# Nutrient and Organic Matter Inputs to Hawaiian Anchialine Ponds: Influences of N-Fixing and Non-N-Fixing Trees[1]

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**Abstract:** Invasive nitrogen-fixing plants often increase energy and nutrient inputs to both terrestrial and aquatic ecosystems via litterfall, and these effects may be more pronounced in areas lacking native $N_2$-fixers. We examined organic matter and nutrient inputs to and around anchialine ponds on Hawai'i Island's leeward coast from an invasive, $N_2$-fixing tree, *Prosopis pallida*, and a non-$N_2$-fixing tree, *Thespesia populnea*. On a monthly basis we quantified: (1) tree basal area and stem density surrounding the ponds, and (2) nutrient content and quantity of *P. pallida* and *T. populnea* litter inputs. Tree density and basal area significantly predicted litterfall mass inputs for both species, but there was no difference in mean total annual litterfall mass, foliar N concentration, or litterfall N between the pond types. Time did not significantly influence litterfall mass, C, or P but did affect litterfall N, likely due to the production of *P. pallida* pods. In contrast, P concentrations were three times greater in *T. populnea* litter than in *P. pallida* litter, resulting in significantly higher P deposition where *T. populnea* was the prevalent tree species. Because this deposition of labile P by the non-$N_2$-fixing *T. populnea* has the potential to strongly influence water quality and soil chemistry, its replacement by *P. pallida* in tree communities of lowland Hawai'i may alter the functioning of anchialine pond ecosystems.

BOTH THE QUANTITY and quality of litterfall exert strong influences over ecosystem processes, population dynamics, and food web and community interactions (Polis et al. 1997). Litterfall often represents the largest energy (i.e., carbon) and nutrient input to ecosystems (Webster et al. 1999, Richardson et al. 2010). It is a fundamental energy source for heterotrophic organisms large and small (Wallace et al. 1997), as well as an important source of nitrogen (N), phosphorus (P), and other nutrients to systems (e.g., Compton et al. 2003, Church et al. 2004, Goldstein et al. 2009, Mineau et al. 2011). Its decomposition and the fate of its products depend in large part on both litter nutrient concentrations and mass, parameters that may vary substantially from one plant species to another (Allison and Vitousek 2004, Hughes and Uowolo 2006).

Litter production and the quality of litter produced may be constrained by a wide variety of environmental factors, including light availability (Jordan 1971), temperature and precipitation regimes (Bray and Gorham 1964, Meentenmeyer et al. 1982), and soil nutrient availability (Vitousek 2004). In addition, litterfall rates can be strongly influenced by interactions among various environmental factors. Riparian zones, where freshwater availability is relatively high and constant, make for particularly interesting study systems. Due to the alleviation of water stress in such systems, plant species generally have

[1] Funding was provided by the National Science Foundation (Hawai'i EPSCoR NSF Grant No. EPS-0903833), with additional logistical support provided by the U.S. Forest Service Institute of Pacific Islands Forestry. Manuscript accepted 2 December 2015.

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Pacific Science (2016), vol. 70, no. 3:333–347
doi:10.2984/70.3.5

higher litter production. However, these patterns will also be influenced by the evolutionary histories of the species (Reich et al. 1994) and nutrient availability (Kozlowski and Pallardy 2002). For example, in riparian zones, species that have evolved the capacity for symbiotic N-fixation add new N to soil/plant cycles that leads to increased soil N mineralization and nitrification rates (Goldstein et al. 2010; Dudley, Hughes, and Ostertag 2014), elevated water nitrate levels (Goldstein et al. 2009, Goldstein et al. 2010, Wiegner et al. 2013), and altered nutrient processing within adjacent stream environments (Mineau et al. 2011). Plant species that are not capable of N-fixation may also exhibit increased litter production when they occur in riparian areas where water availability is relatively high, but such increases in production may not be accompanied by increased N inputs as seen with N-fixing species, especially when nonfixing plant species occur in settings where soil N availability is inherently low (Reynolds and Cooper 2011).

Similar to riparian and stream habitats, anchialine ponds found along the dry leeward regions of Hawai'i Island provide an ideal opportunity to examine productivity of plants in a water-replete setting. Anchialine ponds are landlocked, brackish bodies of water found adjacent to the ocean that provide freshwater access to organisms. They lack surface connection to the sea, but subterranean permeability to the groundwater aquifer and ocean result in wide salinity ranges and daily tidal fluctuations (Holthuis 1973, Brock et al. 1987, Russ et al. 2010). Though sometimes bounded by barren lava substrates, anchialine ponds are often surrounded by vegetation sustained by access to water at the pond/lava flow interface. Terrestrial patterns of succession on Hawai'i Island are periodically reset by lava flows, and anchialine ponds on older flows tend to have greater tree canopy cover. Where riparian cover by vegetation reduces available light below the canopy it may reduce the productivity, diversity, and abundance of aquatic photoautotrophs (Bunn et al. 1999, Skelly et al. 2002). However, energy from riparian trees contributes increasingly to aquatic food webs where canopy cover increases (Doucett et al. 2007). Hence, the mass and quality of riparian litter may also have substantial effects on anchialine pond food webs. The trees *Thespesia populnea* (L.) Sol. ex Corrêa and *Prosopis pallida* (Humb. & Bonpl. ex Willd.) Kunth, are often dominant tree components of this riparian vegetation. *Thespesia populnea* produces taproots that allow for increased access to underground water sources, such as those associated with anchialine ponds, giving them the ability to sustain primary productivity throughout prolonged dry periods and precipitation regimes below their typical range (Friday and Okano 2006). They produce large leaves that decompose slowly (M. Riney, unpubl. data) that can often be seen floating in the ponds or incorporated into the benthic zone. *Thespesia populnea* is not capable of N-fixation, a deficiency that poses a potentially strong constraint on productivity given that bioavailability of N in particular is quite low on young, poorly weathered lava substrates (Vitousek et al. 1987). In contrast, *P. pallida*, commonly referred to as kiawe in Hawai'i, is an invasive N-fixing tree that has become well established on dry, leeward sides of the main Hawaiian Islands (Wagner et al. 1990, Gallaher and Merlin 2010). It often forms dense stands around anchialine ponds and exhibits substantial increases in litter production in such settings relative to upland areas where individuals must rely solely on infrequent, low-volume rain events as their water source (Dudley, Hughes, and Ostertag 2014). The presence of *P. pallida* and *T. populnea*, an N-fixer and non-N-fixer, respectively, around anchialine ponds, where water is relatively abundant and soil N relatively scarce, prompts the following questions: First, under conditions of high water availability, is litterfall production of *P. pallida* greater than that of *T. populnea?* Second, given *P. pallida*'s capacity to symbiotically fix N and *T. populnea*'s inability to do so, will the former species deposit greater amounts of N in litterfall compared with the latter species?

Our objectives here were to determine rates and C, N, and P nutrient concentrations of litterfall for *P. pallida* and *T. populnea* grow-

ing adjacent to anchialine ponds along the dry leeward coast of Hawai'i Island. Specifically, we quantified the following in both *P. pallida*-dominated and *T. populnea*-dominated stands around a series of anchialine ponds: (1) tree basal area and density surrounding the ponds, and (2) the quality (i.e., nutrient concentration) and quantity of *P. pallida* and *T. populnea* litter inputs. We hypothesized that *P. pallida*, due to its $N_2$-fixing capabilities, would exhibit greater basal area, greater stem densities, and higher litterfall rates in comparison with *T. populnea* stands. Further, we expected that *P. pallida* would produce greater amounts of nutrients via its litter compared with *T. populnea*, which could lead to the two types of ponds diverging in their overall ecosystem functioning.

## MATERIALS AND METHODS

### *Study Species*

Native to Peru, Colombia, and Ecuador, *P. pallida*, also known as mesquite or algarroba, and kiawe in Hawai'i, grows from sea level to 610 m elevation in arid to semiarid areas exhibiting annual precipitation between 250 and 1,250 mm (Wagner et al. 1990, Gallaher and Merlin 2010). This salt-tolerant species is a phreatophyte capable of accessing groundwater to 20- to 25-meter depths due to a deep taproot system (Pasiecznik et al. 2001). *Prosopis pallida* has leaf adaptations for arid habitats: bipinnately compound leaves, leaflet folding during periods of high evapotranspiration, and sunken stomata and waxy cuticles (Vilela and Palacios 1997).

Valued as fuel wood and a food source for cattle, *P. pallida* was purposefully introduced to the island of O'ahu in 1828 and to the other main Hawaiian Islands shortly thereafter (Wagner et al. 1990, Gallaher and Merlin 2010). *Prosopis* forest or scrubland currently occupies nearly 4% of the land area of the state (Gon et al. 2006), but it could potentially occupy 34% of the Hawaiian Islands (Gallaher and Merlin 2010).

*Thespesia populnea* (milo) is a Hawaiian tree species belonging to the Malvaceae family that grows from sea level to 275 m elevation (Wagner et al. 1990, Wagner et al. 2005). The species inhabits environments where mean annual precipitation ranges from 500 to 4,000 mm. Similar to *P. pallida*, the salt-tolerant *T. populnea* has a long taproot that can access water sources deep underground, giving it the ability to endure prolonged dry periods and precipitation rates below its typical range (Friday and Okano 2006). *Thespesia populnea*, unlike *P. pallida*, can withstand tidal inundation (Friday and Okano 2006). In addition to the coastal buffering that it provides, *T. populnea* has a wide variety of uses in Hawaiian culture: the wood was used for food bowls, dishes, and platters, and a dye was extracted from the immature fruit capsules to decorate kapa, the traditional clothing material of native Hawaiians (Krauss 1993). In other cultures, *T. populnea* has been exploited for medicinal properties and applications (e.g., Nagappa and Cheriyan 2001, Vasudevan and Parle 2007, Shah and Alagawadi 2011).

### *Study System*

Anchialine ponds occur in the Philippines, the Caribbean, Japan, the Pacific, and the Sinai Peninsula (Santos 2006), They are generally associated with porous coralline or recent volcanic substrates and can be found on the Hawaiian Islands of O'ahu, Maui, Moloka'i, Kaho'olawe, and Hawai'i (Brock et al. 1987). Hawai'i Island supports most of the anchialine ponds in the state (Santos 2006), with more than 70% of the estimated 520 ponds occurring on the Kona coast (Brock et al. 1987). Anchialine ponds are habitat for endemic species, including the orange-black Hawaiian damselfly (pinao 'ula), listed as vulnerable on the International Union for Conservation of Nature (IUCN) Red List (Odonata Specialist Group 1996, Polhemus 1996); the predatory shrimp *Metabetaeus lohena*, candidate for the U.S. Endangered Species List (Russ et al. 2010); and the red shrimp *Halocaridina rubra*, ('ōpae 'ula). Known to Hawaiians as loko wai, anchialine ponds were traditionally used for potable water, bathing, and holding fish.

Our study was conducted in and around 10 individual anchialine ponds located along the South Kohala and North Kona coast on the west side of Hawai'i Island. These sites were selected where an anchialine pond had dominant cover of one or the other of the two riparian tree species *T. populnea* or *P. pallida*. Where possible we selected ponds with monospecific or highly dominant cover of either species. Study locations included 'Anaeho'omalu Bay, Weliweli, Kīholo Bay, and the Kaloko-Honokōhau National Historic Park (Figure 1). The coastline encompassing the study ponds is semiarid and receives approximately 250–500 mm precipitation per year (Giambelluca et al. 2013). Ponds were categorized according to their surrounding dominant tree species and segregated into two pond types: *P. pallida* ($n = 5$) and *T. populnea* ($n = 5$), hereafter referred to as *P. pallida* ponds and *T. populnea* ponds, respectively. Additional woody shrubs [i.e., naupaka (*Scaevola sericea*) and sourbush (*Pluchea carolinensis*)] were minor components of the pond vegetation surrounding the ponds. Surface area, water depth, and proximity to the ocean of each pond were also characterized (Table 1).

Transects were established at each pond for the dual purpose of determining litter trap

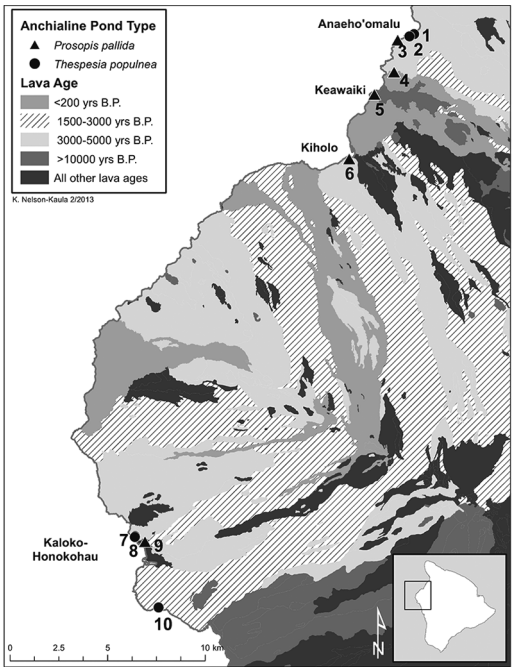


FIGURE 1. Map of anchialine pond study sites on the leeward coast of Hawai'i Island. Refer to Table 1 for information about each numbered study site; pond type refers to dominant vegetation surrounding each pond; ponds 7 and 8 are in close proximity, causing overlapping symbols; lava flow ages based on geologic map of Hawai'i Island (Trusdell 1996).

TABLE 1

Physical Characteristics of Anchialine Pond Study Sites on the Leeward Coast of Hawai'i Island

| Pond | Pond ID | Pond Type | Latitude (°N) | Longitude (°W) | Area[a] ($m^2$) | Max Depth[a] (m) | Max Width[a] (m) | Mean Annual Rainfall[b] (mm) |
|---|---|---|---|---|---|---|---|---|
| 1 | AB4 | *T. populnea* | 19.9116 | 155.89053 | 11.7 | 0.4 | 3.0 | 240 |
| 2 | Pond293 | *T. populnea* | 19.91071 | 155.89269 | 9.1 | 0.4 | 4.2 | 242 |
| 3 | FKAB | *P. pallida* | 19.90903 | 155.89855 | 2.6 | 0.7 | 2.3 | 239 |
| 4 | WW3 | *P. pallida* | 19.89413 | 155.90039 | 45.5 | 0.7 | 4.2 | 244 |
| 5 | Tincan | *P. pallida* | 19.88416 | 155.91049 | 9.2 | 0.5 | 2.5 | 242 |
| 6 | KB1 | *P. pallida* | 19.85457 | 155.92339 | 0.9 | 0.7 | 1.3 | 271 |
| 7 | Kaho50 | *T. populnea* | Available on request | | 17.0 | 0.5 | 5.0 | 449 |
| 8 | Kaho32 | *T. populnea* | Available on request | | N/A | N/A | N/A | 451 |
| 9 | Kaho39 | *P. pallida* | Available on request | | 8.8 | 0.6 | 3.5 | 471 |
| 10 | QLCC | *T. populnea* | Available on request | | 5.9 | 0.4 | 2.2 | 513 |

[a] Provided by Dudley, MacKenzie et al. (2014).
[b] From Giambelluca et al. (2013).

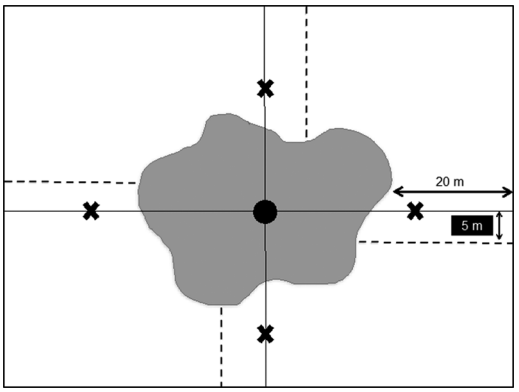


FIGURE 2. Conceptual image of anchialine study pond with transects (solid line), litter traps (x), and vegetation sampling area (area between solid and dashed lines).

placement and surveying surrounding woody vegetation. To maintain consistency among ponds, transects originated from the identified center of each pond. All anchialine ponds have a unique shape, but each study pond was approximated as an ellipse to find the center. Transects began at the edge of each pond and radiated from the pond's center in each cardinal direction (Figure 2).

*Basal Area and Density*

Vegetation surrounding each pond was sampled within a 5-m belt to the right of each transect reference line (Figure 2). Each 5-m-wide transect began at the pond's edge and extended either to the canopy edge or to a maximum length of 20 m, whichever came first. Diameter at breast height (DBH) was measured for all trees of all species rooted within each transect. Rooted individuals were defined as any individual having any percentage of its base originating within the 5-m-wide transect. Trees with multiple stems at DBH level had multiple DBH measurements recorded. Stand basal area was calculated as the sum of the tree area (all stems) divided by the sum of land area measured. Stem density was calculated on an individual plant basis and did not include multiple stems.

*Litterfall Quantity and Nutrient Quality*

We collected litterfall from underneath the vegetation surrounding each pond on a monthly basis from March 2012 to February 2013. Litter collections were conducted over a span of 2 days due to the traveling time required to reach each pond. Ponds were small (Table 1), and the canopy of trees extended into the ponds, so the leaf area falling into the pond water was not expected to differ from the leaf area falling on land at the pond margin. We placed a litter trap on the ground along each established transect within 5 m from the edge of the pond ($n = 4$ per pond) (Figure 2). Similar to stream studies, the placement of litter traps on the edge of the pond was considered a suitable surrogate for measuring direct litter inputs into the pond (Urgenson 2006, Urgenson et al. 2009). Litter traps were constructed with trays (0.18 $m^2$ by 6 cm deep) lined with 1-mm mesh fiberglass to minimize loss of litterfall and provide sufficient drainage. Traps were secured in place using galvanized wire tied to either large rocks or four 0.45-kg diving weights. We sorted litter samples into the following categories: (1) *P. pallida* leaves and flowers; (2) *P. pallida* wood, bark, and stem; (3) *P. pallida* seeds and seed pods; (4) *T. populnea* leaves; (5) *T. populnea* wood, bark, and stem; (6) *T. populnea* reproductive parts; and (7) other species: all tissue types. We grouped *P. pallida* leaves and flowers (called leaves in the text hereafter) because flowers formed a small proportion (<1%) of the combined biomass of this grouping and were typically broken into small pieces similar to size of leaflets, making complete separation difficult. Flowers, including those of N-fixing species, are typically more N- and P-rich than leaf litter (e.g., 0.4%–2% greater N, 0.22%–0.27% greater P in dry mass [Zarrouk et al. 2005, Viera and Schumacher 2010, Lee et al. 2011]). Sorted samples were dried to a constant mass at 70°C and weighed to determine litterfall quantity. For each tissue type, values from all four subsamples per study site were averaged by month, summed across months, and divided by litter trap area to estimate annual litterfall biomass

inputs (g $m^{-2}$ $yr^{-1}$) according to litter tissue type.

We determined nutrient concentrations from combined monthly samples of each litter type per pond during both wet (November–April) and dry (May–October) seasons. Dried litter was ground through a 40-mesh screen using a Wiley Mill and analyzed for %C and %N (detection limit [DL] 0.005 mg, EPA 440) using a Costech 4010 Elemental Analyzer (Costech Analytical Technologies, Valencia, California). To determine %P, approximately 0.25 g of the dried litter sample was ashed at 500°C for 5 hr, cooled, and resuspended with 5 ml of 1 N HCl. After allowing the sample to digest for 0.5 hr, 20 ml of reagent-grade water was added. These extracts were analyzed with a Varian Vista MPX ICP-OES Spectrometer (Varian Analytical Instruments, Walnut Creek, California) using methods of Hue et al. (2000). Mass of C, N, and P in litter inputs from each site was calculated by multiplying biomass values for each litter category by C, N, and P concentrations of that litter type for each season. Because we found no difference in litter nutrients between wet and dry seasons (data not presented), we summed values for each season and presented them as annual inputs.

### *Data Analyses*

To test for differences in basal area and density of trees around the ponds, we used Mann-Whitney tests. To examine how the ponds might differ in litterfall patterns over the course of an annual cycle, we analyzed the monthly litterfall data using a linear mixed effects model (lme function), where canopy type and time are fixed factors, and pond is a random factor, and included the interaction of time*pond type. We used a separate model for each response variable: litterfall mass, litterfall N mass, litterfall P mass, and litterfall C mass inputs. For nutrient concentrations we used Mann-Whitney tests because these samples were bulked by dry and wet season, and so the monthly time component was not explored. We also performed the following correlations for each species across all 10 sites: (1) stem basal area versus litterfall mass and litter nutrient inputs; (2) stem density versus litterfall mass and litter nutrient inputs.

## RESULTS

### *Basal Area and Density of Trees Surrounding Ponds*

The vegetation survey revealed no significant differences in total basal area (all species combined) ($W = 18$, $P = .310$, $n_1 = n_2 = 5$) or density ($W = 6$, $P = .222$, $n_1 = n_2 = 5$) of the trees surrounding the two pond types (Table 2). Basal area of *P. pallida* ranged widely from 4.7 to 76.0 $m^2$ $ha^{-1}$, and densities ranged from 397 to 2,000 trees $ha^{-1}$ (Table 2). Basal area of *T. populnea* ranged from 7.5 to 24.7 $m^2$ $ha^{-1}$, and densities ranged from 402 to 4,828 trees $ha^{-1}$ (Table 2). Although no *T. populnea* individuals were present around *P. pallida* ponds, *P. pallida* individuals were found within the vegetation transects around two of the five *T. populnea* ponds (Table 2). Additional woody plant species that contributed to the "Other" litter category included koa haole (*Leucaena leucocephala*), Christmas berry (*Schinus terebinthifolius*), and noni (*Morinda citrifolia*). These other species composed <1% of the total basal area and <10% of the total density around both pond types (Table 2).

### *Litterfall Mass and Nutrients*

For litterfall mass, there was no significant effect of pond type, time, or a significant interaction. Mean total annual litterfall was 507 (±124 SE) g $m^{-2}$ $yr^{-1}$ around *P. pallida* ponds and 869 (±225 SE) g $m^{-2}$ $yr^{-1}$ around *T. populnea* ponds (Figure 3). High variability in annual litterfall mass among ponds within the same vegetation type resulted in total annual litterfall mass not differing between the two pond types. However, as expected, we observed positive correlations between *P. pallida* basal area and density and *P. pallida* litterfall mass inputs into the ponds; we saw similarly positive correlations between basal area and density of *T. populnea* and litterfall mass inputs from *T. populnea* (Table 3).

Although litterfall mass did not differ between *T. populnea* and *P. pallida* ponds, con-

TABLE 2

Basal Area and Density of the Main Tree Species Surrounding Anchialine Pond Study Sites on the Leeward Coast of Hawai'i Island

| | | Basal Area ($m^2$ $ha^{-1}$) | | | | Density [No. of Individual Trees/Transect Area (ha)] | | | |
|---|---|---|---|---|---|---|---|---|---|
| Pond | Pond Type | *P. pallida* | *T. populnea* | Other | Total | *P. pallida* | *T. populnea* | Other | Total |
| 3 | *P. pallida* | 76.0 | 0.0 | 0.0 | 76.0 | 397 | 0 | 0 | 397 |
| 4 | *P. pallida* | 29.3 | 0.0 | 0.0 | 29.3 | 457 | 0 | 0 | 457 |
| 5 | *P. pallida* | 31.9 | 0.0 | 0.0 | 31.9 | 2,000 | 0 | 0 | 2,000 |
| 6 | *P. pallida* | 34.8 | 0.0 | 0.0 | 34.8 | 1,545 | 0 | 0 | 1,545 |
| 9 | *P. pallida* | 4.7 | 0.0 | 1.5 | 6.2 | 438 | 0 | 500 | 938 |
| | Mean ± SE | 35.3 ± 11.5 | 0.0 | 0.3 ± 0.3 | 35.6 ± 11.3 | 967 ± 337 | 0 | 100 ± 100 | 1,067 ± 311 |
| 1 | *T. populnea* | 9.8 | 24.7 | 0.0 | 34.5 | 126 | 402 | 0 | 528 |
| 2 | *T. populnea* | 13.5 | 7.5 | 0.0 | 21.0 | 1,211 | 1,380 | 0 | 2,592 |
| 7 | *T. populnea* | 0.0 | 15.0 | 0.1 | 15.1 | 0 | 4,828 | 86 | 4,914 |
| 8 | *T. populnea* | 0.0 | 11.2 | 0.0 | 11.2 | 0 | 2,417 | 0 | 2,417 |
| 10 | *T. populnea* | 0.0 | 21.1 | 0.02 | 21.1 | 0 | 629 | 45 | 674 |
| | Mean ± SE | 4.6 ± 2.9 | 15.9 ± 3.1 | 0.02 ± 0.02 | 20.6 ± 4.0 | 267 ± 237 | 1,931 ± 805 | 26 ± 17 | 2,225 ± 796 |

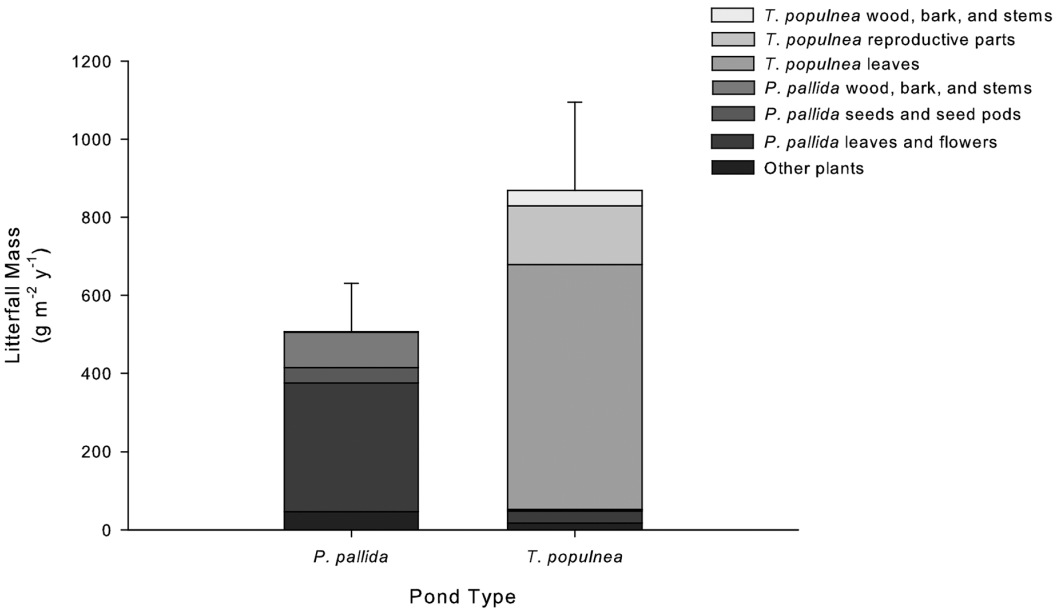


FIGURE 3. Average (±SE) total annual litterfall mass from *P. pallida*- versus *T. populnea*-dominated anchialine ponds on the leeward coast of Hawai'i Island. Litter fractions categorized as "Other plants" included tissues from *S. sericea*, *P. carolinensis*, fountain grass (*Pennisetum setaceum*), and *S. terebinthifolius*.

centrations of C, N, and P did differ among litter categories for the two pond types (Table 4). For example, the leaves and reproductive parts collected from *T. populnea* ponds had P concentrations that were almost three times greater than those from *P. pallida* ponds (Mann-Whitney, $W = 1$, $P = .016$; $W = 0$, $P = .008$; respectively) (Table 4). C:P values

TABLE 3

Correlations between Litterfall Mass According to Litter Categories and Basal Area and Density of the Two Tree Species Surrounding the Anchialine Pond Study Sites on the Leeward Coast of Hawai'i Island

| Parameter | *T. populnea* Leaves | *T. populnea* Reproductive | *T. populnea* Wood, Bark, and Stem | *P. pallida* Leaves and Flowers | *P. pallida* Seeds and Seed Pods | *P. pallida* Wood, Bark, and Stem | Other Plants | Total |
|---|---|---|---|---|---|---|---|---|
| *P. pallida* basal area | –0.664* | –0.530 | –0.770** | 0.882*** | 0.515 | 0.846** | 0.307 | 0.153 |
| *P. pallida* density | –0.636* | –0.462 | –0.747** | 0.922*** | 0.680* | 0.884*** | 0.237 | 0.078 |
| *T. populnea* basal area | 0.968*** | 0.907*** | 0.959*** | –0.783** | –0.530 | –0.932*** | –0.322 | 0.399 |
| *T. populnea* density | 0.936*** | 0.847*** | 0.997*** | –0.740** | –0.449 | –0.933*** | –0.167 | 0.256 |
| Total basal area | –0.205 | –0.131 | –0.313 | 0.349 | 0.031 | 0.339 | 0.282 | 0.515 |
| Total density | 0.222 | 0.132 | 0.443 | –0.257 | 0.143 | –0.270 | 0.244 | –0.225 |

*Note:* Correlation values ($r$) with asterisks indicate significant $P$ values: *, $P \leq .05$; **, $P \leq .01$; ***, $P \leq .001$; all variables were log transformed.

of reproductive parts and leaves from *P. pallida* ponds were more than two times greater than those from *T. populnea* ponds (Table 4). Woody litter from *P. pallida* ponds exhibited higher N concentrations, low C:N, and high C:P compared with that from *T. populnea* ponds (Table 4).

The significance of the litterfall nutrient inputs varied depending on the nutrient, using linear mixed effect models. For litterfall C, there were no significant effects of pond type, time, or their interaction. For litterfall N inputs, there was a significant time effect ($F = 4.26$; df = 1, 108; $P = .0415$) (Figure 4), which we attribute to the timing of pod development for *P. pallida*. In contrast, litterfall P was influenced by pond type but not by timing or the interaction; *T. populnea* ponds had significantly more litterfall P inputs ($F = 5.58$; df = 1, 8; $P = .0458$).

## DISCUSSION

*Prosopis pallida* and *T. populnea* stands measured in this study had high litterfall rates in comparison with other Hawaiian dry forest tree species (Austin 2002), as well as *P. pallida* stands within the same region (Dudley, Hughes, and Ostertag 2014), and are comparable to wetter forest ecosystems on Hawai'i Island (Austin 2002). A recent study found that *P. pallida* stands growing along the coastline have greater access to groundwater and thus have higher annual litterfall mass ($186.8 \pm 270.3$ g $m^{-2}$ $yr^{-1}$) compared with *P. pallida* stands with little access to groundwater growing farther upslope ($10.5 \pm 34.4$ g $m^{-2}$ $yr^{-1}$) (Dudley, Hughes, and Ostertag 2014). In our study, annual litterfall mass from *P. pallida* adjacent to ponds was 2.5 and 50 times higher than that recorded in coastal and upland *P. pallida* stands, respectively, by Dudley, Hughes, and Ostertag (2014). In addition, the *P. pallida* and *T. populnea* ponds in this study had 4.5 and 14 times, respectively, more litterfall per unit basal area than the coastal *P. pallida* stands of Dudley, Hughes, and Ostertag (2014). That *P. pallida* and *T. populnea* around anchialine ponds are substantially more productive than the coastal *P. pallida* stands of Dudley, Hughes, and Ostertag (2014), which were situated less than 10 m above sea level and were shown to have at least some access to groundwater, implies restriction to productivity where groundwater is accessible but at considerable depth. This also suggests that both *T. populnea* and *P. pallida* that inhabit the low-lying terrain in the vicinity of anchialine ponds are largely released from the constraints of water availability that typically occur in arid systems (Noy-Meir 1973). Where *P. pallida* stands are able to access groundwater, both litterfall production and $N_2$-fixation increase because growth is less tied to sporadic rainfall events, resulting in higher soil organic matter and

TABLE 4

Mean (±SE) Litter Nutrient Concentrations by Litter Type Collected around *P. pallida*- versus *T. populnea*-Dominated Anchialine Ponds on the Leeward Coast of Hawai'i Island

| | Mean % N | | Mean % P | | Mean % C | | Mean C:N | | Mean C:P | |
|---|---|---|---|---|---|---|---|---|---|---|
| Litter Type | *P. pallida*-Dominant | *T. populnea*-Dominant | *P. pallida*-Dominant | *T. populnea*-Dominant | *P. pallida*-Dominant | *T. populnea*-Dominant | *P. pallida*-Dominant | *T. populnea*-Dominant | *P. pallida*-Dominant | *T. populnea*-Dominant |
| Leaves | 1.86 ± 0.08 | 1.8 ± 0.1 | 0.09 ± 0.02a | 0.21 ± 0.04b | 43.2 ± 0.9 | 43.9 ± 0.41 | 23.6 ± 1.3 | 27.2 ± 1.9 | 569.4 ± 72.6a | 269.4 ± 62.1b |
| Wood | 1.48 ± 0.07a | 1.10 ± 0.07b | 0.05 ± 0.01 | 0.08 ± 0.02 | 44.48 ± 0.63 | 43.58 ± 0.38 | 30.1 ± 1.3a | 41.8 ± 2.5b | 1,029.8 ± 140.5a | 655.7 ± 109.4b |
| Reproductive Parts | 1.26 ± 0.16 | 1.44 ± 0.11 | 0.08 ± 0.02a | 0.24 ± 0.03b | 39.26 ± 1.93a | 43.69 ± 0.37b | 43.3 ± 11.9 | 34.87 ± 4.2 | 657.5 ± 201.5a | 305.4 ± 63.2b |
| Other | 1.45 ± 0.25 | 1.61 ± 0.42 | 0.14 ± 0.04 | 0.18 ± 0.09 | 42.42 ± 1.55 | 42.34 ± 1.72 | 32.6 ± 4.0 | 32.8 ± 6 | 373.3 ± 80.2 | 370.4 ± 91.4 |

*Note:* Nutrient concentrations from wet and dry seasons were averaged to obtain mean values; means followed by different letters in the same row indicate significant differences between means (Mann-Whitney test, $P \leq .05$).

nutrient content (Dudley, MacKenzie, et al. 2014).

Although invasive $N_2$-fixing species have been shown to alter ecosystem properties in many environments, including wet forests and streams in Hawai'i (e.g., Vitousek and Walker 1989, Hughes and Denslow 2005, Hughes and Uowolo 2006, Wiegner et al. 2013), in this study presence of the invasive $N_2$-fixing species *P. pallida* was not correlated with increased N inputs to soil and anchialine pond water when compared to a non-N-fixing species. Litterfall mass increased with increasing stem density and basal area, but because neither these variables nor litter N content varied greatly between ponds dominated by one or the other of the two species, the presence of *P. pallida* around ponds was, in isolation, not a good predictor of nutrient deposition rates. In conditions of high water availability around anchialine ponds, we would expect *P. pallida* to have sufficient C and water required for high N fixation rates (Serraj et al. 1999) and resources for P acquisition from soils (Houlton et al. 2008). Because all the ponds surrounded by *T. populnea* were on relatively young lava flows (<5,000 ybp), where we would also expect N availability from soils to restrict plant growth (Vitousek et al. 1987), it was surprising that C and N deposition by *T. populnea* matched or exceeded that of *P. pallida*, and P deposition was considerably higher. One possible explanation for this is uptake of nutrients from groundwater. Riparian tree communities can take up substantial quantities of dissolved nutrient concentrations in groundwater (Peterjohn and Correl 1984, Hefting et al. 2005). Peterjohn and Correl (1984) reported assimilation of 15 kg $ha^{-1}$ $yr^{-1}$ of N by riparian forest bordering cultivated cropland, substantially more than the annual N additions estimated by Vitousek et al. (1987) to Hawaiian soils in forest area without N-fixing trees (5.5 kg $ha^{-1}$ $yr^{-1}$). Uptake of groundwater nutrients may form a considerable portion of tree nutrient requirements (Arndt et al. 2004), and at 15 kg $ha^{-1}$ $yr^{-1}$ of N would compose around 20% and 28% of litterfall N deposition measured for *T. populnea* and *P. pallida*, respectively, at sites where they dominate. Nutrient

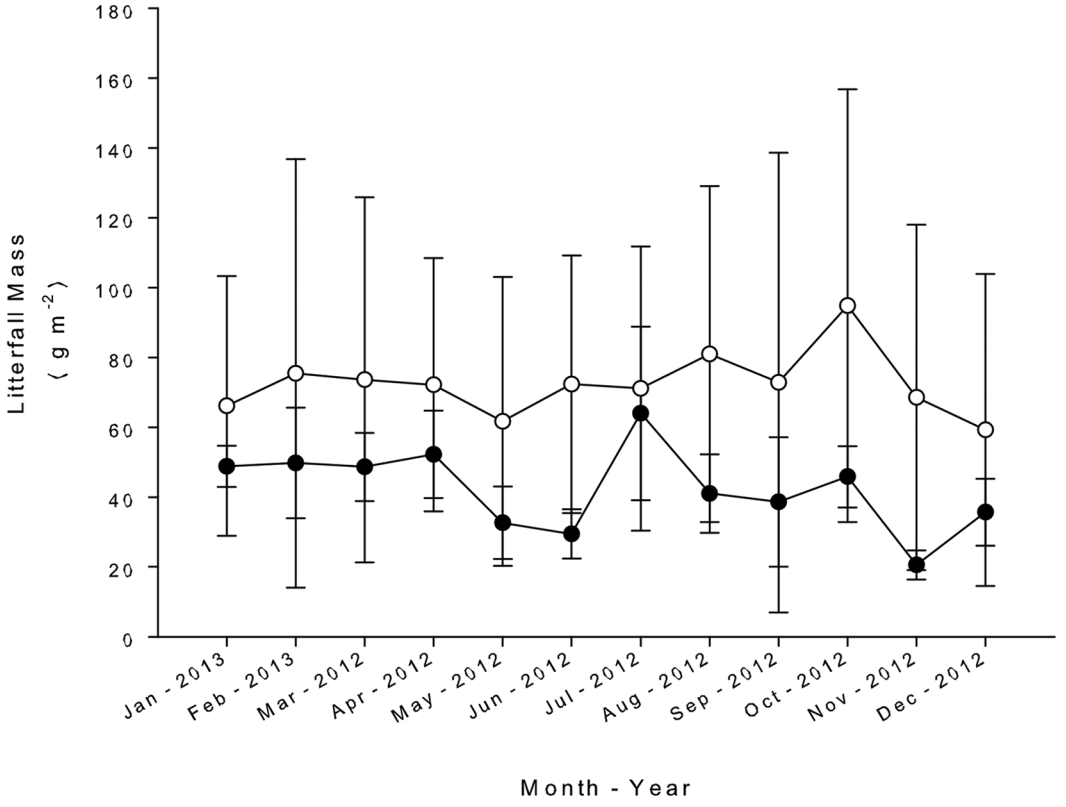


FIGURE 4. Average (±SE) monthly litterfall N mass for *P. pallida*- versus *T. populnea*-dominated anchialine ponds on the leeward coast of Hawai'i Island. The dry season spans May–October and the wet season spans November–April.

concentrations in groundwater in the vicinity of anchialine ponds on this coast are on the order of 60 μM liter$^{-1}$ total dissolved N and 2–6 μM liter$^{-1}$ dissolved reactive phosphorus (Dudley, MacKenzie et al. 2014), within the range at which groundwater has been observed to provide a substantial portion of N supply to riparian trees (Hefting et al. 2005).

A second explanation for the high productivity of *T. populnea* is the co-occurrence of *P. pallida* in ponds dominated by the former species. Although every effort was made to select sites with monospecific cover, *P. pallida* was present in litter collected from all ponds on at least one occasion, symptomatic of the prevalence of *P. pallida* through tree communities in low-lying areas of this coast. N deposition by *P. pallida* in *T. populnea*-dominated ponds ranged from >0.05% to 22% (>0.01 to 26.6 kg ha$^{-1}$ yr$^{-1}$) but was below 5% of total N deposited in all but one pond. It seems unlikely that *T. populnea* was reliant on N fixed by *P. pallida* to maintain its high rates of productivity and nutrient deposition.

Previous studies demonstrate that where phreatophytes invade ecosystems, they have the capacity to strongly alter the functioning of those ecosystems (Di Tomaso 1998). It is not known whether *T. populnea* represents native vegetation for lowland Hawai'i or was an early Polynesian introduction to the Hawaiian Islands; however it seems possible that both of the deep-rooted species in this study have the capacity to introduce considerable quantities of nutrients to soils. It is therefore possible that in areas of this coast where

phreatophytes have access to groundwater, nitrogen limitation of plant growth, characteristic of young Hawaiian soils (Vitousek et al. 1987), may have less influence on plant community development than at higher elevations where groundwater is inaccessible.

As well as enriching soils near anchialine ponds, litter deposited directly onto the water surface is likely to provide a substantial subsidy to aquatic food webs that may be measured against losses of autochthonous primary production caused by riparian light reduction. Ecosystem-level impacts of invasive $N_2$-fixers on aquatic communities have been well documented and include elevated water nutrient levels (Goldstein et al. 2010, Wiegner et al. 2013) and alteration and shifts in food webs (Atwood et al. 2010). Our results also indicated that high litter mass and P content of nonfixing tree *T. populnea* litter has the potential to influence the nutrient cycling processes in these ponds and their surroundings where it was present. This result is supported by the finding of high soluble reactive phosphorus in anchialine pond water with *T. populnea* canopy (Dudley, Hughes, and Ostertag 2014). In addition, *T. populnea* ponds were found to be more heterotrophic compared with *P. pallida* ponds, as evidenced by their higher respiration rates (E. Johnson, unpubl. data). However, it remains to be seen what consequences this heavy litter deposition has on biota within ponds, particularly for native *H. rubra*, which is considered a keystone species in sustaining benthic communities within anchialine ponds (Bailey-Brock and Brock 1993, Dalton et al. 2012, Sakihara 2012). Currently, it is also unknown whether riparian tree communities of either species result in net increases (e.g., Mineau et al. 2011) or reductions (e.g., Hefting et al. 2005) in nutrients entering adjacent marine ecosystems via groundwater discharge.

It is curious to note that although *P. pallida* leaf litter was present at all five *T. populnea* ponds, *T. populnea* leaves were only retrieved from one of five *P. pallida* ponds. This observation brings to mind whether *T. populnea* is spatially restricted by its dispersal method of coastal drift to ponds that are in close proximity to the coastline, or if there are other factors controlling the distribution of both *T. populnea* and *P. pallida*. Dispersal of *P. pallida* seeds is not restricted to coastal drift, because feral animals, such as goats and cattle, aid in germination and act as efficient dispersal agents (Gallaher and Merlin 2010). This was exploited in the late 1800s and early 1900s in Hawai‘i, and the spread of *P. pallida* in the Hawaiian Islands can be attributed to its use as fodder for the then-growing cattle industry (Gallaher and Merlin 2010). Thus, the historical land use of the studied sites could explain differences in species distribution among ponds. Because this study lacked *T. populnea* ponds that were completely free of *P. pallida*, it is difficult to determine how *T. populnea* behaves on its own. There are currently no statewide monitoring programs nor conservation and preservation laws for the protection of anchialine ponds from anthropogenic threats such as coastal development, pollution, and invasive species (Wiegner et al. 2006) despite their relative rarity, cultural significance, and biological importance. As a result, roughly one-third of anchialine ponds in the district of South Kohala on Hawai‘i Island have been destroyed by hotel and residential development (Stone 1989). Without comprehensive and ongoing studies, it is difficult to determine what defines a pristine anchialine habitat in terms of water quality, pond biota, and even surrounding plant species' identity and abundance, or lack thereof, making pond restoration back to a prehuman state nearly impossible.

## ACKNOWLEDGMENTS

For help in the field we thank Nick Wilhoite, Koa Matsuoka, Troy Sakihara, Justin Yeh, Michael Riney, Molly Murphy, Richard MacKenzie, Scarlett Kettwich, Chloe Hughes, and Claire Hughes. Lucas Mead, Tara Holitzki, and Erik Johnson ran the nutrient samples at the University of Hawai‘i at Hilo Analytical Laboratory. We recognize the staff at the Kaloko-Honokōhau National Historic Park and the Queen Lili‘uokalani Children's Center for their hospitality and access to field sites.

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