta^{18}\text{O}$ values. Further, this technique currently assumes a linear relationship between J_s and groundwater access; this relationship could be better parameterized by including additional locations for measurement of J_s that more fully represent the gradient of groundwater availability.

We suggest that this study can serve as an example of how interactions between geology, hydrology, and ecology control not only the geographical extent of biological invasions in drylands, but also spatial

patterns of impacts within the invasion range. We see multidisciplinary approaches that integrate remote sensing data with detailed, plot-scale measurements as valuable for increasing our understanding of these patterns of invasion impact.

Acknowledgements

This research was supported by funding from NSF Hawai'i Experimental Program to Stimulate Competitive Research (EPSCoR) Grant Number EPS-0903833, NSF REU 1005186 for student funds, and in-kind support from the USDA Forest Service Pacific Southwest Research Station. GAO data collection, processing and analysis were supported by the Gordon and Betty Moore Foundation and the Carnegie Institution for Science. The Global Airborne Observatory has been made possible by grants and donations to G.P. Asner from the Avatar Alliance Foundation, Margaret A. Cargill Foundation, David and Lucile Packard Foundation, Gordon and Betty Moore Foundation, Grantham Foundation for the Protection of the Environment, W. M. Keck Foundation, John D. and Catherine T. MacArthur Foundation, Andrew W. Mellon Foundation, Mary Anne Nyburg Baker and G. Leonard Baker Jr, and William R. Hearst III. We thank the community of Kiholo, particularly the MacDonald family and Jenny Mitchell for their support for this research. Hawai'i Department of Land and Natural Resources staff provided access to the Hawai'i Experimental Tropical Forest. The Pacific Internship Program for Exploring Science helped with coordination of student interns. J. VanDeMark, N. Wilhoite, J. Schulten, E. Parsons, M. Murphy, T. Gene, K. Matsuoka, J. Yeh, T. Sakihara, K. Nelson-Kaula, M. Riney, and T. Winthers-Barcelona assisted us greatly in the field.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2019.117653>.

References

- Adams, W.M., Peterson, F.L., Mathur, S.P., Lepley, L.K., Warren, C., Huber, R.D., 1971. A hydrogeophysical survey using remote-sensing methods from Kawaihae to Kailua-Kona, Hawai'i. *Ground Water* 9, 42–50.
- Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.-H., Allard, G., Running, S.W., Semerci, A., Cobb, N., 2010. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management* 259, 660–684.
- Aplet, G.H., Hughes, R.F., Vitousek, P.M., 1998. Ecosystem development on Hawaiian lava flows: biomass and species composition. *Journal of Vegetation Science* 9, 17–26.
- Asner, G., Clark, J.K., Mascaro, J., Galindo García, G., Chadwick, K., Navarrete Encinales, D., Paez-Acosta, G., Cabrera Montenegro, E., Kennedy-Bowdoin, T., Duque, Á., 2012. High-resolution mapping of forest carbon stocks in the Colombian Amazon. *Biogeosciences* 9, 2683–2696.
- Asner, G.P., Hughes, R.F., Mascaro, J., Uowolo, A.L., Knapp, D.E., Jacobson, J., Kennedy-Bowdoin, T., Clark, J.K., 2011. High-resolution carbon mapping on the million-hectare Island of Hawai'i. *Frontiers in Ecology and the Environment* 9, 434–439.
- Asner, G.P., Knapp, D.E., Kennedy-Bowdoin, T., Jones, M.O., Martin, R.E., Boardman, J., Field, C.B., 2007. Carnegie Airborne Observatory: In-flight fusion of hyperspectral imaging and waveform light detection and ranging (LiDAR) for three-dimensional studies of ecosystems. *Journal of Applied Remote Sensing* 1. <https://doi.org/10.1117/1.2794018>.
- Austin, A.T., Yahdjian, L., Stark, J.M., Belnap, J., Porporato, A., Norton, U., Ravetta, D.A., Schaeffer, S.M., 2004. Water pulses and biogeochemical cycles in arid and semiarid ecosystems. *Oecologia* 141, 221–235.
- Bassiouni, M., Oki, D.S., 2013. Trends and shifts in streamflow in Hawai'i, 1913–2008. *Hydrological Processes* 27, 1484–1500.
- Bauer, G.R., 2003. A study of the ground-water conditions in North and South Kona and South Kohala districts, Island of Hawai'i, 1991–2002. Department of Land and Natural Resources, Commission on Water Resource Management.
- Bush, S.E., Hultine, K.R., Sperry, J.S., Ehleringer, J.R., 2010. Calibration of thermal dissipation sap flow probes for ring-and diffuse-porous trees. *Tree Physiology* 30, 1545–1554.
- Canadell, J., Jackson, R., Ehleringer, J., Mooney, H., Sala, O., Schulze, E.-D., 1996. Maximum rooting depth of vegetation types at the global scale. *Oecologia* 108, 583–595.
- Clark, J.S., Carpenter, S.R., Barber, M., Collins, S., Dobson, A., Foley, J.A., Lodge, D.M., Pascual, M., Pielke, R., Pizer, W., Pringle, C., Reid, W.V., Rose, K.A., Sala, O.,

- Schlesinger, W.H., Wall, D.H., Wear, D., 2001. Ecological forecasts: An emerging imperative. *Science* 293, 657–660.
- Constable, S.C., Parker, R.L., Constable, C.G., 1987. Occam's inversion: A practical algorithm for generating smooth models from electromagnetic sounding data. *Geophysics* 52, 289–300.
- Dahm, C.N., Cleverly, J.R., Coonrod, J.E.A., Thibault, J.R., McDonnell, D.E., Gilroy, D.F., 2002. Evapotranspiration at the land/water interface in a semi-arid drainage basin. *Freshwater Biology* 47, 831–843.
- Dewson, Z.S., James, A.B.W., Death, R.G., 2007. A review of the consequences of decreased flow for instream habitat and macroinvertebrates. *Journal of the North American Benthological Society* 26, 401–415.
- Dimova, N.T., Swarzenski, P.W., Dulaiova, H., Glenn, C.R., 2012. Utilizing multichannel electrical resistivity methods to examine the dynamics of the fresh water–seawater interface in two Hawai'i an groundwater systems. *Journal of Geophysical Research Oceans*, 117.
- Duarte, T.K., Pongkijvorasin, S., Roumasset, J., Amato, D., Burnett, K., 2010. Optimal management of a Hawaiian Coastal aquifer with nearshore marine ecological interactions. *Water Resources Research* 46.
- Dudley, B.D., Hughes, R.F., Ostertag, R., 2014. Groundwater availability mediates the ecosystem effects of an invasion of *Prosopis pallida*. *Ecological Applications* 24, 1954–1971.
- Dudley, B.D., MacKenzie, R.A., Sakihara, T.S., Riney, M.H., Ostertag, R., 2017. Effects of invasion at two trophic levels on diet, body condition, and population size structure of Hawai'i an red shrimp. *Ecosphere* 8.
- Farley, K.A., Jobbágy, E.G., Jackson, R.B., 2005. Effects of afforestation on water yield: a global synthesis with implications for policy. *Global Change Biology* 11, 1565–1576.
- Frazier, A.G., Giambelluca, T.W., 2017. Spatial trend analysis of Hawaiian rainfall from 1920 to 2012. *International Journal of Climatology* 37, 2522–2531.
- Gallaher, T., Merlin, M., 2010. Biology and Impacts of Pacific Island Invasive Species. 6. *Prosopis pallida* and *Prosopis juliflora* (Algarroba, Mesquite, Kiawe) (Fabaceae). *Pacific Science* 64, 489–526.
- Giambelluca, T.W., Chen, Q., Frazier, A.G., Price, J.P., Chen, Y.L., Chu, P.S., Eischeid, J.K., Delporte, D.M., 2013. Online Rainfall Atlas of Hawai'i. *Bulletin of the American Meteorological Society* 94, 313–316.
- Giambelluca, T.W., Nullet, M.A., Schroeder, T.A., 1986. Hawai'i Rainfall Atlas. Honolulu, HI, USA.
- Giambelluca, T., Shuai, X., Barnes, M., Alliss, R., Longman, R., Miura, T., Chen, Q., Frazier, A., Mudd, R., Cuo, L., 2014. Evapotranspiration of Hawai 'i. Final report submitted to the US Army Corps of Engineers—Honolulu District. State of Hawai 'i.
- Granier, A., 1987. Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements. *Tree Physiology* 3, 309–320.
- Hatton, T.J., Ruprecht, J., George, R.J., 2003. Preclearing hydrology of the Western Australia wheatbelt: Target for the future? *Plant and Soil* 257, 341–356.
- Hawai'i Community Foundation. 2015. A Blueprint for Action: Water Security for an Uncertain Future 2016–2018. Hawai'i Community Foundation, Honolulu, HI 96813.
- Hsieh, J.C., Chadwick, O.A., Kelly, E.F., Savin, S.M., 1998. Oxygen isotopic composition of soil water: quantifying evaporation and transpiration. *Geoderma* 82, 269–293.
- Hughes, R.F., Asner, G.P., Baldwin, J.A., Mascaro, J., Bufile, L.K.K., Knapp, D.E., 2018. Estimating aboveground carbon density across forest landscapes of Hawaii: combining FIA plot-derived estimates and airborne LiDAR. *Forest Ecology and Management* 424, 323–337.
- Hughes, R.F., Asner, G.P., Mascaro, J., Uwololo, A., Baldwin, J., 2014. Carbon storage landscapes of lowland Hawai'i : the role of native and invasive species through space and time. *Ecological Applications* 24, 716–731.
- Hultine, K.R., Koepke, D.F., Pockman, W.T., Fravolini, A., Sperry, J.S., Williams, D.G., 2006. Influence of soil texture on hydraulic properties and water relations of a dominant warm-desert phreatophyte. *Tree Physiology* 26, 313–323.
- Huxman, T.E., Wilcox, B.P., Breshears, D.D., Scott, R.L., Snyder, K.A., Small, E.E., Hultine, K., Pockman, W.T., Jackson, R.B., 2005. Ecohydrological implications of woody plant encroachment. *Ecology* 86, 308–319.
- Jackson, R.B., Jobbágy, E.G., Noretto, M.D., 2009. Ecohydrology in a human-dominated landscape. *Ecohydrology* 2, 383–389.
- James, S.A., Clearwater, M.J., Meinzer, F.C., Goldstein, G., 2002. Heat dissipation sensors of variable length for the measurement of sap flow in trees with deep sapwood. *Tree Physiology* 22, 277–284.
- Johnson, A.G., Glenn, C.R., Burnett, W.C., Peterson, R.N., Lucey, P.G., 2008. Aerial infrared imaging reveals large nutrient-rich groundwater inputs to the ocean. *Geophysical Research Letters* 35.
- Knee, K.L., Street, J.H., Grossman, E.E., Boehm, A.B., Paytan, A., 2010. Nutrient inputs to the coastal ocean from submarine groundwater discharge in a groundwater-dominated system: Relation to land use (Kona coast, Hawai'i, U.S.A.). *Limnology and Oceanography* 55, 1105–1122.
- Kumagai, T., Aoki, S., Shimizu, T., Otsuki, K., 2007. Sap flow estimates of stand transpiration at two slope positions in a Japanese cedar forest watershed. *Tree Physiology* 27, 161–168.
- Lau, L.-K.S., Mink, J.F., 2006. Hydrology of the Hawaiian Islands. University of Hawaii Press.
- Le Maitre, D.C., Versfeld, D.B., Chapman, R.A., 2000. The impact of invading alien plants on surface water resources in South Africa: A preliminary assessment. *Water Sa* 26, 397–408.
- Lefsky, M.A., Cohen, W.B., Parker, G.G., Harding, D.J., 2002. Lidar remote sensing for ecosystem studies: Lidar, an emerging remote sensing technology that directly measures the three-dimensional distribution of plant canopies, can accurately estimate vegetation structural attributes and should be of particular interest to forest, landscape, and global ecologists. *BioScience* 52, 19–30.
- Loke, M., Chambers, J., Rucker, D., Kuras, O., Wilkinson, P., 2013. Recent developments in the direct-current geoelectrical imaging method. *Journal of Applied Geophysics* 95, 135–156.
- Maly, K., and O. Maly. 2011. He mo'olelo 'aina no napu'u — traditions of Pu'u wa'awa'a and Pu 'u Anahulu lands of Kiholo state wilderness park district of Kona, island of Hawai'i. An ethnography of Kiholo at Napu'u prepared as part of a cultural impact assessment consultation study for the Kiholo State Wilderness Park master plan and EIS, Kumu Pono Associates LLC, Honolulu, HI, USA.
- Mascaro, J., Detto, M., Asner, G.P., Muller-Landau, H.C., 2011. Evaluating uncertainty in mapping forest carbon with airborne LiDAR. *Remote Sensing of Environment* 115, 3770–3774.
- Meinzer, F.C., Woodruff, D.R., Eissenstat, D.M., Lin, H.S., Adams, T.S., McCulloh, K.A., 2013. Above- and belowground controls on water use by trees of different wood types in an eastern US deciduous forest. *Tree Physiology* 33, 345–356.
- Miyazawa, Y., Dudley, B.D., Hughes, R.F., Vandemark, J., Cordell, S., Nullet, M.A., Ostertag, R., Giambelluca, T.W., 2016. Non-native tree in a dry coastal area in Hawai'i has high transpiration but restricts water use despite phreatophytic trait. *Ecohydrology* 9, 1166–1176.
- Naumburg, E., Mata-Gonzalez, R., Hunter, R.G., McIendon, T., Martin, D.W., 2005. Phreatophytic Vegetation and Groundwater Fluctuations: A review of current research and application of ecosystem response modeling with an emphasis on great basin vegetation. *Environmental Management* 35, 726–740.
- Nelson-Kaula, K.K., Ostertag, R., Hughes, R.F., Dudley, B.D., 2016. Nutrient and organic matter inputs to Hawai'i an anchialine ponds: influences of N-fixing and non-N-fixing trees. *Pacific Science* 70, 333–347.
- Newman, B.D., Wilcox, B.P., Archer, S.R., Breshears, D.D., Dahm, C.N., Duffy, C.J., McDowell, N.G., Phillips, F.M., Scanlon, B.R., Vivoni, E.R., 2006. Ecohydrology of water-limited environments: A scientific vision. *Water Resources Research* 42.
- Noy-Meir, I., 1973. Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics* 4, 25–51.
- Orlowski, N., Pratt, D.L., McDonnell, J.J., 2016. Intercomparison of soil pore water extraction methods for stable isotope analysis. *Hydrological Processes* 30, 3434–3449.
- Peterson, R.N., Burnett, W.C., Glenn, C.R., Johnson, A.G., 2009. Quantification of point-source groundwater discharges to the ocean from the shoreline of the Big Island, Hawai'i. *Limnology and Oceanography* 54, 890–904.
- Phillips, D.L., Gregg, J.W., 2001. Uncertainty in source partitioning using stable isotopes. *Oecologia* 127, 171–179.
- R Core Team. 2018. R: A language and environment for statistical computing R Foundation for Statistical Computing, Vienna, Austria.
- Raich, J.W., Russell, A.E., Crews, T.E., Farrington, H., Vitousek, P.M., 1996. Both nitrogen and phosphorus limit plant production on young Hawaiian lava flows. *Biogeochemistry* 32, 1–14.
- Rascher, K.G., Hellmann, C., Maguas, C., Werner, C., 2012. Community scale 15N isoscapes: tracing the spatial impact of an exotic N2-fixing invader. *Ecology Letters* 15, 484–491.
- Rempe, D.M., Dietrich, W.E., 2018. Direct observations of rock moisture, a hidden component of the hydrologic cycle. *of Sciences*.
- Rengasamy, P., 2006. World salinization with emphasis on Australia. *Journal of Experimental Botany* 57, 1017–1023.
- Schenk, H.J., Jackson, R.B., 2002. Rooting depths, lateral root spreads and below-ground/above-ground allometries of plants in water-limited ecosystems. *Journal of Ecology* 90, 480–494.
- Scholl, M.A., Ingebritsen, S.E., Janik, C.J., Kauahikaua, J.P., 1996. Use of precipitation and groundwater isotopes to interpret regional hydrology on a tropical volcanic island: Kilauea volcano area, Hawaii. *Water Resources Research* 32, 3525–3537.
- Scott, R.L., Cable, W.L., Huxman, T.E., Nagler, P.L., Hernandez, M., Goodrich, D.C., 2008. Multiyear riparian evapotranspiration and groundwater use for a semiarid watershed. *Journal of Arid Environments* 72, 1232–1246.
- Scott, R.L., Edwards, E.A., Shuttleworth, W.J., Huxman, T.E., Watts, C., Goodrich, D.C., 2004. Interannual and seasonal variation in fluxes of water and carbon dioxide from a riparian woodland ecosystem. *Agricultural and Forest Meteorology* 122, 65–84.
- Scott, R.L., Shuttleworth, W.J., Goodrich, D.C., Maddock, T., 2000. The water use of two dominant vegetation communities in a semiarid riparian ecosystem. *Agricultural and Forest Meteorology* 105, 241–256.
- Street, J.H., Knee, K.L., Grossman, E.E., Paytan, A., 2008. Submarine groundwater discharge and nutrient addition to the coastal zone and coral reefs of leeward Hawai'i. *Marine Chemistry* 109, 355–376.
- Thorburn, P.J., Hatton, T.J., Walker, G.R., 1993. Combining measurements of transpiration and stable isotopes of water to determine groundwater discharge from forests. *Journal of Hydrology* 150, 563–587.
- Warshauer, F.R., Jacobi, J.D., Price, J., 2009. Native coastal flora and plant communities in Hawai'i: Their composition, distribution, and status. Hawai'i Cooperative Studies Unit Technical Report HCSU-014. University of Hawai'i at Hilo.
- West, A.G., Patrickson, S.J., Ehleringer, J.R., 2006. Water extraction times for plant and soil materials used in stable isotope analysis. *Rapid Communications in Mass Spectrometry* 20, 1317–1321.
- West, J.M., Salm, R.V., 2003. Resistance and resilience to coral bleaching: implications for coral reef conservation and management. *Conservation Biology* 17, 956–967.
- White, D.A., Dunin, F.X., Turner, N.C., Ward, B.H., Galbraith, J.H., 2002. Water use by contour-planted belts of trees comprised of four Eucalyptus species. *Agricultural Water Management* 53, 133–152.
- Wolfe, E. W., and J. Morris. 1996. Geologic map of the Island of Hawai'i . Miscellaneous investigations series map I-2524-A. US Geological Survey, Reston.
- Zeppel, M., Lewis, J.D., Phillips, N.G., Tissue, D.T., 2014. Consequences of nocturnal water loss: a synthesis of regulating factors and implications for capacitance, embolism and use in models. *Tree Physiology* 34, 1047–1055.
- Zohdy, A.A., Jackson, D.B., 1969. Application of deep electrical soundings for groundwater exploration in Hawai'i. *Geophysics* 34, 584–600.
- Zwieniecki, M.A., Newton, M., 1995. Roots growing in rock fissures: Their morphological adaptation. *Plant and Soil* 172, 181–187.