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Impacts of an Invasive N_2-Fixing Tree on Hawaiian Stream Water Quality

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ABSTRACT

N_2-fixing trees can affect stream water quality. This has been documented in temperate streams, but not in tropical ones, even though N_2-fixing trees are prevalent in the tropics. We investigated the effects of the introduced, invasive tree, *Falcataria moluccana* (albizia) on water quality of Hawaiian streams. Nutrient concentrations were measured in reaches above and below *F. moluccana*-dominated riparian zones of four streams over 14 mo, and benthic algal nutrient limitation was examined in one stream. NO_3^-+NO_2^- concentrations were up to 600 percent higher in reaches below *F. moluccana* stands than in ones above them. In contrast, dissolved organic nitrogen concentrations were 24 percent lower in most reaches below *F. moluccana* stands, and NH_4^+ and particulate nitrogen concentrations were similar above and below the stands. Dissolved organic carbon concentrations were up to 30 percent lower below *F. moluccana* stands, but particulate carbon concentrations were similar between reaches. Total dissolved phosphorus concentrations were similar above and below *F. moluccana* stands, whereas H_4SiO_4 concentrations were higher below the stands. In the stream where benthic chlorophyll *a* was measured, concentrations were three times higher below the *F. moluccana* stand than above it. Benthic algae were co-limited by nitrogen and phosphorus above the *F. moluccana* stand, and limited by phosphorus below it. These results suggest that *F. moluccana*'s presence relieved nitrogen-limitation and caused the benthic algae to become solely phosphorus-limited. Overall, our results demonstrate that *F. moluccana* can strongly affect the chemistry and primary producers of these tropical streams.

Key words: *Falcataria moluccana*; Hawaii; nitrogen; nutrient limitation; riparian zone; streams.

NITROGEN (N) CONTROLS SPECIES COMPOSITION, DIVERSITY, DYNAMICS, AND FUNCTIONING OF MANY TERRESTRIAL, FRESHWATER, AND MARINE ECOSYSTEMS (Vitousek *et al.* 1997). Human activities, such as biological N_2-fixing crop cultivation, fossil fuel combustion, N fertilizer synthesis, and invasive N_2-fixing plant introductions, have altered N cycling more than any other element at regional and global scales (Galloway *et al.* 2003). These activities have increased the amount of available N in the environment and its mobility between ecosystems (Vitousek *et al.* 1997). The consequences of large, more mobile N pools are multifaceted and crossecosystem boundaries. For example, elevated atmospheric N emissions from fossil fuel combustion have led to N saturation conditions in temperate forests (Berendse *et al.* 1993), and acidification and eutrophication of temperate freshwaters and estuaries (Vitousek *et al.* 1997). The presence of N_2-fixing trees may also lead to forest N saturation conditions (Vitousek *et al.* 1997), and when these trees are located in riparian areas, they can have interecosystem effects by altering stream water quality, ecosystem processes, and food webs (Compton *et al.* 2003, Atwood *et al.* 2010, Mineau *et al.* 2011).

Impacts of riparian N_2-fixing trees have been largely documented in Pacific Northwest streams, United States (Compton *et al.* 2003), and more recently in the semi-arid western United States (Mineau *et al.* 2011) and South Africa (Jovanovic *et al.* 2009), even though riparian N_2-fixing trees are widespread worldwide (Jacobs *et al.* 2007, Scott *et al.* 2009, Morris & Stanford 2011, Reyes *et al.* 2011). In Pacific Northwest forests, N_2-fixation by the native *Alnus rubra* (red alder) has not only increased N litterfall inputs to the forest floor and increased dissolved inorganic (DIN) and organic N (DON) leaching below the active rooting zone (Binkley *et al.* 1992), but it has increased stream NO_3^- and DON concentrations by an order of magnitude (Compton *et al.* 2003). Increased stream N concentrations from *A. rubra* have led to higher primary productivity and chlorophyll *a* (Chl *a*) concentrations (Goldman 1961, Volk *et al.* 2003), suggesting that N inputs from *A. rubra* may alleviate N-limitation. In addition, microbial colonization, leaf litter breakdown rates, and stream invertebrate densities, biomass, and richness were all greater in streams draining *A. rubra* forests (Sampaio *et al.* 2001, Elliot *et al.* 2004, Richardson *et al.* 2004, Wipfli & Musslewhite 2004). *Elaeagnus angustifolia* (Russian olive), a non-native, N_2-fixing, riparian tree found in the western United States, also affects stream N concentrations and biofilm nutrient limitation (Mineau *et al.* 2011). The mechanisms by which these riparian N_2-fixing trees affect stream nutrient concentrations, processes, and biota remain currently unknown.

In contrast to the growing literature on riparian N_2-fixing tree effects on temperate streams, little is known about their

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effects on tropical streams (Atwood *et al.* 2010), even though they are widespread in this region (ter Steege *et al.* 2006, Benson & Dawson 2007, Tassin *et al.* 2012). Tropical streams, particularly those with little anthropogenic N deposition, like the Hawaiian Islands, may be especially affected by N_2-fixing riparian trees. Anthropogenic N deposition rates are relatively low in Hawaii (0.5–6 kg N/ha/yr), although volcanic activity increases deposition rates locally (Carrillo *et al.* 2002, Vitousek 2004), and young basalt contains little to no N (Vitousek 2004). Soil N concentrations increase across the Hawaiian Islands along a chronological gradient from atmospheric deposition and N_2-fixation from soil bacteria, lichens, and higher plants (Vitousek 2004). Contributing to this soil N gradient, are populations of non-native, N_2-fixing shrubs and trees, which often form invasion fronts emanating from purposeful plantings (Vitousek & Walker 1989, Woodcock 2003, Hughes & Denslow 2005).

A daunting non-native, N_2-fixing tree in Hawaii is *Falcataria moluccana* (albizia). Native to the Moluccas, New Guinea, New Britain, and the Solomon Islands (Wagner *et al.* 1999), it was first introduced to Hawaii in the 1920s–1950s to restore degraded watersheds (Nelson 1965). *Falcataria moluccana* is a large, fast-growing tree, and in windward plantations on Hawaii Island, it has increased soil N pools and availability (*i.e.,* NO_3^- and NH_4^+) well above measured values within monotypic *Eucalyptus saligna* stands (Garcia-Montiel & Binkley 1998). *Falcataria moluccana* invasion into native-dominated lowland wet forests, which previously lacked native N_2-fixing plants, increased N inputs via litterfall 4–55 times, soil N availability 17–121 times, and doubled litter decomposition rates relative to adjacent native-dominated stands (Hughes & Denslow 2005, Hughes & Uowolo 2006). Where it occupies riparian zones, it is anticipated that elevated litterfall N inputs could be as high as 250 kg N/ha/yr (Hughes & Denslow 2005), a value comparable to industrial corn production N fertilizer additions (Jaynes *et al.* 2001), three times greater than atmospheric N deposition from industrial areas of North America and Europe (Berendse *et al.* 1993, Wright & van Breeman 1995) and N_2-fixation rates of *F. moluccana* itself (Binkley & Giardina 1997), and seven times greater than litter inputs from temperate N_2-fixing trees (Binkley *et al.* 1992, Busse & Gunkel 2002).

While effects of *F. moluccana* on terrestrial systems are becoming well documented (Hughes & Denslow 2005, Allison *et al.* 2006, Hughes & Uowolo 2006, Hughes *et al.* 2012); less is known about its impact on streams (Atwood *et al.* 2010). Despite their shared N_2-fixing capacity, impacts of *F. moluccana*, *A. rubra*, and *E. angustifolia* on streams likely differ as a function of their geographic location. *A. rubra* and *E. angustifolia* are present in temperate forests, which are generally N-limited; thus, the amount of N leaching from the forest floor to the stream should be relatively low, except in monotypic stands. In contrast, *F. moluccana* is found in tropical forests, which have a lower capacity to retain N (Matson *et al.* 1999), a condition speculated to result from high N inputs from asymbiotic biological N_2-fixation in the soil litter layer (Hedin *et al.* 2009, Brookshire *et al.* 2012a,b). Therefore, more N from the forest is probably leaching into streams as compared to temperate forests. In addition, tropical streams experience year-round leaf litter inputs, whereas temperate ones receive seasonal inputs (Compton *et al.* 2003). The consequence is that a greater amount of N is entering tropical streams via leaf litter annually compared to temperate ones. It is hypothesized that this increase in N from *F. moluccana* will impact freshwater and coastal water quality – as both tend to be N-limited in the tropics (Laperriere 1995, Neill *et al.* 2001, Flecker *et al.* 2002) and may lead to coastal eutrophication.

The goal of our study was to investigate effects of *F. moluccana* on water chemistry and benthic algal nutrient limitation of Hawaii Island streams. Water samples were collected from stream reaches above and below *F. moluccana*-dominated riparian zones of four streams, five to ten times, over 14 mo.

METHODS

SITE DESCRIPTION.—Four streams in three watersheds on Hawaii Island were sampled for this project including: Ainako Stream, Kolekole River, and Waipuhi and Waipunalau Gulches (Table 1), five to ten times from June 2005 to August 2006. Water samples were collected from the thalweg at two to four stations that were 0.5–1.5 km apart within each stream primarily during the dry season (May–October, HDOH 2009) under baseflow conditions. Stations were located above and below *F. moluccana* stands to assess their effects on stream water quality using a design similar to Hurd and Raynal (2004). Water was sampled using plastic buckets, pre-rinsed with stream water. Water for nutrient analyses was filtered through pre-combusted (500°C for 6 h) GF/F filters (Whatman, Piscataway, New Jersey, U.S.A.), and unfiltered water for total suspended solids (TSS), as well as particulate carbon (PC) and nitrogen (PN) was placed into two 1-L HDPE acid-washed bottles, pre-rinsed with stream water. All water samples were immediately placed on ice, transported to the laboratory, and stored frozen until analysis. Water samples for TSS, PC, and PN were immediately processed at the laboratory.

ANALYTICAL METHODS.—Filtered nutrient samples were analyzed for total dissolved N (TDN), ammonium (NH_4^+), nitrate plus nitrite ($NO_3^- + NO_2^-$), total dissolved phosphorus (TDP), phosphate (PO_4^{3-}), silicic acid (H_4SiO_4), and dissolved organic carbon (DOC). NH_4^+ [USGS I-2525, detection limit (d.l.) 1 μmol/L], $NO_3^- + NO_2^-$ (USEPA 353.4, d.l. 0.1 μmol/L), TDP (USGS I-4650-03, d.l. 0.1 μmol/L), PO_4^{3-} (USEPA 365.5, d.l. 0.1 μmol/L), and H_4SiO_4 (USEPA 366, d.l. 5 μmol/L) were analyzed on a Technicon Pulse II Autoanalyzer. Dissolved organic phosphorus (DOP) was determined from the difference between TDP and PO_4^{3-}. TDN was analyzed using high-temperature combustion, followed by chemiluminescent detection of nitric oxide on a Shimadzu TOC-V, TNM-1 (d.l. 1 μmol/L). DON was determined from the difference between TDN and DIN (DIN = $NH_4^+ + NO_3^- + NO_2^-$). DOC was also measured using high-temperature combustion on a Shimadzu TOC-V, TNM-1 (d.l. 10 μmol/L). All nutrient samples were analyzed within 2 weeks of collection. In addition, known volumes of

TABLE 1. *Characteristics of streams examined in this study on Hawaii Island. Conservation, agriculture, and urban zone are abbreviated as Cons-Ag-Urb. Mean annual temperature and precipitation are abbreviated as MAT and MAP. NA indicates where data were not available.*

Stream	Stream order	Watershed area (km^2)[a]	Zoning Cons-Ag-Urb (%)[a]	*Falcataria moluccana* area (km^2)[b]	Population[a]	Volcano complex	Substrate age (kyr)[c]	Elevation range (m asl)[d]	MAT (°C)[e]	MAP (mm)[a]
Ainako	1	3.1	84-2-14	0.30	275	Mauna Loa	3–5	100–250	22	4834
Kolekole	3	52	71-29-0	0.11	24	Mauna Kea	65–70	400–450	20–22	3900
Waipuhi	1	1.0	38-62-0	0.76	NA	Kohala	120–230	425–550	20–22	2420
Waipunalau	1	1.7	38-62-0	0.76	NA	Kohala	120–230	425–550	20–22	2420

[a] Michaud & Wiegner 2011.

[b] Area estimated using remote sensing imagery (Worldview2 for Ainako Stream and Kolekole River; Carnegie Institution for Science at Stanford University courtesy of G. Asner for Waipunalau and Waipuhi Gulches) and ArcGIS v. 10 software.

[c] Wolfe & Morris 1996.

[d] USGS topographic series W833.

[e] Sanderson 1993.

water from the 1-L water samples transported back to the laboratory were filtered through two pre-combusted, pre-weighed, GF/F filters, and dried to a constant weight at 70°C. One filter was analyzed for TSS (APHA, AWWA, & WEF 1995) and the other for PC and PN on a CHN analyzer (Costech Analytical Technologies, Valencia, California, U.S.A.). Total N (TN) was calculated as the sum of TDN and PN, and total C (TC) was calculated as the sum of DOC and PC. All nutrient samples were analyzed at the University of Hawaii at Hilo Analytical Laboratory.

BENTHIC ALGAL NUTRIENT LIMITATION.—Nutrient-diffusing substrates were used to assess benthic algal nutrient limitation in Ainako Stream in summer 2006 (Tate 1990). Nutrient-diffusing substrates were constructed out of 10-cm diameter clay saucers glued to Petri dishes. Saucers were filled with 2 percent agar solutions, with one set of saucers serving as controls (C; no nutrient additions), and the others being enriched with nutrients: + N (0.5 mol/L $NaNO_3$), + P (0.1 mol/L KH_2PO_4), and + N + P (same level as in the + N and + P treatments alone). Saucers were attached to the streambed using concrete nails and placed in a cross-shape configuration, with the C saucer upstream, + N and + P saucers placed side by side and below the C, and + N + P saucers placed downstream of all other treatments. This configuration minimized contamination among saucers and treatments. Six sets of treatment configurations were deployed, three above the *F. moluccana* stand and three below it, in water with similar water depths, light levels, and stream water velocities. After 3 weeks, the saucers were retrieved, placed into separate zip-lock bags, and transported to the laboratory. Algae were scraped from the saucer into a known volume of deionized water, which was then sub-sampled and filtered through a GF/F filter. Filters were stored frozen in the dark until analysis. Chl *a* samples were analyzed on a Turner 10-AU fluorometer using USEPA method 445.0.

STATISTICAL ANALYSES.—Differences in concentrations for dissolved and particulate nutrients, as well as N and C pools' compositions were examined using a general linear model (GLM) with location (above or below *F. moluccana* stands), stream, and year as factors; stream was used as a blocking factor. All observations for a particular station were first log transformed, averaged across sampling dates within a year, and then used in the GLM. When observations had zeros for values, a constant was added prior to logging the data, where the constant was one-half of the smallest positive value. A two-way analysis of variance (ANOVA) and a Tukey HSD multiple comparison test were used to examine differences in Chl *a* concentrations with location and treatment (C, + N, + P, and + N + P) as factors. Correlations were used to examine associations among variables. Statistics were run using Systat® 11 and SAS 9.3, and an α-level of 0.05 was used.

RESULTS

Falcataria moluccana's presence affected stream water N concentrations (Fig. 1). Specifically, NO_3^-+NO_2^- concentrations were significantly higher below *F. moluccana* stands than above them ($P = 0.0051$) (Fig. 1). In contrast, DON concentrations were lower below *F. moluccana* stands than above them ($P = 0.0841$), although the difference was not significant (Fig. 1). Concentrations of NH_4^+ and PN were similar above and below *F. moluccana* stands (Fig. 1). Percent contribution of DIN to the TN pool significantly increased below *F. moluccana* stands in all streams ($P = 0.0282$), whereas the percent contribution of DON to the TN pool significantly decreased ($P = 0.0312$) (Table S1). Percent contribution of PN to the TN pool was similar above and below *F. moluccana* stands (Table S1). Most forms of N had similar concentrations among streams, except for DON ($P = 0.0194$), where its concentration was highest in Waipunalau Gulch and lowest in Ainako Stream.

Falcataria moluccana presence did not consistently affect organic C concentrations in the streams (Table 2). DOC concentrations were up to 30 percent lower below *F. moluccana* stands, although this difference was not significant ($P = 0.1571$). In

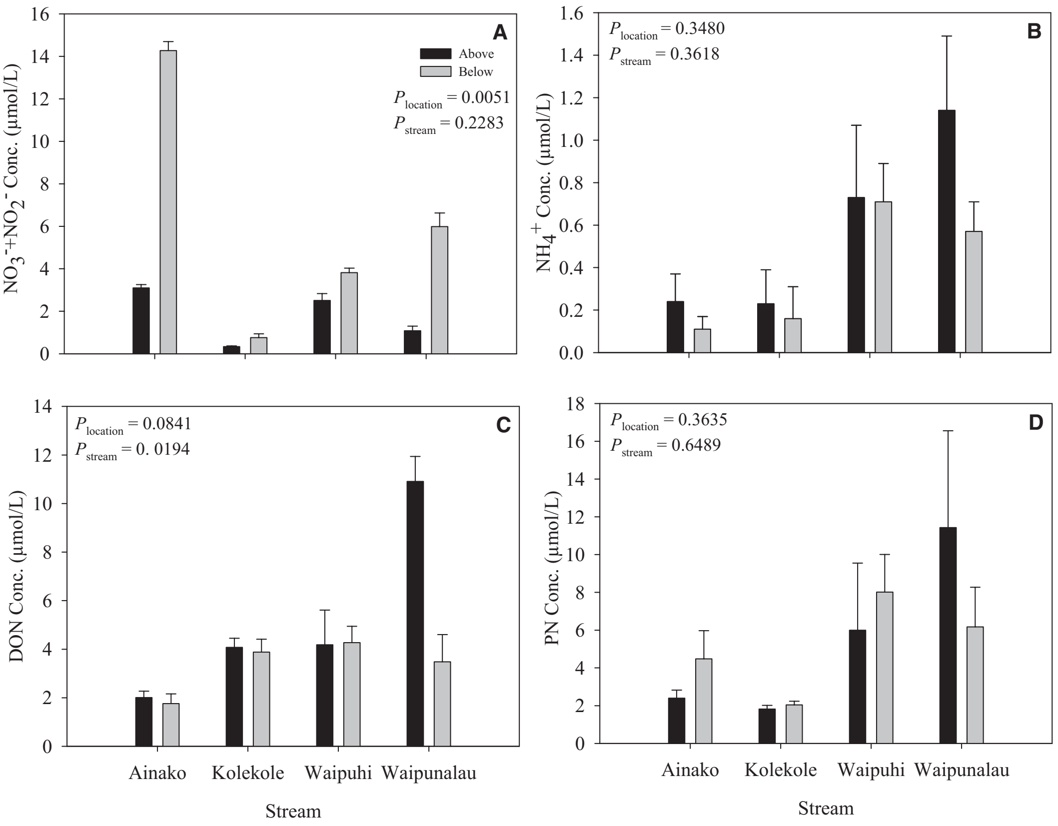

FIGURE 1. Comparison of average (± SE) (A) $NO_3^-+NO_2^-$, (B) NH_4^+, (C) dissolved organic nitrogen (DON), and (D) particulate nitrogen (PN) concentrations in Hawaiian streams above and below *Falcataria moluccana* stands. Results from GLM are shown on figure ($\alpha = 0.05$).

contrast, PC concentrations were similar above and below *F. moluccana* stands. Percent contribution of DOC to the TC pool was significantly lower ($P = 0.0252$) below *F. moluccana* stands, whereas percent contribution of PC to the TC pool was significantly higher ($P = 0.0005$) (Table S1). DOC concentrations differed among streams ($P = 0.0023$), whereas PC concentrations were similar. The DOC difference was driven by Ainako Stream, which had the lowest values.

TDP concentrations were similar above and below *F. moluccana* stands, but significantly differed among streams, where Waipuhi and Waipunalau Gulches had significantly higher concentrations than Ainako Stream and Kolekole River ($P = 0.0003$) (Table 2). Almost 100 percent of the TDP in Ainako Stream and Kolekole River was DOP, whereas DOP and PO_4^{3-} comprised 70 percent and 30 percent of the TDP, respectively, in Waipuhi and Waipunalau Gulches. H_4SiO_4 concentrations were higher

TABLE 2. *Comparison of average (± SE) nutrient concentrations in Hawaiian streams above and below* Falcataria moluccana *stands. All concentrations are reported in μmol/L, except for TSS, which is reported as mg/L.*

Location	Stream	Stations	*N*	TN	TDN	TC	DOC	PC	TDP	H_4SiO_4	TSS
Above	Ainako	2	20	8 ± 1	5 ± 0	86 ± 11	55 ± 6	31 ± 5	0.0 ± 0.0	92 ± 11	3.6 ± 1.1
	Kolekole	2	16	7 ± 0	5 ± 0	216 ± 25	194 ± 24	22 ± 3	0.1 ± 0.1	84 ± 12	2.3 ± 1.2
	Waipuhi	1	5	13 ± 5	7 ± 2	191 ± 86	108 ± 38	83 ± 49	1.4 ± 1.0	94 ± 20	22.1 ± 14.8
	Waipunalau	1	5	25 ± 6	13 ± 1	501 ± 95	342 ± 33	159 ± 69	1.4 ± 0.4	16 ± 7	69.4 ± 40.5
Average			46	10 ± 1	6 ± 1	188 ± 24	140 ± 17	47 ± 11	0.4 ± 0.1	81 ± 7	12.3 ± 5.3
Below	Ainako	2	20	21 ± 2	15 ± 1	100 ± 24	43 ± 7	56 ± 18	0.2 ± 0.1	149 ± 17	5.7 ± 1.6
	Kolekole	1	8	7 ± 0	5 ± 0	195 ± 32	171 ± 31	24 ± 3	0.1 ± 0.0	95 ± 13	4.5 ± 3.3
	Waipuhi	2	10	17 ± 3	9 ± 1	248 ± 41	127 ± 12	121 ± 30	0.9 ± 0.2	140 ± 19	28.6 ± 9.4
	Waipunalau	2	10	16 ± 3	10 ± 1	214 ± 56	124 ± 29	89 ± 29	1.0 ± 0.2	123 ± 15	31.5 ± 11.6
Average			48	16 ± 1	11 ± 1	170 ± 20	98 ± 11	72 ± 12	0.5 ± 0.1	132 ± 9	15.6 ± 3.6

below *F. moluccana* stands than above them, but the difference was not significant ($P = 0.1178$), and concentration levels were similar among streams (Table 2).

Benthic Chl *a* concentrations were three times higher ($P < 0.0001$) below the *F. moluccana* stand than above it in Ainako Stream (Fig. 2). Above the stand, benthic algae were significantly higher on the + N + P treatment compared to the control ($P = 0.037$), and below the stand, they were significantly higher on the + P treatment compared to the control ($P = 0.005$) and + N treatment ($P = 0.022$).

DISCUSSION

EFFECTS ON STREAM WATER QUALITY.—N_2-fixing trees found within riparian and greater watershed areas affect stream N concentrations. The most commonly documented effect is an increase in stream and groundwater NO_3^-+NO_2^- concentrations (Goldman 1961, Compton *et al.* 2003, Hurd & Raynal 2004, Jovanovic *et al.* 2009, Mineau *et al.* 2011). In our study, NO_3^-+NO_2^- concentrations significantly increased below *F. moluccana* stands in all streams. The greatest concentration increase was in Ainako Stream, where NO_3^-+NO_2^- increased ~ 12 μmol/L, a 500 percent increase, and may be attributed to the dense *F. moluccana* canopy over the relatively narrow stream channel.

It remains unknown how N_2-fixing trees increase NO_3^-+NO_2^- in streams, but several mechanisms are possible. First, litter from the N_2-fixing trees may fall directly into streams, where it is physically, chemically, and biologically broken down, releasing either particulate or dissolved N into the water (*a la* Compton *et al.* 2003). In the Pacific Northwest, stream litter inputs were three times greater in an *A. rubra* forest (348 g/m^2) than in an old-growth coniferous one (104 g/m^2) (Volk *et al.* 2003). This translated into significantly higher PC concentrations, but not PN ones (Volk *et al.* 2003). *Falcataria moluccana* has been shown to increase litter inputs to wet lowland forests in Hawaii 1.3–8.6 times and N mass of litterfall 4–55 times (Hughes & Denslow 2005); these inputs are 2.9–3.4 times greater (1000–1200 g/m^2) than *A. rubra* litter inputs to streams (Volk *et al.* 2003). Second, soluble nutrients either derived from breakdown of N_2-fixing tree leaf litter on land or exudation from their roots may be mobilized through surface runoff and groundwater (Goldman 1961, Wondzell & Swanson 1996). At Castle Lake, California, high NO_3^- concentrations in spring water beneath *Alnus tenuifolia* (mountain alder) were thought to be from nitrification of NH_4^+ released from decomposing leaf litter (Goldman 1961), as extractable soil N concentrations, primarily NH_4^+, were an order of magnitude higher below the alders than other deciduous trees (Goldman 1961). A third possibility is leaching of N_2-fixing tree leaves on land and lateral transport of the solubilized N from upland stands via groundwater to streams (Compton *et al.* 2003, Sigleo *et al.* 2010, Steinberg *et al.* 2011). In Oregon, *A. rubra* cover within entire watersheds explained a much greater proportion of NO_3^- variability (66%) than cover within 30–120 m (< 42%) of the stream, suggesting that this mechanism was the major N source to streams (Compton *et al.* 2003).

Further research is needed to determine which of these mechanisms is responsible for elevated stream NO_3^-+NO_2^- concentrations draining *F. moluccana* stands in Hawaii. *Falcataria moluccana* leaf litter decomposes rapidly, however, particularly under *F. moluccana*-dominated canopies with no evidence of immobilization (Hughes & Uowolo 2006) and soil inorganic N availability is up to 120 times greater than in native-dominated forests on comparably aged lava flows (Hughes & Denslow 2005). These results suggest that *F. moluccana* leaves are decomposed on land into soluble N forms transported either through surface runoff or groundwater to streams.

Like NO_3^-+NO_2^-, stream DON concentrations have also been reported to primarily increase in the presence of N_2-fixing trees (Compton *et al.* 2003, Volk *et al.* 2003, Mineau *et al.* 2011), although no detectable effects have also been reported (Sigleo *et al.* 2010). In downstream reaches where *E. angustifolia* was the dominant riparian vegetation, DON was the dominant dissolved N form (65% of TDN) and its concentrations were higher than those in above stream reaches without *E. angustifolia* (Mineau *et al.* 2011). A similar result was found in streams draining *A. rubra* forests in Washington, where organic N (ON) concentrations were higher than those measured in streams draining old-growth coniferous forests and ON was the dominant N form (58% of the TN) (Volk *et al.* 2003). In Oregon and Washington, stream DON and total ON concentrations increased with increasing *A. rubra* cover; however, NO_3^-+NO_2^- was the dominant dissolved N form in these streams (Compton *et al.* 2003, Steinberg *et al.* 2011). At Harvard Forest, increased N availability enhanced DON leaching from the forest floor, but not from deeper mineral soil, suggesting that overland flow, not groundwater, was responsible for increases in stream DON concentration (Currie *et al.* 1996, McDowell *et al.* 1998). In addition, it is speculated that N_2-fixing trees, like *A. rubra*, may increase stream DON concentrations through root or symbiont exudation (Compton *et al.* 2003); a similar mechanism has been proposed to explain elevated soil and stream DON concentrations in high atmospheric N deposition areas (Brookshire *et al.* 2007).

In contrast to previously reported increases, DON concentrations decreased in three of the four streams studied below *F. moluccana* stands. We speculate that the soil DON that typically leaches into the streams is broken down by extracellular N-mineralizing enzymes in the soil whose activities are significantly higher in *F. moluccana* stands than in native ones (Allison *et al.* 2006), and nitrified. Nitrification rates were higher in *A. rubra* forests compared to old-growth coniferous ones (Verburg *et al.* 2001, Rothe *et al.* 2002); this has yet to be documented for *F. moluccana*. Nitrification is probably not occurring in the streams because DON concentration decreases do not account for NO_3^-+NO_2^- concentration increases (Fig. 1).

Documented effects of N_2-fixing trees on stream NH_4^+ concentrations are less consistent in sign and magnitude than those reported for NO_3^-+$NO_2^-$and DON. Several studies have reported no effect of N_2-fixing trees on stream NH_4^+ concentrations (Compton *et al.* 2003, Volk *et al.* 2003), whereas one reported an increase (Goldman 1961) and another a decrease

(Stottlemyer 1992). In our study, small decreases in NH_4^+ were observed from the reach above the *F. moluccana* stand to below it and this pattern was consistent across streams; however, it was not significant.

In comparison to dissolved N forms, few studies have investigated the effects of N_2-fixing trees on stream PN concentrations. To date, only one study has reported values as %N of suspended material and found that it was similar between streams draining *A. rubra* and old-growth coniferous forests (Volk *et al.* 2003). In our study, stream reaches above and below *F. moluccana* stands had similar PN concentrations, suggesting that the largest effect of *F. moluccana* was on dissolved N in the stream, not particulate matter. Similar stream PN concentrations above and below *F. moluccana* stands suggest that changes in stream chemistry were not likely from PN degradation within the stream and later N transformations, but rather from processes occurring on land.

Few studies assessing the effects of N_2-fixing trees on stream water quality have measured DOC concentrations. In an Alaskan study, DOC concentrations nearly doubled below an *Alnus crispa* (green alder) stand (Stottlemyer 1992). Studies have shown that increased N availability in forests may stimulate microbial organic matter mineralization and increase release of DOC from the forest floor (Zech *et al.* 1994). In contrast to the Alaskan study, we found stream DOC concentrations were lower below *F. moluccana* stands, a pattern similar to what we found with respect for DON. A similar pattern of decreasing DOC and DON soil water concentrations was observed in Norwegian forests exposed to chronic N inputs (Vestgarden *et al.* 2001). Our results are coincidental with increased rates of litter decomposition and net N mineralization in *F. moluccana*-dominated forests in Hawaii (Hughes & Denslow 2005, Hughes & Uowolo 2006). These observations suggest a scenario whereby N amendments stimulate microbial utilization of soil dissolved organic matter and lead to decreased soil water DOC and DON concentrations. *Falcataria moluccana* invasion into lowland wet forests has been shown to increase litter decomposition rates (Hughes & Uowolo 2006) and levels of extracellular enzymes responsible for C and N mineralization (Allison *et al.* 2006). Therefore, it is possible that increased N inputs from *F. moluccana* to the riparian forests of the studied streams stimulated microbial utilization of soil water DOC and DON, decreasing the amount available for leaching into the streams. The strong correlation ($r = 0.888$) between stream DOC and DON concentrations further suggests common controls (Fig. 3). These controls are likely the ones affecting, soil organic matter (SOM), as soil C:N is strongly correlated with stream DOC and DON concentrations in unpolluted forests (Brookshire *et al.* 2007). In young Hawaiian soils, terrestrial primary production and stabilization of SOM onto minerals affect soil organic C:N (Vitousek 2004).

Like DOC, only one study to our knowledge has examined the effects of N_2-fixing trees on stream PC concentrations. This study found that PC concentrations were significantly higher in streams with *A. rubra* compared to streams with old-growth coniferous trees (Volk *et al.* 2003). This was expected because of the greater litter input to *A. rubra* streams than to old-growth coniferous ones (Volk *et al.* 2003). While litter inputs from *F. moluccana* stands are significantly higher than from native-dominated stands (Hughes & Denslow 2005), PC concentrations in our streams were similar between reaches above and below *F. moluccana* stands. This suggests that most of the tree litter falls and is processed on the forest floor rather than in the stream. One difference to note is that higher PC and PN concentrations were found in the streams draining older substrates compared to younger ones, and this may be explained by higher soil C and N content found at these sites, as SOM becomes stabilized on minerals found on substrates this age (Vitousek 2004).

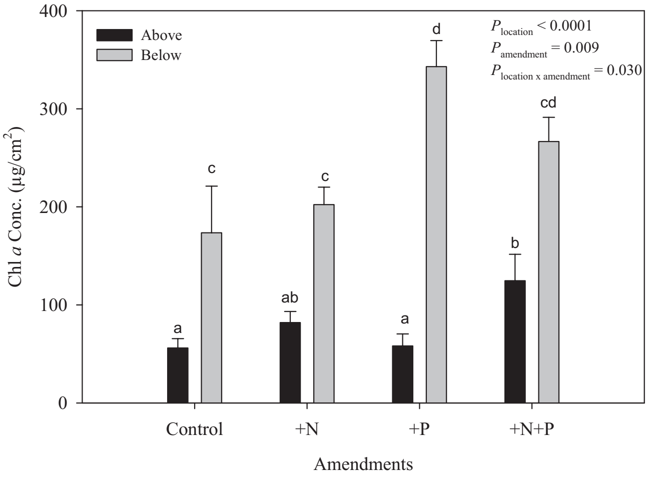

FIGURE 2. Average (± SE) Chlorophyll *a* (Chl *a*) concentrations in Ainako Stream, Hawaii, above and below *Falcataria moluccana* stands in response to nutrient amendments: control (no nutrient amendments), +N (plus nitrogen), +P (plus phosphorus), and + N + P (plus nitrogen and phosphorus) ($N = 3$). Results from two-way ANOVA and Tukey HSD multiple comparison test are shown on figure ($\alpha = 0.05$). Tukey HSD multiple comparison test results are from one-way ANOVAs where locations (above and below *F. moluccana*) were individually analyzed because there was a significant interaction between location and nutrient amendment. Bars with different letters are significantly different from one another (above *F. moluccana* – letters a-b are used, below *F. moluccana* – letters c-d are used). Details on nutrient amendments can be found in the methods.

As with DOC and PC concentrations, effects of N_2-fixing trees on stream P concentrations have not been well documented and reported effects are variable. Total phosphorous concentrations significantly increased in Pacific Northwest streams draining *A. rubra* forests compared to old-growth coniferous ones (Volk *et al.* 2003). In contrast, *E. angustifolia* in the riparian zone of Idaho and Wyoming streams had no effect on PO_4^{3-} concentrations (Mineau *et al.* 2011). We also found TDP concentrations were similar in stream reaches above and below *F. moluccana* stands. *Falcataria moluccana* in Hawaiian plantations decreases soil P availability (Binkley & Ryan 1998, Binkley *et al.* 2000, Kaye *et al.* 2000), but increases P supply from litter, as well as soil P availability in young lowland wet forests (Hughes & Denslow 2005). Soil age and rock-derived P availability have been proposed as possible factors explaining these discrepancies (Hughes

& Denslow 2005), as primary mineral phosphates in young soils are available to plants, whereas P in older soils, particularly those with lengthy periods of agriculture, is more occluded (Vitousek 2004). In our study, streams draining older substrates had higher TDP concentrations than streams draining young substrates. This difference may be explained by high P concentrations found in Hawi lavas of the Kohala Volcano compared to lavas from other volcanoes (Spengler & Garcia 1988).

N_2-fixing tree effects on stream H_4SiO_4 concentrations remain unknown. We observed consistently higher concentrations in reaches below *F. moluccana* stands, although the difference was not significant. Increases may be from either leaf litter decomposition on land or in streams (Derry *et al.* 2005), or from groundwater inputs (Dollar & Atkinson 1992). Sixty-eight to 90 percent of silica (Si) released into Hawaiian streams has cycled through plants and has not been directly released from silicate mineral weathering (Derry *et al.* 2005). In addition, *F. moluccana* leaves have more Si than native *Metrosideros polymopha* and *Acacia koa* leaves, but a lower amount than invasive *Trema orientalis* and *Psidium cattleianum* leaves (Hughes unpubl. data). Additional data are needed to determine whether *F. moluccana* does significantly increase H_4SiO_4 concentrations in streams.

EFFECTS ON PRIMARY PRODUCERS AND HIGHER TROPHIC LEVELS.—While it has been argued that increased forest N inputs from either N_2-fixing trees or atmospheric pollution will not lead to eutrophication in temperate freshwaters because they are generally P-limited (Hecky & Kilham 1988, Stoddard 1994), these increased inputs may lead to eutrophication in tropical freshwaters, which tend to be N-limited (Laperriere 1995, Neill *et al.* 2001, Flecker *et al.* 2002). In Ainako Stream, benthic Chl *a* concentrations were three times higher below the *F. moluccana* stand than above it (Fig. 2). In contrast, benthic Chl *a* concentrations were similar between streams draining *A. rubra* and old-growth coniferous forests (Hernadez *et al.* 2005, Volk *et al.* 2008). Presence of *A. rubra* also did not affect nutrient limitation, as benthic algae were limited by both N and P in streams with and without *A. rubra* (Volk *et al.* 2008). In contrast, presence of *E. angustifolia* alleviated N-limitation of benthic algae, and in some streams, it appeared to induce P-limitation (Mineau *et al.* 2011). In Hawaii, benthic algae were limited by both N and P above the *F. moluccana* stand in Ainako Stream. Below the stand, benthic algae Chl *a* was higher across all nutrient treatments compared to the ones above the stand suggesting that *F. moluccana*'s presence relieved N-limitation (Fig. 2). In addition, benthic algal Chl *a* was 1.3–2 times higher in treatments with P than those without it (Fig. 2), suggesting that benthic algae switched from being co-limited by N and P above the *F. moluccana* stand to P-limited below it. While our results are limited to Ainako Stream, they suggest that *F. moluccana*'s presence can increase benthic algal Chl *a* and cause streams to become P-limited.

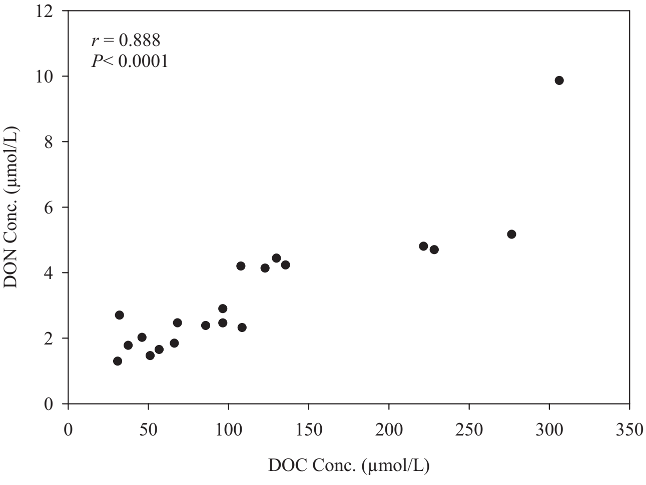

FIGURE 3. Association of dissolved organic carbon (DOC) concentrations with dissolved organic nitrogen (DON) ones in Hawaiian streams that were sampled above and below *Falcataria moluccana* stands. Results from correlation analysis are shown on figure (α = 0.05).

The probability is high that increased stream N loads from *F. moluccana* contribute to coastal eutrophication. First, N inputs from litter are as high as industrial corn production N fertilization rates (Jaynes *et al.* 2001) and higher than atmospheric N deposition rates in industrialized areas (Berendse *et al.* 1993, Wright & van Breeman 1995). Second, coastal waters are generally N-limited (Hecky & Kilham 1988) and N limitation occurs in Kaneohe Bay, Hawaii, during prevailing non-storm conditions (Ringuet & MacKenzie 2005). Third, *F. moluccana* leaves are rapidly transported to coastal waters during storms, where they may breakdown faster than in streams, as was observed with *A. rubra* leaves in the Pacific Northwest (Sakamaki & Richardson 2007).

While our study focused on changes in stream water quality from *F. moluccana*, N_2-fixing trees, like other riparian trees (Wallace *et al.* 1999), also affect leaf litter breakdown rates and stream invertebrates (Sampaio *et al.* 2001, Elliot *et al.* 2004, Richardson *et al.* 2004, Wipfli & Musslewhite 2004). In Hawaii, *F. moluccana* affected Ainako Stream's food web (Atwood *et al.* 2010). Its litter replaced stream macroalgae and particulate organic matter as a major food source to lower level consumers, and through this substitution became an important indirect C and N source for higher level consumers.

CONCLUSION

Falcataria moluccana is affecting both forests (Hughes & Denslow 2005, Allison *et al.* 2006, Hughes & Uowolo 2006) and streams (Atwood *et al.* 2010). In three of our four streams, $NO_3^- + NO_2^-$ concentrations exceeded Hawaii Department of Health's dry season standards below *F. moluccana* stands (HDOH 2009). *Falcataria moluccana* removal may improve stream water quality as decreased soil NO_3^- levels were documented following removal in American Samoan forests (Hughes *et al.* 2012). Our study highlights the need to better understand effects of terrestrial vegetation shifts on aquatic ecosystems, especially in the face of environmental change. This knowledge is central to our ability to predict how these changes will impact these linked ecosystems, as well as our ability to manage them under new conditions (Ball *et al.* 2010).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. *Comparison of average (± SE) percent contributions of different forms of N and C to the total N and C pools in Hawaiian streams above and below F. moluccana stands.*

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