

## **Leaf-litter inputs from an invasive nitrogen-fixing tree influence organic-matter dynamics and nitrogen inputs in a Hawaiian river**

Author(s): Richard A. MacKenzie , Tracy N. Wiegner , Frances Kinslow , Nicole Cormier and Ayron M. Strauch

Source: Freshwater Science, 32(3):1036-1052. 2013.

Published By: The Society for Freshwater Science

DOI: <http://dx.doi.org/10.1899/12-152.1>

URL: <http://www.bioone.org/doi/full/10.1899/12-152.1>

---

BioOne ([www.bioone.org](http://www.bioone.org)) is a nonprofit, online aggregation of core research in the biological, ecological, and environmental sciences. BioOne provides a sustainable online platform for over 170 journals and books published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Web site, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at [www.bioone.org/page/terms\\_of\\_use](http://www.bioone.org/page/terms_of_use).

Usage of BioOne content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

## Leaf-litter inputs from an invasive nitrogen-fixing tree influence organic-matter dynamics and nitrogen inputs in a Hawaiian river

Richard A. MacKenzie<sup>1,4</sup>, Tracy N. Wiegner<sup>2,5</sup>, Frances Kinslow<sup>2,6</sup>,  
Nicole Cormier<sup>1,7</sup>, AND Ayrton M. Strauch<sup>3,8</sup>

<sup>1</sup> US Department of Agriculture Forest Service, Pacific Southwest Research Station, Institute of Pacific Islands Forestry, 60 Nowelo Street, Hilo, Hawaii 96720 USA

<sup>2</sup> Marine Science Department, University of Hawaii at Hilo, 200 West Kawili Street, Hilo, Hawaii 96720 USA

<sup>3</sup> Department of Natural Resources and Environmental Management, University of Hawaii at Manoa, 1910 East-West Road, Honolulu, Hawaii 96822 USA

**Abstract.** We examined how invasion of tropical riparian forests by an exotic N-fixing tree (*Falcataria moluccana*) affects organic-matter dynamics in a Hawaiian river by comparing early stages of leaf-litter breakdown between the exotic *F. moluccana* and native *Metrosideros polymorpha* trees. We examined early decomposition stages because of low leaf-litter retention rates (<20 d) that result from the flashy nature of tropical Pacific Island streams. Leaf breakdown rates, fungal biomass, and invertebrate abundances were 40, 120, and 30% greater, respectively, for *F. moluccana* than *M. polymorpha* leaves. Leaf-litter breakdown was largely a result of stream flow and to a lesser extent fungal colonization. Invertebrates were not an important factor in leaf-litter breakdown. Initial tannin content, leaf C:N, and toughness were important intrinsic factors inhibiting leaf breakdown and fungal colonization. Regression analyses between remaining N content (%) and ash-free dry mass of leaf litter revealed that the early stages of *F. moluccana* leaf-litter breakdown are a source of N to streams invaded by *F. moluccana* and contribute a conservatively estimated 2.1 to 5.7% to the available total dissolved N pool. Direct input of *F. moluccana* leaf litter influences early stages of leaf-litter breakdown in tropical streams with low leaf-litter retention rates. Direct input of leaf litter also contributes somewhat to N inputs, but subsurface flows through N-rich soils of *F. moluccana*-invaded riparian forests probably are a greater source.

**Key words:** nitrogen fixing, invasive species, *Falcataria moluccana*, leaf litter decomposition, tropical stream.

Riparian forests are a major source of nutrients and organic matter that shape community structure, foodweb dynamics, and productivity of lotic ecosystems (Vannote et al. 1980, Webster and Benfield 1986, Wallace et al. 1997). Invasion by exotic plants can significantly alter energy inputs from riparian forests to riverine faunal assemblages. For example, shifts from native to exotic leaf-litter inputs can significantly alter microbial, fungal, and invertebrate communities

that colonize leaves, leaf-litter breakdown rates, and the higher trophic levels supported by allochthonous resources (Royer et al. 1999, Thompson and Townsend 2003). Invasion of riparian forests by N-fixing trees can alter nutrient dynamics of forested ecosystems through increased N inputs and decomposition of N-rich organic matter within ecosystems (Vitousek et al. 1987, Hughes and Uowolo 2006). Increased N inputs have been reported from streams draining stands of native N-fixing alder (*Alnus rubra* Bong) (Compton et al. 2003, Shaftel et al. 2011), exotic N-fixing Russian olive (*Elaeagnus angustifolia*) (Mineau et al. 2011), and exotic N-fixing albizia trees (*Falcataria moluccana*) (Atwood et al. 2010, Wiegner et al., in press). However, it is unclear how increased N inputs from exotic N-fixing trees coupled with increased inputs of N-rich, high-food-quality leaf litter will

<sup>4</sup> E-mail addresses: rmackenzie@fs.fed.us

<sup>5</sup> wiegner@hawaii.edu

<sup>6</sup> kinslow@hawaii.edu

<sup>7</sup> Present address: US Geological Survey, National Wetlands Research Center, 700 Cajundome Blvd., Lafayette, Louisiana 70506 USA. E-mail: cormiern@usgs.gov

<sup>8</sup> astrauch@hawaii.edu

affect ecological functions, such as leaf-litter decomposition, in temperate or tropical streams.

*Albizia* (*Falcataria moluccana* Barnaby & Grimes) is an exotic N-fixing tree that is rapidly invading native Pacific Island watersheds (e.g., Hawaii, American Samoa). It was first introduced to Hawaii from New Guinea in the 1900s (Nelson 1965, Wagner et al. 1999) and has since invaded native lowland forests across Hawaii (Asner et al. 2008). It is considered a major threat to Hawaiian biodiversity because it can alter stand structure (Hughes and Denslow 2005), shift faunal communities (Allison et al. 2006), and create habitat for other invasive plants (Hughes and Denslow 2005). *Falcataria moluccana* also can alter nutrient cycles of native ecosystems via inputs of N-rich leaves, which significantly increase N concentrations in soils (Hughes and Denslow 2005, Hughes and Uowolo 2006) and stream water of invaded watersheds (Atwood et al. 2010, Wiegner et al., in press). Enrichment of stream water is hypothesized to be the result of subsurface flows through N-saturated soils in *F. moluccana*-invaded forests or of direct inputs of N-rich leaf litter to streams.

Increased nutrient loads and N-rich leaf-litter inputs to streams from invasive N-fixing trees could increase the nutritional value of leaf litter in Pacific Island streams by stimulating microbial colonization of those leaves (Graça et al. 2001, Sampaio et al. 2001, Gulis and Suberkropp 2003). Microbially conditioned leaves could then provide an alternative food source to stream fauna that do not commonly feed on leaf litter (e.g., atyid shrimp, snails), increasing leaf-litter breakdown in Pacific Island streams that lack classic leaf-shredding organisms (e.g., stoneflies) (Resh and deSzalay 1995, Benstead et al. 2009). This shift could increase the importance of allochthonous inputs in Pacific Island streams largely supported by autochthonous material (Larned et al. 2008) and alter stream organic-matter dynamics and invertebrate community composition. Nutrients released to the water column from leaf-litter breakdown also could increase nutrient loads to streams, rivers, and nearshore waters.

We documented how invasion of riparian forests by N-fixing trees would affect organic-matter cycling in tropical streams by conducting a series of short-term leaf-litter-breakdown experiments in the Wailuku River on the Island of Hawaii, Hawaii, USA. We focused on the early stages of leaf-litter decomposition because of low leaf-litter-retention rates (<20 d) that result from the flashy nature of these ecosystems (Larned 2000). During the wet and dry seasons of 2006 and 2007, we deployed leaf-litter packs and litter bags containing leaves from either *F. moluccana* or the

native *Metrosideros polymorpha* (Gaudichaud) in a forested and an urban reach of the Wailuku River. We compared leaf-litter-breakdown rates, fungal biomass, and invertebrate abundances between leaf-litter species, reaches, and types of leaf-litter pack, and among seasons. We hypothesized that: 1) leaf-litter nutrients and structural differences would result in higher breakdown rates for *F. moluccana* vs *M. polymorpha* leaves, 2) differences in leaf-litter nutrients would result in a greater role for invertebrates in leaf-litter breakdown of *F. moluccana* vs *M. polymorpha* leaves, and 3) elevated nutrient levels in streams from development or invasive species would increase leaf-litter breakdown of both species.

## Methods

### Study site

We selected 2 study reaches in the upper forested and lower urban areas of the Wailuku River on the island of Hawaii, Hawaii, USA. The forested reach was a 10-m-long, 3<sup>rd</sup>-order river reach (lat 19.709716°N, long -155.160951°W) at an elevation of 670 m asl (Fig. 1). The riparian forest was dominated by native koa (*Acacia koa* Gray), *M. polymorpha*, and uluhe fern (*Dicranopteris linearis* Burm). The forested reach had a 598-km<sup>2</sup> drainage basin with 48% forest, 20% grassland, and 32% barren area. The urban reach was a 10-m-long, 4<sup>th</sup>-order river reach (lat 19.752964°N, long -155.0938°W) at an elevation of 16.7 m asl. The urban reach was ~7.0 km downstream of the forested reach. The riparian forest of the urban reach was dominated by exotic clidemia (*Clidemia hirta* Linnaeus), strawberry guava (*P. cattleianum*), rose apple (*Syzygium jambos* Linnaeus), and *F. moluccana*. The urban reach had a 659-km<sup>2</sup> drainage basin with ~50% forest, ~21% grassland, ~29% barren land, <1% agricultural land, and <1% urban area. Both forested and urban reaches flowed through bedrock and boulder substrate. We randomly selected 6 stations from a 10-point grid laid over a map of the reaches. We pounded 1 rebar into the river substrate at each station and attached a 3-m-long chain to the rebar. We attached leaf-litter packs and litter bags to the chains. We conducted 3 short-term leaf-litter-breakdown experiments from: 1) February through April 2006 (2006 wet season), 2) June through July 2006 (2006 dry season), and 3) November through December 2006 (2007 wet season). We conducted a longer-term follow-up leaf-litter-breakdown experiment from June 2011 through March 2012. This study encompassed both wet and dry seasons (2011).

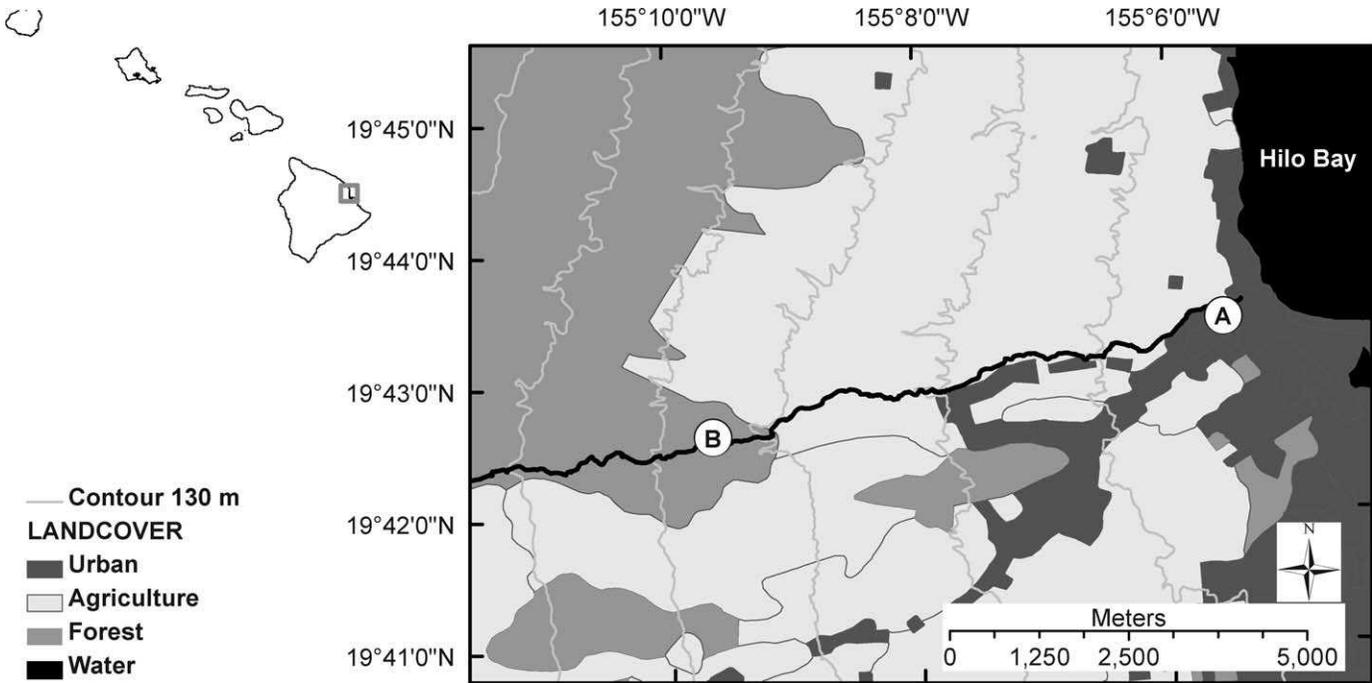


FIG. 1. Map of study site showing the lower urban (labeled A) and upper forested (labeled B) reaches and the 3 main land covers (urban, forest, agriculture).

#### Water-quality variables

We estimated mean, minimum, and maximum discharge values ( $\text{m}^3/\text{s}$ ) from the Piihonua gage (US Geological Survey [USGS] station 16704000), which was  $\sim 100$  m downstream of the forested reach. River discharge measurements were not available for the urban reach. We averaged stream discharge values over the duration of each experiment. Because of a major storm in the 2006 wet season, discharge values are from the first 3 wk of the experiment only. Data are available at <http://nwis.waterdata.usgs.gov/nwis/sw>.

We measured dissolved  $\text{O}_2$  (%), temperature, and specific conductance of the surface water of the forested and urban reaches with a handheld YSI<sup>TM</sup> 85 probe (Yellow Springs Instruments, Yellow Springs, Ohio). In the 3<sup>rd</sup> experiment (2007 wet season), we also made river depth and flow velocity measurements. We measured river depth with a meter stick and river velocities with a USGS pygmy flow meter (Rickly Hydrological Co., Columbus, Ohio). We made measurements once a week during each experiment. We estimated depth and velocity values for the forested reach in the 2006 wet and dry seasons from ratios of depth and velocity measured in the forested reach in the 2007 wet season. We used the same approach to estimate depth and velocity values

for the urban reach but with data from the urban reach.

We collected water samples at the beginning of the 2006 wet and dry seasons during baseflow conditions as part of another project that ended in the 2006 dry season. We did not collect water samples during the 2007 wet season. We filtered water samples through glass-fiber filters and stored them frozen until analysis for nutrients. We analyzed filtered samples for  $\text{NO}_2^-$  and  $\text{NO}_3^-$  ( $\Sigma\text{NO}_3$ , detection limit [DL] =  $0.1 \mu\text{M}$ ; USEPA 1983),  $\text{NH}_4^+$  (DL =  $1.0 \mu\text{M}$ ; Fishman 1993), and soluble reactive P (SRP; DL =  $0.1 \mu\text{M}$ ; USEPA 1983) with a Technicon AutoAnalyzer II (Pulse Instrumentation, Saskatoon, Canada).

#### Leaf-litter decomposition

We collected senescent *F. moluccana* and *M. polymorpha* leaf litter 1 mo before each experiment by placing leaf-litter traps under *F. moluccana* or *M. polymorpha* trees adjacent to the Wailuku River. We air-dried the leaf litter in the laboratory for 1 wk. We used  $\sim 2.5$  g of leaves to create each leaf-litter pack or litter bag. We used leaf-litter packs and litter bags to assess the importance of invertebrates in leaf-litter breakdown (invertebrates could access leaves in litter packs but not in litter bags). We constructed leaf-litter packs by stringing *F. moluccana* or *M. polymorpha*

leaves onto an 80-cm-long nylon thread. We reweighed the litter packs prior to deployment. We constructed 10 × 10-cm litter bags from 3-mm nylon mesh. We cable tied 1 leaf-litter pack and 1 litter bag of either *F. moluccana* or *M. polymorpha* to the inside of an 8.5-cm-diameter tubular wire cage. We constructed cages of 1-cm-mesh, plastic-coated hardware cloth and left them open on both ends. We used the cages to secure the leaf-litter packs during the extreme floods that can occur in the Wailuku River. Cages also provided habitat for any invertebrates that might feed on the leaf litter. We acknowledge the artifacts created by this treatment design (i.e., artificial habitat for potential detritivores), but we thought it suitable to test our hypotheses because *F. moluccana* and *M. polymorpha* leaf-litter packs and litter bags were treated the same in the forested and urban river reaches and in all 3 sampling seasons.

For each short-term experiment, we constructed 35 *F. moluccana* and 35 *M. polymorpha* tubular cages, each with a leaf-litter pack and a litter bag ( $n = 70$ ). We deployed 15 cages of each species in each reach. We cable-tied 5 *F. moluccana* cages or 5 *M. polymorpha* cages to chains at randomly selected stations, and we oriented cages so that the lengths and, thus, the tube openings were perpendicular to river flow. We returned the remaining 10 cages (5 *F. moluccana* and 5 *M. polymorpha*) to the laboratory where we used them to calculate initial dry mass for the deployed cages. We removed leaves from the leaf-litter packs and litter bags, oven-dried them at 60°C to a constant mass, and weighed them to the nearest 0.01 g.

We analyzed leaf-litter subsamples for total C and N with a Costech<sup>TM</sup> model elemental analyzer (Costech Analytical Technologies, Valencia, California). We quantified structural and secondary compounds in leaves with sequential C analysis. We sequentially separated samples into nonpolar, water soluble, and acid-soluble (i.e., cellulose) fractions, with the remaining residue representing lignin or lignin-based material (McClagherty 1985, Ryan 1990). We estimated tannin from the water-soluble fraction with the Follin–Denis method (Allen et al. 1974) and cellulose content from the acid-soluble fraction with a phenol–sulfuric acid assay (Dubois et al. 1956). We calculated fractions on an ash-free dry mass (AFDM) basis and expressed them as % initial litter mass (Ryan 1990). We measured leaf toughness from subsamples with a penetrometer with a 0.79-mm punch. We placed a beaker on the top of the punch and filled it with water until the punch broke through a veinless area of the leaf (Pearson and Connolly 2000). We combusted the remaining leaves in the samples at 550°C for 4 h and calculated AFDM. The

initial AFDM of the deployed cages was equal to the product of the initial fresh leaf-litter mass of the deployed cages and the fresh leaf-litter mass:AFDM ratio calculated from the 10 cages returned to the laboratory.

We removed leaf cages from the river once a week over a 5-wk period during each season. The 5-wk duration was based on results of previous leaf-litter studies done in the region (Archer 1983, Benstead 1996, Larned 2000) and was necessary because of the short retention time of leaf litter in these flashy systems (Larned 2000). We randomly selected 1 cage for removal from each of the 6 forested and urban reach stations. We enclosed leaf cages in plastic bags before removing them from the river, placed them on ice, and returned them to the laboratory where they were disassembled. We removed leaves from the leaf-litter packs and litter bags and gently washed them over a 500-mm-mesh sieve with tap water to remove any invertebrates, algae, or sediments. We dried the leaf litter to a constant mass at 60°C, weighed it to the nearest 0.01 g, subsampled for total N and C analyses, and combusted the remainder at 550°C for 4 h to calculate AFDM. We calculated % AFDM remaining by dividing the ending AFDM of each leaf pack by the initial AFDM. We  $\ln(x)$ -transformed % AFDM remaining and plotted it as a function of time for each station. We fit the data with a linear regression, and estimated leaf-litter decay coefficients ( $k$ ) from the slope of the regression (Benfield 1996). We averaged  $k$  values for each leaf-litter type across stations in each reach.

For the longer-term experiment, we weighed 5.0 g of *F. moluccana* and *M. polymorpha* leaves, placed them in litter bags, and deployed them in the forested reach. We used only litter bags in the forested reach because decomposition rates did not differ between litter bags and leaf-litter packs or between the forested and urban reach (see Results). We removed leaf-litter packs on days 3, 7, 14, 46, 72, 116, and 259 and processed them as described above.

#### *Fungal biomass*

We extracted ergosterol from a subsample of leaf litter from the litter bags to estimate fungal biomass (Gessner and Chauvet 1993, Gessner and Schmitt 1996) on day 0 and during weeks 1, 3, and 5 of each short-term experiment. We used whole *F. moluccana* leaves because of their small size (<1 cm), but we took subsamples of *M. polymorpha* leaves with a 6-mm-diameter leaf punch. We froze, lyophilized, and weighed the leaf subsamples and extracted ergosterol from the leaf litter with the techniques described by

Gessner and Schmitt (1996). We converted ergosterol mass to fungal biomass with a conversion factor of 5.5 mg ergosterol/g fungal biomass (Gessner and Newell 2002) and averaged values across stations in each reach.

#### *Invertebrate abundance*

We sorted invertebrates from leaf-litter packs and litter bags and identified them to family (Merritt and Cummins 1996). We estimated invertebrate abundance by summing the total number of invertebrates per litter bag or leaf pack and dividing by the remaining AFDM of leaf litter from the litter bag or leaf pack on each date.

#### *Contribution of leaf-litter N to the water column*

We plotted %N remaining in leaf litter from each *F. moluccana* and *M. polymorpha* short-term leaf-litter pack against %AFDM remaining for that leaf-litter pack for all 3 seasons to examine changes in leaf-litter N. We ran linear regressions in Sigma Plot (version 8.0; SYSTAT Software Inc., San Jose, California). We estimated the change in %N relative to the change in total leaf biomass, and thus time, from the slope of the line (Aber and Melillo 1980, 1982). Positive slopes indicated N immobilization from the water column, whereas negative slopes indicated N release to the water column.

We estimated the potential % contribution of *F. moluccana* leaf-litter breakdown to the total N budget of a heavily invaded stream (Ainaloa Stream) (Wiegner et al. in press) with a series of calculations as

$$N_{\text{rem}} = (SS_{\text{Fmol}})(\%N_{\text{leaf}})r$$

where  $N_{\text{rem}}$  is the amount of N remineralized ( $\text{mg}/\text{m}^2$ ) from *F. moluccana* leaf-litter breakdown,  $SS_{\text{Fmol}}$  is the standing stock of *F. moluccana* leaf litter ( $\text{mg}/\text{m}^2$ ),  $\%N_{\text{leaf}}$  is %N content of *F. moluccana* leaf litter, and  $r$  is the %N released. We estimated  $SS_{\text{Fmol}}$  from randomly collected,  $30 \times 30$ -cm Surber samples from Ainaloa Stream. We sorted all *F. moluccana* leaf litter from samples, dried it to constant mass, weighed it, and divided by the area of the Surber sampler ( $0.04 \text{ m}^2$ ). The flux of total dissolved N (TDN) above a  $1.0\text{-m}^2$  area of stream ( $\text{mg}/\text{m}^2$ ) at any instant ( $\Phi_{\text{TDN}}$ ) was

$$\Phi_{\text{TDN}} = (\text{TDN}_{\text{H}_2\text{O}})h$$

where  $\text{TDN}_{\text{H}_2\text{O}}$  was the average water-column TDN concentration ( $\text{mg}/\text{m}^3$ ) from an *F. moluccana*-invaded reach of the Ainaloa stream (Wiegner et al. in press) and  $h$  was the average water depth (cm). The % contribution of N released from *F. moluccana* break-

down to the overall N budget of the invaded Ainaloa stream ( $\%N_{\text{Fmol}}$ ) was

$$\%N_{\text{Fmol}} = N_{\text{rem}}/\Phi_{\text{TDN}}.$$

#### *Statistical analysis*

We compared dissolved  $\text{O}_2$ , temperature, and specific conductance between reaches (urban vs forested) and among seasons (2006 wet season, 2006 dry season, 2007 wet season) with a 2-way analysis of variance (ANOVA). We compared initial chemical and structural components of leaf litter between leaf species (*F. moluccana* vs *M. polymorpha*) with a 1-way ANOVA. For short-term experiments, we compared  $\ln(x)$ -transformed leaf-litter decay coefficients from each station between leaf species, reaches, and treatments (leaf-litter packs vs litter bags), and among seasons with a 4-way factorial ANOVA. Fixed effects included leaf species, reach, treatment, and season and all 2-, 3-, and 4-way interactions. For the longer-term experiment, we compared  $\ln(x)$ -transformed leaf-litter decay coefficients between leaf species with a 1-way ANOVA.

Initial examination of fungal biomass over time between the 2 leaf species revealed that peak fungal biomass occurred at different times for the 2 species. Furthermore, patterns of fungal biomass over time were not consistently linear or quadratic, and therefore, regression analyses could not be used to calculate fungal colonization rates and compare fungal biomass over time. Instead, we used Functional Data Analysis (FDA) to examine how fungal biomass on leaf litter changed over time. FDA represents time series of various data sets as functions and conducts analyses on the functions rather than on the data (Ramsey and Silverman 2005). FDA integrated fungal biomass over time for each leaf type at each reach and each season. Functions were run from the starting time point (day 0) to the day of maximum fungal biomass in Sigma Plot. Patterns in invertebrate abundances over time were neither linear nor quadratic. Thus, functions of invertebrate abundance over time were calculated in a way similar to the approach taken for fungal biomass over time, with the exception that the area under the plot was determined over the entire study period. We compared fungal biomass and invertebrate abundance from each station between leaf species, reaches, and treatments (invertebrate abundance only), and among seasons using 3- and 4-way ANOVAs, respectively.

We used Pearson's product-moment correlation analysis to identify relationships among leaf-litter breakdown rates, invertebrate abundances, physico-chemical variables, and intrinsic qualities of leaf litter in leaf-litter packs and litter bags. We included fungal

TABLE 1. Mean ( $\pm 1$  SE) values for environmental variables measured at the upper forested and lower urban reaches of the Wailuku River, Hawaii, USA. Dissolved O<sub>2</sub> (DO), temperature (Temp), and specific conductance (SpC) were compared between reaches and among seasons with 2-way analysis of variance. Q = discharge, min = minimum, max = maximum,  $\Sigma\text{NO}_3 = \text{NO}_2^- + \text{NO}_3^-$ , SRP = soluble reactive P. Asterisks denote significant differences between reaches: \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ . Means with the same superscript after asterisks are not significantly different among seasons.

Variable	2006 wet season		2006 dry season		2007 wet season	
	Forested	Urban	Forested	Urban	Forested	Urban
Q (m <sup>3</sup> /s)	2.1 $\pm$ 0.3	–	1.7 $\pm$ 0.1	–	1.2 $\pm$ 0.3	–
Q <sub>min</sub> (m <sup>3</sup> /s)	1.0	–	0.8	–	0.5	–
Q <sub>max</sub> (m <sup>3</sup> /s)	7.3	–	4.3	–	9.7	–
Depth (cm)	31.8	70.4	27.9	65.8	19.7 $\pm$ 1.8	46.6 $\pm$ 6.9
Velocity (cm/s)	76.0	3.0	61.6	2.5	43.4 $\pm$ 6.6	1.8 $\pm$ 1.4
DO (% saturation)	89.4 $\pm$ 1.7	91.7 $\pm$ 1.1***	87.9 $\pm$ 4.59	103.5 $\pm$ 2.6***	93.5 $\pm$ 2.4	97.8 $\pm$ 2.5***
Temperature (°C)	19.5 $\pm$ 0.4	21.7 $\pm$ 0.5***a	20.1 $\pm$ 0.4	22.7 $\pm$ 0.4***b	16.9 $\pm$ 0.4	19.7 $\pm$ 0.5***c
SpC (mS/cm)	32.7 $\pm$ 1.7	74.2 $\pm$ 8.6***b	34.3 $\pm$ 1.0	68.4 $\pm$ 9.1***a	33.4 $\pm$ 1.3	46.7 $\pm$ 3.0***a
$\Sigma\text{NO}_3$ ( $\mu\text{M}$ )	0.8	2.4	0.6	0.6	–	–
NH <sub>4</sub> <sup>+</sup> ( $\mu\text{M}$ )	<1.0	<1.0	<1.0	<1.0	–	–
SRP ( $\mu\text{M}$ )	<0.1	<0.1	<0.1	<0.1	–	–

biomass values in tests done on data from litter bags because they were measured only from litter bags. We used mean and maximum discharge values from the forested reach for the urban reach because discharge values were not available for the urban reach and because reach did not affect % remaining AFDM, leaf-litter decay coefficients, or fungal biomass.

We ran post hoc analyses on seasonal comparisons with the Tukey–Kramer method. We ran all ANOVAs with PROC MIXED (SAS, version 9.1; SAS Institute, Cary, North Carolina), whereas we ran correlations in SYSTAT (version 10; Systat Software, Inc., San Jose, California). We set  $\alpha = 0.05$  for all analyses.

## Results

### Environmental variables

River velocities were higher and water depths were shallower in the forested than in the urban reach (Table 1). Dissolved O<sub>2</sub> ( $F_{1,25} = 10.95$ ,  $p < 0.001$ ), temperature ( $F_{1,25} = 66.9$ ,  $p < 0.001$ ), and specific conductance ( $F_{1,25} = 52.61$ ,  $p < 0.001$ ) were all lower in the forested than the urban reach (Table 1). Nutrient ( $\Sigma\text{NO}_3$ , NH<sub>4</sub><sup>+</sup>, and SRP) concentrations did not differ between the forested and urban reaches except in the 2006 wet season when  $\Sigma\text{NO}_3^-$  values were higher in the urban (2.4  $\mu\text{M}$ ) than in the forested reach (0.8  $\mu\text{M}$ ; Table 1). NH<sub>4</sub><sup>+</sup> and SRP were generally below detection limits.

Mean, minimum, and maximum discharge values were available only from the Piihonua gaging station 100 m downstream of the forested reach. Mean and minimum discharge values decreased over time such that 2006 wet season > 2006 dry season > 2007 wet

season. Maximum discharge was greater in the wet seasons than the dry season, and water temperatures were significantly greater in the dry season than in the wet seasons ( $F_{2,25} = 32.09$ ,  $p < 0.001$ ). Dissolved O<sub>2</sub> was similar among seasons.

### Leaf-litter chemistry

Initial cellulose and lignin levels were higher in *F. moluccana* than in *M. polymorpha* leaves ( $F_{1,10} = 5.80$ ,  $p < 0.05$ ;  $F_{1,10} = 67.44$ ,  $p < 0.001$ ; respectively) (Table 2). Initial N content was 3 $\times$  higher in *F. moluccana* leaves than in *M. polymorpha* leaves ( $F_{1,10} = 4840.20$ ,  $p < 0.001$ ). Initial tannin content was 5 $\times$  greater in *M. polymorpha* than in *F. moluccana* leaves ( $F_{1,10} = 253.10$ ,  $p < 0.001$ ). *Metrosideros polymorpha* leaves also had higher C:N ( $F_{1,10} = 558.70$ ,  $p < 0.001$ ),

TABLE 2. Mean ( $\pm 1$  SE;  $n = 6$ ) initial values of chemical and physical characteristics of *Falcataria moluccana* and *Metrosideros polymorpha* leaf litter collected from riparian forests along the Wailuku River, Hawaii, USA. Values were compared between species with 1-way analysis of variance. Asterisks denote significant differences between leaf species: \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ .

Characteristic	<i>F. moluccana</i>	<i>M. polymorpha</i>
%C	43.01 $\pm$ 0.17	45.34 $\pm$ 0.13***
%N	1.48 $\pm$ 0.01	0.48 $\pm$ 0.01***
C:N	29.05 $\pm$ 0.13	94.73 $\pm$ 2.78***
Cellulose (%)	38.33 $\pm$ 0.87	34.89 $\pm$ 1.08*
Tannins (%)	3.88 $\pm$ 0.69	20.79 $\pm$ 0.81***
Lignin (%)	38.84 $\pm$ 2.15	19.89 $\pm$ 0.83***
Lignin:N	26.21 $\pm$ 1.38	41.58 $\pm$ 2.27***
Toughness (mg)	74.48 $\pm$ 9.08	184.17 $\pm$ 18.58***

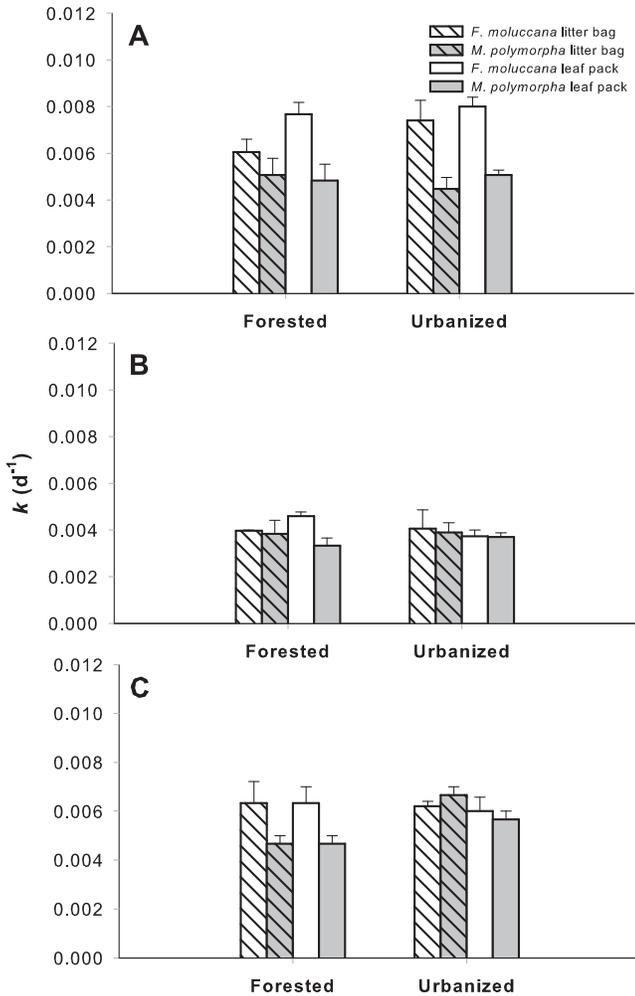


FIG. 2. Mean (+1 SE) breakdown rates ( $k$ ;  $\text{d}^{-1}$ ) from *Falcattaria moluccana* and *Metrosideros polymorpha* leaf-litter packs and litter bags in short-term experiments in the 2006 wet season (A), 2006 dry season (B), and 2007 wet season (C) in the Wailuku River, Hawaii, USA.

lignin:N ( $F_{1,10} = 33.5$ ,  $p < 0.001$ ), and leaf toughness ( $F_{1,15} = 33.90$ ,  $p < 0.001$ ) than *F. moluccana* leaves.

#### Leaf-litter breakdown

A 30-d storm strongly increased river discharge over a prolonged period after week 3 of the 2006 wet-season sampling period. Remaining leaf-litter packs and litter bags were either missing or severely damaged. As a result, leaf-litter decomposition rates for the 2006 wet season could be measured only from leaf packs and litter bags collected from weeks 1 through 3. Analysis of data from the 2006 dry and 2007 wet seasons showed no differences in leaf-litter  $k$ -values calculated with and without data for weeks 4 and 5. Therefore, we used the full 2006 dry- and 2007

wet-season data sets and the partial 2006 wet-season data set in subsequent analyses.

Leaf-litter  $k$ -values averaged across years, reaches, and treatments from the short-term experiments were nearly  $2\times$  greater for *F. moluccana* than for *M. polymorpha* ( $F_{1,47} = 27.99$ ,  $p < 0.001$ ; Fig. 2A–C). Average  $k$ -values also differed among seasons ( $F_{2,47} = 45.44$ ,  $p < 0.001$ ).  $k$ -values were greater in the 2006 and 2007 wet seasons than in the 2006 dry season for both species (season  $\times$  leaf,  $F_{2,47} = 5.28$ ,  $p < 0.01$ ). The interaction between season and leaf also revealed that *F. moluccana* generally broke down faster than *M. polymorpha* in all seasons, but the difference was significant only in the 2006 wet season (Fig. 2A). Leaf-litter  $k$ -values were similar between reaches and between litter bags and leaf-litter packs. In the long-term experiment, leaf-litter  $k$ -values were 20% higher for *F. moluccana* ( $0.0050 \pm 0.0001/\text{d}$ ) than for *M. polymorpha* ( $0.0042 \pm 0.0001/\text{d}$ ) ( $F_{1,4} = 31.14$ ,  $p < 0.001$ ).

In leaf-litter packs,  $k$ -values were positively correlated with leaf lignin content ( $r = 0.42$ ,  $p < 0.01$ ,  $n = 36$ ), mean discharge ( $r = 0.46$ ,  $p < 0.01$ ,  $n = 36$ ), and maximum discharge ( $r = 0.54$ ,  $p < 0.001$ ,  $n = 36$ ), and negatively correlated with C:N ( $r = -0.49$ ,  $p < 0.01$ ,  $n = 36$ ), leaf toughness ( $r = -0.43$ ,  $p < 0.01$ ,  $n = 36$ ), and initial leaf tannin content ( $r = -0.48$ ,  $p < 0.01$ ,  $n = 36$ ) (Table 3). In litter bags,  $k$ -values were positively correlated to initial leaf cellulose content ( $r = 0.33$ ,  $p < 0.05$ ,  $n = 36$ ), leaf lignin content ( $r = 0.32$ ,  $p < 0.05$ ,  $n = 36$ ), and maximum discharge ( $r = 0.32$ ,  $p < 0.05$ ,  $n = 36$ ) and negatively correlated to initial leaf tannin content ( $r = -0.35$ ,  $p < 0.05$ ,  $n = 36$ ). Fungal biomass was positively correlated to initial leaf cellulose content ( $r = 0.41$ ,  $p < 0.05$ ,  $n = 36$ ), invertebrate abundance ( $r = 0.34$ ,  $p < 0.05$ ,  $n = 36$ ), and lignin content ( $r = 0.80$ ,  $p < 0.001$ ,  $n = 36$ ) and negatively correlated to C:N ( $r = -0.84$ ,  $p < 0.001$ ,  $n = 36$ ), initial leaf toughness ( $r = -0.75$ ,  $p < 0.001$ ,  $n = 36$ ), and initial leaf tannin content ( $r = -0.82$ ,  $p < 0.001$ ,  $n = 36$ ). Invertebrate abundance was negatively correlated to dissolved  $\text{O}_2$  ( $r = -0.51$ ,  $p < 0.001$ ,  $n = 36$ ) and mean river discharge ( $r = -0.30$ ,  $p = 0.07$ ,  $n = 36$ ).

#### Fungal biomass

Initial fungal biomass was greater on *F. moluccana* than on *M. polymorpha* leaves (Fig. 3A–C). Fungal biomass on *F. moluccana* leaves peaked after the 1<sup>st</sup> or 2<sup>nd</sup> sampling event and then declined. Fungal biomass on *M. polymorpha* leaves increased linearly over time. Fungal biomass was greater on *F. moluccana* than on *M. polymorpha* leaves by the end of 2006 wet-season experiment (Fig. 3A), but was similar between

TABLE 3. Pearson's correlation coefficients for litter-breakdown rates of *Falcataria moluccana* and *Metrosideros polymorpha*, fungal biomass, and invertebrate abundance in leaf-litter packs and litter bags, and environmental variables in the Wailuku River, Hawaii 2006–2007. DO = dissolved O<sub>2</sub>, Q = mean discharge, Q<sub>max</sub> = maximum discharge, ind = individuals, AFDM = ash-free dry mass.

Variable	Factor	<i>r</i>	<i>p</i>
Leaf-litter-pack-breakdown rate (/d)	C:N	-0.49	<0.01
	% lignin	0.42	<0.01
	Leaf toughness (mg)	-0.43	<0.01
	% tannins	-0.48	<0.01
	Q (m <sup>3</sup> /s)	0.46	<0.01
	Q <sub>max</sub> (m <sup>3</sup> /s)	0.54	<0.001
Litter bag breakdown rate (/d)	% cellulose	0.33	<0.05
	% lignin	0.32	<0.05
	% tannins	-0.35	<0.05
	Q <sub>max</sub>	0.32	<0.05
	% cellulose	0.41	<0.05
Fungal biomass (mg/g leaf AFDM remaining)	C:N	-0.84	<0.001
	Invertebrate abundance	0.34	<0.05
	% lignin	0.80	<0.001
	Leaf toughness	-0.75	<0.001
	% tannins	-0.82	<0.001
	%DO	-0.51	<0.001
	Q	-0.30	0.07

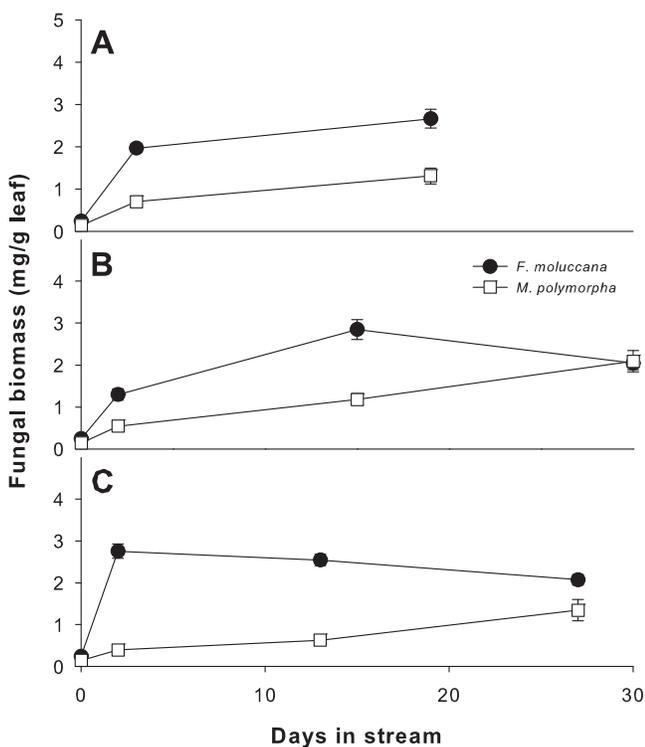


FIG. 3. Mean ( $\pm 1$  SE) fungal biomass values plotted over time from *Falcataria moluccana* and *Metrosideros polymorpha* leaf litter in short-term experiments in the 2006 wet season (A), 2006 dry season (B), and 2007 wet season (C) in the Wailuku River, Hawaii, USA. Week 5 values from the 2006 wet season are missing because of a major storm that happened after week 3.

the 2 leaf species by the end of the other experiments (Fig. 3B, C).

Mean (SE) fungal biomass was >120% higher on *F. moluccana* leaf litter ( $1.82 \pm 0.07$  mg/g leaf) than on *M. polymorpha* litter ( $0.82 \pm 0.08$  mg/g leaf) ( $F_{1,24} = 170.26$ ,  $p < 0.001$ ; Table 4). Fungal biomass did not differ among seasons, but the leaf species  $\times$  season interaction was significant ( $F_{2,24} = 7.41$ ,  $p < 0.01$ ). Fungal colonization rates were greater on *M. polymorpha* leaves in the 2006 dry season than in the wet seasons. Fungal biomass tended to be higher on *F. moluccana* leaves during the wet seasons, but this trend was not significant. The leaf species  $\times$  season  $\times$  reach interaction also was significant ( $F_{2,24} = 3.65$ ,  $p < 0.05$ ). Fungal biomass was greater on *F. moluccana* than on *M. polymorpha* leaves in both reaches and all seasons except in the urban reach in the 2006 dry season, when fungal biomass tended to be greater on *F. moluccana* than *M. polymorpha* leaves, but this trend was not significant.

#### Invertebrate abundance

Invertebrate abundance was greater on *F. moluccana* ( $27.4 \pm 4.2$  individuals [ind]/g leaf) than *M. polymorpha* leaves ( $19.0 \pm 3.0$  ind/g leaf) ( $F_{1,48} = 33.78$ ,  $p < 0.001$ ), was greater in the forested ( $27.8 \pm 4.0$  ind/g leaf) than in the urban reach ( $18.6 \pm 3.3$  ind/g leaf) ( $F_{1,48} = 105.39$ ,  $p < 0.001$ ), and was greater in the 2007 wet season ( $29.3 \pm 4.0$  ind/g leaf) and 2006 dry season ( $27.5 \pm 5.0$  ind/g leaf) than in the wet season ( $12.8 \pm$

TABLE 4. Mean ( $\pm 1$  SE) daily fungal biomass values on *Falcataria moluccana* and *Metrosideros polymorpha* leaves in the Wailuku River, Hawaii, 2006–2007. Leaf averages were calculated across season and reach. Asterisks denote significant differences between leaf species: \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ ).

	Fungal biomass (mg/g leaf)	
	<i>F. moluccana</i>	<i>M. polymorpha</i>
2006 wet season		
Forested	2.10 $\pm$ 0.18	1.04 $\pm$ 0.14***
Urban	1.64 $\pm$ 0.07	0.50 $\pm$ 0.06***
Average	1.87 $\pm$ 0.13	0.77 $\pm$ 0.14***
2006 dry season		
Forested	1.83 $\pm$ 0.09	1.07 $\pm$ 0.10*
Urban	1.54 $\pm$ 0.10	1.08 $\pm$ 0.23
Average	1.68 $\pm$ 0.09	1.08 $\pm$ 0.11***
2007 wet season		
Forested	1.70 $\pm$ 0.26	0.74 $\pm$ 0.06**
Urban	2.13 $\pm$ 0.05	0.46 $\pm$ 0.02***
Average	1.91 $\pm$ 0.15	0.60 $\pm$ 0.07***
Leaf average	1.82 $\pm$ 0.07	0.82 $\pm$ 0.08***

3.8 ind/g leaf) ( $F_{2,48} = 154.52$ ,  $p < 0.001$ ). The season  $\times$  reach  $\times$  leaf species interaction was significant ( $F_{2,48} = 7.08$ ,  $p < 0.01$ ). All main-effect differences were driven by differences in the urban reach in the 2006 wet season (Fig. 4A–F). Mean daily invertebrate abundance was greater on leaf packs ( $40.0 \pm 3.8$  ind/g leaf) than on litter bags ( $8.5 \pm 1.0$  ind/g leaf) ( $F_{1,48} = 343.53$ ,  $p < 0.001$ ) in all seasons (season  $\times$  treatment,  $F_{2,48} = 6.51$ ,  $p < 0.01$ ; Fig. 4A–F).

#### N mineralization

We calculated N mineralization from full data sets in the 2006 dry and 2007 wet seasons and the partial data set in the 2006 wet season, and we pooled data from both reaches for each season. Percent N content remaining of *F. moluccana* leaves decreased as % AFDM remaining decreased in each season (Fig. 5A–C). For every 1% of *F. moluccana* AFDM decomposed, 0.4 to 1.1% of the N content of *F. moluccana* leaves was released into the Wailuku River. The N released to the water column during breakdown of *F. moluccana* was 20.7 to 56.9% of the water-column TDN ( $55.4 \pm 2.6$  mg/m<sup>2</sup>) (Fig. 6). These estimates were based on standing stocks of *F. moluccana* that had accumulated in depositional areas of the Ainaloa Stream. Assuming that depositional areas constituted only 10% of the reach (RAM, unpublished data), a more accurate estimate of TDN contribution from *F. moluccana* breakdown at any instant in time would be 2.1 to 5.7%. Percent N content of *M. polymorpha* leaves

increased as % AFDM decreased during the 2006 wet and dry seasons, but not in the 2007 wet season. For every 1% of *M. polymorpha* AFDM decomposed, N content of *M. polymorpha* leaf litter increased by 1 to 10%.

#### Discussion

Replacement of native riparian forests by exotic species can shift the intrinsic quality of leaf-litter inputs to adjacent rivers, thereby altering riverine-community structure and function. Invasion of riparian forests by exotic N-fixing species is expected to have even greater effects on nutrient and organic-matter inputs, but few investigators have examined this hypothesis in tropical regions. Breakdown was significantly faster for exotic *F. moluccana* than native *M. polymorpha* leaf litter in short- and long-term experiments. These results support our 1<sup>st</sup> hypothesis that the higher N content in *F. moluccana* leaf litter would lead to greater breakdown rates than *M. polymorpha*, but mechanical fragmentation by river discharge strongly affected litter fragmentation. The similarity of leaf-litter breakdown rates in leaf-litter packs and litter bags did not support our 2<sup>nd</sup> hypothesis. High N content of *F. moluccana* leaves, and thus high food quality, did not provide an alternative food resource for nondetritivorous invertebrates. Last, leaf-litter breakdown rates were similar in the urban and forested reaches, a result we attribute to similar nutrient concentrations between reaches. Thus, we were unable to test our 3<sup>rd</sup> hypothesis that differences in water-column nutrients would increase leaf-litter breakdown rates.

#### Interspecific differences in leaf-litter breakdown

The short-term experiments probably reflected dynamics of organic-matter processing in these tropical streams better than the long-term experiment because leaf-litter retention rates are low (<20 d) (Larned 2000). These watersheds also are spatially compact, and distances between headwaters and stream mouths are often only a few km (Resh and deSzalay 1995). Thus, initial decomposition of leaf litter before organic matter is flushed and used by nearshore nekton communities is an important regulator of organic-matter dynamics in tropical island ecosystems (Atwood et al. 2012). Invasion of riparian areas by *F. moluccana* probably will alter organic matter and nutrient inputs to streams and nearshore areas because initial decomposition rates are greater for *F. moluccana* than *M. polymorpha*. Moreover, *F. moluccana* leaf-litter inputs occur year round and are nearly 10 $\times$  greater than native leaf-litter inputs (Hughes and Denslow 2005).

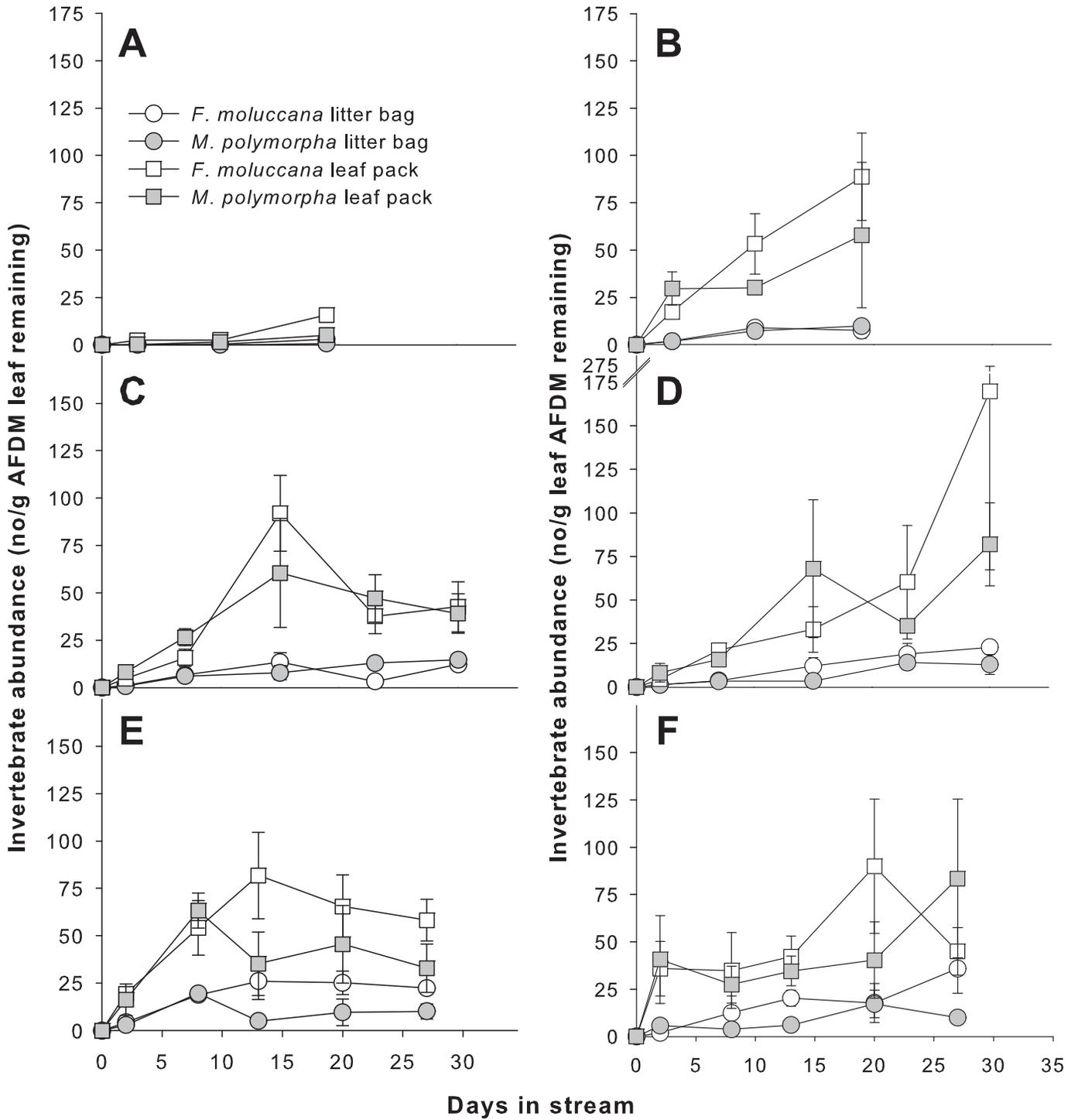


FIG. 4. Mean ( $\pm 1$  SE) invertebrate abundance over time from *Falcataria moluccana* and *Metrosideros polymorpha* litter bags and leaf-litter packs in the 2006 wet season (A, B), 2006 dry season (C, D), and 2007 wet season (E, F) in urban (A, C, E) and forested (B, D, F) reaches of the Wailuku River, Hawaii, USA. Week 4 and 5 values from the 2006 wet season are missing because of a major storm that happened after week 3. AFDM = ash-free dry mass.

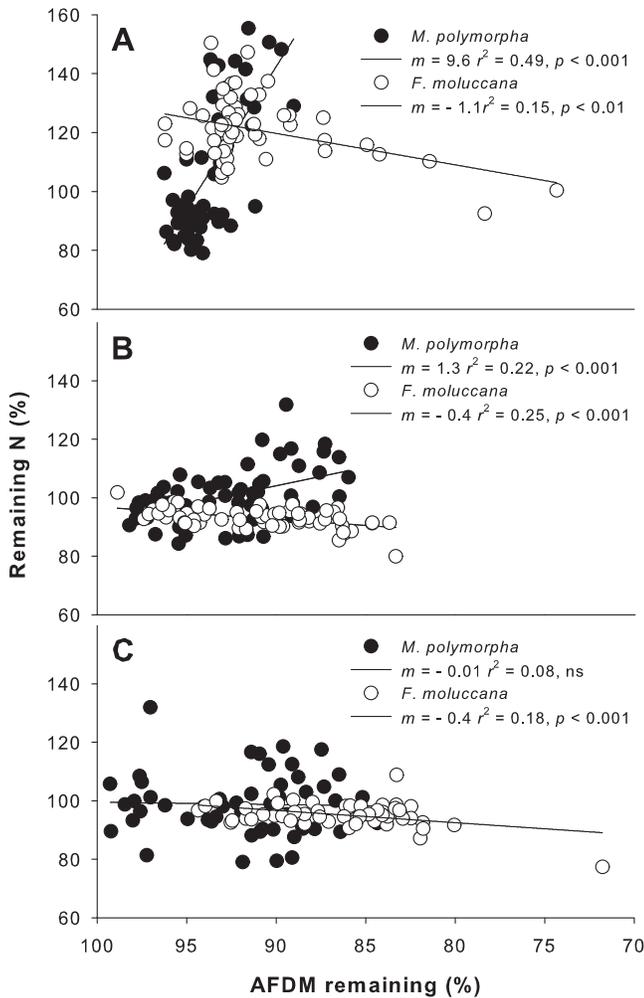


FIG. 5. Percent N remaining in *Falcataria moluccana* and *Metrosideros polymorpha* leaves removed from the Wailuku River during the short-term experiments vs leaf ash-free dry mass (AFDM) remaining in the 2006 wet season (A), 2006 dry season (B), and 2007 wet season (C). Slope ( $m$ ) and goodness of fit ( $r^2$ ) values for the regressions are given in the key to symbols. Positive slopes indicate that leaves are an N sink, whereas negative slopes indicate leaves are an N source to the water column. Breakdown rates did not differ between the forested and urban reaches, so data from the 2 reaches were pooled.

Leaf chemistry and structure can influence fungal and microbial colonization and, thus, leaf-litter breakdown (Ardón et al. 2009, Kominoski et al. 2009). *Falcataria moluccana* leaf litter was expected to break down significantly faster than *M. polymorpha* because of its higher N content and, thus, higher fungal colonization rates. Comparison of other intrinsic factors revealed that lignin and cellulose concentrations were also significantly greater in *F. moluccana* than in *M. polymorpha* leaves (Table 2). Higher lignin and cellulose content should have inhibited bacterial

and fungal colonization (Alexander 1977, Ardón and Pringle 2008) and, thus, slowed leaf breakdown rates (Webster and Benfield 1986, Gessner and Chauvet 1994, Ostrofsky 1997, Richardson et al. 2004) of *F. moluccana* compared to *M. polymorpha*. However, we found no evidence for inhibition, possibly because the high N content of *F. moluccana* leaf litter may have offset the inhibitory effect of lignin and cellulose (Melillo et al. 1982). Alternatively, increased nutrients could have been provided by excretion from significantly greater numbers of invertebrates on *F. moluccana* leaves (Pringle and Triska 1991). Last, cellulose content was higher in *F. moluccana* than in *M. polymorpha* leaves, but differences in cellulose content between *F. moluccana* and *M. polymorpha* (4%) were smaller than differences reported among leaf species (12%) in other studies in which cellulose content affected leaf-litter breakdown rate (Ardón et al. 2006, Ardón and Pringle 2008).

Differences in leaf-litter breakdown rates between *F. moluccana* and *M. polymorpha* also could have been influenced by the higher tannin levels in *M. polymorpha* leaves. Tannins can inhibit fungal growth (Feeny and Bostock 1968) and, thus, leaf-litter breakdown rates (Irons et al. 1994, Ostrofsky 1997, Mathuriau and Chauvet 2002). *Metrosideros polymorpha* leaves may require a long conditioning period for tannins to leach out of the leaves to make them suitable for fungal colonization (Ardón and Pringle 2008). Tannin content might explain the slow linear increase of fungal biomass on *M. polymorpha* leaves during the short-term experiments. This hypothesis is further supported by the high fungal biomass measured on the few litter bags that survived the 2006 flood. Values from these leaf-litter packs (3.25–4.27 mg/g leaf) exceeded values from *F. moluccana* leaves measured throughout the study. If high concentrations of tannins and other phenolics (not measured here) inhibited fungal colonization, then the longer immersion period for surviving packs in the 2006 wet-season experiment than in the other short-term experiments (60 d vs 28–30 d) may have allowed more time for tannins and other phenolic compounds to leach out of the leaf litter. However, the short retention rates of leaf litter (<20 d) reported for a nearby stream (Larned 2000) coupled with the short lengths of these streams suggest that *M. polymorpha* leaves are not in streams long enough for leaching to affect microbial biomass. Other leaf-litter characteristics (described below) are probably more important regulators of fungal colonization and, thus, leaf-litter breakdown.

Leaf toughness can influence leaf-litter breakdown in temperate (Ostrofsky 1997, Quinn et al. 2000) and

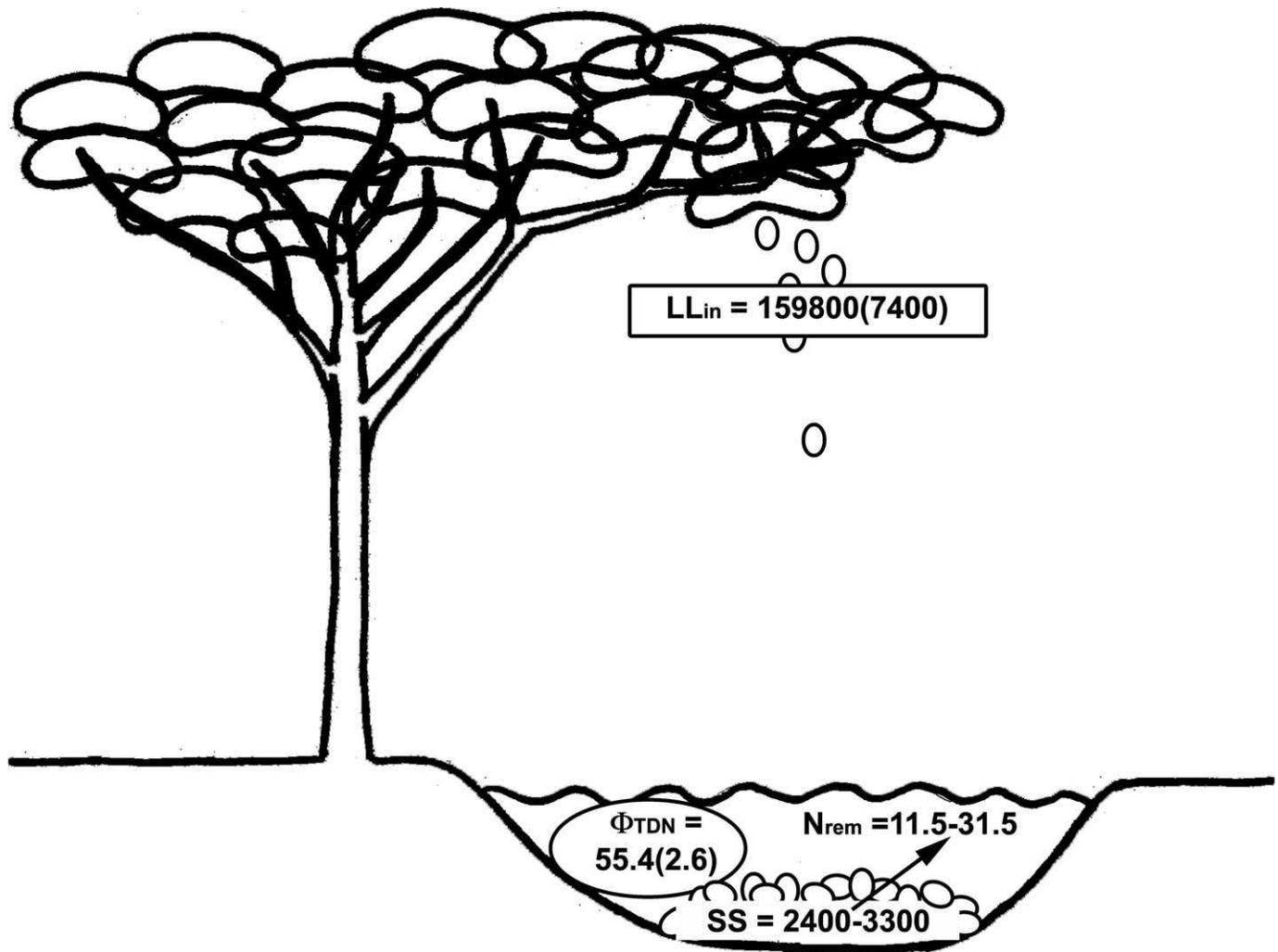


FIG. 6. Conceptual diagram showing estimated N input to a stream with a riparian zone invaded by *Falcataria moluccana*. N pools include the instantaneous standing stock of N from *F. moluccana* leaf litter ( $SS$ ;  $\text{mg}/\text{m}^2$ ), total N remineralized to stream water column from that standing stock of leaf litter ( $N_{rem}$ ;  $\text{mg}/\text{m}^2$ ), and the flux of total dissolved N ( $\Phi_{TDN}$ ) above a  $1.0\text{-m}^2$  area of stream ( $\text{mg}/\text{m}^2$ ) (Wiegner et al., in press). The amount of N entering the stream from leaf-litter inputs from *F. moluccana* trees ( $LL_{in}$ ;  $\text{mg m}^{-2} \text{y}^{-1}$ ) (Hughes and Denslow 2005) is presented to demonstrate the potentially large amounts of N that could be entering the streams in the form of leaf litter. Values are presented as either means ( $\pm 1$  SE) or as ranges.

tropical streams (Ardón and Pringle 2008, Li et al. 2009). Correlations between decomposition rates of leaf-litter packs, discharge, leaf toughness, and leaf C:N in our study suggest that the structural complexity of leaves is an important regulator of leaf-litter breakdown in the Wailuku River. Breakdown of structurally complex leaves should require more fungal processing and mechanical fragmentation by flow than breakdown of structurally simple leaves (Webster and Benfield 1986, Quinn et al. 2000, Li et al. 2009).

#### Leaf-litter breakdown in Hawaiian rivers

Leaf-litter breakdown rates did not differ between leaf-litter packs and litter bags, and invertebrate

abundances were not correlated with intrinsic properties of leaf litter. These results indicate that invertebrates played a minor role in leaf-litter breakdown in the Wailuku River, as has been reported for other Hawaiian rivers (Archer 1983, Larned 2000). High N content, low tannin content, and low leaf toughness are characteristics of high-quality food for invertebrates, so we expected *F. moluccana* leaf litter to be a novel food source for omnivorous invertebrates (i.e., atyid shrimps), which are important detritivores in other tropical rivers (Crowl et al. 2001, Williams 2002). However, the Wailuku River lacks established populations of detritivores, so the expected response to shifts in the

TABLE 5. Peak fungal biomass values (mean  $\pm 1$  SE when available) and time of peak fungal biomass (d) from our study and other studies conducted in temperate (temp), Mediterranean (Med), arid, and tropical (tropics) streams. Mean streamwater nutrient concentrations are reported when available. AFDM = ash-free dry mass,  $\Sigma\text{NO}_3 = \text{NO}_2^- + \text{NO}_3^-$ , SRP = soluble reactive P. \* indicates values reported as mg/g leaf AFDM.

Leaf type	Fungal biomass (mg/g leaf)	Time of peak biomass	Climate	$\text{NH}_4^+$ ( $\mu\text{M}$ )	$\Sigma\text{NO}_3$ ( $\mu\text{M}$ )	SRP ( $\mu\text{M}$ )
<i>Phragmites australis</i>	71.3 $\pm$ 4.2 <sup>a</sup>	–	Temp	–	–	–
<i>Alnus glutinosa</i>	21.1 $\pm$ 1.5 <sup>a</sup>	14 d	Temp	–	–	–
<i>Alnus glutinosa</i>	77.3 <sup>b</sup>	56 d	Temp	1.4	48.4	1.1
<i>Salix fragilis</i>	69.7 <sup>b</sup>	56 d	Temp	1.4	48.4	1.1
<i>Protium brasiliense</i>	95.0 $\pm$ 14.6 <sup>c*</sup>	30 d	Temp	–	70.0	0.17
<i>Alnus glutinosa</i>	76.7 $\pm$ 17.7 <sup>d*</sup>	24 d	Temp	–	50.0	0.004
<i>Alnus glutinosa</i>	61.8 $\pm$ 9.0 <sup>d*</sup>	7 d	Med	–	17.1	0.01
<i>Castanea sativa</i>	280.8 $\pm$ 54.0 <sup>e*</sup>	24 d	Med	–	–	–
<i>Elaeagnus angustifolia</i>	47.6 $\pm$ 8.3 <sup>f</sup>	–	Arid	–	–	–
<i>Populus deltoides</i>	76.2 $\pm$ 19.0 <sup>f</sup>	–	Arid	–	–	–
<i>Alnus glutinosa</i>	105.4 $\pm$ 14.4 <sup>d*</sup>	75 d	Tropics	–	3.6	0.08
<i>Croton gossypifolius</i>	81.9 <sup>g*</sup>	10 d	Tropics	–	8.9	0.7
<i>Clidemia</i> sp.	92.8 <sup>g*</sup>	16 d	Tropics	–	8.9	0.7
<i>Protium brasiliense</i>	19.3 <sup>c*</sup>	75 d	Tropics	–	3.6	0.08
<i>M. polymorpha</i>	2.2 $\pm$ 0.2	This study	Tropics	0.09	1.7	0.006
<i>F. moluccana</i>	3.1 $\pm$ 0.2	This study	Tropics	0.09	1.7	0.006

<sup>a</sup> Gessner and Schmitt 1996

<sup>b</sup> Hieber and Gessner 2002

<sup>c</sup> Gonçalves et al. 2007

<sup>d</sup> Gonçalves et al. 2006

<sup>e</sup> Abelho 2009

<sup>f</sup> Harner et al. 2009

<sup>g</sup> Mathuriau and Chauvet 2002

intrinsic quality of leaf-litter inputs (Piccolo and Wipfli 2002, Wipfli and Musslewhite 2004, Hernandez et al. 2005) did not occur.

Peak fungal biomass was 10 to 100 $\times$  lower in the Wailuku River than in other tropical and temperate streams. This result suggests that fungi may be less important for leaf-litter breakdown in Hawaiian streams than in other streams (Table 5). The reason for low fungal biomass in the Wailuku River is unclear, but several explanations are possible. First, we measured fungal biomass only during early stages of decomposition. Second, nutrient concentrations in the Wailuku River are extremely low. Low fungal biomass in a tropical stream in Cerrado (Table 5) was partially attributed to low nutrient levels (Gonçalves et al. 2007). The  $\text{NO}_3^-$  values (3.6  $\mu\text{M}$ ) reported by Gonçalves et al. (2007) are similar to concentrations in our study, but  $\text{PO}_4^{3-}$  concentrations in their stream (80.6  $\mu\text{M}$ ) were orders of magnitude higher than in the Wailuku River (undetectable;  $<0.01$   $\mu\text{M}$ ). In temperate streams, fungal biomass increases with elevated nutrient levels (Suberkropp 1995, Suberkropp and Chauvet 1995, Pascoal and Cássio 2004, Pascoal et al. 2005, Gulis et al. 2006) and in experimental manipu-

lations of stream nutrients (Ferreira et al. 2006, Gulis et al. 2006, 2008, Ferreira and Chauvet 2011). The ranges of nutrient levels reported from low-nutrient reference streams in these studies ( $\text{NH}_4^+$ : 1.2–3.9  $\mu\text{M}$ ,  $\text{NO}_3^-$ : 3.0–99.3  $\mu\text{M}$ ,  $\text{PO}_4^{3-}$ : 0.4–3.2  $\mu\text{M}$ ) are much higher than concentrations in the Wailuku River. Third, the lignin and cellulose content of *F. moluccana* and *M. polymorpha* were higher than values reported by Gessner (2005). Gonçalves et al. (2007) attributed low fungal biomass in their study in a tropical stream to high lignin and cellulose content of leaves. Fourth, invertebrate densities and biomass are low in Pacific Islands, presumably because they are remote (Bright 1982, Barnes and Shiozawa 1985, Benstead et al. 2009). Remoteness could have similarly affected aquatic fungi and, thus, their role in leaf-litter decomposition. Pascoal and Cássio (2004) reported higher levels of fungal biomass in streams with greater fungal species richness. Last, the differences among studies could reflect differences in analytical technique among laboratories or the fact that some studies reported fungal biomass as mg/g leaf AFDM and others mg/g leaf. Additional studies from remote tropical island streams are needed to examine these factors.

### Effect of *F. moluccana* leaf-litter breakdown on river N

*Falcataria moluccana* and *M. polymorpha* differed in the leaf-litter N content remaining after the early stages of decomposition. N content of *M. polymorpha* litter was positively correlated with % AFDM remaining in the 2006 wet and dry seasons (Fig. 5A, B) as would be expected if leaf litter were colonized by fungi and microbial organisms over time (Triska and Sedell 1976, Gessner and Chauvet 1994). The lack of change in the N content of *M. polymorpha* leaves in 2007 probably was a consequence of lower discharge because fungal biomass was positively correlated with discharge. In contrast, N content of *F. moluccana* litter was negatively correlated with % AFDM remaining, a result suggesting that the breakdown of *F. moluccana* litter released N to the river. N release during decomposition can be reversed over time (Triska and Sedell 1976, Melillo et al. 1982, Ardón et al. 2006), but the flashy nature of Wailuku Stream and the low residence time of leaf litter (Larned 2000) suggests that decomposition may not progress far enough for N immobilization to occur on *F. moluccana* leaves. Thus, early stages of breakdown of *F. moluccana* leaf litter may be increasing N inputs to invaded streams. An N budget for Ainaloa Stream showed that the early stages of *F. moluccana* litter decomposition contributed 2.1 to 5.7% of the TDN pool. This small addition of N probably is important for biological processes in invaded stream reaches (e.g., increased algal growth), but reports of increased N in forest soils from litter inputs of N-fixing trees (Bormann et al. 1994, Hughes and Denslow 2005, Hughes and Uowolo 2006) suggest that subsurface groundwater flows through invaded riparian forest soils may be a greater source of N than leaf decomposition in invaded streams (Wondzall and Swanson 1996, Compton et al. 2003). Future work is needed to verify this hypothesis.

### Conclusion

Invasion of riparian forests by the N-fixing *F. moluccana* tree alters tropical streams via increased leaf-litter breakdown rates and, to an extent, release of N during that breakdown. Most of our experiments focused on early stages of decomposition, but these stages are influential regulators of organic matter and nutrient dynamics in tropical island streams because their flashy nature decreases organic-matter retention (Larned 2000). Decreased in-stream processing time can potentially increase inputs of particulate organic matter or nutrients to streams and nearshore receiving waters, thereby altering nearshore processes (Atwood et al. 2012). Breakdown of *F.*

*moluccana* leaf litter that is retained in depositional areas increases inputs of fine particulate material and elevates N levels in invaded streams to some degree before the litter is flushed to lower stream reaches or nearshore areas. This litter is replaced quickly by the large amount of leaf litter that enters the stream from invaded riparian forests (Hughes and Denslow 2005, Wiegner and Tubal 2010). Our results highlight another effect of *F. moluccana* on Pacific Island watersheds and adds to a growing body of information that underscores the need for strategies to restore dominance of native tree species in riparian forests invaded by N-fixing trees.

### Acknowledgements

Janet “Oli” Kondo, Mark Manuel, Lindsey Shimizu, Kari Shozuya, Emily Siegel, Micah Brewer, and Caitlin Kryss assisted with field work and laboratory analysis. John Kominoski, Amanda Uowolo, and Paul Scowcroft provided valuable comments on an earlier draft of this manuscript, and Jim Baldwin and Ken Gerow provided valuable advice on statistical models. We thank Sharon Ziegler-Chong and her staff at the University of Hawaii Pacific Internship Programs for Exploring Science for providing support and guidance for the interns that worked on this project. We also thank the Hawai'i State Department of Land and Natural Resources and Barbara Green for providing access to the Wailuku River through their property. This research was funded by a grant and cooperative agreement from the National Oceanic and Atmospheric Administration (NOAA), Project RIEL-38, which is sponsored by the University of Hawai'i Sea Grant College Program, School of Ocean and Earth Science and Technology, under Institutional Grant No. NA050AR4171048 from NOAA Office of Sea Grant, Department of Commerce and by National Science Foundation's Research Experience for Undergraduates. The views expressed herein are those of the authors and do not necessarily reflect the view of NOAA or any of its subagencies.

### Literature Cited

- ABELHO, M. 2009. ATP and ergosterol as indicators of fungal biomass during leaf decomposition in streams: a comparative study. *International Review of Hydrobiology* 94:3–15.
- ABER, J. D., AND J. M. MELILLO. 1980. Litter decomposition: measuring relative contributions of organic matter and nitrogen to forest soils. *Canadian Journal of Botany* 58: 416–421.
- ABER, J. D., AND J. M. MELILLO. 1982. Nitrogen immobilization in decaying hardwood litter as a function of initial

- nitrogen and lignin content. *Canadian Journal of Botany* 60:2263–2269.
- ALEXANDER, M. 1977. *Soil microbiology*. John Wiley and Sons, New York.
- ALLEN, S. E., H. M. GRIMSHAW, J. A. PARKINSON, AND C. QUARMBY. 1974. *Chemical analysis of ecological materials*. Blackwell Publishing, Oxford, UK.
- ALLISON, S. D., C. NIELSEN, AND R. F. HUGHES. 2006. Elevated enzyme activities in soils under the invasive nitrogen-fixing tree *Falcataria moluccana*. *Soil Biology and Biochemistry* 38:1537–1544.
- ARCHER, K. M. 1983. *Leaf litter decomposition in Hawaiian streams*. MS Thesis, University of Hawaii, Honolulu, Hawaii.
- ARDÓN, M., AND C. M. PRINGLE. 2008. Do secondary compounds inhibit microbial- and insect-mediated leaf breakdown in a tropical rainforest stream, Costa Rica? *Oecologia* (Berlin) 155:311–323.
- ARDÓN, M., C. M. PRINGLE, AND S. L. EGGERT. 2009. Does leaf chemistry differentially affect breakdown in tropical vs temperate streams? Importance of standardized analytical techniques to measure leaf chemistry. *Journal of the North American Benthological Society* 28:440–453.
- ARDÓN, M., L. A. STALLCUP, AND C. M. PRINGLE. 2006. Does leaf quality mediate the stimulation of leaf breakdown by phosphorous in Neotropical streams? *Freshwater Biology* 51:618–633.
- ASNER, G. P., R. F. HUGHES, P. M. VITOUSEK, D. E. KNAPP, T. KENNEDY-BOWDOIN, J. BOARDMAN, R. E. MARTIN, M. EASTWOOD, AND R. O. GREEN. 2008. Invasive plants transform the three-dimensional structure of rain forests. *Proceedings of the National Academy of Sciences of the United States of America* 105:4519–4523.
- ATWOOD, T. B., T. WIEGNER, AND R. A. MACKENZIE. 2012. Effects of hydrological forcing on the structure of a tropical estuarine food web. *Oikos* 121:277–289.
- ATWOOD, T. B., T. N. WIEGNER, J. P. TURNER, AND R. A. MACKENZIE. 2010. Potential effects of an invasive N-fixing tree on a Hawaiian stream food web. *Pacific Science* 64:367–379.
- BARNES, J. R., AND D. K. SHIOZAWA. 1985. Drift in Hawaiian streams. *Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie* 22: 2119–2124.
- BENFIELD, E. F. 1996. Leaf breakdown in stream ecosystems. Pages 579–589 in F. R. Hauer and G. A. Lamberti (editors). *Methods in stream ecology*. Academic Press, San Diego, California.
- BENSTEAD, J. P. 1996. Macroinvertebrates and the processing of leaf litter in a tropical stream. *Biotropica* 28:367–375.
- BENSTEAD, J. P., J. G. MARCH, C. PRINGLE, K. C. EWEL, AND J. W. SHORT. 2009. Biodiversity and ecosystem function in species-poor communities: community structure and leaf litter breakdown in a Pacific island stream. *Journal of the North American Benthological Society* 28: 454–465.
- BORMANN, B. T., K. J. CROMACK, AND W. O. I. RUSSELL. 1994. The influence of red alder on soils and long-term ecosystem productivity. Pages 47–56 in D. E. Hibbs, D. S. DeBell, and R. F. Tarrant (editors). *The biology and management of red alder*. Oregon State University Press, Corvallis, Oregon.
- BRIGHT, G. R. 1982. Secondary benthic production in a tropical island stream. *Limnology and Oceanography* 27:472–480.
- COMPTON, J. E., M. R. CHURCH, S. T. LARNED, AND W. E. HOGSETT. 2003. Nitrogen export from forested watersheds in the Oregon Coast Range: the role of N<sub>2</sub>-fixing red alder. *Ecosystems* 6:773–785.
- CROWL, T. A., W. H. MCDOWELL, A. P. COVICH, AND S. L. JOHNSON. 2001. Freshwater shrimp effects on detrital processing and nutrients in a tropical headwater stream. *Ecology* 82:775–783.
- DUBOIS, M., K. A. GILLES, J. K. HAMILTON, P. A. REBERS, AND F. SMITH. 1956. Colorimetric method for determination of sugars and related substances. *Analytical Chemistry* 28: 350–356.
- FEENY, P. P., AND H. BOSTOCK. 1968. Seasonal changes in the tannin content of oak leaves. *Phytochemistry* 7:871–880.
- FERREIRA, V., AND E. CHAUVET. 2011. Synergistic effects of water temperature and dissolved nutrients on litter decomposition and associated fungi. *Global Change Biology* 17:551–564.
- FERREIRA, V., V. GULIS, AND M. A. S. GRAÇA. 2006. Whole-stream nitrate addition affects litter decomposition and associated fungi but not invertebrates. *Oecologia* (Berlin) 149:718–729.
- FISHMAN, M. J. 1993. *Methods of analysis by the U.S. Geological Survey National Water Quality Laboratory—Determination of inorganic and organic constituents in water and fluvial sediments*. U.S. Geological Survey Open-File Report 93-125. US Geological Survey, Reston, Virginia.
- GESSNER, M. O. 2005. Proximate lignin and cellulose. Pages 115–120 in M. A. S. Graça, F. Bärlocher, and M. O. Gessner (editors). *Methods to study litter decomposition: a practical guide*. Springer, Houten, The Netherlands.
- GESSNER, M. O., AND E. CHAUVET. 1993. Ergosterol-to-biomass conversion factors for aquatic hyphomycetes. *Applied and Environmental Microbiology* 59:502–507.
- GESSNER, M. O., AND E. CHAUVET. 1994. Importance of stream microfungi in controlling breakdown rates of leaf litter. *Ecology* 75:1807–1817.
- GESSNER, M. O., AND S. Y. NEWELL. 2002. Biomass, growth rate, and production of filamentous algae in plant litter. Pages 390–408 in C. J. Hurst, R. L. Crawford, G. Knudsen, M. McInerney, and D. L. Stetzenbach (editors). *Manual of environmental engineering*. ASM Press, Washington, DC.
- GESSNER, M. O., AND A. L. SCHMITT. 1996. Use of solid-phase extraction to determine ergosterol concentrations in plant tissue colonized by fungi. *Applied and Environmental Microbiology* 62:415–419.
- GONÇALVES, J. F., M. A. S. GRAÇA, AND M. CALLISTO. 2006. Leaf-litter breakdown in 3 streams in temperate, Mediterranean, and tropical Cerrado climates. *Journal of the North American Benthological Society* 25:344–355.

- GONÇALVES, J. F., M. A. S. GRAÇA, AND M. CALLISTO. 2007. Litter decomposition in a Cerrado savannah stream is retarded by leaf toughness, low dissolved nutrients and a low density of shredders. *Freshwater Biology* 52:1440–1451.
- GRAÇA, M. A. S., R. C. F. FERREIRA, AND C. N. COIMBRA. 2001. Litter processing along a stream gradient: the role of invertebrates and decomposers. *Journal of the North American Benthological Society* 20:408–420.
- GULIS, V., V. FERREIRA, AND M. A. S. GRAÇA. 2006. Stimulation of leaf litter decomposition and associated fungi and invertebrates by moderate eutrophication: implications for stream assessment. *Freshwater Biology* 51:1655–1669.
- GULIS, V., AND K. SUBERKROPP. 2003. Leaf litter decomposition and microbial activity in nutrient-enriched and unaltered reaches of a headwater stream. *Freshwater Biology* 48:123–134.
- GULIS, V., K. SUBERKROPP, AND A. D. ROSEMOND. 2008. Comparison of fungal activities on wood and leaf litter in unaltered and nutrient-enriched headwater streams. *Applied and Environmental Microbiology* 74:1094–1101.
- HARNER, M. J., C. L. CRENSHAW, M. ABELHO, M. STURSOVA, J. J. F. SHAH, AND R. L. SINSABAUGH. 2009. Decomposition of leaf litter from a native tree and an actinorhizal invasive across riparian habitats. *Ecological Applications* 19:1135–1146.
- HERNANDEZ, O., R. W. MERRITT, AND M. S. WIPFLI. 2005. Benthic invertebrate community structure is influenced by forest succession after clearcut logging in southeastern Alaska. *Hydrobiologia* 533:45–59.
- HIEBER, M., AND M. O. GESSNER. 2002. Contribution of stream detritivores, fungi, and bacteria to leaf breakdown based on biomass estimates. *Ecology* 83:1026–1038.
- HUGHES, R. F., AND J. S. DENSLOW. 2005. Invasion by an N<sub>2</sub>-fixing tree alters function and structure in wet lowland forests of Hawaii. *Ecological Applications* 15:1615–1628.
- HUGHES, R. F., AND A. UOWOLO. 2006. Impacts of *Falcataria moluccana* invasion on decomposition in Hawaiian lowland wet forests: the importance of stand-level controls. *Ecosystems* 1–16.
- IRONS, J. G., M. W. OSWOOD, R. J. STOUT, AND C. M. PRINGLE. 1994. Latitudinal differences in leaf litter breakdown: is temperature really important? *Freshwater Biology* 32:401–411.
- KOMINOSKI, J. S., T. J. HOELLEIN, J. J. KELLY, AND C. M. PRINGLE. 2009. Does mixing litter of different qualities alter stream microbial diversity and functioning on individual litter species? *Oikos* 118:457–463.
- LARNED, S. T. 2000. Dynamics of coarse riparian detritus in a Hawaiian stream ecosystem: a comparison of drought and post-drought conditions. *Journal of the North American Benthological Society* 19:215–234.
- LARNED, S. T., P. M. ELDRIDGE, AND R. A. KINZIE. 2008. Modeling C and N flows through a stream food web: an inverse approach. *Journal of the North American Benthological Society* 27:674–689.
- LI, A. O. Y., L. C. Y. NG, AND D. DUDGEON. 2009. Effects of leaf toughness and nitrogen content on litter breakdown and macroinvertebrates in a tropical stream. *Aquatic Sciences* 71:80–93.
- MATHURIAU, C., AND E. CHAUVET. 2002. Breakdown of leaf litter in a neotropical stream. *Journal of the North American Benthological Society* 21:384–396.
- MCCLAUGHERTY, C. A. 1985. Forest litter decomposition in relation to soil nitrogen dynamics and litter quality. *Ecology* 66:266–275.
- MELILLO, J. M., J. D. ABER, AND J. F. MURATORE. 1982. Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology* 63:621–626.
- MERRITT, R. W., AND K. W. CUMMINS (EDITORS). 1996. An introduction to the aquatic insects of North America. 3<sup>rd</sup> edition. Kendall/Hunt, Dubuque, Iowa.
- MINEAU, M. M., C. V. BAXTER, AND A. M. MARCARELLI. 2011. A non-native riparian tree (*Elaeagnus angustifolia*) changes nutrient dynamics in streams. *Ecosystems* 14:353–365.
- NELSON, R. E. 1965. A record of forest plantings in Hawaii. USDA Forest Service Resource Bulletin PSW-1. US Department of Agriculture Forest Service, Pacific Southwest Research Station, Albany, Georgia.
- OSTROFSKY, M. L. 1997. Relationship between chemical characteristics of autumn-shed leaves and aquatic processing rates. *Journal of the North American Benthological Society* 16:750–759.
- PASCOAL, C., AND F. CÁSSIO. 2004. Contribution of fungi and bacteria to leaf litter decomposition in a polluted river. *Applied and Environmental Microbiology* 70:5266–5273.
- PASCOAL, C., F. CÁSSIO, A. MARCOTEGUI, B. SANZ, AND P. GOMES. 2005. Role of fungi, bacteria, and invertebrates in leaf litter breakdown in a polluted river. *Journal of the North American Benthological Society* 24:784–797.
- PEARSON, R. G., AND N. M. CONNOLLY. 2000. Nutrient enhancement, food quality and community dynamics in a tropical rainforest stream. *Freshwater Biology* 43:31–42.
- PICCOLO, J. J., AND M. S. WIPFLI. 2002. Does red alder (*Alnus rubra*) in upland riparian forests elevate macroinvertebrate and detritus export from headwater streams to downstream habitats in southeastern Alaska? *Canadian Journal of Fisheries and Aquatic Sciences* 59:503–513.
- PRINGLE, C. M., AND F. J. TRISKA. 1991. Effects of geothermal groundwater on nutrient dynamics of a lowland Costa Rican stream. *Ecology* 72:951–965.
- QUINN, J. M., G. P. BURRELL, AND S. M. PARKYN. 2000. Influences of leaf toughness and nitrogen content on in-stream processing and nutrient uptake by litter in a Waikato, New Zealand, pasture stream and streamside channels. *New Zealand Journal of Marine and Freshwater Research* 34:253–271.
- RAMSEY, J. O., AND B. W. SILVERMAN. 2005. Functional data analysis. 2<sup>nd</sup> edition. Springer, New York.
- RESH, V. H., AND F. A. DE SZALAY. 1995. Streams and rivers of Oceania. Pages 717–736 in C. E. Cushing, K. W. Cushing, and G. W. Minshall (editors). *River and stream ecosystems*. Elsevier, Amsterdam, The Netherlands.
- RICHARDSON, J. S., C. R. SHAUGHNESSY, AND P. G. HARRISON. 2004. Litter breakdown and invertebrate association with three types of leaves in a temperate rainforest stream. *Archiv für Hydrobiologie* 159:309–325.

- ROYER, T. V., M. T. MONAGHAN, AND G. W. MINSHALL. 1999. Processing of native and exotic leaf litter in two Idaho (U.S.A.) streams. *Hydrobiologia* 400:123–128.
- RYAN, M. G. 1990. A comparison of methods for determining proximate carbon fractions of forest litter. *Canadian Journal of Forest Research* 20:166–171.
- SAMPAIO, A., R. CORTES, AND C. LEO. 2001. Invertebrate and microbial colonisation in native and exotic leaf litter species in a mountain stream. *International Review of Hydrobiology* 86:4–5.
- SHAFTEL, R. S., R. S. KING, AND J. A. BACK. 2011. Alder cover drives nitrogen availability in Kenai lowland headwater streams, Alaska. *Biogeochemistry* 107:135–148.
- SUBERKROPP, K. 1995. The influence of nutrients on fungal growth, productivity, and sporulation during leaf breakdown in streams. *Canadian Journal of Botany* 73: 1361–1369.
- SUBERKROPP, K., AND E. CHAUVET. 1995. Regulation of leaf breakdown by fungi in streams: influences of water chemistry. *Ecology* 76:1433–1445.
- THOMPSON, R. M., AND C. R. TOWNSEND. 2003. Impacts on stream food webs of native and exotic forest: an intercontinental comparison. *Ecology* 84:145–161.
- TRISKA, F. J., AND J. R. SEDELL. 1976. Decomposition of four species of leaf litter in response to nitrate manipulation. *Ecology* 57:783–792.
- USEPA (US ENVIRONMENTAL PROTECTION AGENCY). 1983. Methods for chemical analysis of water and wastes. EPA-600/4 4-79-020. US Environmental Protection Agency, Cincinnati, Ohio.
- VANNOTE, R. L., G. W. MINSHALL, K. W. CUMMINS, J. R. SEDELL, AND C. E. CUSHING. 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* 37:130–137.
- VITOUSEK, P. M., L. R. WALKER, L. D. WHITEAKER, D. MUELLER-DOMBOIS, AND P. A. MATSON. 1987. Biological invasion by *Myrica faya* alters ecosystem development in Hawaii. *Science* 238:802–803.
- WAGNER, G. A., D. R. HERBST, AND S. H. SOHMER. 1999. Manual of the flowering plants of Hawaii. University of Hawaii Press, Honolulu, Hawaii.
- WALLACE, J. B., S. L. EGGERT, J. L. MEYER, AND J. R. WEBSTER. 1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. *Science* 277:102–104.
- WEBSTER, J. R., AND E. F. BENFIELD. 1986. Vascular plant breakdown in freshwater ecosystems. *Annual Review of Ecology and Systematics* 17:567–594.
- WIEGNER, T. N., R. F. HUGHES, L. M. SHIZUMA, D. K. BISHAW, AND M. E. MANUEL. Impacts of an invasive N<sub>2</sub>-fixing tree on Hawaiian stream water quality. *Biotropica* (in press).
- WIEGNER, T., AND R. L. TUBAL. 2010. Comparison of dissolved organic carbon bioavailability from native and invasive vegetation along a Hawaiian river. *Pacific Science* 64: 545–555.
- WILLIAMS, J. L. 2002. Effects of the tropical freshwater shrimp *Caridina weberi* (Atyidae) on leaf litter decomposition. *Biotropica* 34:616–619.
- WIPFLI, M. S., AND J. MUSSLEWHITE. 2004. Density of red alder (*Alnus rubra*) in headwaters influences invertebrate and detritus subsidies to downstream fish habitats in Alaska. *Hydrobiologia* 520:153–163.
- WONDZELL, S. M., AND F. J. SWANSON. 1996. Seasonal and storm dynamics of the hyporheic zone of a 4<sup>th</sup>-order mountain stream. *Journal of the North American Benthological Society* 15:20–34.

Received: 18 October 2012

Accepted: 7 June 2013