

# Drought in an Invaded Hawaiian Lowland Wet Forest<sup>1</sup>

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**Abstract:** In this study we examined historic drought frequency and hydrologic effects of removing invasive plants from one of the few remaining Hawaiian wet lowland forests, near Hilo, Hawai‘i. We developed a conceptual and statistical model of Hilo droughts using historic rainfall and pan evaporation data and discovered that episodes of low soil moisture were most likely from January to March but also occurred in June or July. Field measurements were taken in four pairs of plots. Nonnative woody and herbaceous species were removed from four plots; control plots were undisturbed. Soil water potential measurements documented partial soil drying in control plots, but not removal plots, during droughts with recurrence intervals of 2–3 yr. Drier soils exhibited strong small-scale heterogeneity in soil water potential that presumably reflects macroporosity in the young ‘a‘ā lava flow substrate. Transpiration from and rainfall interception by the dense canopy of nonnative species were most likely responsible for drier conditions in control plots. Removal plots experienced changes to shading, mid-day vapor pressure deficit, albedo, and aerodynamic resistance, but it appears that hydrologic impact of these variables was minor. We suggest that efforts to restore Hawaiian tropical rain forests should consider drought resilience as one objective, among many, of a restoration program. Germinating seeds, shallow-rooted saplings and deeper-rooted mature trees may respond differently to hydrologic effects of removing invasive plants.

MANY AREAS on the windward coasts of the main Hawaiian Islands receive more than

60 mm of rain in each month and therefore fall into the Köppen-Geiger classification of tropical rainfall climate (Kottek et al. 2006). Within this zone, most of the native forests have been converted to other uses and only a few patches remain of native Hawaiian lowland wet forests (Price et al. 2012). These forests are heavily invaded, and their long-term survival is uncertain; their loss will further reduce native biodiversity. Nonnative invasive species are considered the greatest threat to this ecosystem (Zimmerman et al. 2008, Ostertag et al. 2009), with climate change as a potential exacerbating stress. The study reported here is motivated by the hypothesis that resilience to drought is one factor that affects forest composition and that climate-related changes to soil moisture can potentially affect the distribution of species in tropical forests (Engelbrecht et al. 2006).

Numerous investigations have examined droughts in tropical forests that experience a dry season, but only a few studies have documented droughts in rain forests that are wet year-round (Walsh and Newberry 1999,

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Allen et al. 2010) or examined impacts using “rain out” experiments (Nepstad et al. 2007). To our knowledge there are only two studies that have examined drought in Hawaiian rain forests that are wet year-round. Pau et al. (2010) used satellite data to document drought-associated greening of Hawaiian wet forests at midelevations. They attributed this positive response to reduction in cloud cover. Loope and Giambelluca (1998) proposed that Hawaiian cloud forests may serve as a barometer of climate change.

The purpose of this study is to contribute to our understanding of drought in Hawaiian lowland wet forests, focusing on climatology and the hydrologic effects of invader removal during times of low rainfall. Because our field measurements span only a few years, modeling was used to improve our understanding of drought occurrence during the last six decades. Specifically, we used historic meteorological data to develop a conceptual and mathematical model of droughts; the model describes the magnitude-frequency relationship of historic droughts at the study site. Soil water potential ( $\Psi_s$ ) measurements taken during a series of mild droughts provided the link between field conditions and the model’s drought index. To demonstrate the influence of invasive species removal, measurements were taken in four pairs of plots. Control plots contained heavily invaded native forest; invasive herbaceous and woody plant species were mechanically removed from the paired “removal” plots. Field observations of interception and vapor pressure deficit, along with  $\Psi_s$  responses to an artificial drought, were used to evaluate hydrologic response to invader removal.

#### MATERIALS AND METHODS

##### *Field Site and Paired Plots*

The study site, which is described in detail in Ostertag et al. (2009), is part of a Hawaiian lowland wet forest near the town of Hilo on the island of Hawai‘i and within the Keaukaha Military Reservation (KMR) (19° 42.15' N, 155° 2.40' W). The forest canopy is dominated by the native ‘ōhi‘a (*Metrosideros poly-*

*morpha*) with lesser amounts of lama (*Diospyros sandwicensis*); the invasive bingabing (*Macaranga mappia*) occupies a lower level of the overstory. The canopy, whose height ranges from 23 to 35 m, is sparse; the mid- and understories are dense. One of our control plots contains native hala (*Pandanus tectorius*) in the midstory, but otherwise the midstory and understory are occupied by invasive trees such as strawberry guava (*Psidium cattleianum*) and melastoma (*Melastoma septemnerium*) and the shrub *Clidemia hirta*. Today this ‘ōhi‘a/lama forest is found only on the windward side of Hawai‘i Island (Gagné and Cuddihy 1999), and its future is uncertain because of low levels of recruitment by native species. There are only a few remaining stands of native-dominated Hawaiian lowland wet forests because most of them have been cleared for agriculture (Price et al. 2012). One reason that the KMR site has not been cleared for agriculture is that it sits on a 750–1,500-yr-old ‘a‘ā lava flow with immature soils. ‘A‘ā morphology develops when the cooling surface of a lava flow tears and breaks into many jagged pieces that overlie a relatively unfractured core. The upper portion of the flow is composed of exceptionally permeable cobble- to boulder-sized basalt clasts. These overlie a very dense but vertically fractured ‘a‘ā core whose top surface lies at a depth of 0.5–1 m. In spite of high rainfall, soils are well drained in most locations, and there are no defined surface water channels; unless disturbed there is no surface runoff. Soils (Papai extremely stony muck) are classified as Euic isohyperthermic Typic Udifolists (Soil Survey Staff 2010). The mapped available water storage, which is defined as the amount of water between field capacity and the permanent wilting point, is 2.7 cm in the top 25 cm of soil and 5.2 cm in the top 1.5 m.

Four pairs of 10 × 10 m plots were established in 2004 (Ostertag et al. 2009). Each pair of plots was about 100 m from other pairs, and each removal plot was about 20 m from its paired control plot. All nonnative plant species were mechanically removed from the managed plots and from a 2.5 m perimeter buffer strip. Herbaceous plants, grasses, ferns, seedlings, and some saplings

were hand pulled. Trees and shrubs were cut and stumps were immediately poisoned with a triclopyr-based herbicide to prevent resprouting. To prevent reestablishment, hand weeding of all invasive species was performed approximately every 8 months through the end of the study reported here. Before removal the leaf area index (LAI) of the forest was approximately 5.5 m<sup>2</sup> leaf/m<sup>2</sup> ground; removal treatments reduced LAI to about 2 m<sup>2</sup> leaf/m<sup>2</sup> ground (Ostertag et al. 2009). Five repeat measurements demonstrated that LAI did not change over the next several years.

Weather data were obtained from the U.S. National Weather Service for the Automated Surface Observing System (ASOS) station at the Hilo International Airport (WBAN no. 21504), located approximately 1.6 km from the study site. From 1981 to 2010, rainfall averaged 3,219 mm/yr, and air temperature averaged 23.3°C. Minimum and maximum daily relative humidity averaged 68% and 80%, respectively. From 1966 to 1968 pan evaporation at the Hilo Airport averaged 1,637 cm/yr (Western Region Climate Center 2007). Although the climate has seasonal variations, they are not strong; the driest month (June) receives an average of 187 mm of precipitation, placing the site into the Köppen-Geiger category of Tropical Rain Forest (Kottek et al. 2006).

### *Field and Laboratory Measurements*

Air temperature and humidity were measured at a height of 20 cm using sensors (HOBO H8 Pro, Onset Computer Corp., Pocasset, Massachusetts) placed 1 m from the northeast corner of each plot. Vapor pressure deficit, defined as the difference between vapor pressure in the air and vapor pressure of a free water surface, was calculated from air temperature and relative humidity.

Soil water potential ( $\Psi_s$ ) and soil temperature were measured using a psychrometer (Wescor model HR-33T) and PCT-55 (ceramic) sensors. Each sensor was calibrated to determine its MPa/ $\mu$ V coefficient. The measured  $\Psi$  represents the sum of matric and osmotic potential, but osmotic potential was assumed to be negligible. Precision of the in-

strument is  $\pm 0.03$  MPa. When drought was imminent, as judged by several weeks of low rainfall, one psychrometer was deployed in a removal plot and an additional psychrometer was deployed in the paired control plot. Each instrument was equipped with four sensors located within 1 m of each other. Sensors were placed vertically in mineral soil at a depth of about 10 cm. Although there are four pairs of plots, there was only one pair of psychrometers. Consequently for each drought event the  $\Psi_s$  measurements were made on a single pair of plots.

Measurements of  $\Psi_s$ , soil temperature, and offset voltage, which was measured by the psychrometer during the course of the  $\Psi_s$  measurement, were taken at 1-hr intervals. Transient saturated conditions, deteriorating sensors, and measurements taken at the wrong time during the psychrometer's cooling cycle can contribute to invalid measurements. Data from individual sensors were therefore examined to locate anomalous values, which were discarded. For treatment averages, data quality was considered acceptable if at least three control sensors and at least three removal sensors reported valid data.  $\Psi_s$  measurements are less accurate when vertical soil thermal gradients are present, a condition that can be identified by large offset voltages (Brown and Shouse 1992). For this reason daily averages were calculated from data collected at times of the day when offsets were small (1800 to 0100 hours and 0800 to 1000 hours).

Statistical differences in  $\Psi_s$  treatment means were analyzed by two methods. *T* tests were used to examine the lowest daily-average  $\Psi_s$  recorded by a given sensor during the course of a drought. In the *t* test the sample size for each treatment was therefore the number of drought events times the number of plots. Repeated measures analysis of variance (rANOVA) was performed on daily time series of  $\Psi_s$ , with different days serving as repeats and different sensors serving as subjects.

Throughfall was measured using trough-type collectors (effective surface area of 2,700 cm<sup>2</sup>) that discharged into containers that were emptied weekly. Interception was calculated as precipitation less throughfall less stemflow. Precipitation was measured

~1.6 km away at the Hilo Airport. Flat topography minimized spatial gradients in precipitation due to aspect or orographic forcing. Stemflow was estimated at 2.5% (control) or 2.0% (removal) of gross precipitation. These numbers are similar to values measured in other tropical rain forests (Scatena 1990, Dietz et al. 2006, Park and Cameron 2008).

Each of the eight plots had one throughfall collector that was randomly sited within the plot and not moved thereafter. Forty-seven weekly measurements were taken beginning in July 2004 and ending August 2005. Data from weeks with heavy rainfall (throughfall > ~7 cm week<sup>-1</sup>) were discarded because fully saturated conditions were not relevant to the question at hand. Data were also discarded if operator error or equipment failure led to a loss of data from any of the eight plots. Measurements were sometimes taken at intervals of slightly less or more than 7 days, so to avoid inconsistencies all data are reported in units of cm day<sup>-1</sup>. Weekly throughfall measurements are not normally distributed, so differences in plot medians were evaluated using the Mann-Whitney rank sum test (SigmaStat ver. 3.5).

Soil samples (~3,000 cm<sup>3</sup>) were collected from each of the eight plots to characterize soils and evaluate  $\Psi_s$  response under controlled conditions. Samples were placed in a cylindrical metal pot (~15 cm diameter, soil ~19 cm deep), moved to a climate-controlled laboratory, saturated, and then allowed to dry for 62 days. The dry-down period was followed by an 11-day wet-up period during which samples were lightly watered each day. Samples were weighed periodically to obtain soil moisture.  $\Psi_s$  was measured using a psychrometer and a single sensor placed in the center of the container at a depth of 5–8 cm.

#### *Hilo/KMR Drought Model*

Droughts can be identified in a variety of ways depending on the issues of concern and data availability (Dracup et al. 1980, Tsakiris et al. 2007). In this study we identify droughts as periods during which soil moisture remains below a threshold. The drought model has

three parts: (1) simulation of daily soil moisture, (2) identification of drought events, and (3) statistical estimation of the magnitude-frequency relationship for drought events.

The soil moisture model was used to simulate daily soil moisture from 1950 to 2010. Model inputs (drivers) were daily rainfall and monthly average pan evaporation. The only parameter was field capacity, which was estimated as 115 mm based on laboratory measurements of soil samples and an assumed rooting depth of 0.5 m. Daily soil moisture content (the model's state variable and output) was simulated using a bucket-type model that tracks the balance between precipitation and evapotranspiration. In implementing the soil moisture model it was assumed that:

- (a) the demand for evapotranspiration (hereinafter evaporative demand) equals 75% of pan evaporation;
  - (b) evaporative demand is first satisfied by rainfall and then by soil moisture;
  - (c) water in excess of field capacity becomes groundwater recharge. (There is no surface runoff at the study site.);
  - (d) evapotranspiration proceeds at the potential rate until soil moisture falls below a critical threshold; below the critical threshold the ratio of actual to potential evapotranspiration declines linearly to zero for perfectly dry soil.
- This conceptualization, which is sometimes called the Feddes model, is supported by experimental data and has been applied widely (Chen et al. 2008). In the study reported here 60% of field capacity was selected as the critical threshold, in part because this value produced a credible number of droughts. In the sensitivity analysis we also tested a version of the model that assumes that evapotranspiration begins to drop below the potential rate whenever soil moisture falls below field capacity.

To analyze drought seasonality, we examined the time series of simulated soil moisture. If soil moisture was less than 50% of field capacity, that day was classified as experiencing strong drought; if soil moisture was

more than 50% but less than 60% of field capacity, that day was classified as experiencing mild drought.

Following the recommendations of Dracup et al. (1980), we identified drought events as periods when soil moisture remains below a threshold. Specifically, we adopted a criterion of soil moisture less than 60% of field capacity for at least 3 consecutive days. This criterion is a choice based on local experience; moreover a value of 60% produced a credible number of droughts. To evaluate the sensitivity of results to this choice, we also implemented an alternate version of the model that uses a threshold of 50% of field capacity.

Drought events were characterized by duration and magnitude, which was defined as the cumulative amount of unmet evaporative demand, measured from the first time that soil moisture fell below the threshold. Our statistical model of drought interarrival times (described later in this section) assumes that drought events are independent events. Sequential droughts were considered related if they were separated by fewer than 10 days and during that time the soil moisture did not exceed 80% of field capacity. Related sequential droughts and the period between them were combined.

Statistical treatment of the drought magnitude-frequency relationship was based on the partial duration approach, which is appropriate for events that exceed a threshold. The partial duration approach is also better suited than the annual maxima approach for analyzing events of low recurrence interval. Following Stedinger et al. (1993), drought interarrival times were modeled by a Poisson probability distribution and drought magnitude was modeled with a generalized Pareto distribution. The generalized Pareto distribution is appropriate for events that exceed a threshold. For the Poisson and Pareto distributions, the annual recurrence interval,  $T_a$ , is then given by:

$$G(x) = 1 - \left[ \frac{1 - \exp[-(1 - G(x))]}{1 - \frac{\kappa x}{\alpha}} \right]^{1/\lambda}$$

where

$x$  = magnitude of drought (cumulative unmet evaporative demand)

$\lambda$  = average number of events per year

$G(x)$  = cumulative generalized Pareto distribution.

The statistical model has three parameters:  $\lambda$ ,  $\kappa$ , and  $\alpha$ . The Poisson parameter  $\lambda$  was set equal to the average number of events per year, and Pareto parameters  $\kappa$  and  $\alpha$  were estimated using the method of L moments (Hosking 1990, Stedinger et al. 1993):

$$\kappa = \frac{\bar{x}}{\text{second L moment of } x} - 2$$

$$\alpha = \bar{x}(1 + \kappa)$$

second L moment of  $x$

$$= -\bar{x} + \frac{2}{n(n-1)} \sum_{i=1}^{n-1} (n-i)x_i$$

where

$\bar{x}$  = mean drought magnitude

$n$  = number of droughts

$x_i$  = drought magnitude; ranked from small  $x_1$  to large  $x_n$ .

## RESULTS

### Hilo/KMR Drought Model

The model identified two drought seasons (Figure 1): the main drought season occurred in winter (January–March, peaking in February), and a secondary season occurred in summer (June–July). Severe droughts were most likely to occur in February and March.

The model predicts that mild droughts occur almost twice a year on average (Table 1). The average drought lasted for 3 weeks and incurred 13 mm of unsatisfied evaporative demand. The most severe drought in the period of record occurred in 1983 and was associated with a strong El Niño. The 1983 drought lasted nearly 3 months and incurred 117 mm of unsatisfied atmospheric demand. It had an estimated recurrence interval of 50 yr (Table 2). The three droughts for which



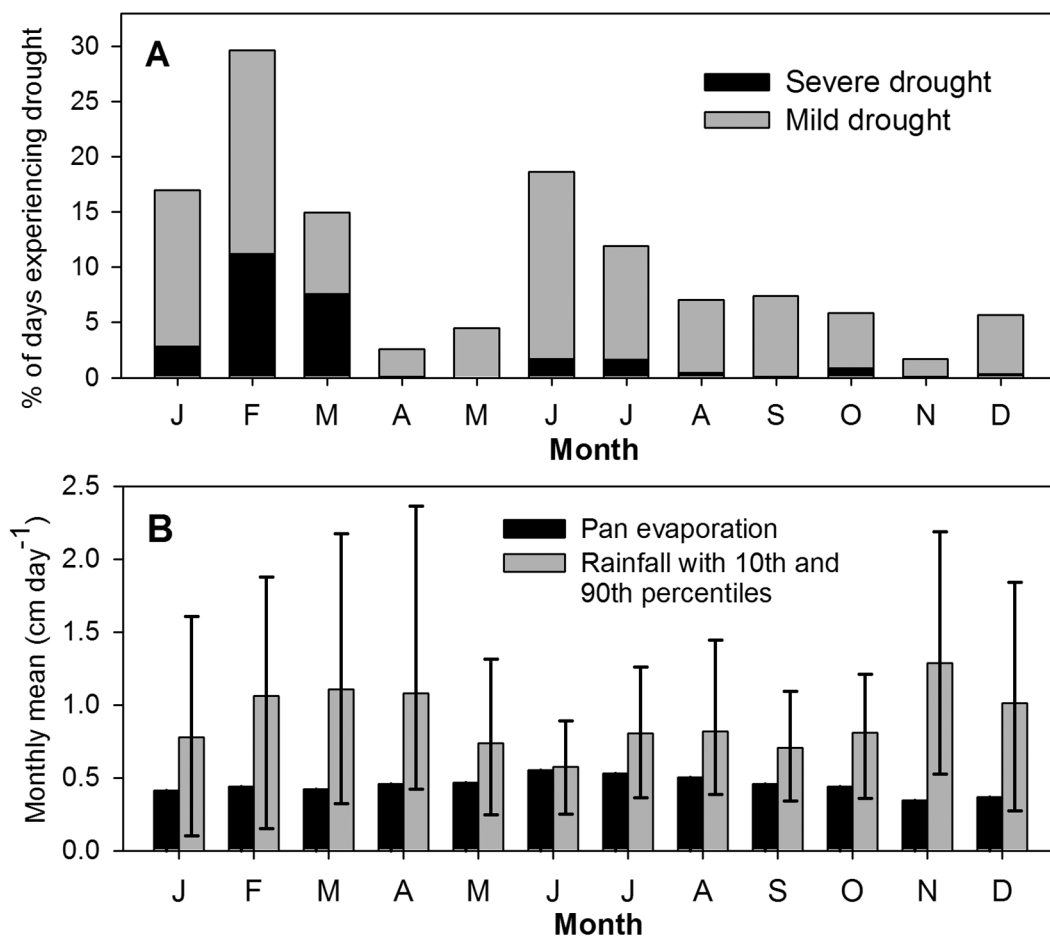


FIGURE 1. Climatology of modeled droughts during 1950–2010. (A) Prevalence by month. Days with soil moisture less than half of field capacity were classified as experiencing strong drought, and days with soil moisture between 50% and 60% of field capacity were classified as experiencing mild drought. (B) Seasonal rainfall (1950–2010) and pan evaporation (1966–1968).

we have measured  $\Psi_s$  have recurrence intervals of 1.5, 1.6, and 2.9 yr (Table 2).

Sensitivity studies were used to evaluate the influence of parameters whose values were selected somewhat arbitrarily. Two alternate versions of the model were run. In alternate model no. 1, the threshold used to identify droughts was dropped from 60% of field capacity to 50% of field capacity. In alternate model no. 2, the threshold used to identify droughts was raised to 70% of field capacity, while simultaneously assuming that evapotranspiration begins to drop below the poten-

tial rate whenever soil moisture falls below field capacity (as opposed to when soil moisture falls below 60% of field capacity). The first alternate version of the model used the most stringent definition of drought and identified 33% fewer droughts than the original model. The second alternate version of the model, which assumes that plants are more likely to conserve water, identified 2% more droughts than the original model. All three versions of the model made similar estimates of (1) seasonal patterns, and (2) the recurrence interval of the small May 2005

TABLE 1

Drought Model Parameters Fitted from 1950–2010 Data

| Parameter                                            | Value                           |
|------------------------------------------------------|---------------------------------|
| Average number of events per year ( $\lambda$ )      | 1.77                            |
| Mean magnitude of drought ( $\bar{x}$ ) <sup>a</sup> | 12.6 mm (maximum 117. mm)       |
| Mean duration of drought                             | 22 days (median 13, range 3–91) |
| $\kappa$ (Pareto parameter)                          | –0.63                           |
| $\alpha$ (Pareto parameter)                          | 4.69                            |

<sup>a</sup> Magnitude is defined as the accumulated unsatisfied evaporative demand.

drought. Estimates of the latter were within 3% of each other. Estimates of the recurrence interval for the 1983 drought were 50, 56, and 61 yr for the original model, alternate no. 1, and alternate no. 2, respectively. Because alternate model no. 1 neglects the smallest droughts, it is arguably the most appropriate for evaluation of large infrequent events.

Field Soil Water Potential during Droughts

Soil water potential ( $\Psi_s$ ) was measured during three mild droughts with recurrence intervals ranging from 1.5 to 2.9 yr. Taken as a whole,  $\Psi_s$  in the control plots was lower (drier) and more variable than  $\Psi_s$  in the removal plots (Table 3). For each of the droughts the lowest measured  $\Psi_s$  (among the eight sensors) occurred in a control plot (Figure 2).

According to both *t* tests and rANOVA, the difference between control  $\Psi_s$  and removal  $\Psi_s$  was statistically significant for the

TABLE 3

Summary of  $\Psi_s$  Data for Droughts in May 2005, January 2006, and June 2007

| Soil Water Potential Statistic                                                                | Control         | Removal |
|-----------------------------------------------------------------------------------------------|-----------------|---------|
| Percentage of sensors reporting moist conditions ( $\Psi_s \geq 0.1$ MPa)                     | 36%             | 58%     |
| Percentage of sensors reporting slightly dry conditions ( $\Psi_s$ between –0.1 and –0.3 MPa) | 27%             | 42%     |
| Percentage of sensors reporting very dry conditions ( $\Psi_s \leq -0.3$ MPa)                 | 36%             | 0%      |
| Mean $\Psi_s$ (MPa)                                                                           | –0.26           | –0.11   |
| Standard deviation $\Psi_s$ (MPa)                                                             | 0.19            | 0.06    |
| <i>n</i> (three droughts times four sensors)                                                  | 11 <sup>a</sup> | 12      |

Note: This table is based on the lowest daily-average  $\Psi_s$  observed by each sensor during each of these droughts.

<sup>a</sup> One sensor malfunctioned during the December 2005 drought.

June 2007 event (*t* test: *t* = –2.516, *df* = 6, *P* = .046; rANOVA: *F* = 6.122, *df* = 1, *P* = .048). Differences were not significant for the other two drought events, which according to the Hilo/KMR drought model were smaller than the 2007 event. Because of low statistical power (0.05 compared to the desired power  $\geq 0.80$ ) it is possible that control plots were drier than removal plots in May 2005 and January 2006, but differences were not detected with only four sensors.

$\Psi_s$  varied considerably between adjacent sensors that were installed within 1 m of each other (Figure 2). Also, intraplot variability of  $\Psi_s$  increased as  $\Psi_s$  dropped, as evidenced by negative correlation (*r* = –0.84, *P* < .01,

TABLE 2

Recurrence Intervals of Selected Droughts

| Date                             | Recurrence Interval (yr) | Magnitude (mm) | Duration (days) |
|----------------------------------|--------------------------|----------------|-----------------|
| 17 January 1983–10 April 1983    | 50                       | 116.8          | 84              |
| 7 January 2010–6 March 2010      | 25                       | 71.6           | 59              |
| 11 May 2005–4 June 2005          | 1.5                      | 3.0            | 25              |
| 30 December 2005–10 January 2006 | 1.6                      | 3.6            | 12              |
| 27 May 2007–14 June 2007         | 2.9                      | 10.8           | 19              |

Note: The 1983 event is the largest during the period of record, and the 2010 event is the largest in the twenty-first century.

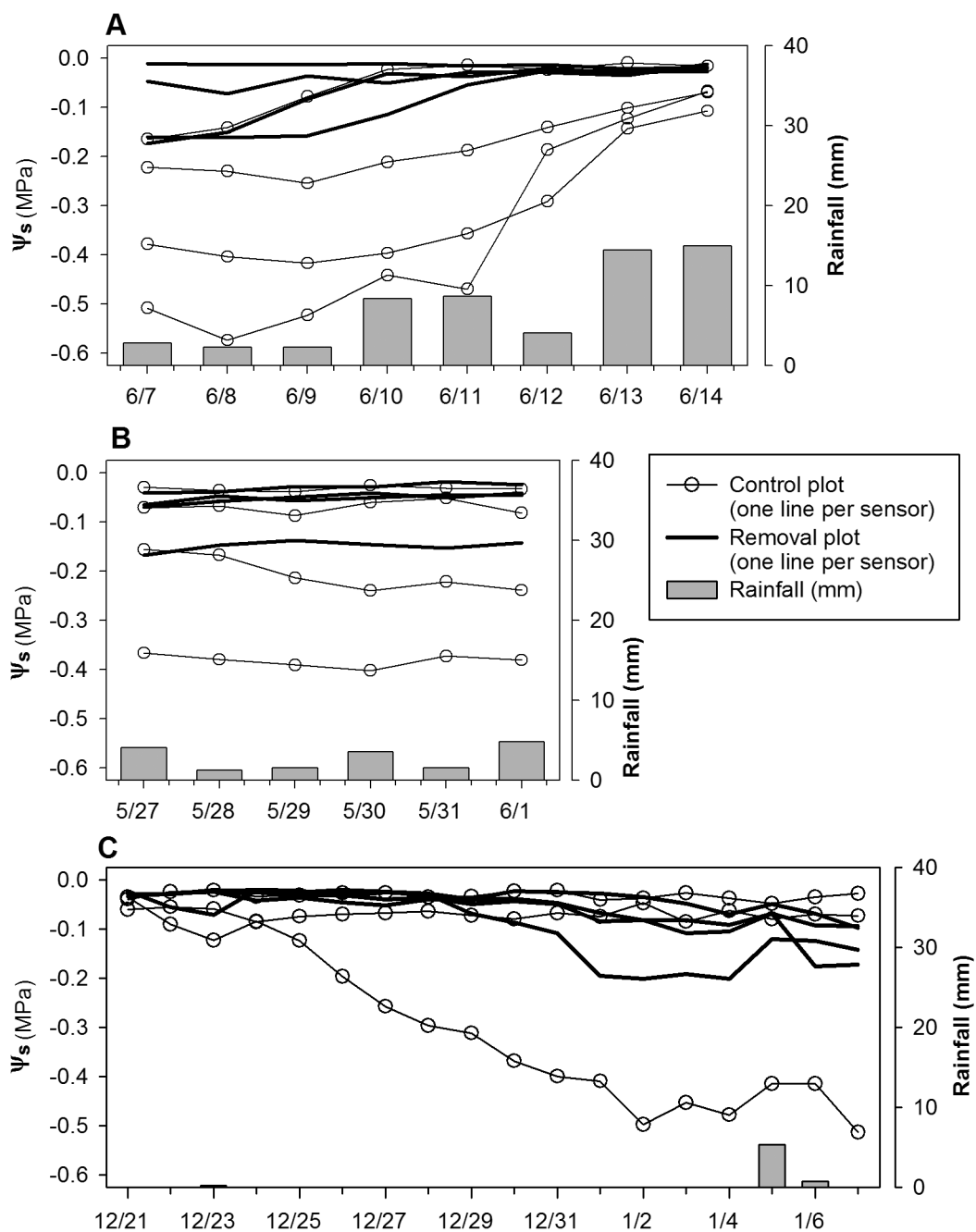


FIGURE 2. Soil water potential during three drought periods. (A) June 2007, observations span the recovery period but not the period of drought development. (B) May 2005. (C) December 2005–January 2006.



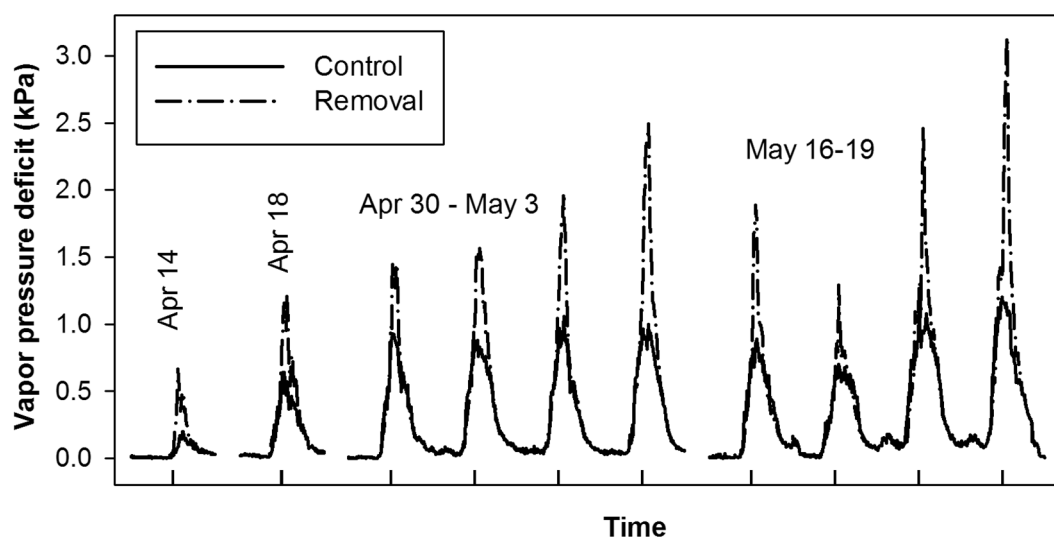


FIGURE 3. Vapor pressure deficit (VPD) during dry weather. Selected representative days in 2005 are shown. VPD was calculated from ground-level measurements of air temperature and relative humidity.

$n = 54$ , daily time step) between the plot mean and the plot standard deviation. Under dry conditions  $\Psi_s$  exhibited a crude diurnal cycle, with lower values during the afternoon.

#### *Soil Water Potential during Artificial Laboratory Drought*

Soil samples collected for the laboratory experiment ( $n = 8$ ) had an average porosity of 54% (SE 1%) and an average field capacity of 23% (SE 2%). Rocks greater than 2.5 cm diameter constituted 85.1% of the soil samples' dry weight. Soil texture did not vary systematically between removal and control plots.

During the course of the laboratory experiment  $\Psi_s$  varied greatly between the eight soil samples even though each sample was subjected to identical irrigation and drying schedules. Minimum recorded  $\Psi_s$  during the 62-day dry-down period ranged from  $-3.22$  to  $-0.18$  MPa (mean  $-1.53$ , standard deviation 1.09,  $n = 8$ ). Examination of time series showed that sometimes  $\Psi_s$  temporarily increased during the dry-down period (when a consistent downward trend was expected) or temporarily decreased during the wet-up period (when a consistent upward trend was expected).

#### *Microclimate Diurnal Variations*

During dry weather the midday and afternoon vapor pressure deficit (VPD) was larger in the removal plots than in the control plots (Figure 3). On the days shown in Figure 3, the minimum relative humidity was 71% in the control plots and 58% in the removal plots. Differences in VPD were largest from noon to 1500 hours and were negligible from 1700 hours to 1100 hours. During multiday spells of dry weather there were progressive increases in the midday VPD of the removal plots; comparable increases in the control plots were absent or attenuated (Figure 3). In both removal and control plots VPD was near zero between midnight and 0800 hours (Figure 4).

#### *Interception*

Interception was measured in all eight plots during 23 weeks of light to moderate rainfall (Figure 5). During those weeks, precipitation averaged  $3.2 \text{ mm day}^{-1}$ . In control plots 39% of rainfall was intercepted versus 27% in the removal plots; the average difference was  $0.39 \text{ mm day}^{-1}$ . Median weekly interception was  $0.60 \text{ mm day}^{-1}$  in the control plots and

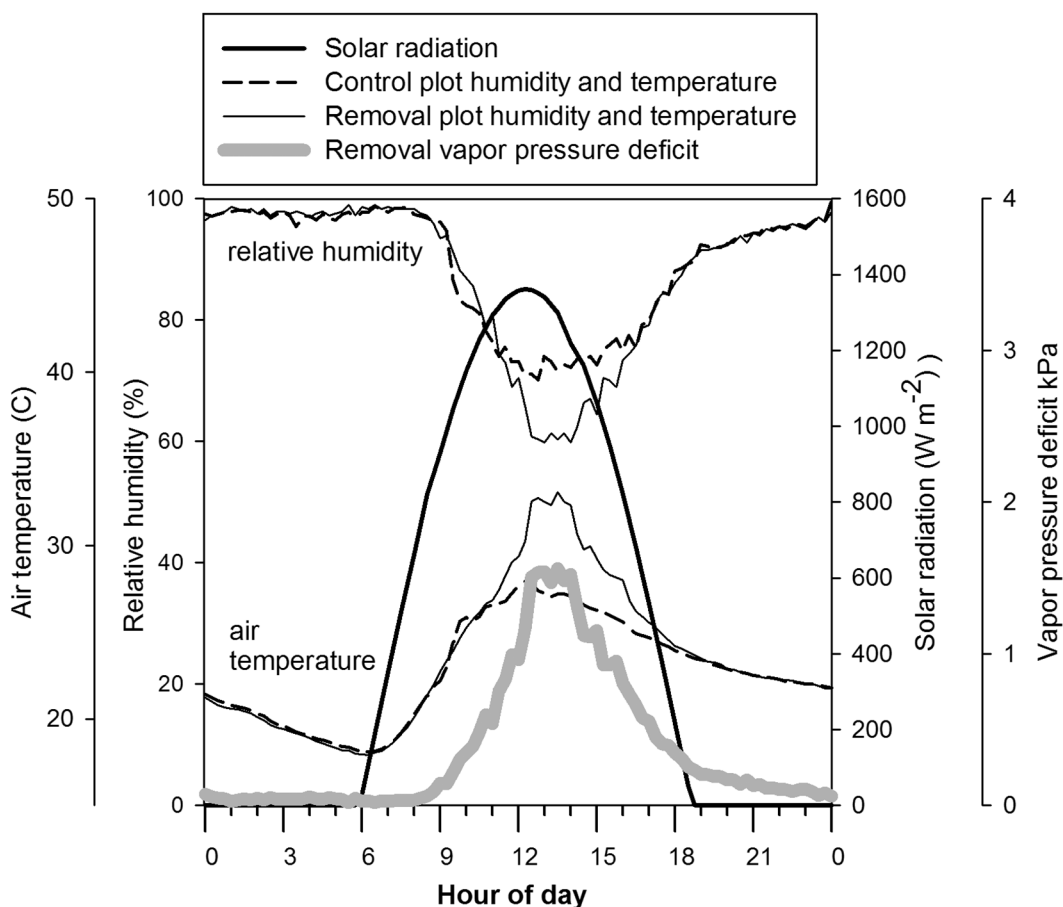


FIGURE 4. Microclimate diurnal cycle during a dry day (1 May 2005). Solar radiation is the value at the top of the atmosphere and is calculated from the solar constant and the solar zenith angle.

0.40 mm day<sup>-1</sup> in the removal plots. This difference is marginally significant (Mann-Whitney rank sum test,  $U = 3554$ ,  $P = .06$ ,  $n_1$  (small) = 92,  $n_2$  (big) = 92). There is considerable variability within a treatment (Figure 5), reflecting spatial variability in canopy density and architecture.

#### DISCUSSION

##### *Drought Model and Drought Climatology*

Daily soil moisture predictions made by our soil moisture model are correlated with observed  $\Psi_s$  in the control plots ( $r = 0.82$ ,  $P < .001$ , 27 days of observations), lending credi-

bility to model results. In the removal plots the correlation between modeled soil moisture and observed  $\Psi_s$  is not significant, suggesting that the model's soil moisture estimates are most accurate under conditions of high LAI.

Our field data document partial soil drying during three mild droughts in 2005–2007; recurrence intervals of these events are 1.5, 1.6, and 2.9 yr, according to estimates made by the Hilo/KMR drought model. This suggests that in stands with high LAI, episodes of soil drying can be expected once every 2 or 3 yr, on average. Studies in similar forests in Panama also found a drought recurrence interval of 2 yr (Engelbrecht et al. 2006), suggest-

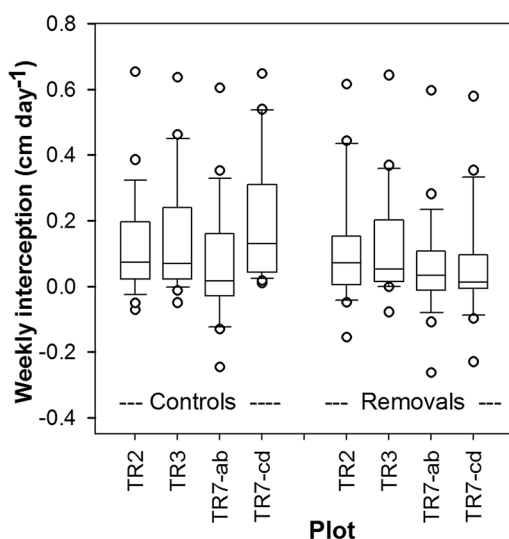


FIGURE 5. Variation of interception among plots during weeks of low to moderate rainfall between July 2004 and August 2005. Each box plot represents 23 weeks of measurements and shows the median value, outliers, and 90th, 75th, 25th, and 10th percentiles. All plots have concurrent measurement periods. Negative values mean that throughfall exceeded rainfall recorded 1.6 km away at a location with similar elevation and aspect.

ing that drought conditions need to be considered in the life history of rain forest trees, even when rainfall is aseasonal.

The model identified two drought seasons: the main one in January–March, and a secondary one in June–July. Because soil dries slowly, low rainfall in December and May sometimes contributed to drought development in subsequent months. Winter is the rainy season and experiences lower evaporative demand, but rainfall is inconsistent (Figure 1B). Winter droughts were associated with anomalously low seasonal rainfall in particular years. In contrast summer rainfall is more consistent, but average amounts are lower. It is not surprising that droughts sometimes occur in the months with the least rainfall and the highest evaporative demand.

Across the main Hawaiian Islands the El Niño phase of the El Niño Southern Oscillation (ENSO) is often associated with reduced winter precipitation, but low precipitation can also occur in the absence of El Niño

(Chu and Chen 2005). We found similar results in Hilo precipitation records. Empirical evidence suggests that in Hawai'i the combination of El Niño and the positive-phase Pacific Decadal Oscillation, which is similar to ENSO but more persistent, is a better predictor of reduced November–February Hawaiian rainfall than either index alone (Chu and Chen 2005). In the western tropical Pacific ENSO has been linked to rain forest droughts (Walsh and Newberry 1999). ENSO is expected to remain an important source of climate variability in the future (IPCC 2013).

### Soil Water Potential ( $\Psi_s$ )

Interpretation of the  $\Psi_s$  data requires an understanding of the unusual character of the soil at the KMR site. This immature soil, which is developed on a very young 'a'ā lava flow, contains a high percentage of minimally weathered pebbles, cobbles, and boulders, with clasts greater than 2.5 cm composing 85% of the dry weight. Some of the spaces between large clasts are empty (macrovoids exceeding 2 cm), and some are filled with fine-grained mineral soil. We hypothesize that macrovoids served as capillary barriers and were partly responsible for the fact that as the soil became drier  $\Psi_s$  became spatially variable at the scale of meters. The small-scale spatial variability made it more difficult to establish statistical significance of differences between treatment means. In the laboratory,  $\Psi_s$  varied over an order of magnitude between soil samples even though (1) all samples experienced identical atmospheric forcing, (2) the absence of plants eliminated variability due to root water extraction, and (3) all samples had similar soil texture. Again, we attribute this to macropores serving as capillary barriers. Unexpected fluctuations in  $\Psi_s$  could have resulted from episodic movement of "fingers" of water through macrovoids, a phenomenon known as unstable flow (Nimmo 2009).

### Hydrologic Impact of Invader Removal

The study reported here was part of a larger effort to better understand the potential for restoring invaded Hawaiian lowland wet

TABLE 4

Potential Hydrologic Impacts of Removing Nonnative Midcanopy and Understory Plants

| Mechanism                                                                                     | Result                                                                                                                                   | Effect on Woody Species during Times of Drought                                                                                       |
|-----------------------------------------------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------|---------------------------------------------------------------------------------------------------------------------------------------|
| Less transpiration from nonnative vegetation }<br>Reduction in interception }                 | Soil profile will become wetter                                                                                                          | Mature trees and shallow rooted saplings will experience less water stress                                                            |
| Reduced shading and less mulchlike litter                                                     | Soil surface will dry faster during midday                                                                                               | Reduced germination; shallow-rooted seedlings will experience water stress                                                            |
| Increase in air temperature and decrease in relative humidity (at ground level and at midday) | VPD will increase at ground level, leading to (1) increased evaporation from soil and (2) increased transpiration from understory leaves | Increased water stress due to drying of the soil surface and possibly deeper layers                                                   |
| Hydraulic pumping triggered by afternoon drying and warming of soil surface                   | Upward movement of water from deeper soil layers in response to thermal and $\Psi_s$ gradients                                           | This feedback softens the stress on shallow-rooted seedlings at the expense of deeper-rooted mature trees                             |
| Decreased albedo <sup>a</sup>                                                                 | More energy available for evapotranspiration; surface soil and soil profile will become drier                                            | Increased water stress; these may be minor effects but should not be entirely neglected in holistic examinations of the water balance |
| Reduction in aerodynamic roughness                                                            | Greater efficiency of soil-atmosphere exchange of water vapor (Thom 1971); soil surface and profile will become drier                    |                                                                                                                                       |
| Increase in throughfall intensity; raindrops have more kinetic energy                         | Greater potential for runoff and erosion of litter and organic matter                                                                    |                                                                                                                                       |

<sup>a</sup> The sign of the change to albedo may vary with local conditions.

forests by removing invasive herbaceous and woody plants, which were located primarily in the midstory and understory. The diverse hydrologic effects of invasive removal are therefore of interest. Table 4 summarizes the mechanisms by which invasive removal affected hydrologic variables and processes. We have emphasized impacts on soil moisture but neglected groundwater recharge, which is not important at this site but could be at others. The mechanisms vary in terms of whether they make the soil wetter or drier and the depth at which they do so. Mechanisms therefore vary in their impacts to germination, shallow-rooted seedlings, and deeper-rooted mature trees. Tropical seedlings are particularly vulnerable to droughts in the wet season (Engelbrecht et al. 2006). An ill-timed drought of only short duration could endanger the success of an outplanting project.

The KMR experiments showed that invasive removal prevented drying of shallow soil. What processes were responsible? Removal would be expected to alter albedo, aerodynamic resistance, and vapor pressure deficit in a way that would have *increased* evapotranspiration in the removal plots, thereby making the soil drier (Table 4). Because the removal plots did not dry out, however, we can infer that these variables were of minor importance. It is possible that vapor pressure deficit and aerodynamic resistance would be more influential in larger plots.

The lack of soil drying in the removal plots could be explained by reduction of interception and transpiration. Our measurements document probable reduction of interception when LAI was reduced from  $\sim 5.5$  m<sup>2</sup> leaf/m<sup>2</sup> ground to  $\sim 2.0$  m<sup>2</sup> leaf/m<sup>2</sup> ground. The amount of the interception reduction is less than we originally hypothesized, however.

Possibly some species have leaves that shed water efficiently, or interception was sometimes limited by saturation of canopy storage. Our measurements suggest that invasive vegetation would be expected to intercept 5–20 mm of rainfall during time spans typical of drought development (2–8 weeks), assuming light to moderate rainfall. Because this is not a large amount, it is likely that reduction in transpiration was more important than reduction in interception.

At a molecular level vapor pressure deficit drives evaporation and transpiration, so evapotranspiration would have been negligible from midnight to 0800 hours, when vapor pressure deficit was near zero in both removal and control plots. Evapotranspiration is also driven by net radiation, and on dry days the time of maximum evapotranspiration was approximately 1100 hours to 1600 hours, as indicated by the times of maximum solar radiation and vapor pressure deficit (Figure 4). Early afternoon differences between evapotranspiration in the removal plot and evapotranspiration in the control plot would have been controlled by several variables, including but not limited to vapor pressure deficit, LAI, soil moisture, and possibly albedo. We did not measure differences in canopy conductance, but others have found that the sensitivity of canopy conductance to vapor pressure deficit is a function of incident radiation and soil moisture (Chen et al. 2014).

Under dry conditions our  $\Psi_s$  data show a crude diurnal cycle, with water loss through the day and moisture recovery at night, presumably from upward movement of water from deeper in the soil (hydraulic pumping). Bruno et al. (2006) found similar diurnal cycles at shallow depths in Amazon rain forest soils.

One limitation of our study is that soil moisture was measured at only a single shallow depth (10 cm); emplacement of sensors deeper in the rocky soil would have been problematic. Other studies, however, have documented vertical variations in soil moisture depletion. In the Amazon basin, for example, Bruno et al. (2006) found that during drier conditions trees withdrew water from depths of 2–10 m. At KMR the dense core of

the lava flow may inhibit root penetration below 0.5–1 m, although it is likely that roots from larger trees exploit the vertical cooling cracks that usually fracture lava flows. Unfortunately we know little of root structure at this site and how it varies by species.

### *Response to Water Stress*

Plants employ two main strategies for tolerating or avoiding drought. The first strategy is presented by isohydric species (drought avoiders) that regulate water deficit through stomatal closure, and the second strategy is represented by anisohydric species (drought tolerant) that maintain high stomatal conductance at the cost of water loss (McDowell et al. 2008). Isohydric species are generally more vulnerable to drought than anisohydric species and tend to succumb to carbon starvation, particularly when droughts are lengthy. Anisohydric species, especially tall individuals, are vulnerable to hydraulically mediated cavitation under conditions of intense drought (McDowell et al. 2008). Studies have shown that resistance to cavitation tends to decline with increasing mean annual precipitation (Choat et al. 2012). It is therefore inferred that trees in a tropical rain forest would be dominated by isohydric species. When isohydric and anisohydric species are in competition, the isohydric species will likely perish first (McDowell et al. 2008). According to a global meta-analysis, ecosystems dominated by invasive species tend to use more water per unit ground area than those dominated by native species, particularly where climates are wetter and hotter (Cavaleri and Sack 2010). This implies that these invasive species tend to employ a more anisohydric strategy of water use and during times of drought this may disadvantage native species that adopt a more conservative and protective isohydric strategy. Evaluation of this hypothesis requires more information on the water use characteristics of species found in Hawaiian lowland wet forests.

*Metrosideros polymorpha*, the dominant canopy tree at KMR, is highly conservative in its water use compared with agroforestry species grown in the region (Kagawa et al. 2009)

and is unusual in that it is established in both very dry and very wet climates. Cornwell et al. (2007) showed that although many *M. polymorpha* traits vary with rainfall, some key traits associated with drought tolerance (e.g., xylem resistance to embolism) do not. This suggests that *M. polymorpha* growing at high-rainfall sites ( $5,400 \text{ mm yr}^{-1}$ ) may be as drought tolerant as those in very dry sites ( $600\text{--}700 \text{ mm yr}^{-1}$ ). Also, as a pioneer species on new lava flows, *M. polymorpha* is able to withstand soils with very low water storage capacity. Based on this understanding, we hypothesize that a downside of conservative traits in tropical wet systems is the vulnerability toward displacement by nonnative or invasive species that are adapted to high resource use. If climate change brings drier conditions, *M. polymorpha* may be at a disadvantage.

#### *Restoration Implications and Future Outlook*

Restoration and protection of the few remaining patches of Hawaiian lowland wet forests is a priority if we are to prevent further losses to native biodiversity (Zimmerman et al. 2008). To date there have been several small pilot projects that have explored restoration strategies of invaded Hawaiian lowland wet forests (Cordell et al. 2009, Ostertag et al. 2009, Schulten et al. 2014), but feasible restoration techniques suitable for this ecosystem are still under development. We regard restoration of invaded primary forest, and long-term maintenance to prevent nonnative recruitment, as the best strategy for preservation of this unique ecosystem (Ostertag et al. 2009). Although native species are present in the seed bank, canopy opening appears to be necessary for them to germinate (Cordell et al. 2009).

We believe that it is worthwhile to consider drought resilience as one objective, among many, of a restoration program. In this context, resilience can be defined as the ability of target native species to recruit in spite of ill-timed droughts, and the ability of mature trees to fare as well or better than invasive species during prolonged severe drought. Following the suggestions of Funk et al. (2008), one possible strategy is to pre-

empt invasion by establishing native species whose water-use strategies are similar to those of the invasive species of concern.

In principle, it is possible to consider the impact of proposed restoration programs on interception, evaporative demand, surface drying, and deeper soil moisture. Table 4 may be useful as a starting point for a systematic evaluation. There are many open questions, however, including species-specific response to water stress and interspecies competition. We propose several avenues for future data collection efforts. Seedling hardiness is easily evaluated with potted plant experiments (Tyree et al. 2003, Schulten et al. 2014). To characterize species traits one can measure  $\delta^{13}\text{C}$ , xylem specific conductivity, stomatal conductance, and stemwater potential (Pérez-Harguindeguy et al. 2013). During times of severe drought, we recommend field documentation of mortality, midday leaf water potential, and subsequent attacks by biotic agents.

The possibility that future climate change will change forest composition should not be neglected. Because species vary in their drought resiliency, changes to soil moisture climatology could have an impact on tropical forests (Engelbrecht et al. 2006). A wide variety of atmospheric, hydrologic, and plant processes affect soil moisture, and therefore it is difficult to make robust predictions of how the climatology of drought will change as climate warms (McDowell et al. 2008, IPCC 2013). Global climate models include soil moisture as a state variable and can be used to holistically evaluate future changes to soil moisture, although the limitations of such predictions must be borne in mind. Wang (2005) used 15 Intergovernmental Panel on Climate Change (IPCC) models to compare preindustrial simulations with simulations of post-2100 ( $\text{CO}_2$  stabilized) conditions. In warm seasons the models predicted increased evapotranspiration; models generally predicted decreased soil moisture in the tropics and subtropics. The most recent suite of climate models (IPCC Fifth Assessment) predicts, however, that soil moisture droughts will not become more frequent until the latter



half of the twenty-first century and that currently dry regions will be hit hardest (IPCC 2013).

In Hawai'i there is evidence that relative humidity has declined in the last 50 yr (Diaz et al. 2011) and that winter precipitation has decreased during a similar time frame (Chu et al. 2010), although the observed precipitation trends are not spatially consistent. Other factors being equal, lowering relative humidity increases atmospheric evaporative demand. Regarding future rainfall, downscaled IPCC climate models predict that Hawaiian precipitation is likely to decrease slightly in the winter and increase slightly in the summer (Timm and Diaz 2009, Lauer et al. 2013). There is disagreement between models, however, and predictions are spatially inconsistent. Nevertheless, the data discussed here suggest that it is possible that wintertime droughts could become more prevalent in Hawaiian lowland wet forests over the next century. To better understand the potential impacts to forest composition we need more species-specific data on native and invader water-use strategies and traits.

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