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Groundwater availability mediates the ecosystem effects of an invasion of *Prosopis pallida*

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Abstract. Groundwater levels in arid environments are dropping worldwide due to human extraction, and precipitation events are predicted to become rarer and more intense in many arid areas with global climate change. These changes will likely alter both primary productivity and plant–soil nutrient cycles. To better understand the nature of such alterations, we examined effects of groundwater availability on plant–soil nitrogen (N) cycling in areas invaded by the N-fixing phreatophyte, *Prosopis pallida*, on the dry leeward coast of Hawai'i Island. Our aims were to quantify effects of groundwater availability to *P. pallida* on rates of litterfall N inputs and accretion in soils and to quantify effects of groundwater availability on N mineralization and leaching rates of inorganic N under natural rainfall conditions and simulated rain events. Stem water $\delta^{18}O$ values indicate that *P. pallida* trees in lowland plots accessed shallow groundwater, while in upland plots they relied solely on rainfall. During drought periods, *P. pallida* at upland plots experienced water stress, evidenced by lower stem water potentials, higher water-use efficiency, and lower predawn photosynthetic performance than at lowland plots. *Prosopis pallida* basal area was 5.3 times greater at lowland plots, and these plots exhibited 17 times higher carbon (C), 24 times higher N, and 35 times higher phosphorus (P) additions via litterfall, indicating that productivity of this phreatophyte was decoupled from rainfall where groundwater was present. Total N mass in soils was 4.7 times greater where groundwater was accessible, supporting the case that groundwater access increased N_2 fixation at a stand level. In contrast, N mineralization and leaching losses from soils, though substantially greater in lowland relative to upland areas, were strongly controlled by rainfall. Results provide clear examples of how invasive species with particular functional attributes (i.e., N-fixing phreatophytes) exploit otherwise inaccessible resources to dramatically alter the functioning of the systems they invade and how anthropogenic changes to hydrological processes can also alter ecosystem-level impacts of biological invasions. Results also illustrate a mechanism by which regional groundwater drawdown may reduce soil nutrient accretion and availability in arid regions.

Key words: *^{15}N; ^{18}O; arid; carbon; groundwater; Hawai'i Island; invasion; leaching; litterfall; mesquite; phosphorus;* Prosopis pallida.

Introduction

Demand for water currently exceeds renewable freshwater supply in much of the world's arid and semiarid lands (Oki and Kanae 2006), which collectively represent 30–40% of the world's terrestrial surface (Dregne 1991, Austin et al. 2004). Human population growth in these regions has risen rapidly in recent decades with totals now exceeding one billion people (Koohafkan and Stewart 2008). Today, these systems face two distinct changes to water regimes and water supply. First, many of the people in these regions are heavily dependent on groundwater resources for agriculture and domestic use, and water consumption in excess of recharge rates has resulted in region-wide reductions in groundwater tables (Stromberg et al. 1992, Postel 1993, Shah et al. 2003, Yang et al. 2003, Scanlon et al. 2006, Rodell et al. 2009). Because the masses of water in many such aquifers are high relative to natural inputs or outputs (McMahon et al. 2011, Currell et al. 2012), groundwater levels in these aquifers may be slow to recover from withdrawals by humans (Vitousek et al. 1997). Second, rainfall in arid regions is forecast to change due to increases in global surface temperatures; many arid regions are expected to experience declines in overall rainfall (CSIRO 2001, Parry et al. 2007) with extended dry periods (i.e., drought) and increases in intensity of rainfall events (Burke et al. 2006, Huntington 2006, Oki and Kanae 2006, Durack et al. 2012). These changes in water availability are likely to result in periods of increased dependence on groundwater availability for both natural and irrigated systems and vegetation die-off and dieback (Breshears et al. 2005, Adams et al. 2009, Munson et al. 2012), as well as

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alterations to plant productivity, water use, nutrient cycling, and, ultimately, ecosystem function.

Rainfall is not only seasonal but episodic in ecosystems that receive very low precipitation (Noy-Meir 1973), and such pulses determine the functioning of these arid ecosystems. Large rainfall events allow for more rapid growth periods, during which limitation of primary production shifts towards a dependence on nutrient availability, especially N (Fisher et al. 1988, Burke et al. 1997, Austin et al. 2004). Fixation and mineralization of N in arid soils is, in turn, strongly dependent on temporal and spatial patterns of water availability. For example, N fixation by lichen and microbial communities in arid soils increases following rainfall (Belnap 2002, 2003), and the fixation rates of symbiotic N-fixing plants are sensitive to drought (Serraj et al. 1999, Abdelhamid et al. 2011). Microbial processes responsible for release of N from litter to inorganic soil pools are also tied to water availability. Rates of leaf litter break down increase with rainfall (Austin and Vitousek 2000, Yahdjian et al. 2006), and mineralization of soil organic N increases rapidly following rainfall events (Schimel and Parton 1986, Austin et al. 2004). These microbial processes may be more sensitive to small rain events than are responses of plants. Small rain events with sufficient frequency, large enough only to wet the surface layers of soil and not increase nutrient movement to the root surface, provide a mechanism by which mineralization of N may occur significantly in excess of plant uptake (Singh et al. 1989). This asynchrony of N availability and plant demand in arid regions allows N to be lost at higher rates relative to total pools than in temperate systems and those with higher, more consistent rainfall (Austin and Vitousek 1998, Austin et al. 2004). The mechanisms for this N loss are via leaching of mineralized N to deep soils and groundwater at rates higher than plants are able to negate through uptake (Walvoord et al. 2003, Johnson et al. 2007), leaching of dissolved organic compounds (Perakis and Hedin 2002), or gaseous losses from surface soils (Peterjohn and Schlesinger 1991, Schlesinger and Peterjohn 1991, Mummey et al. 1994, Seitzinger et al. 2006). Determinants of the magnitude of leaching and gaseous losses in arid soils remain poorly understood (Austin et al. 2004), but these processes transfer considerable amounts of N below the depth of desert plants roots (Walvoord et al. 2003) and to the atmosphere (Houlton and Bai 2009).

In arid and semiarid landscapes, symbiotic N-fixing tree and shrub species often contribute a large portion of the total, new fixed N added to soils (Cleveland et al. 1999). Nitrogen-fixing phreatophytes, deep rooted species that obtain much of their water from the saturated zone, are common in arid and semiarid regions worldwide and have been further spread through these regions globally for human need (Pasiecznik et al. 2001, Richardson et al. 2011). The dual ability to access groundwater and acquire N via symbiotic N fixation alleviates water and N limitations, respectively, allowing such species to contribute significantly to nutrient cycling and productivity in arid systems outside of seasonal periods of high rainfall (Rundel et al. 1982). Increased water availability to otherwise drought-stressed N fixers is likely to provide C and water required for increased N fixation rates (Serraj et al. 1999) and resources for P acquisition from soils (Houlton et al. 2008). Phreatophytic plants may also extract nutrients from groundwater (Arndt et al. 2004), which may be redistributed to surface soils via litter inputs, providing nutrients that can sustain plant or microbes or be lost from the ecosystem. Previous studies demonstrate that where phreatophytes or N-fixing species invade ecosystems, they have the capacity to fundamentally alter the functioning of those ecosystems (Vitousek et al. 1987, Di Tomaso 1998). Where species are both N fixers and phreatophytes, we would expect their capacity to alter function to be amplified further. We would also expect such capacity to be constrained where critical resources are limited. For example, rates of N fixation and productivity by leguminous phreatophytes may be relatively high where groundwater is abundant and available and severely constrained where it is not.

The volcanic lava flows of Hawai'i Island provide standardized soil environments in which to study nutrient dynamics in plant communities. Lava laid down in individual flows provides substrate of a single age that is chemically homogenous at the time of deposition. Nitrogen is virtually absent from this parent material (Vitousek 1995), and the relative abundance of nutrients available to plants growing on these flows change predictably through time (Vitousek and Farrington 1997, Hedin et al. 2003). Most rainfall along leeward Hawai'i occurs at relatively high elevations and percolates to groundwater (Giambelluca et al. 2013); this flow of groundwater is the primary land to sea hydrologic connection on this coast. At the coastline, freshwater originating upslope is present at shallow depths in the lava substrates (i.e., 3–5 m), presumably within the potential rooting zone of phreatophytic tree species. These conditions create an ideal setting in lowland, leeward Hawai'i in which to examine the influence of shallow groundwater availability and rainfall pulses on primary productivity and N cycling in arid soils.

Invasion by *Prosopis pallida* across much of coastal leeward Hawai'i, areas formerly occupied by native dry forest communities, offers an opportunity to examine changes in the cycling of both water and N in a low-rainfall system. The genus *Prosopis* is a dominant component of native vegetation across millions of square kilometers of Central and South America, southwest USA, Asia, central and north Africa, and the Middle East (Rundel et al. 1982, Johnson and Mayeux 1990, Pasiecznik et al. 2001). This genus also now occurs as a nonnative introduction throughout

much of Australia, the Sahel region, and South Africa, in pockets through east and north Africa, throughout India, and Hawaii (Pasiecznik et al. 2001, Adams et al. 2010). *Prosopis pallida* was introduced to Hawaii in the early 19th century and has naturalized from early planting efforts to now cover approximately 3.5% of the total land area of the Islands (~59 000 hectares). It is found almost exclusively on leeward coasts of the main Hawaiian Islands (Gallaher and Merlin 2010), areas that approximate environmental conditions found in its native range. Within this system, we asked firstly, how do the physiological functions of this dry-system legume respond to variations in rainfall, with and without groundwater access? Secondly, how does groundwater access alter N input rates of *P. pallida*, and does this lead to differences in nutrient accretion in soils? Thirdly, how does groundwater availability affect soil N mineralization and leaching rates of inorganic N under low rainfall conditions and heavy rain events? Our hypotheses were (1) groundwater access would release lowland stands from physiological effects of dry season drought; (2) groundwater access would increase acquisition rates of C, N, and P by *P. pallida* and thus their input to lowland soils; and (3) net N mineralization rates and leaching losses would increase in proportion to mean daily rainfall and soil N pools, resulting in higher mineralization and leaching rates in lowland areas, where we predicted N input rates would be highest. We address these hypotheses using a data time series from a single lava flow, where *P. pallida* had established and proliferated from plantings in 1894 (Maly and Maly 2011). The high porosity of the basalt lava layers present in leeward Hawai'i results in low surface water flow and a consistent groundwater flow at heights close to sea level driven by high altitude recharge (Johnson et al. 2008, Peterson et al. 2009). We measured physiological responses of upland and lowland stands to rainfall, stem density and basal area, nutrient input rates through litterfall and soil nutrient accretion, and cycling between areas of the stand with and without groundwater access.

Methods

Study system

Our study was conducted along the coastline and upslope from Kīholo, within the boundaries of Kīholo State Park located on the western, leeward coast of Hawai'i Island (19.84° N, 155.93° W). Lowland, leeward areas of the Hawaiian Islands are typically very dry, and rainfall in our study area occurs as sporadic small events in summer months and larger events from October to March (Giambelluca et al. 2013). While original coastal dry forests in this area were typically composed of native trees *Erythrina sandwicensis* (Wiliwili), *Reynoldsia sandwicensis* ('Ohe), *Abutilon incanum* (Ma'o), and the grass *Heteropogon contortus* (Pili), most leeward areas are now dominated by nonnative grasses and N-fixing trees, particularly *P. pallida* and *Leucaena leucocephala* (Cuddihy and Stone 1990, D'Antonio and Vitousek 1992, Wagner et al. 1999). We focused on a lava flow of age ~3000 yr BP (Wolfe and Morris 1996). Mean annual precipitation of the area is ~270 mm based on a 30-year average (Giambelluca et al. 2013), and mean annual temperature in the park over the two years of the study was 24.9°C. Physical soil conditions consist of a discontinuous layer of soil over fractured pāhoehoe basalt bedrock; soils throughout the area of study are clayey, isotic, nonacid, isohyperthermic, lithic torriorthents (Web Soil Survey, data *available online*)[4]. Near the coastline, groundwater is present at a height very close to that of sea level, affording potential groundwater access to vegetation growing in that zone. During dry periods, vegetation consists almost exclusively of monospecific stands of *Prosopis pallida*; these are augmented by an ephemeral understory cover of the native herbs, *Sida fallax* ('Ilima) and *Waltheria indica* ('Uhaloa) that emerge following large rain events (see Plate 1).

Experimental design

Our various tree- and stand-level measurements were made within 10 circular plots of 40 m diameter, five of which were located in a coastal band of the pāhoehoe flow centered at 19.8506° N, 155.9321° W, and five located on the same flow ~1.5-km inland and centered at 19.8381° N, 155.9300° W. Lowland plots (L1–L5) were situated between 0 and 15 m above sea level, and upland plots (U1–U5) were located between 60 and 70 m above sea level. Rainfall was measured only at plots U1 and L1. Upland site measurements were made using an 8 inch diameter tipping bucket rain gauge connected to a Hobo event logger (Onset Computer Corporation, Cape Cod, Massachusetts, USA). Lowland site rainfall measurements were made using a CS700 rain gauge (Campbell Scientific, Logan, Utah, USA) connected to a CR3000 data logger (Campbell Scientific, Logan, Utah, USA). We monitored temperature at these two plots with Onset Hobo H8 Pro loggers, shielded from direct sunlight by plastic dishes. Humidity was also recorded at the lowland site (plot L1) with an HMP45C humidity probe (Vaisala, Vantaa, Finland).

Determination of plant water sources

We used oxygen stable isotope ratios ($\delta^{18}O$ values) to evaluate the differences in water sources for *P. pallida* in upland and lowland plots. We characterized groundwater sources from quarterly collections (December 2010–September 2012) of water-filled lava tube caves at two locations within the study area. We collected precipitation samples at plots U1 and L1 using funnels linked to PVC containers with mineral oil to prevent evaporation. Precipitation was collected as composite samples accumulated from 11 November to 22 December 2010, from 22 December 2010 to 22 March 2011, from 22 March 2011 to 7 June 2011, and thereafter at weekly intervals

[4] http://websoilsurvey.sc.egov.usda.gov/App/WebSoilSurvey.aspx

from 7 June 2011 to 22 September 2012. All water samples were collected in acid washed syringes and filtered through Whatman GF/F filters (GE Healthcare Life Sciences, Little Chalfont, Buckinghamshire, UK) into crimp seal vials without headspace. We collected soil samples for water extraction from 3–5 cm depth in all plots on 22 June, 22 September, and 22 December 2011. We collected *P. pallida* stem samples in each of the ten plots, sampling quarterly from December 2010 to September 2012. We collected one fully suberized *P. pallida* stem segment approximately 5 cm in length from four trees within each plot ($n = 5$ composite samples for each site and date). Stem segments and soil samples were immediately placed in 20-mL glass vials with screw-top lids and sealed with Parafilm (Bemis Flexible Packaging, Neenah, Wisconsin, USA), kept on ice during transport, and frozen until analyzed.

We analyzed relative contributions of rainwater and groundwater to stem water with single isotope, two source Bayesian mixing models (Moore and Semmens 2008, Jackson et al. 2009). Calculations were performed for each area and season (wet, 23 September–22 March; dry, 23 March–22 September) from wet season 2010–2011 to dry season 2012. We calculated seasonal $\delta^{18}O$ end-members and their standard deviations from $\delta^{18}O$ values of individual water samples taken throughout the season (i.e., six samples in each site for groundwater, and one value for each rainfall sample). We used precipitation $\delta^{18}O$ values rather than those of soil water for this analysis due to the observations that *P. pallida* sap flow in upland areas was strongly dependent on rainfall and reduced to near zero during dry periods (Y. Miyazawa et al., *unpublished manuscript*), and during these dry periods we saw depletion in soil $\delta^{18}O$ values below those of the most recent rainfall, due possibly to the diurnal adsorption of atmospheric water vapor (Agam and Berliner 2004, Wen et al. 2012). This approach assumes that ^{18}O-enrichment of soil water associated with evaporation prior to plant uptake was minor compared to the differences in source (groundwater and rainwater) signatures and equal between sites. These assumptions are supported by tendencies toward low fractionation of water isotopes in permeable soils (Gat 1996) and very similar air temperatures near ground level at the two sites (Appendix 1). Results of the SIAR model (Jackson et al. 2009) are presented as upper and lower 95% highest density region (HDR) estimates of groundwater contribution.

Stem water extraction and $\delta^{18}O$ analysis of all water samples were performed at the Stable Isotope Ratio Facility for Environmental Research (SIRFER) at the University of Utah (Salt Lake City, Utah, USA). Stem water extraction was performed following West et al. (2006). $\delta^{18}O$ 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, California, USA). Samples were analyzed against three lab reference materials calibrated to Vienna Standard Mean Ocean Water (VSMOW). Instrument precision for $\delta^{18}O$ values was ±0.2‰.

Plant water stress and foliar nutrient concentrations

We measured water potential values quarterly within plots U1 and L1 at the upland and lowland sites using a Scholander-type pressure chamber (PMS, Corvallis, Oregon, USA). Water potential was measured in the three hours before dawn (Ψ_{PD}) as an estimate of maximum daily water availability, and again on the same day between 11:30 and 14:00 (Ψ_{MD}) as an indicator of midday water stress. Two replicate canopy stems were measured and averaged for eight haphazardly selected trees within each plot on each date ($n = 8$ per plot). The maximum quantum yield of photosystem II (F_v/F_m) was measured quarterly at plots U1 and L1 using an Aquation portable shutter fluorometer (Aquation, Umina Beach, New South Wales, Australia). We measured two mature canopy leaves of eight trees ($n = 8$) within each plot in the three hours before dawn as an estimate of water stress effects on photosynthetic performance (Maxwell and Johnson 2000, Resco et al. 2008).

We collected eight mature leaves from four haphazardly selected trees at all plots for leaf mass per area analysis (LMA). Leaf area was measured using an LI-1300 leaf area meter (LI-COR Biosciences, Lincoln, Nebraska, USA). Leaves were dried at 70°C to a constant mass and weighed. LMA values for individual leaves within each plot were averaged prior to analysis (n = ~~5~~ plots per site). We pulverized dried leaves using a Wig-L-Bug grinding mill (Crescent Dental, Chicago, Illinois, USA) to make a composite sample for each plot ($n = 5$ plots per site) and analyzed for percentages of C, N, and P and $\delta^{13}C$ and $\delta^{15}N$ at the Experimental Program to Stimulate Competitive Research (EPSCoR) analytical laboratory at the University of Hawai'i at Hilo. Percent C and N were determined by thermal combustion using a Costech 4010 Elemental Analyzer (Costech Analytical Technologies, Valencia, California, USA). Samples were dry ashed (500°C for 5.5 h), dissolved in 1 mol/L HCl, and analyzed using a Varian Vista MPX ICP-OES (Varian Analytical Instruments, Walnut Creek, California, USA) to determine percentage of P. Duplicate samples of 2.5 mg of powder were loaded into tin capsules and analyzed for C and N isotope composition using a Costech 4010 elemental combustion system interfaced to a Thermo Delta V Advantage isotope ratio mass spectrometer (Thermo Fisher Scientific, Waltham, Massachusetts, USA). All $\delta^{13}C$ and $\delta^{15}N$ values were normalized to Pee Dee Belemnite and air standards respectively, using USGS samples 40 and 41. The standard analytical error between duplicate analyses was calculated using National Institute of Standards and Technology (NIST) standard 1547 and was lower than ±0.3‰ for N and ±0.1‰ for C. We collected eight leaves from each of

four *Sida fallax* plants within each plot on four, quarterly sampling dates from March 2011 to December 2011 as a reference to assess N fixation by *P. pallida* using $\delta^{15}N$ natural abundance (Shearer and Kohl 1986). The contribution of symbiotic fixation to foliar N was estimated using a single isotope, two source mixing model for the upland site, as described in *Methods: Determination of plant water sources*, and a three source model for the lowland site, where groundwater was accessible. At the lowland site, the midpoint of the N contribution for groundwater was constrained at 4.4% using prior information from transpiration data (Y. Miyazawa et al., *unpublished manuscript*) and dissolved inorganic N concentrations in groundwater (B. Dudley, *unpublished data*). The $\delta^{15}N$ value of biologically available soil N was estimated from *S. fallax* leaf tissue averaged over all time periods and plots; the standard deviation for this value was calculated from variation in mean values between plots. The $\delta^{15}N$ value and standard deviation of N from fixation were estimated at 0‰ and 1‰, respectively (Högberg 1997, Bedard-Haughn et al. 2003). A groundwater $\delta^{15}N$ value and standard deviation of 3.16‰ and 0.24‰, respectively, were used based on results of sampling beneath the lowland site (B. Dudley, *unpublished data*). This method assumes negligible $^{14}N/^{15}N$ fractionation during N uptake and assimilation of all N sources for both reference and N-fixing plants and that the reference and N-fixing plants utilize components of the soil N pool with differing $\delta^{15}N$ values equally (Högberg 1997).

Basal area, stem density, and litterfall

We determined *P. pallida* stand-level basal area and stem density by measuring the basal diameter (i.e., diameter near ground level, but above any root collar flaring or buttressing) for all stems encountered within each plot. We collected litterfall from each plot using four 0.18 m^2, 6 cm deep trays lined with 1-mm mesh fiberglass screen. We placed litter traps 15 m from the center point at each of the plots at bearings of 45°, 135°, 225°, and 315° and collected litter at monthly intervals between 9 August 2011 and 8 August 2012. Collected litter was dried to a constant mass at 70°C, weighed, and sorted into categories: *P. pallida* leaves; *P. pallida* wood, bark, and stems; *P. pallida* flowers, pods, and beans; and other plants (all parts). *Prosopis pallida* components were considered separately because this species contributed the vast majority (>95%) of litter to each plot. For each tissue type, litter mass of the plot was averaged by month. We estimated annual litterfall biomass inputs in each site (upland and lowland) by tissue type from the sum of the monthly litter mass. We calculated nutrient concentrations in litter at each plot at each site from two composite samples collected over three months of each litter type from within the wet season, and two further composite samples collected over three months from within the dry season. Composites were 9 August–7 November, 7 November–5 February, 5 February–5 May, and 5 May–3 August. Composite samples were initially ground to ~2 mm using a Wiley Mill (Thomas Scientific, Swedesboro, New Jersey, USA), homogenized by vigorous shaking and stirring, and subsampled. The subsample was pulverized using a Wig-L-Bug grinding mill and analyzed for percentages of C, N, and P, $\delta^{13}C$ and $\delta^{15}N$ as described in *Methods: Plant water stress and foliar nutrient concentrations*. Carbon, N, and P percentages were determined for the dominant litter type (*P. pallida* leaves) and all other litter types combined. We examined relative constraints on nutrient availability to *P. pallida* in upland and lowland sites by determining resorption efficiency of N and P (the percentage of nutrients resorbed from senesced leaf litter compared to attached green leaves, e.g., (foliar N − litter N) × 100/foliar N) and C:N, C:P, and N:P in leaf and litter. We compared values from attached leaves in quarterly samplings in December 2011–September 2012 to mean quarterly values for litter (e.g., December 2011 leaf values were compared to pooled litter values for November–January). Because we found no seasonal differences in these relationships, we compared yearly averages for upland and lowland sites. We estimated monthly and yearly mass of C, N, and P falling as litter inputs at each plot by multiplying dry mass of each litter category by the C, N, and P concentrations of that litter type.

Soil nutrient content and soil N responses to rainfall

We examined soil N pools, net N mineralization rates, and leaching losses of NH_4^+ and NO_3^- from surface soils using soil core incubations. We used intact soil cores that were fitted at both ends with bags of ion exchange resin (DiStefano and Gholz 1986). Cores were 80 mm in length, with a 34-mm internal diameter. Resin bags were made of nylon stocking material, filled with 2.5 g of mixed-bed ion exchange resins (IONAC NM-60 H+/OH-form, type I 16–50 mesh beads; J. T. Baker, Phillipsburg, New Jersey, USA), formed around a thin PVC ring with an external diameter slightly smaller than the internal diameter of the tube. Bags were covered with 2-mm mesh-size nylon webbing to reduce damage during deployment and retrieval. All materials used in the construction of the resin bags were acid washed, rinsed thoroughly in deionized water, pH checked, and dried prior to construction. Resins were not acid washed. The upper resin bag was not analyzed and was present to remove dissolved N from rainwater entering the soil core.

We placed soil cores at three randomly selected points within each of the five upland and five lowland plots for each incubation. At each point, we extracted an initial core in the nearest patch of soil sufficiently deep to accommodate it, removed it, and placed it in a cooler for transport to the laboratory for analysis of N pools and soil moisture. We extracted a second core immediately adjacent to the extraction point, placed mixed-bed resin bags above and below the plug within

the core sleeve, and returned it to its extraction point where it remained in place for the duration of the incubation. Net mineralization was calculated by subtracting extractable inorganic N per gram dry mass of soil in the initial soil sample from that in the incubated sample. Initially, we deployed and recovered soil cores over the course two in situ incubations (i.e., from November 2011 to February 2011 and from February to May 2012), during which time no additional water was added. We subsequently carried out four additional 30-day soil core incubations (i.e., from March to April 2012, July to August 2012, and two sets from January to February 2013) in which we added deionized water to the cores at weekly intervals to simulate rainfall events. In the first two water addition incubations, water was added in amounts to match rainfall conditions in December 2010 and January 2011, which stimulated a significant amount of herbaceous and tree growth in the site. At each deployment, 50 ml of deionized water was added to each core and 10 ml weekly for three subsequent weeks. During January and February 2013, we deployed two additional sets of cores concurrently; in the first set of cores, 25 mL H_2O was added at deployment and 5 mL H_2O added weekly for the three following weeks. In the second, 10 mL H_2O was added at deployment, followed by 2.5 mL in the three subsequent weeks. At the conclusion of each deployment, we removed the incubated core, placed it on ice, and returned it to the laboratory for analysis of N pools. Each soil core, whether initial or incubated, was passed through a 2-mm sieve before extraction. Pools of NH_4^+ and NO_3^- were determined for each core sample from 10 g of fresh soil added to 100 mL of 2 mol/L potassium chloride (KCl). This solution was agitated on a shaker table for 6 h, after which time the solution from each sample was filtered through Whatman #1 filter paper. Resin bags were treated in a manner similar to soil extracts. We removed the outer mesh of the bottom resin bag from each soil core, rinsed the bags with deionized water to remove attached soil, shook them vigorously to remove excess water, placed each bag in 50 mL of 2 mol/L KCl, and agitated them on a shaker table for 6 h. Sample extracts and standards were frozen immediately after filtration. All KCl extracts were analyzed colorimetrically for NO_3-N (method modified from EPA 353.2) and NH_4-N (method modified from USGS I-2525-89) using a Technicon II Autoanalyzer (Pulse Instrumentation, Milwaukee, Wisconsin, USA) at the University of Hawai'i at Hilo. Soil samples from the time zero cores of the August 2012 deployment were analyzed to determine total C, N, and P percentages and organic content, as well as $\delta^{13}C$ and $\delta^{15}N$ values. This soil was passed through a 2-mm sieve, dried at 70°C to a constant weight, ground to a fine powder using a Wig-L-Bug grinder, and analyzed at the University of Hawai'i at Hilo for C, N, and P content and $\delta^{13}C$ and $\delta^{15}N$ values in the same manner as leaf and litter samples. While carbonates were not expected to be present in the parent basalt that form these soils, we confirmed the absence of marine-derived carbonates by adding subsamples of the soils used in $\delta^{13}C$ analysis to 1 mol/L HCl and watching for bubbling. Gravimetric moisture content was determined by drying soil samples at 105°C to a constant mass. We combusted an additional subsample in a muffle furnace for 6 h at 500°C to calculate organic matter content. We calculated soil texture from pooled samples of two further randomly placed soil cores from each plot. Because these soils had high organic matter content, we removed organic material by mixing soil with deionized water, adding 10 mL of 30% H_2O_2 solution, and heating to 80°C. We repeatedly added 10-mL measures of H_2O_2 until reactions slowed and soils became bleached. Excess water and H_2O_2 was removed by boiling. Samples were then dried at 105°C for 48 h, and 30 g of this sample analyzed for particle size using the hydrometer method (Gee and Bauder 1979) with sodium hexametaphosphate as a dispersant. We classified soil texture from particle sizes according to the USDA system (Soil Survey Staff 1999). Soil bulk density at each site was calculated from initial soil cores collected November 2011 ($n = 3$ for each plot) and January 2013 ($n = 6$ for each plot). Soil from each core was passed through a 2-mm sieve, weighed, and adjusted to rock-free dry bulk density using site and date specific gravimetric water content and the volume of the soil core. Soil depths at upland and lowland sites were estimated during April and May 2012 using transects centered on the midpoint of each of the five upland and five lowland plots. At each plot, five 40-m transects were laid out in parallel, spaced 8 m apart, and soil depth was measured at 0.5-m intervals along each transect by pushing thin steel rods into the soil until they reached bedrock. Soil mass per hectare was calculated as the product of rock-free dry bulk density and soil volume at each plot and multiplied by site specific soil C, N, and P content to obtain soil C, N, and P mass per hectare.

Data analysis

We examined changes in leaf and stem nutrient allocation, water use, and productivity indices using linear mixed models (LMM) performed with PROC GLIMMIX in SAS version 9.3 (SAS 2009). We examined differences in foliar N and P content, foliar $\delta^{15}N$ and $\delta^{13}C$, and leaf mass per area where the fixed effects were site, time, and their interaction. We modeled correlations among observations from the same plot due to repeated measures over time for each response variable. Based on Akaike's information criterion corrected for small sample sizes (AIC_c), we used the compound symmetric correlation structure for responses of $\delta^{15}N$, leaflet size, and leaf mass per area. The first-order autoregressive, ante-dependence and heterogeneous Toeplitz correlation structures were used for

TABLE 1. Estimated groundwater contributions to stem water in upland and lowland stands of *Prosopis pallida*.

Seasons and sites	Groundwater $\delta^{18}O$	Precipitation $\delta^{18}O$	Soil water $\delta^{18}O$	Stem water $\delta^{18}O$	Upper 95% HDR	Lower 95% HDR
Wet 2010–2011						
Upland	−7.57 ± 0.06	−5.56 ± 3.05	...	−7.50 ± 1.00	...	...
Lowland	−7.21 ± 0.06	−5.75 ± 2.85	...	−7.72 ± 0.60	...	...
Dry 2011						
Upland	−7.47 ± 0.02	−0.72 ± 1.54	−1.96 ± 5.66	−3.34 ± 2.40	0.63	0.18
Lowland	−7.16 ± 0.01	−1.14 ± 0.85	1.06 ± 1.90	−7.39 ± 1.33	1	0.85
Wet 2011–2012						
Upland	−7.40 ± 0.09	−2.30 ± 1.43	−8.06 ± 4.57	−2.34 ± 1.39	0.21	0
Lowland	−7.26 ± 0.10	−1.88 ± 1.40	−1.71 ± 3.43	−7.09 ± 1.21	1	0.80
Dry 2012						
Upland	−7.29 ± 0.01	−0.90 ± 0.87	...	1.09 ± 1.62	0.19	0
Lowland	−7.14 ± 0.003	−0.52 ± 1.39	...	−6.04 ± 3.41	1	0.85

Notes: Shown are measured $\delta^{18}O$ values for groundwater, precipitation, soil water, and *P. pallida* stem water for wet season (October to March) 2011 to dry season (April to September) 2012. Error terms listed for water source and stem water $\delta^{18}O$ values are standard deviations. The two rightmost columns give upper and lower 95% highest density region (HDR) estimates of the proportion of *P. pallida* stem water derived from groundwater, based on mixing between precipitation and groundwater sources. Ellipses indicate no data possible.

foliar N content, foliar P content, and $\delta^{13}C$, respectively, again based on the AIC_c. Fixed effects for water potential and F_v/F_m were site, time, and the interaction between site and time. Tree nested with site and leaves within tree were the random effects. Comparisons were made between sites for each time period in all LMM analyses using the slice function in PROC GLIMMIX, which tests the significance of one fixed effect at each level of another fixed effect. Nutrient translocation prior to leaf abscission and yearly nutrient additions via *P. pallida* litterfall and soil characteristics were compared between upland ($n = 5$) and lowland ($n = 5$) plots using Welch's *t* tests. A natural log transformation was performed on soil P per hectare data prior to analysis to reduce differences in variances between upland and lowland sites. Except for LMM analysis, statistical tests were conducted with the base and SIAR packages of the statistical software R, (R Development Core Team 2011). Error terms for means are reported as standard error, unless otherwise specified.

RESULTS

Water sources

Stem water $\delta^{18}O$ values indicated that groundwater was the dominant source of water at lowland plots and rainwater the dominant source of water for upland plots during dry periods (Table 1; Fig. 1). Although the $\delta^{18}O$ values of groundwater were relatively consistent through time at the two sites, the $\delta^{18}O$ values of rainfall events varied seasonally; values tended to be more depleted of ^{18}O in heavy wet season rains and more enriched in ^{18}O in small rainfall events. Importantly, $\delta^{18}O$ values of heavy rainfall events during winter 2010–2011 overlapped those of groundwater. As a result, it was not possible to determine contributions of these two water sources to stem water for winter 2010–2011, and the apparent contribution of groundwater to stem water in upland plots during summer 2011 should be viewed with some caution.

Climate

Patterns of rainfall and temperature were similar at the two sites over the course of the study (Fig. 2; Appendix A). Seasonal high temperatures of between 35°–36°C were recorded at both sites between July and August in 2011 and 2012. The minimum temperature recorded during the study was 15.9°C.

Measurements of plant water stress and foliar nutrient concentrations

With the exception of a single sampling event in March 2011 following sustained rainfall, predawn stem water potential (Ψ_{PD}) and midday stem water potential

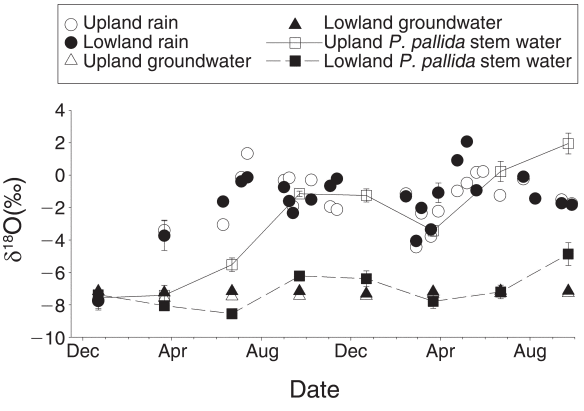

FIG. 1. Shown are $\delta^{18}O$ values (mean ± SE) of water sources and stem water of *Prosopis pallida* from December 2010 to September 2012 in a coastal stand near Kīholo, a semiarid area on the leeward coast of Hawai'i Island. Upland plots were situated 60–70 m above sea level, while lowland plots were less than 15 m above sea level.

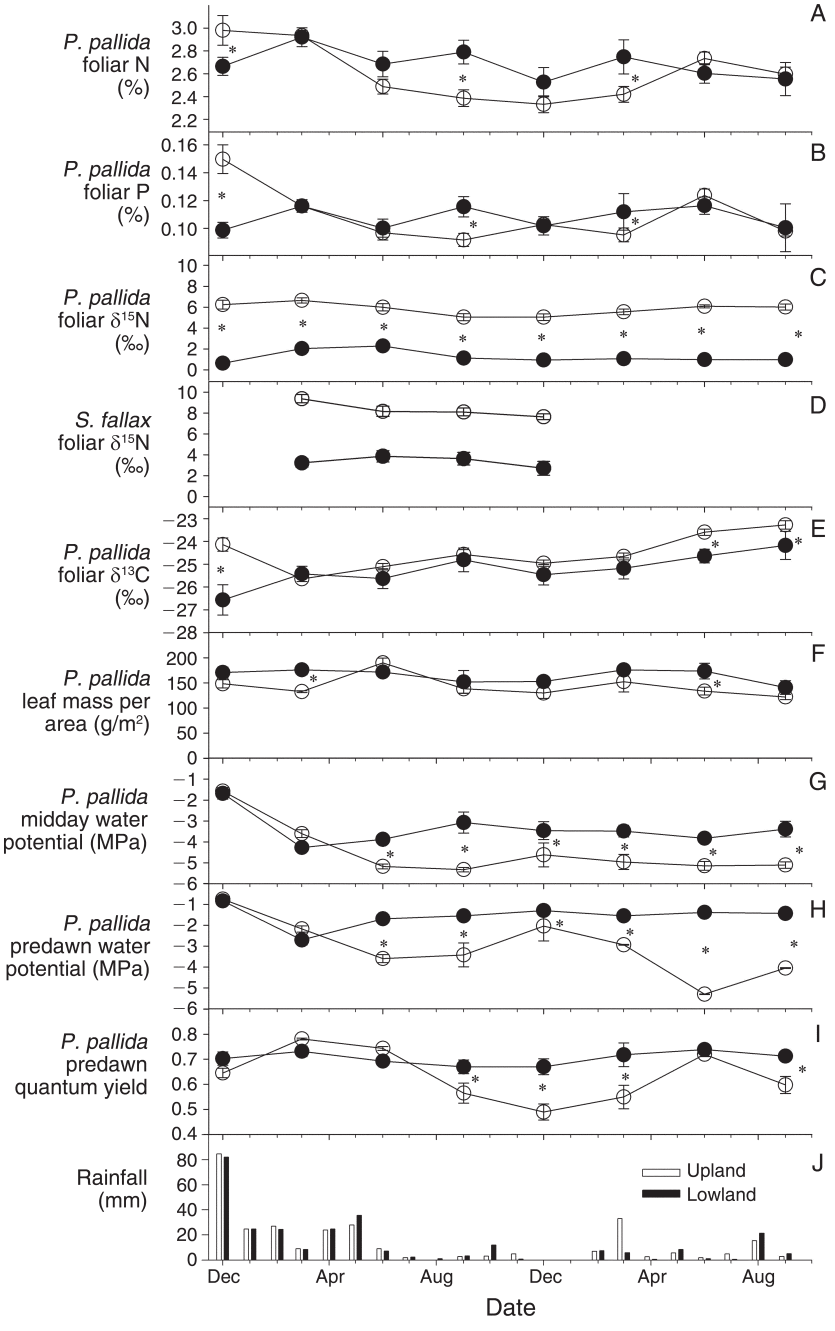

FIG. 2. Patterns of allocation indices, water use, and productivity in leaves and stems of *P. pallida* from 22 December 2010 to 27 September 2012, and foliar $\delta^{15}N$ values for *Sida fallax* from March to December 2011. Error bars show ± SE. Panels (A–F) show site means ($n = 5$ plots) for canopy leaves on each date. Panels (G–I) show means for stems (water potential) and canopy leaves (F_v/F_m) from trees ($n = 8$) from a single upland and a single lowland plot. With the exception of panel (D), asterisks at individual time points of indicate upland and lowland means are statistically different at $P < 0.05$.

(Ψ_{MD}) values were lower at the upland site relative to the lowland site (Fig. 2F, G). Both upland and lowland sites showed significant decreases in Ψ_{PD} and Ψ_{MD} during periods of low rainfall in the latter months of the study, and interactions between site and time likely reflect a significantly greater response of Ψ_{PD} and Ψ_{MD} to intermittent rainfall at the upland site compared to the lowland site. Mean leaf $\delta^{13}C$ values were consistently higher at upland plots, indicating higher integrated water-use efficiency, and increased through time. The lack of a significant interaction indicates that this trend was similar for upland and lowland plots. (Fig. 2D).

TABLE 2. Results of Type III tests of fixed effects from linear mixed model (LMM) analyses for nutrient allocation, water use, and productivity indices in leaves and stems of *P. pallida*.

Variables and effects	df	*F*	*P*
Foliar N content			
Site	1, 64	3.03	0.086
Time	7, 64	5.24	<0.001
Site × time	7, 64	3.07	0.008
Foliar P content			
Site	1, 5.08	0.03	0.878
Time	7, 5.86	3.59	0.072
Site × time	7, 5.86	6.61	0.019
Foliar $\delta^{15}N$			
Site	1, 8.00	252.83	<0.001
Time	7, 56.09	5.36	<0.001
Site × time	7, 56.09	2.44	0.030
Foliar $\delta^{13}C$			
Site	1, 8.71	6.76	0.030
Time	7, 7.16	5.08	0.023
Site × time	7, 7.16	1.86	0.214
Leaflet area			
Site	1, 8.01	14.23	0.005
Time	7, 55.14	6.49	<0.001
Site × time	7, 55.14	3.10	0.008
Leaf mass per area			
Site	1, 8.03	2.34	0.164
Time	7, 55.02	3.82	0.002
Site × time	7, 55.02	1.98	0.074
Predawn stem water potential			
Site	1, 14.1	62.87	<0.001
Time	7, 222.7	33.80	<0.001
Site × time	7, 222.7	17.26	<0.001
Midday stem water potential			
Site	1, 14.01	30.72	<0.001
Time	7, 226.1	44.58	<0.001
Site × time	7, 226.1	13.16	<0.001
Predawn F_v/F_m			
Site	1, 14.01	14.69	0.002
Time	7, 224.5	10.74	<0.001
Site × time	7, 224.5	6.19	<0.001

Note: Shown are comparisons of upland and lowland sites (site) over eight quarterly sampling periods (time) from December 2010 to September 2012.

Prosopis pallida leaf $\delta^{15}N$ values at upland plots were 4–6‰ greater than those at lowland plots through the duration of the study (Fig. 2C). Mixing model analysis suggested symbiotic fixation contributions made up between 23–41% of foliar N at the upland site and 37–69% of foliar N at the lowland site over the period studied. Predawn quantum yield (F_v/F_m) values showed an interaction between site and time. This was driven by reduced values at the upland site, which coincided with seasonal patterns or rainfall, rather than values at the lowland site, which remained consistent throughout changes in seasonal rainfall (Fig. 2H). *P. pallida* leaflet size was consistently greater in lowland plots and greater at both upland and lowland plots following rainfall, leading to a significant time effect (Table 2). Leaf mass per area was not different between sites and tended toward higher values in spring (March) and early summer months. Foliar N values of *P. pallida* varied between 2.98% ± 0.13% (mean ± SE) and 2.33 ± 0.07%, and there was an interaction between site and time for both foliar N and P values, as leaves from upland plots tended to have greater increases in N and P content following rainfall and lower content during low-rainfall periods (Fig. 2A, B).

Basal area, stem density, and litterfall

Mean stem density at lowland plots was approximately twice that of upland plots, and lowland trees had greater average basal area, resulting in 5.3 times the basal area per hectare in lowland plots (Fig. 3). Upland trees mobilized greater amounts of foliar N and P prior to leaf abscission; N resorption, P resorption, leaf litter C:N, and leaf litter C:P values were all greater at upland plots (Table 3). A greater leaf litter N:P indicated a particular tendency to mobilize P prior to abscission in

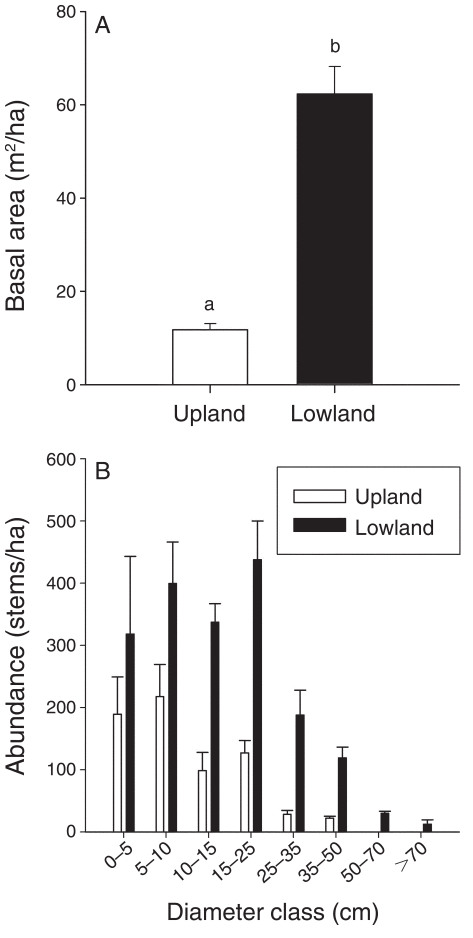

FIG. 3. (A) Basal area of *P. pallida* in upland and lowland areas of the Kīholo stand. Different lowercase letters indicate significantly different means at $P < 0.05$. (B) Size distribution of *P. pallida* in upland and lowland sites. *X*-axis categories are basal diameters. Bars in both panels show means of plots ($n = 5$) ± SE for each site.

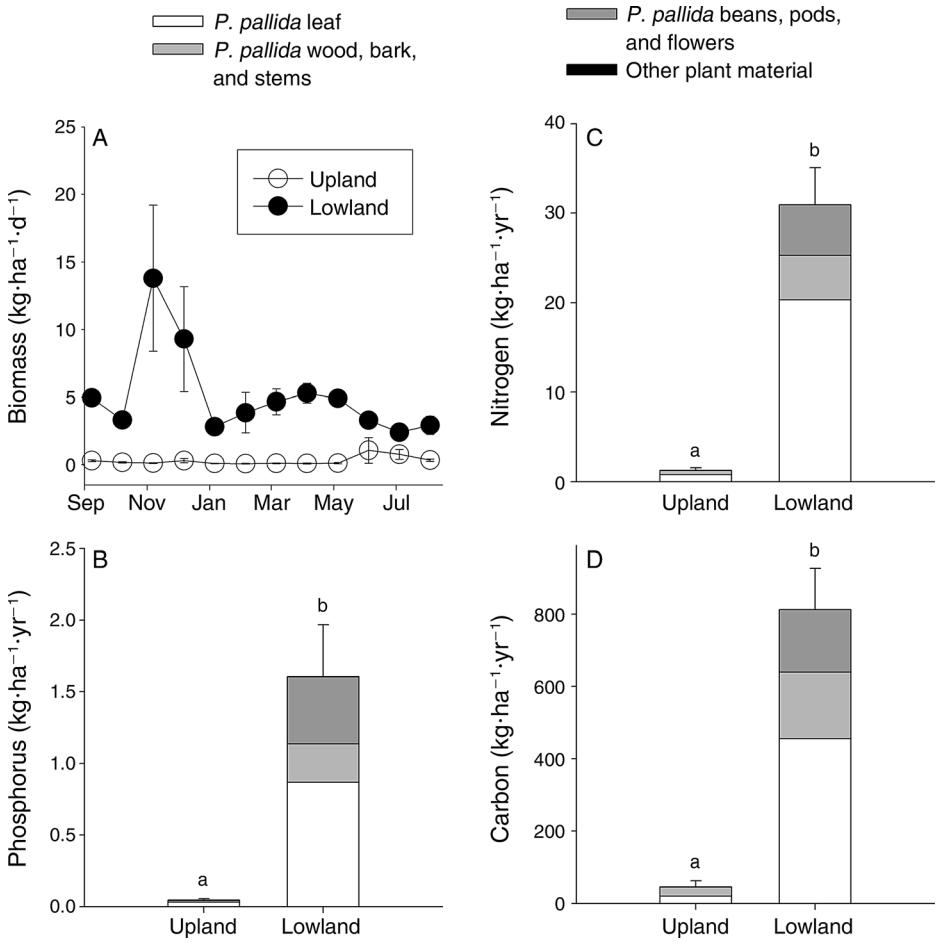

FIG. 4. Mass and nutrient content of litter fall from 8 August 2011 to 8 August 2012. Panel (A) gives mean daily litter masses calculated from monthly collections on plots at upland ($n = 5$) and lowland ($n = 5$) sites. Panels (B, C, and D) give nutrient masses per unit area over the year measured. Different lowercase letters in each panel indicate significantly different mean nutrient masses for the sum of all litter categories at $P < 0.05$. Error bars show ±SE for the sum of all litter categories.

upland plots (Table 2). Litter mass inputs in upland plots were 17 times lower compared to lowland plots, of which *P. pallida* contributed >96% of total litterfall at upland plots and >99.9% at lowland plots (Fig. 4A). Concentrations of N and P in composited *P. pallida* leaf litter samples ranged from 1.52% to 2.22% and between 0.05–0.10%, respectively. *P. pallida* wood, bark, and stem litter ranged from 0.72% to 1.57% N and from 0.02% to 0.09% P, while bean, pod, and flower litter of this species contained between 1.20–1.59% N and from

TABLE 3. Nutrient resorption efficiencies and nutrient ratios for *P. pallida* leaves and leaf litter.

Variable	Upland ($n = 5$)	Lowland ($n = 5$)	t	df	P
N resorption efficiency (%)	32.2 ± 1.1	21.8 ± 2.6	4.51	6.46	0.003
P resorption efficiency (%)	35.3 ± 2.3	19.2 ± 1.7	5.09	7.94	<0.001
Leaf C:N	18.88 ± 0.13	17.50 ± 0.29	−4.39	5.55	0.006
Litter C:N	26.49 ± 0.25	21.566 ± 0.44	−9.70	6.36	<0.001
Leaf C:P	447.87 ± 10.43	419.41 ± 17.61	−1.39	6.50	0.210
Litter C:P	672.69 ± 24.45	500.87 ± 19.98	18.18	9	<0.001
Leaf N:P	23.69 ± 0.54	23.94 ± 0.57	0.26	7.20	0.801
Litter N:P	25.13 ± 0.68	23.13 ± 0.48	−2.39	7.18	0.047

Notes: $P < 0.05$ indicates a significant difference between upland and lowland means. Resorption efficiency was determined from nutrient content of attached leaves in quarterly samplings from December 2011 to September 2012 and mean nutrient content for leaf litter collections over the same dates (see *Methods*). Shown are mean ± SE. The t values, df, and P values are for Welch's t tests for differences between upland and lowland sites.

TABLE 4. Mean soil physical and chemical characteristics at upland and lowland sites, all of which had silt loam soil texture as defined by USDA.

Soil variable	Upland ($n = 5$)	Lowland ($n = 5$)	t	df	P
Depth (cm)	2.96 ± 0.26	3.54 ± 0.45	1.11	6.46	0.305
Organic content (%)	11.94 ± 0.77	55.81 ± 4.18	10.30	4.27	>0.001
Clay (%)	12.38 ± 1.67	11.03 ± 1.47	−0.61	7.88	0.559
Silt (%)	55.86 ± 2.02	44.75 ± 5.19	−2.00	5.19	0.100
Sand (%)	31.76 ± 1.76	44.22 ± 4.68	2.49	5.11	0.054
Bulk density (g/cm^3)†	0.50 ± 0.02	0.33 ± 0.03	−4.45	7.48	0.002
%C	5.13 ± 1.11	32.19 ± 0.46	22.56	5.34	>0.001
Soil C (kg/ha)	7127 ± 1061	39169 ± 8959	3.55	4.11	0.023
$\delta^{13}C$	−20.83 ± 0.27	−25.03 ± 0.16	−13.55	6.53	>0.001
%N	0.54 ± 0.09	2.90 ± 0.10	17.75	7.99	>0.001
Soil N (kg/ha)	753.9 ± 77.6	3546 ± 817	3.40	4.07	0.026
Extractable soil NO_3^--N (kg/ha)	8.05 ± 1.05	77.35 ± 16.08	4.28	4.02	0.013
Extractable soil NH_4^+-N (kg/ha)	1.95 ± 0.44	9.74 ± 0.73	9.11	6.59	>0.001
$\delta^{15}N$	11.53 ± 0.56	3.81 ± 0.26	−12.58	5.69	>0.001
%P (total)	0.05 ± 0.02	0.22 ± 0.03	5.21	7.45	0.001
Total soil P (kg/ha)	68.99 ± 24.03	288.7 ± 100.3	3.55	8.00	0.008

Notes: Shown are mean ± SE. The t values, df, and P value shown are for Welch's t tests for differences between upland and lowland sites.

† Dry bulk density after rocks >2 mm removed.

0.07% to 0.17% P. Nitrogen input through litterfall was ~24 times greater, P ~35 times greater, and C ~17 times greater at lowland plots over the year measured, due to proportionally greater input of N- and P-rich litter types and higher nutrient content of leaf litter at lowland plots (Table 2; Fig. 4B–D).

Soil nutrient content

Lowland soils had greater organic content and contained 4.7 times higher total N than did upland soils (Table 4). Total extractable N (the sum of extractable ammonium, nitrate, and nitrite) per hectare was 8.7 times higher at lowland plots than upland plots. Lowland soils had over five times greater mass of C per hectare and 5.5 times greater total P content. The isotopic composition of soil C and N differed strongly between upland and lowland soils. Mean soil $\delta^{13}C$ and $\delta^{15}N$ values were higher at the upland site by 4.2‰ and 7.58‰, respectively (Table 4).

Soil N responses to rainfall

Net N mineralization showed greater temporal variability in lowland soils over the spread of rainfall/water additions tested, ranging from 0.18 ± 0.06 (mean ± SE) to −1.22 ± 0.52 kg ha^{-1} d^{-1}, than in upland soils, where daily N mineralization ranged from 0.057 ± 0.05 to −0.191 ± 0.05 kg ha^{-1} d^{-1}. Patterns of mineralization appeared to be influenced by rainfall, with immobilization occurring during very dry periods in both upland and lowland soils, mineralization in both sites following light rains, and variable, generally net immobilization of N over periods of heavy rainfall (Fig. 5A). Nitrogen leached into resin bags at the base of the cores was dependent on rainfall and around 10 times greater in lowland soils for a given rainfall volume. Lowland soil leaching losses ranged from 0.021 ± 0.005 to 1.256 ± 0.186 kg ha^{-1} d^{-1} and were linearly correlated to average daily rainfall during the incubation period ($r^2 = 0.94$, $P < 0.001$; Fig. 5B). Upland leaching losses ranged from 0.005 ± 0.005 to 0.124 ± 0.011 kg ha^{-1} d^{-1} and were best represented by quadratic relationship to rainfall during the incubation period ($r^2 = 0.95$, $P < 0.001$; Fig. 5B, C).

DISCUSSION

Coupling of hydrological, C, and nutrient cycles

We hypothesized that *P. pallida* in lowland areas would be able to access groundwater sources unavailable to upland trees and that this availability of groundwater would release lowland stands from the physiological effects of drought. Evidence for lowland tree access to groundwater was strong; during periods of low rainfall when $\delta^{18}O$ values of rainfall and groundwater sources were well separated, we saw clear differences between the $\delta^{18}O$ values of stem water in upland and lowland *P. pallida*. Lowland trees had stem water $\delta^{18}O$ values indicative of groundwater, while stem water $\delta^{18}O$ values for trees at upland plots followed the $\delta^{18}O$ values of light rainfall events from the 2011 dry season through to the dry season of 2012. That lowland trees could access groundwater was supported by greater consistency in predawn water potential and F_v/F_m in lowland trees over the course of the study and greater predawn and midday stem water potentials at the lowland site, particularly during periods of low rainfall (Fig. 2). In addition, upland trees showed responses to water shortage in the form of higher $\delta^{13}C$ values, which in arid system plants of the same species likely represent a shift to greater integrated water-use efficiency (Ehleringer and Cooper 1988). Upland trees also showed a tendency to produce smaller leaves without significantly increasing leaf mass per unit area. Reduction in leaf size is a well-established response to water stress in desert plants, serving to reduce transpiration water loss and

leaf temperature by sensible heat dissipation at the expense of productivity (Chaves et al. 2003, Farooq et al. 2009). Leaf mass per area often increases in response to drought stress (Nilsen and Schlesinger 1981, Schulze et al. 1998, Chaves et al. 2003, Poorter et al. 2009), although this trend does not seem to apply for species of the genus *Prosopis* (Nilsen et al. 1986, Vilela et al. 2003).

At a stand level, we saw markedly larger trees and greater stem density at the lowland site where groundwater was used as a water source during dry periods, indicating that growth rates are very likely higher. This pattern matches that of stands of phreatophytic species in other arid and semiarid areas (e.g., Rundel et al. 1982, Stromberg 1992, Stromberg et al. 1993, Gries et al. 2003), where productivity and stand biomass tend to increase with decreasing depth to groundwater. Stand density in arid zones where shallow groundwater is not present tends to be driven by rainfall (Fensham et al. 2005, Pekin et al. 2009), and in this case, rainfall appears to be insufficient to maintain upland stand densities to the degree that groundwater availability does at the lowland site.

Importantly, the distinct physiological advantages of *P. pallida* trees with access to groundwater profoundly influence ecosystem function via our two hypothesized mechanisms: increased nutrient inputs to soils and greater nutrient loss. Resorption of both N and P in upland trees was more efficient than in lowland trees, suggesting that nutrient acquisition was more limited relative to requirements at upland plots (Reed et al. 2012). Lowland stands also produced proportionally greater quantities of litter types rich in N and P and relatively discretionary in terms of energy investment (i.e., seeds, pods, and flowers). As a result, total litter mass falling over the course of the year studied was 17 times greater the at lowland site, but lowland litterfall contributed ~24 times the N and 35 times the P of the upland site. Thus, groundwater access contributed to the total mass of N and P deposited in the form of litter through higher litter quantity and quality. The greater N accretion in lowland soils and denser, larger stands of trees in lowland plots suggest strong differences in patterns of N-cycling between areas with and without groundwater access. The processes that could contribute to greater N accretion at the lowland site are an increase in N acquisition by *P. pallida* at a stand level, either through increases in fixation or N uptake from groundwater, and reduced losses of N in lowland areas via leaching or gaseous loss from soils. Comparison of $\delta^{15}N$ values of *P. pallida* with those of the ephemeral shrub *S. fallax* suggest that *P. pallida* was obtaining a portion of its N from symbiotic fixation. Only a single reference plant was available for this comparison, and in the absence of information on the mycorrhizal associations of these species, these data should be viewed with some caution (Högberg 1997, Spriggs et al. 2003). Nevertheless N fixation is a common feature of *Prosopis* species in other semiarid areas (Rundel et al. 1982, Bai et

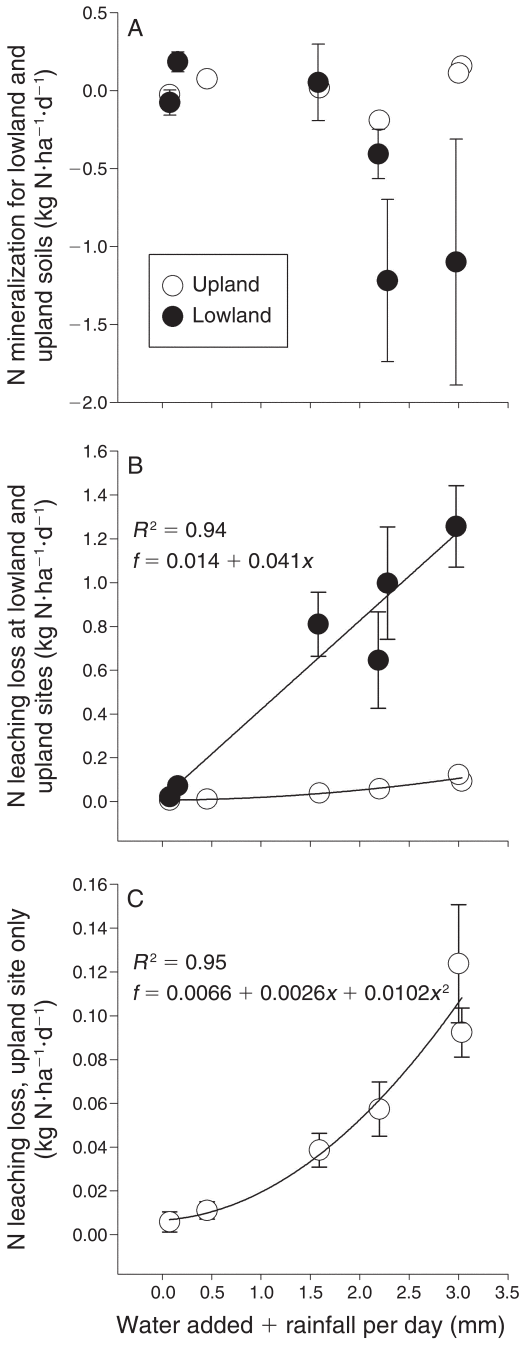

FIG. 5. Net N mineralization in and leaching losses from soils in upland ($n = 5$) and lowland ($n = 5$) plots. The x-axes of all panels give the sum of rainfall and water added to cores during each deployment divided by the number of days deployed. Panel A shows net in N mineralization for lowland and upland soils. Panel B shows relative leaching losses from cores at lowland and upland sites, while panel C shows leaching losses at the upland site on a reduced y-axis scale.

al. 2013), and comparable contributions of newly fixed N to *P. pallida* foliar N at the two sites would result in far greater contributions of newly fixed N to lowland soils where productivity and litterfall are higher. While our estimates of the proportion of foliar N derived from fixation at upland and lowland sites overlapped during the period the reference plant was present, the rates of both fixation and nutrient uptake from soils tend to be reduced in legumes experiencing water stress (DeVries et al. 1989, Serraj et al. 1999, Zahran 1999, Abdelhamid et al. 2011). Reduced fixation rates can be due to reductions in the availability of photosynthetic products that follow drought (Kuo and Boersma 1971, Nambiar et al. 1983), reductions in O_2 availability for nodule respiration (Denison 1998), and feedback regulation by N compounds (Parsons et al. 1993); all three of these processes are likely to be exacerbated by reductions in leaf water potential, such as those seen at upland plots, and hence phloem flow rates (Serraj et al. 1999).

Another important consequence for N-cycling differences between the two sites is that access to groundwater provides lowland trees with a direct source of both N and P. The contribution of these nutrient sources to the requirements of arid system phreatophytes has been suggested to be substantial in some arid zones; Arndt et al. (2004) found greater than half the N contribution to N-fixing phreatophytes with groundwater access in a hyperarid desert was sourced from groundwater. In our study, this source would appear to be less significant. Groundwater beneath the study area contains these nutrients at concentrations of ~50μ mol/L dissolved inorganic N and 2 μ mol/L soluble reactive P (B. Dudley et al., *unpublished data*), and at lowland stand-level transpiration rates calculated by Y. Miyazawa et al. (*unpublished manuscript*) could account for an uptake of 1.3 kg ha^{-1} yr^{-1} and 0.11 kg ha^{-1} yr^{-1} of groundwater N and P, respectively. This N amount is virtually identical to that calculated for groundwater N uptake by *Prosopis glandulosa* stands in the Sonoran Desert (Rundel et al. 1982). These values could account for ~4.4% of the N and 7% of the P deposited to lowland soils through litterfall, and while not trivial, they do suggest that at both upland and lowland sites the majority of these nutrients are sourced from soils, or in the case of N, either soils or symbiotic fixation. Whether increased N availability to *P. pallida* in the lowland plots occurs via fixation, soil N mineralization, or uptake of N from groundwater, it is reasonable to expect that this facilitated increased investment in P acquisition from soils through the production of N-rich phosphatases and increased root biomass (Allison et al. 2006, Houlton et al. 2008). Diffusion of nutrients and extracellular enzymes, and thus the uptake of soil-derived nutrients by plants, is limited in very dry soils (Barber 1995, Stark and Firestone 1995, Borken and Matzner 2009), and these results suggest that in arid environments, groundwater influences not only N-cycling, but P- and C-cycling as well.

In addition to the effects of groundwater on growth and nutrient inputs into the ecosystem, mineralization and losses of nutrient pools were influenced by pulsed water availability through rainfall. Our prediction that N mineralization in all areas would be positively correlated with both the size of rainfall pulses and the size of the soil organic N pools was based on low soil C:N (9.46 and 11.0 for upland and lowland soils, respectively) and the previous findings that N mineralization in arid systems typically increases with rainfall when the available substrate is N rich (Austin et al. 2004). Soil N mineralization at both sites was negative at very low rainfall, likely due to immobilization of mineral N by bacteria (Austin et al. 2004), and positive at both upland and lowland sites for daily water additions to cores between 0.45–1.6 mm/day for the upland site and 0.15–1.6 mm/d for the lowland site. With water additions greater than 1.6 mm/d, net N mineralization was consistently negative at the lowland site but showed substantial variation between plots and showed no clear pattern at the upland site. Much of the apparent net loss in N from the lowland site with high water additions could be accounted for by leaching, and leaching rates were highly dependent on the amount of water entering cores. Soil texture was similar between upland and lowland sites, and differences in leaching rates at a given water addition could largely be accounted for by nearly nine times higher extractable inorganic N pools in lowland soils. These leaching estimates may be conservative; the capture of ions by the mixed-bed resins as water passed out of the core was likely to be less than complete. While not measured in this study, gaseous losses of N from soils are also rainfall dependent in arid systems and may contribute considerably to soil N losses (Austin et al. 2004). Hence, the dependence of the major avenues of N loss at both sites on rainfall, combined with a decoupling of N additions acquired by *P. pallida* from rainfall through groundwater access at the lowland site, could explain differences in soil N accretion between the two stands.

Two potential mechanisms may have contributed to differences in $\delta^{15}N$ values between the upland and lowland areas. Firstly, buildup of ^{15}N-depleted N as the product of fixation could have shifted soil N below a ^{15}N-enriched starting point (prior to invasion) more rapidly at the lowland site than at the upland site if N fixation rates of the lowland site were higher at a stand level (Rascher et al. 2012). Uptake of inorganic N from groundwater also could have contributed to this effect. Secondly, the proportion of N entering the soil–plant N cycle eventually lost as ^{15}N-depleted gas efflux from soils may be higher at the upland than the lowland site. This mechanism would not rely on a greater rate of gaseous N loss from the upland site, but that these losses are higher relative to additions. Losses of N through leaching seem unlikely to account for the differences in soil $\delta^{15}N$ values; fractionation during mineralization and leaching losses of N from soils typically accounts for

PLATE 1. A view toward the upland site in January 2011, one month following a large rain event. The ground cover of *Sida fallax* ('Ilima) and *Waltheria indica* ('Uhaloa) died off during subsequent dry weather to leave only the larger *Prosopis pallida* trees. Photo credit: B. D. Dudley.

differences of 1–2‰ between soil and leached N pools (Houlton and Bai 2009). Losses of the ^{15}N-depleted gaseous products of denitrification and ammonification reactions can cause considerable increases in soil $\delta^{15}N$ values (Houlton et al. 2006, Houlton and Bai 2009), as these processes discriminate against ^{15}N substantially (Bedard-Haughn et al. 2003) and can be responsible for considerable losses of N from arid soils (Hartley and Schlesinger 2000). The contribution of gaseous losses to differences in the $\delta^{15}N$ values of the two soil pools is supported by the lack of a ^{15}N-enriched source of N to the study area; bulk nitrate deposition in Hawai'i was measured by Houlton et al. (2006) as close to 0‰, and concentrations of nitrate in rainfall at our study site are very low, typically less than 1 μmol/L (J. Fackrell, *unpublished data*). Biological fixation of N within the soil–plant system imparts only small isotope fractionation effects, enriching or depleting the ammonium product less than 2‰ from that of atmospheric N_2 (Högberg 1997). It is possible that the relative scarcity of inorganic N in soils at the upland site may contribute to reductions in leaching following rainfall through higher plant and microbial uptake of mineral N (Hedin et al. 2003). This effect could enhance the effects of the mechanism put forward by Houlton and Bai (2009) for ^{15}N-enrichment of soil N pools by shifting the major loss of soil N further towards gaseous losses following rain (Schlesinger and Peterjohn 1991, Peterjohn and Schlesinger 1991).

Ecosystem-level consequences of invasion

Our results show that effects of *P. pallida* on nutrient availability are altered by depth to groundwater; while this species is able to persist without groundwater in this system, stands with groundwater access exhibited substantially higher soil N pools and leaching losses of inorganic N. As such, these lowland invaded areas are likely to contribute disproportionately to N loading via groundwater discharge. Groundwater access also allowed this nonnative, N-fixing species to form dense canopies in the coastal lowlands, with up to five times the basal area and considerably higher leaf area index than was exhibited in upland stands (Y. Miyazawa et al., *unpublished manuscript*). Given these differences, it is likely that long-term effects of this species on ecosystem functioning and development will differ as a function of access to groundwater and may extend to the plant community level by altering species diversity, relative abundances, and light availability as seen elsewhere in Hawai'i (Hughes and Denslow 2005).The effects of groundwater depth on the ecosystem level effects of invasive phreatophytes are not restricted to Hawai'i. Increases in groundwater depth alter the community composition of riparian communities in the arid southwest of the USA (Stromberg et al. 1996),

increasing susceptibility of these communities to invasion by *Tamarix* spp., a genus of phreatophyte native to Eurasia (Horton et al. 2001, Lite and Stromberg 2005). Where *Tamarix* spp. are present in these systems, groundwater depth alters their impacts to hydrology and soil chemistry (Di Tomaso 1998). Thus, alterations to groundwater levels have the potential to affect arid ecosystem structure and function well beyond their direct effects on water availability.

Our results also highlight that the consequences of the invasion of N-fixing trees on young lava flows are highly dependent on climate. Most of the examples of N-fixing invaders in Hawai'i occur in wet forests, where substantial change to the relative availability of resources for primary producers has been documented, resulting in changes in ecosystem development (Vitousek et al. 1997) and positive feedbacks that lead to increased rates of invasion by other nonnative species (Hughes and Denslow 2005). Changes caused by these N-fixing trees are so marked because N is the resource least available relative to the demands of primary producers in these systems (Vitousek and Farrington 1997). In contrast, in Hawaiian dry forests where lack of rainfall seasonally limits primary production, the magnitude and nature of the ecosystem-level impacts of *P. pallida* as an N-fixing invader are mediated by water availability, both via groundwater supply and rainfall. For example, although a substantial amount of N accumulates in the ecosystem in litter or mineral soil, mineralization rates to and leaching losses of reactive N from these soils were dependent on the magnitude of rainfall events. Soils showed a high potential for N loss during heavy rain events, but these events are infrequent in comparison to wet forest ecosystems. Hence, the effects of invasion by *P. pallida* may be altered by changes to groundwater levels, but also by climate change that results in changes to the timing or intensity of rainfall.

Conclusion

Viewed with a global context, our results indicate that current patterns in groundwater drawdown across arid regions will likely increase the susceptibility of this phreatophytic desert species to physiological stress associated with seasonal drought. *Prosopis* is the dominant genus of vegetation through millions of square kilometers of the world's arid and semiarid regions (Rundel et al. 1982, Pasiecznik et al. 2001), and drought events in many of these regions are predicted to worsen as a result of climate change. There is considerable evidence to suggest that the physiological effects of regional reductions in groundwater levels currently extend to phreatophyte species in other arid systems (Stromberg et al. 1993, 1996, Smith et al. 1998, Cooper et al. 2006); interactions between groundwater levels and climate change are likely to be important in structuring plant communities in arid regions. Our results also show that access to groundwater for N-fixing phreatophytes in arid regions disconnects productivity of these trees from the pulse-driven nature of these systems (Noy-Meir 1973), i.e., productivity and nutrient additions to soils are decoupled from surface soil moisture, on which processes of organic matter breakdown, mineralization, and uptake and loss of nutrients from arid soils rely (Austin et al. 2004). Hence, regional reductions in groundwater levels may reduce N accretion in arid soils, but may also reduce soil accretion of other nutrients, as evidenced by the reduced buildup of C and P at the upland site in our study. *Prosopis pallida* is an extremely successful invader in much of its range, and our study provides an example of how changes to hydrological cycles may not only alter the geographical ranges of invasive species, but mediate impacts to nutrient cycling and resource availability within invaded areas.

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Supplemental Material

Ecological Archives

The Appendix is available online: http://dx.doi.org/10.1890/13-1262.1.sm