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Article in Pacific Science · April 2016

DOI: 10.2984/70.2.7

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Leaf Litter Breakdown of Native and Exotic Tree Species in Two Hawaiian Streams that Differ in Flow¹

Megan Roberts,² Ayron M. Strauch,^{3,5} Tracy Wiegner,² and Richard A. Mackenzie⁴

Abstract: Riparian leaf litter is a major source of allochthonous organic material to temperate and tropical streams, promoting primary and secondary productivity in lotic and nearshore habitats. In tropical island streams, where native leaf-shredding macroinvertebrates are absent, physical fragmentation from stream flow is an important factor affecting leaf litter breakdown and, thus, organic matter dynamics. Additionally, the invasion of exotic plants into riparian areas is expected to affect litter composition and, consequently, its degradation. We compared the interactions of stream flow and inputs of leaf litter from native and exotic plants on leaf litter breakdown in two streams of varying flows on Hawai'i Island. Decay rates were greater in the high flow stream than in the low flow one for exotic *Spathodea campanulata* (0.037 vs. 0.023 day⁻¹), but not significantly different for exotic *Psidium cattleianum* (0.003 vs. 0.003 day⁻¹), and native *Metrosideros polymorpha* (0.005 vs. 0.002 day⁻¹). In contrast, the exotic *Falcataria moluccana* (a nitrogen fixer) decomposed more rapidly in the low flow stream (0.017 day⁻¹) than in the high flow stream (0.010 day⁻¹). Breakdown rates also varied among species, with *S. campanulata* > *F. moluccana* > *M. polymorpha* > *P. cattleianum*. Breakdown rates were generally positively correlated to leaf nitrogen content and negatively correlated with leaf structure characteristics (toughness, organic carbon content, percentage lignin). Our findings indicate that stream flow regimes altered by climate change are likely to influence leaf litter decomposition, and *S. campanulata* and *F. moluccana* will likely impact organic matter dynamics in Hawaiian and other Pacific Island streams. However, predicted changes depend on the species composition of riparian leaf litter.

RIPARIAN VEGETATION CONTRIBUTES allochthonous organic material to rivers and is an important source of carbon and nutrients to lotic ecosystems (Webster and Meyer 1997; Meyer, Wallace, and Eggert 1998; Moretti, Gonçalves, and Callisto 2007). Leaf litter decomposition within streams is driven by physical and biological processes leading to the reduction, chemical, and physical transformation and consumption of litter material

(Peterson and Cummins 1974, Webster and Benfield 1986). The initial breakdown of litter material produces particulate organic matter, an important food source for many lotic fauna, and dissolved organic matter, a source of carbon and nutrients for bacteria, fungi, and algae (Ward 1986). Particulate organic matter and dissolved organic matter exported to nearshore environments also support estuarine metabolism (Schlesinger and Melack

¹ This research was funded by the U.S. Forest Service Pacific Southwest Research Station. Additional support was also provided by the Marine Science Department of the University of Hawai'i at Hilo for the analysis of leaf samples. Manuscript accepted 16 October 2015.

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1981; Wiegner, Tubal, and MacKenzie 2009; Atwood, Wiegner, and MacKenzie 2012) and marine food webs (Mann and Lazier 1991, Polis and Hurd 1996, Sakamaki and Richardson 2008). Reduced export, in both the amount and quality, of organic matter to streams and nearshore coastal areas is expected to negatively impact these ecological processes.

Stream flow provides an important control on leaf litter breakdown in temperate and tropical stream ecosystems. This is especially true in remote tropical island streams where shredding stream invertebrates are generally lacking (Resh and Deszalay 1995, Larned 2000, Benstead et al. 2009, MacKenzie et al. 2013). Hence, in tropical islands, stream flow is the primary mechanism that mechanically fragments leaf litter into finer particulate and dissolved forms that are more readily available for consumption by invertebrates and microbes (Benstead et al. 2009, MacKenzie et al. 2013). Stream flow can influence the residence time of litter, which affects the colonization of litter by bacterial and fungal communities that break down leaf structural compounds (Dubey, Stephenson, and Edwards 1995; Larned 2000; Chadwick et al. 2006; Gaudes et al. 2009). This suggests that future changes in stream flow (e.g., increased length and severity of drought leading to lower flows or more frequent, larger magnitude flood events) will impact leaf litter breakdown, organic matter dynamics, and the many stream and nearshore processes that rely on them.

The invasion of riparian areas by exotic plant species is another factor that is expected to impact leaf litter breakdown and organic matter dynamics in tropical island streams. Changing species composition may alter the quantity, quality, and timing of litter production. Throughout the tropical Pacific (e.g., Hawai'i, Guam, American Samoa, Pohnpei), native riparian plant species are quickly being displaced by exotic invasive species (Denslow, Space, and Thomas 2009; Hughes, Uowolo, and Togia 2012). Shifts in litter inputs can alter stream microbial, fungal, and invertebrate communities (Royer, Monaghan, and Minshall 1999; Thompson and Townshend 2003). In Hawai'i, native riparian forests dominated by *Metrosideros polymorpha* (ohia), *Acacia koa*

(koa), and *Dicranopteris linearis* (uluhe fern) are being rapidly replaced by exotic stands of *Psidium cattleianum* (strawberry guava), *Falcataria moluccana* (albizia), and/or *Spathodea campanulata* (African tulip) (Meyer 2000, Asner et al. 2008). Previous studies have found that some of these exotic plant species have faster growth rates (Hughes and Denslow 2005), greater litter inputs to streams, and faster litter degradation rates with consequences for stream water chemistry (Atwood et al. 2010, Wiegner and Tubal 2010, MacKenzie et al. 2013, Wiegner et al. 2013). The higher litter production of these exotic trees coupled with intrinsic differences in litter quality and structure are expected to impact leaf litter decomposition and organic matter cycling. In particular, *F. moluccana* and *S. campanulata* have more nitrogen (N)-rich leaves with lower percentage tannin content compared to *M. polymorpha* (Odoh, Ezugwu, and Ugwoke 2012; MacKenzie et al. 2013) and is, therefore, expected to decompose faster.

While the decomposition of the exotic *F. moluccana* is known to alter stream nutrient dynamics compared to the native *M. polymorpha* (Wiegner et al. 2013), *F. moluccana* is not the only exotic species invading riparian forests. We examined how differing stream flow (high vs. low) affects the decomposition rate of leaf litter from one native (*M. polymorpha*) and three exotic, invasive tree species (*P. cattleianum*, *F. moluccana*, *S. campanulata*). All leaves were expected to break down faster in the high flow stream compared to the low flow stream. Additionally, we hypothesized that due to differences in leaf physical and chemical properties, *M. polymorpha* and *P. cattleianum* would break down slower than *F. moluccana* or *S. campanulata*.

MATERIALS AND METHODS

Site Description

Study sites were selected in two streams at similar elevations (400–500 m above sea level), underlying geomorphology (USDA 2010), and surrounding land-cover on the windward side of Hawai'i Island (Figure 1). Three stations were selected in each stream with

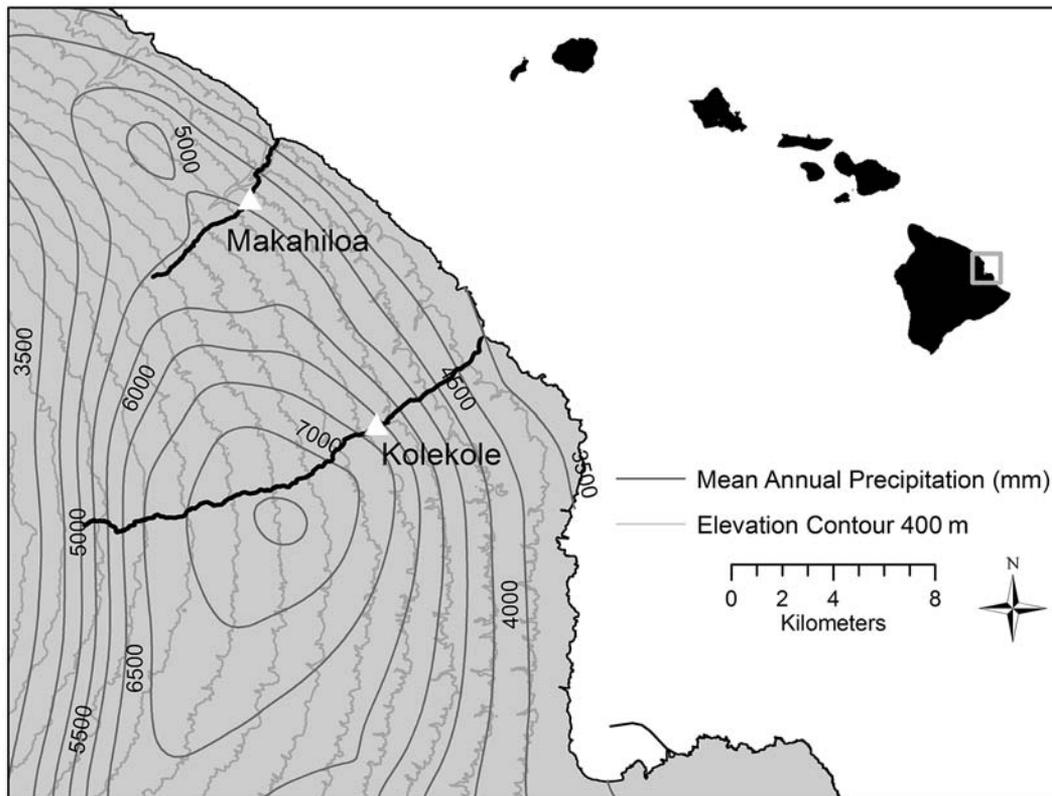


FIGURE 1. Map of the windward coast, Hawai'i Island, with study sites on each river indicated by triangles and mean annual precipitation isohyets based on Giambelluca et al. (2013).

similar water depths and velocities, although depths varied substantially with flow. The high flow stream, Kolekole, was located 19.3 km north of Hilo and the upstream watershed receives 6,426 mm of mean annual rainfall, while the low flow site, Makahiloa, was located 33.8 km north of Hilo, and receives 4,663 mm mean annual rainfall (Giambelluca et al. 2013). Both sites were directly downstream from a large plunge pool and located in runs with consistent bed material composed mostly of cobble and gravel (Fouk, unpubl. data). For more detailed site descriptions, see Strauch et al. (2015).

Stream Characteristics

Stream stage was monitored at 15-min intervals using HOBO logger pressure transducers

(Onset Corporation, Bourne, Massachusetts) and stream flow was calculated using a rating curve developed for each stream (Strauch et al. 2015). Mean flow, low flow (Q_{90}), and high flow (Q_{10}) were calculated for the study period as the average, 90th percentile (low), and 10th percentile (high) size flows, respectively. Flow variability was calculated over this interval as $Q_{90}:Q_{10}$. Stream water temperature was also measured at 15-min intervals by the pressure transducers and the daily mean, minimum, and maximum temperatures calculated for the study period. Filtered (0.7 μ m Whatman G/F filter; GE Healthcare Bio-Sciences, Pittsburgh, Pennsylvania) water samples were collected at monthly intervals from each stream, placed on ice in the field, and stored frozen in the laboratory until analysis. Samples were analyzed for sum nitrate + nitrite

—1
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(ΣNO_3^-), ammonium (NH_4^+), phosphate (PO_4^{3-}), dissolved organic carbon (DOC), and total dissolved nitrogen (TDN). ΣNO_3^- (U.S. Environmental Protection Agency [USEPA] 353.4, detection limit [d.l.] $0.1 \mu\text{mol l}^{-1}$), NH_4^+ (U.S. Geological Survey [USGS] I-2525, d.l. $1 \mu\text{mol l}^{-1}$), PO_4^{3-} (USEPA 365.5, d.l. $0.1 \mu\text{mol l}^{-1}$) were analyzed on a Technicon Pulse II Autoanalyzer (SEAL Analytical Inc., Mequon, Wisconsin). DOC and total dissolved nitrogen were analyzed by high-temperature combustion (Shimadzu TOC-V, TNM-1, Tokyo, Japan; d.l. $10 \mu\text{mol l}^{-1}$ and $5 \mu\text{mol l}^{-1}$, respectively). All nutrient samples were analyzed within 2 weeks of collection at the University of Hawai'i at Hilo Analytical Laboratory. Dissolved oxygen was measured in the field using a YSI 85 probe (YSI Corp., Yellow Springs, Ohio).

Leaf Collection

Leaf litter was collected weekly from tarps placed under each tree species between September and November 2011. *Psidium cattleianum* and *S. campanulata* grow in stands of multiple individuals resulting in one tarp collecting leaves from several trees. In contrast, tarps for *M. polymorpha* and *F. moluccana* collected leaves from individual trees. Once collected from tarps, leaves were air-dried for 30–60 days and sorted for whole leaves, removing sticks, stems, and seeds. Leaves were then stored in paper bags in a cool, dry place.

Leaf Analyses

Subsamples ($n=6$) of each species were ground up, weighed, combusted at 500°C for 3 hr, and then reweighed to determine percentage organic matter (Benfield 2007). A penetrometer was used to determine leaf toughness ($n=6$) by measuring the force (g) needed to puncture fresh leaf tissue with a 0.79 mm punch (Pearson and Connolly 2000). Subsamples ($n=6$) were also analyzed for percentage carbon (%C) and nitrogen (%N) content using a Costech model elemental analyzer (Costech Analytical Technologies, Inc., Valencia, California) at the University of Hawai'i at Hilo Analytical Laboratory. Ground samples were

separately analyzed for carbon fractions (soluble cell contents, hemicellulose and bound proteins, cellulose, and lignin) using an Ankom A200 Fiber Analyzer at the Carnegie Institute for Science at Stanford University (Rowland and Roberts 1994). One-half gram samples were placed in Ankom filter bags in a neutral detergent (to remove soluble cellular contents), followed by an acid detergent (to remove hemicellulose). Then, a 3-hr 72% sulfuric acid soak removed cellulose. Residual material (lignin and ash) was combusted at 550°C for 4 hr to determine ash content.

Experimental Setup

Approximately 5.00 g (weighted to the nearest 0.01 g) of each species was placed in an individual, 1 mm mesh, $10.5 \times 13 \text{ cm}$ nylon litterbag. Litterbags with a small mesh size were used due to the small size of *F. moluccana* leaves and because previous studies in Hawaiian streams found that decomposition was largely due to microbial activity and physical fragmentation, not from shredders that might be excluded from a small mesh bag (Larned 2000, MacKenzie et al. 2013). Twenty-four litterbags of each species were deployed in each stream in January 2012. Eight bags of each species were attached by cable ties to each of three 4.57 m chains and secured to pieces of rebar hammered into the stream bed. Three bags were collected from each stream at 1, 3, 7, 15, 37, 59, 120, and 240 days after initial deployment. The length of deployment was based on decomposition of tropical leaves in previous experiments in Hawai'i (MacKenzie et al. 2013). On each collection day, one litterbag of each replicate chain for each species was randomly selected, removed from each chain, and placed in a plastic bag and bucket for transport back to the laboratory ($n=3$ per species per site per date). Six additional bags of each species were used as transport controls and were carried to the stream on the initial day of deployment and returned to the laboratory where they were rinsed, oven dried at 70°C , and reweighed. The ratio of air-dried to oven-dried mass of these transport controls were then used to convert the initial air-dried weights of all leaf samples deployed in the

streams to initial oven-dried weights. These transport controls also corrected for any initial leaf mass lost due to transport or handling in the field or laboratory.

After returning to the laboratory, leaves were removed from litterbags and immediately rinsed in a 0.25 mm sieve with cold tap water to remove sediments, algae, and micro-invertebrates that may have accumulated. Organisms larger than 0.25 mm were removed from the samples by hand. Samples were then dried in a 70°C oven to a constant mass (~1 week) and weighed to the nearest 0.01 mg to determine dry mass. The organic fraction of leaf mass was determined by combusting approximately 0.5 g of ground sample (weighted to the nearest 0.01 mg) at 500°C for 3 hr. Subtracting the mass of mineral ash from the initial dry mass provided the ash free dry mass (AFDM) of each sample. Percentage remaining AFDM was calculated by dividing the AFDM of each sample at collection by the initial AFDM. Some bags were missing following high flow events: one bag from each species was missing from Kolekole and two bags from each species (except only one from *M. polymorpha*) were missing from Makahiloa. Missing values resulted in $n=2$ for that particular species, site, and date of litterbag collection.

Statistical Analysis

Mean \pm SE concentration of each water parameter was calculated and differences between streams were determined using a two-tailed unequal-variance t -test. A one-way analysis of variance was used to determine differences in nutrient composition (%C, %N, C:N, percentage organic matter) and toughness among tree species.

The mean \pm SE percentage remaining AFDM was plotted against time for each leaf litter species for each stream. Leaf litter decay constants (k) were calculated as the exponent coefficient in the two-parameter exponential decay regression model for each replicate of each species (Olson 1963). Differences in mean k values were determined using a fully fixed two-way analysis of variance to examine the effect of stream flow (high vs.

low), leaf litter species (*M. polymorpha*, *F. moluccana*, *S. campanulata*, and *P. cattleianum*), and their interactions. We acknowledge that replications within streams represent a level of pseudoreplication; however, a larger scale study was not feasible and replication of stream flow conditions across multiple streams is not possible as they do not exist. Following a significant interaction effect, we tested the hypothesis that litter breakdown would be greater in the higher flowing stream for each species using a one-sided unequal-variance t -test. Relationships between k and leaf characteristics were examined using a Spearman correlation for each stream. All analyses were completed using SigmaPlot (version 12.0, Systat Software, San Jose, California) with $\alpha=0.05$.

RESULTS

Stream Characteristics

Low (Q_{90}) and storm flows (Q_{10}) were 1.8 \times and 4.4 \times greater, respectively, in Kolekole Stream compared to Makahiloa Stream (Table 1). During the first 14 days of the experiment, a drought resulted in the mean flow in Makahiloa of $<0.01 \text{ m}^3 \text{ sec}^{-1}$ compared to $0.15 \text{ m}^3 \text{ sec}^{-1}$ for Kolekole, while the mean flow for the whole study for the two streams was $1.05 \text{ m}^3 \text{ sec}^{-1}$ and $1.79 \text{ m}^3 \text{ sec}^{-1}$, respectively. Flow variability ($Q_{10}:Q_{90}$) was greater in Kolekole (11.07) compared to Makahiloa (4.42). Nutrient concentrations were similar between streams (Table 1). Average, minimum, and maximum stream water temperatures were each significantly different ($P < .01$) between the streams, with Makahiloa consistently warmer than Kolekole.

Leaf Characteristics

Among tree species, there were significant differences in leaf toughness ($F=56.7$, $df=3$, 20 , $P < .001$), percentage organic matter ($F=105.3$, $df=3$, 20 , $P < .001$), %C content ($F=10.5$, $df=3$, 20 , $P < .001$), and %N content ($F=180$, $df=3$, 20 , $P < .001$) (Table 2). Toughness values were similar for *M. polymorpha* and *P. cattleianum*, but both species were about

TABLE 1

Mean \pm SE Physiochemical, Nutrient, and Stream Flow Characteristics in Makahiloa (Low Flow) and Kolekole (High Flow) Streams from Monthly Samples from February 2012 to September 2012, Hawai'i Island

	Makahiloa	Kolekole	<i>t</i> -statistic
DO (mg l ⁻¹)	7.96 \pm 0.20	7.82 \pm 0.64	0.15
NH ₄ ⁺ (μ M)	1.34 \pm 0.22	1.42 \pm 0.31	0.20
Σ NO ₃ ⁻ (μ M)	1.04 \pm 0.65	0.32 \pm 0.09	1.10
PO ₄ ⁻³ (μ M)	0.13 \pm 0.02	0.15 \pm 0.03	0.55
DOC (μ M)	360 \pm 59	314 \pm 54	0.57
TDN (μ M)	19 \pm 8	14 \pm 4	0.52
Mean daily temperature (°C)	19.45 \pm 0.01	18.15 \pm 0.01	10.18*
Min daily temperature (°C)	18.59 \pm 0.10	17.25 \pm 0.07	10.78*
Max daily temperature (°C)	20.36 \pm 0.11	19.11 \pm 0.09	9.01*
<i>Q</i> ₉₀ (m ³ sec ⁻¹)	0.24	0.42	
Mean flow (m ³ sec ⁻¹)	1.05	1.79	
<i>Q</i> ₁₀ (m ³ sec ⁻¹)	1.06	4.65	
<i>Q</i> ₁₀ : <i>Q</i> ₉₀	4.42	11.07	
Depth (m)	0.24 (0.13)	0.41 (0.07)	

Note: Results from Student *t*-statistic (df=16) for two-sided unequal variance *t*-test between streams are shown ($\alpha=0.05$); DO=dissolved oxygen; DOC=dissolved organic carbon TDN=total dissolved nitrogen.

**P*<.01.

4 \times tougher (*P*<.05) than both *F. moluccana* and *S. campanulata*, which had similar leaf toughness. Percentage organic matter was greatest in *M. polymorpha* (~95%) followed by *F. moluccana*, *P. cattleianum*, and *S. campanulata*, with no significant differences between *F. moluccana* and *P. cattleianum*. Percentage C content in *S. campanulata* (~37%) was ~1.3 \times less than the other three species (*P*<.05). *M. polymorpha* and *P. cattleianum* had similar %N content (~0.5%), while %N content in *S. campanulata* and *F. moluccana* was 3.6 \times and 2.5 \times greater, respectively (*P*<.05). There was also a significant difference in C:N among species (*F*=306, df=3, 20, *P*<.001), with *M. polymorpha* having the highest C:N followed by *P. cattleianum*, *S. campanulata*, and *F. moluccana* (Table 2).

Decomposition Rates

There was a significant species effect (*F*=124.38, df=3, 3, *P*<.0001) and a stream \times

species interaction (*F*=14.71, df=3, 3, *P*<.001), but only a trend in stream flow effect (*F*=3.675, df=3, 3, *P*=.073) for the decay constants. Decay constants in both streams were greatest for *S. campanulata*, followed by *F. moluccana*, *P. cattleianum*, and *M. polymorpha*, with no significant difference between *S. campanulata* and *F. moluccana* in the low flow stream, or between *P. cattleianum* and *M. polymorpha* for either stream (Figures 2 and 3). Significant interactions between streams and litter species were due to leaf litter decomposition being nearly 2 \times slower in the low flow stream for *S. campanulata* (*t*=3.56, df=4, *P*<.05), but almost 2 \times faster for *F. moluccana* (*t*=4.76, df=4, *P*<.05) than in the high flow stream. Leaf litter decomposition was also nearly 2 \times slower for *M. polymorpha* in the lower flowing stream, although this was not significant (*t*=1.71, df=4, *P*=.08). There was no significant difference in the decay constants of *P. cattleianum* between streams (*t*=0.3, df=4, *P*=.39). Decay constants were negatively correlated to leaf toughness, %N, and C:N in the high flow and low flow streams (Table 3). Toughness was negatively correlated with %N ($\rho=1.0$, *P*<.001) and C:N ($\rho=1.0$, *P*<.001).

DISCUSSION

Species Differences in Litter Breakdown

Variations in litter decomposition among tree species can be largely attributed to differences in the initial litter quality of those species (Kueffer et al. 2008). We found no difference between the decomposition rates of the *M. polymorpha* and *P. cattleianum*, which could have been due to their relatively close phylogenetic lineage (Myrtaceae family) (Wagner, Herbst, and Sohmer 1999), with similar toughness values and chemical composition (Table 2). Breakdown rates of *S. campanulata* and *F. moluccana* litter were nearly 5 \times to 10 \times faster than the other two species in either stream, related to initial differences in structural composition (e.g., tannins, lignin, cellulose) or nutrient (e.g., %N) content (Gonçalves Jr., Graça, and Callisto 2006; Martin, Tipping, and Reddy 2010; Walpola et al. 2011).

TABLE 2

Means \pm SE Leaf Toughness (g), Percentage Organic Material, Percentage Carbon (%C) and Nitrogen (%N), Carbon to Nitrogen Ratio (C:N) by Species ($n=6$). Percentage carbon fractions based on single samples

Characteristic	<i>M. polymorpha</i>	<i>P. cattleianum</i>	<i>F. moluccana</i>	<i>S. campanulata</i>
Leaf toughness (g)	301.1 \pm 59.3 ^a	269.8 \pm 29.5 ^a	69.2 \pm 17.7 ^b	88.0 \pm 20.2 ^b
% Organic material	94.9 \pm 0.1 ^c	91.3 \pm 0.2 ^b	92.2 \pm 0.1 ^b	85.6 \pm 0.2 ^a
%C	45.8 \pm 0.2 ^a	44.1 \pm 0.2 ^a	45.1 \pm 0.3 ^a	36.6 \pm 0.2 ^b
%N	0.46 \pm 0.03 ^a	0.57 \pm 0.04 ^a	1.81 \pm 0.07 ^c	1.25 \pm 0.05 ^b
C:N	99.3 \pm 0.3 ^c	78.2 \pm 0.4 ^b	24.9 \pm 0.1 ^a	29.3 \pm 0.2 ^a
% Soluble cell contents	51.71	62.00	37.78	61.25
% Hemicellulose and bound proteins	5.73	6.83	6.92	9.00
% Cellulose	22.7	14.86	16.71	12.97
% Lignin	19.43	15.88	38.14	16.34
% Ash	1.16	0.02	0.04	0.80

Note: Identical superscript letters are not statistically different (analysis of variance, $\alpha=0.05$).

Leaf structural characteristics are important factors that can retard litter breakdown in tropical streams (Gonçalves Jr., Graça, and Callisto 2007; Li, Ng, and Dudgeon 2009; MacKenzie et al. 2013). The two invasive species that decomposed fastest had the highest foliar N content (highest %N and lowest C:N), a factor known to affect litter quality. The significantly higher %N content and lower C:N ratios of *S. campanulata* and *F. moluccana* suggests that they also provide a higher quality substrate for fungal and bacterial colonization.

Only litter from the N₂-fixing species *F. moluccana* decomposed faster in the low flow stream than in the high flow stream. *Falcataria moluccana* litter has a greater %N content compared to the other species, and previous research has shown that *F. moluccana* leaf litter is colonized faster by fungi, supports up to 120% more fungal biomass, and breaks down 40% faster than native *M. polymorpha* leaves in Hawaiian streams (MacKenzie et al. 2013). Differences in the molecular composition of *F. moluccana* litter may make it more vulnerable to damage from ultraviolet light (Burger and Edwards 1996, Krause et al. 2003) and thus more likely to decay in certain conditions, such as during low flow periods when water levels are shallow. It is possible that higher stream water temperatures may have affected the decomposition of smaller leaves

more than larger leaves, as *F. moluccana* leaves are 5 \times to 10 \times smaller than the other leaves studied here, and the low flow stream had significantly higher mean daily temperatures.

Species-specific chemical and physical properties can alter the rate of microbial decomposition (Cornelissen et al. 1999, Kominoski et al. 2009). High soluble C content retards litter decomposition, while higher %N and lower C:N ratios result in greater microflora colonization and activity leading to higher rates of decomposition (Webster and Benfield 1986, Suberkropp and Chauvet 1995). *Metrosideros polymorpha* had greater toughness, percentage cellulose, and soluble cell contents compared to *F. moluccana*, while *F. moluccana* had the greatest percentage lignin, suggesting that the physical defenses of *M. polymorpha* may limit decomposition by microbial pathogens. There were negative correlations among decay constants (k), toughness, and C:N in both streams, but only a significant negative correlation between k with percentage organic matter and %C in the high flow stream. Furthermore, only in the low flow stream was there a significant positive correlation with litter decomposition rates and %N leaf content. Riparian vegetation is an important contributor of organic material to stream systems and changes in riparian species composition can alter carbon and nutrients inputs to freshwater and nearshore

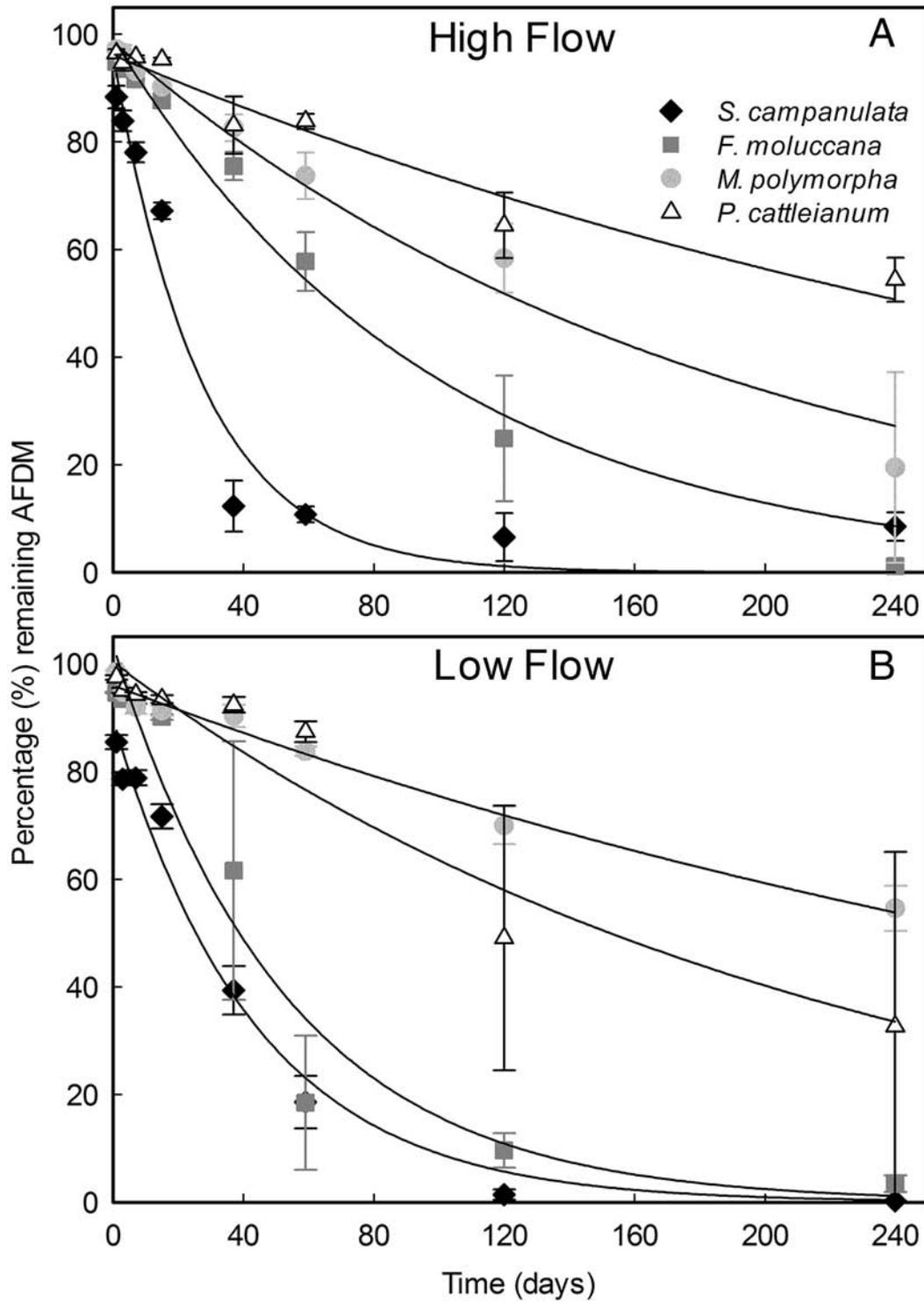


FIGURE 2. Mean \pm SE percent ash-free dry mass (AFDM) remaining in leaf packs ($n=3$) for each litter species in Kolekole (high flow) and Makahiloa (low flow) streams from February 2012 to September 2012, Hawai'i Island.

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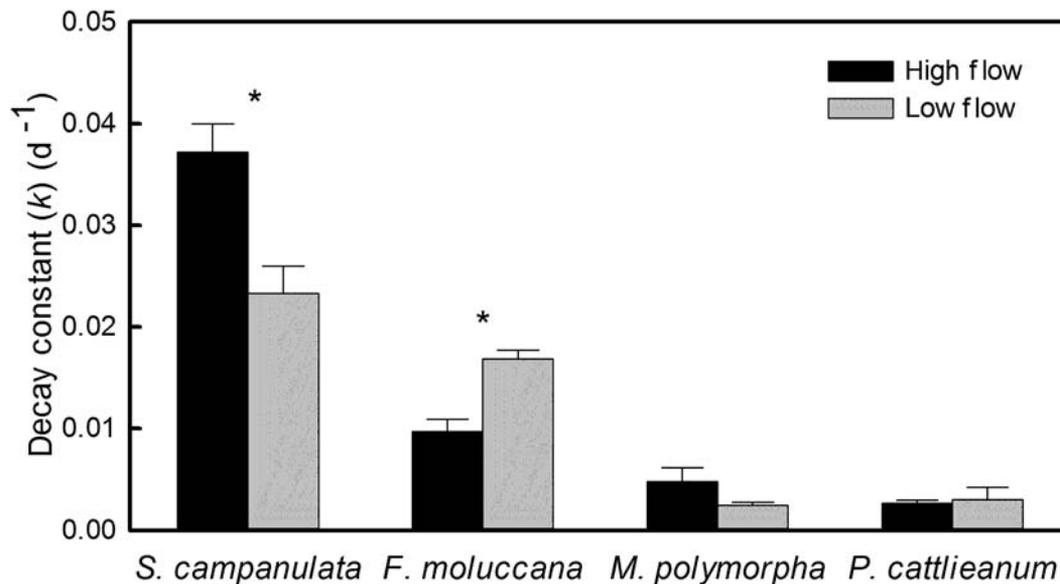


FIGURE 3. Comparison of mean \pm SE decay constants (k) (day^{-1}) for four litter species in Kolekole (high flow) and Makahiloa (low flow) streams, Hawai'i Island from February to September 2012. Asterisks (*) represent significant differences between streams ($P < .05$).

ecosystems (Bailey, Schweitzer, and Whitham 2001; Compton et al. 2003; Wiegner and Tubal 2010; MacKenzie et al. 2013).

Considering only leaf structural and nitrogen composition, replacement of native species (*M. polymorpha*) with closely related exotic species (*P. cattleanum*) may not have much impact on lotic systems. However, potential differences in the quantity and seasonality of litter production among introduced species must be addressed to better understand

TABLE 3

Spearman Correlation Coefficients between Leaf Decay Constant (k) and Leaf Toughness (g), Percentage Leaf Organic Matter, %C, %N, or C:N Ratio for in Makahiloa (Low Flow, $n = 12$) and Kolekole (High Flow, $n = 12$) Streams, Hawai'i Island

Stream	Toughness (g)	% Organic Matter			
		%C	%N	C:N	
Low flow	-0.67*	-0.56	-0.56	0.67*	-0.67*
High flow	-0.59*	-0.45	-0.45	0.59*	-0.59*

Note: Abbreviations as in Table 2.

* $P < .05$.

how shifts in riparian species composition will influence freshwater nutrient dynamics (Wiegner and Tubal 2010). Previous work has demonstrated that native Hawaiian forests have a more open canopy compared with invaded forests (Ostertag et al. 2009), with some seasonality in litter production (Vitousek et al. 1995). Comparing the quantity of litter produced in *P. cattleanum* forests with native *M. polymorpha* forests could elucidate such effects. Other exotic forest species are likely to influence both the quantity and quality of decomposition products. Binkley et al. (1992) demonstrated that *F. moluccana* litter production may peak in December, but the degree to which this is influenced by climate is unknown. This type of information with regard to leaf litter inputs, as well as the bioavailability of DOC leached from *F. moluccana*, *P. cattleanum*, and *M. polymorpha* suggests that these invasive trees can contribute 5 \times to 13 \times more bioavailable DOC—potentially altering nutrient and organic matter dynamics, as well as the food webs that depend on this vegetation as an energy and food source (Wiegner and Tubal 2010).

Differences in Leaf Litter Breakdown between Streams

Previous studies have found a decrease in the physical fragmentation of litter in lower and/or less constantly flowing streams (Maamri, Chergui, and Pattee 1997; Gonçalves Jr., Graça, and Callisto 2006). Similarly, Larned (2000) found that the export of coarse particulate organic matter decreased under decreasing flow conditions compared to normal conditions in Hawaiian streams. Contrary to expectations, we found only one species (*S. campanulata*) with a decomposition rate faster in the high flow stream. At the low flow site, litter bags were in shallower water and exposed to higher stream water temperatures, both of which may have confounded these results, as warmer water increases decomposition. Additionally, a small mesh size may have slowed the physical fragmentation of leaves in this study compared to other studies that used a larger size, but the relatively small leaf size of species used here prohibited use of a larger mesh, and all leaves should have been similarly affected by the mesh size in our experiment. Despite running the experiment to 240 days, the slow breakdown of *P. cattleianum* and *M. polymorpha* resulted in high variation, especially in the last sample collection, and substantial amounts of leaf material remaining in most of the bags. An additional experiment over an extended duration and resulting in a greater loss of leaf material for these slower decomposing species might improve our calculation of decomposition rate.

Potential Impacts of Climate Change on Leaf Litter Breakdown

The breakdown of leaf litter in temperate and tropical continental streams is largely attributed to the macroinvertebrate community (Webster and Benfield 1986; Wallace et al. 1997; Gessner, Chauvet, and Dobson 1999; Boyero, Pearson, and Camacho 2006), where shredders break down leaf material into fine and dissolved organic matter fractions that can then support other trophic guilds. The remote nature of tropical island streams, like those in Hawai'i, generally results in the

absence of invertebrates from the shredding trophic guild (Resh and Deszalay 1995, Yule 1996, Larned 2000, MacKenzie et al. 2013). As a result, leaf litter breakdown in these regions is heavily influenced by physical fragmentation of stream flow coupled with microbial activity (MacKenzie et al. 2013). Therefore, changes in stream flow should greatly affect leaf litter decomposition rates in these locations.

In Hawai'i, climate change is expected to influence rainfall through fewer, but more intense storm events and increased number of dry days between storm events (Solomon et al. 2007; Chu, Chen, and Schroeder 2010; Timm et al. 2011). For example, in Hawai'i, a 10% decrease in stream flow over the last 30 yr has been observed and in part has been attributed to decreased rainfall (Bassiouni and Oki 2012). Organic matter concentrations are highly dependent on stream flow conditions (Wiegner, Mead, and Molloy 2013) and because stream flow is such an important driver in leaf litter breakdown in tropical island streams, climate-driven changes to watershed hydrology are expected to influence future nutrient and organic matter dynamics. Furthermore, concurrent climate change-aided alterations in riparian vegetation (e.g., plant species composition change), which in some cases will decrease stream flow, are expected to affect stream ecosystem dynamics (Davis 2013). While our study design could not effectively isolate how the individual effects of decreased base flow and increased storm flow will influence leaf litter decomposition, it did provide insights into how decreased stream flow overall may alter organic matter dynamics in tropical island streams. In the low flow stream, there were many zero flow days, and flow was nearly half that of the high flow stream. Lower flows may have increased microorganism residence time, allowing a longer period of time for bacteria and fungi to colonize, and potentially influencing the breakdown rates of *F. moluccana*.

Implications for Management

Our results suggest that changes in riparian species composition may impact nutrient and

organic matter dynamics in streams with cascading effects on important stream and nearshore processes (Wiegner, Tubal, and MacKenzie 2009; Wiegner and Tubal 2010; Atwood, Wiegner, and MacKenzie 2012; Wiegner et al. 2013). The breakdown products from some invasive, exotic leaf litter could increase the bioavailability of nutrients compared to native leaf litter, with consequences to food web structures (Atwood et al. 2010, Wiegner and Tubal 2010, Wiegner et al. 2013), although our data demonstrate that replacing *M. polymorpha* with *P. cattleianum* may not alter the rate of nutrient availability. Furthermore, it is unclear whether additional species (*F. moluccana* or *S. campanulata*) will be capable of supporting similar ecological functions (e.g., heterotrophic growth of biofilm, nutrient cycling, nearshore pelagic food webs). Understanding the long-term consequences of changing leaf litter composition may help guide management of riparian forests. Climate projections for Hawai'i forecast continued warming and drying, with fewer, but more intense rain events resulting in altered stream flow regimes. Shifts in the frequency and intensity of storm flows and droughts are expected to alter leaf litter decomposition. However, exactly how changes in riparian leaf litter species composition will affect litter decomposition will depend on the species. Hence, the combined effects of changes in stream flow and riparian vegetation on ecological functions in Hawaiian streams remains unclear.

ACKNOWLEDGMENTS

The authors greatly appreciate access to study sites through Kamehameha Schools/Bishop Estate. Fieldwork was assisted by T. Fraundorf and P. Foulk. Laboratory work was assisted by D. Roberts and J. Troller. Revisions to this manuscript benefited greatly from two anonymous reviewers.

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