

***Hedychium gardnerianum* invasion into Hawaiian montane rainforest: interactions among litter quality, decomposition rate, and soil nitrogen availability**

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Abstract. Few studies have examined the invasion of understory species into closed-canopy forests and, despite inter-specific differences in litter quality and quantity between understory and dominant canopy trees, the influence of understory invasions on soil nitrogen (N) cycling remains unknown. This paper examines litter quality and decomposition of kahili ginger (*Hedychium gardnerianum*), an invasive understory herb, to determine the influence of this species on N cycling in a Hawaiian montane rainforest. To examine the potential feedback between increased soil N availability and litter decomposition, litter from the invasive ginger, a native tree, and native tree fern was collected from unfertilized and fertilized plots and decomposed in a reciprocal transplant design. *Hedychium* litter decomposed faster than litter from the two native species. Across species, decomposition rates were negatively correlated with litter lignin content. Despite rapid decomposition rates of *Hedychium* litter, soil nitrogen availability and rates of net mineralization in the soil were similar in invaded and uninvaded plots. Nitrogen cycling at this site may be more strongly influenced by native species, which contribute the most to overall stand biomass. A negative effect of fertilization on the decomposition of *Hedychium* litter suggests that a negative feedback between litter quality and soil N availability may exist over longer timescales.

Introduction

Through its influence on decomposition and the rate of nutrient return to the soil, plant litter quality plays a critical role in the regulation of nitrogen (N) cycling within ecosystems (Melillo et al. 1982; Hobbie 1992; Scott and Binkley 1997). Individual species vary widely in litter chemistry with patterns emerging across growth forms and habitats (Vitousek et al. 1994; Cornelissen et al. 1997; Reich et al. 1997; Hobbie and Gough 2002). For example, long-lived leaves of perennial species are often characterized by low nutrient and high secondary compound content while short-lived leaves of rapidly growing species display high nutrient and low secondary compound content (Chapin 1980; Aerts and Chapin 2000). Thus, changes in species composition within a community arising from disturbance or biological invasion may significantly alter the quality of litter input and subsequent rates of soil N cycling.

The invasion of understory species into closed-canopy forests can introduce new growth forms (e.g., grasses, herbs, woody shrubs) to systems that are dominated by large-statured trees. The few studies that have examined the

invasion of understory species into forests found faster rates of nutrient cycling in soils under or adjacent to the understory plants compared to soils under native shrubs or trees (Ehrenfeld et al. 2001; Standish et al. 2004). Because the influence of individual species on N cycling within a forest presumably results from a combination of litter quality and quantity (e.g., Ehrenfeld 2003), the results from these studies are intriguing given the relatively low biomass that understory species comprise relative to canopy trees. The invasion of understory species into closed-canopy forests is thought to be uncommon (Baker 1986) and has received little attention. Thus, the generality of increased N cycling following the invasion of understory species into forests remains unknown.

This paper investigates litter quality and decomposition of an invasive understory herb and the subsequent influence on N cycling in an N-limited Hawaiian rainforest. Kahili ginger (*Hedychium gardnerianum*) is an herbaceous plant that is native to the Himalayas. First reported at Hawaii Volcanoes National Park in the 1950s (Wester 1992), *Hedychium* is now the dominant understory species in many montane rainforests throughout the state (Ostertag and Verville 2002), often forming a complete ground cover. In the absence of *Hedychium*, these forests contain a modest understory layer of native grasses, shrubs, and ferns and are dominated by native trees and tree ferns. Thus, the introduction of dense *Hedychium* patches into the understory significantly changes the structure of these forests. The effects of *Hedychium* on ecosystem processes, such as N cycling, have not been examined in this system.

Increased soil N availability resulting from rapid decomposition of high quality herbaceous species litter may further increase litter quality, creating a positive feedback among litter quality, decomposition rates, and soil N availability. Independent of changes in litter quality, high soil N availability has been shown to increase decomposition rates of fern and angiosperm litter in similar Hawaiian sites (Hobbie and Vitousek 2000; Allison and Vitousek 2004a). The potential for an invasive species to create a positive feedback between litter quality and soil N availability is particularly important in infertile systems, such as the Hawaiian rainforest studied here, where low soil N availability is maintained by poor litter quality and slow decomposition rates (Chapin 1980). To examine the potential for positive feedback between increased N availability and litter decomposition dynamics, I studied litter chemistry and decomposition in unfertilized and fertilized plots.

Methods

Site description

This study was conducted adjacent to Hawaii Volcanoes National Park on the island of Hawaii (19°25' W, 155°15' N). The elevation at this site is 1176 m and annual precipitation is 2500 mm (Juvik and Juvik 1998). The soils in this area

consist of 200–400 year-old coarse tephra deposits overlaying an older lava flow (Crews et al. 1995). Previous work at the site demonstrated limitation by several soil nutrients, with plant growth primarily limited by N (Vitousek et al. 1993). Two experiments were performed at this site.

Experiment 1

The first experiment examined the effects of *Hedychium* on soil resource availability in four plots where understory vegetation was dominated by *Hedychium* (invaded plots) and four plots where understory vegetation was scarcely populated by native species (uninvaded plots). In invaded plots, *Hedychium* patches were at least 4 m². In both plot types, canopy species included a native tree (*Metrosideros polymorpha*) and native tree ferns (*Cibotium* spp.). All plots were arbitrarily selected and located in undisturbed forest away from roads and trails. Prior to invasion, it is unlikely that the invaded plots were different (e.g., soil properties, light availability) than the uninvaded plots. *Hedychium gardnerianum* is widespread in Hawaii and is found across sites that vary in the frequency of disturbance, light availability, and substrate age and quality (J. Funk, personal observation). However, because of the ‘natural’ design of Experiment 1, it was not possible to attribute differences in soil properties between invaded and uninvaded plots to an effect of *Hedychium* or to an inherent site characteristic that *Hedychium* selects.

Soil (0–10 cm depth) was collected beneath patches of *Hedychium* in four invaded plots and under canopy trees in four uninvaded plots. In each plot, two cores were taken and soil was placed into bags. One bag was immediately taken to the laboratory and the other was buried at the plot for 10 days. Soil moisture was calculated after drying soils at 100 °C for 4 days. Soil pH was measured in a 10:1 mixture of 0.1 M CaCl₂ to wet soil. Soil subsamples were extracted with 2 M KCl to determine nitrate-N and ammonium-N as in Mack and D’Antonio (2003). Supernatant was analyzed colorimetrically with a Lachat analyzer (Lachat, Milwaukee, WI, USA). Net N mineralization was calculated as nitrate-N plus ammonium-N in the 10 day buried soils (final) minus that in the samples immediately processed in the laboratory (initial). Net nitrification was calculated as final minus initial nitrate-N.

Experiment 2

The second experiment examined the effect of fertilization on litter decomposition. This experiment was conducted in fertilized and unfertilized plots initiated in October 1985 (Vitousek et al. 1993), which were located adjacent to the invaded and uninvaded plots described above. The Vitousek fertilization experiment consists of thirty-two 15×15 m plots, which were assigned to eight treatments with factorial combinations of unfertilized (O), nitrogen (N), phosphorus (P), and

a micronutrient mixture (T) containing K, Ca, and Mg: O, N, P, T, NP, NT, PT, and NPT. Fertilization plots receive semi-annual applications of 100 kg ha⁻¹ yr⁻¹ of N (half as urea, half as ammonium nitrate) and/or P (triple superphosphate). In this study, I examined litter quality and decomposition rates in unfertilized and NPT plots of the Vitousek fertilization experiment.

Green and senesced leaves were collected simultaneously from *Hedychium* and the two canopy tree species *Metrosideros* and *Cibotium* in all NPT and unfertilized plots. Second season mature leaves were collected from the top of *Metrosideros* canopies. Litter traps were placed under *Metrosideros* canopies for 2 weeks to collect senesced leaves. Green and senesced leaves of *Hedychium* and *Cibotium* were collected directly from the plant. Leaf area of green leaves was measured with a LI-3000 portable leaf area meter (LI-COR, Lincoln, NE, USA). Green and senesced leaves were dried at 70 °C for 48 h, weighed to determine specific leaf area (SLA, cm² g⁻¹), and then ground to pass a 20-mesh screen. Leaf N content was analyzed with an elemental analyzer (CE Instruments Flash EA 1112, CE Elantech, Lakewood, NJ, USA). The resorption of N during leaf senescence was calculated as [1 – (litter N concentration)/(foliar N concentration)] × 100.

Ground leaf litter samples were sent to the Pesticide Research Lab at Penn State University for polyphenol and protein analyses. Standards were prepared for each species by crudely purifying phenolics using silica gel (LH20) columns (Appel et al. 2001). Litter lignin content was analyzed with a standardized forest products procedure (Ryan et al. 1989) at the Natural Resources Research Institute at University of Minnesota, Duluth.

A litterbag study was used to measure rates of litter decomposition of the three study species. Senesced leaf tissue was collected as described above and air-dried at 25 °C. I placed 2.2 g of litter into 1 mm mesh fiberglass screen bags, which allowed access by most soil invertebrates (Hobbie and Vitousek 2000). In July, litterbags were placed on top of the litter layer in four replicate unfertilized plots and four replicate NPT plots. Both unfertilized and fertilized plots contained *Hedychium*, but the litterbags were placed at least 1 m from any understory vegetation. Each plot received litterbags containing litter from each plot type (unfertilized and NPT) for each species (3 species × 2 litter types). This design can elucidate the relative importance of soil and litter quality in determining litter decomposition rates. Enough litterbags of each species and litter type were placed in plots to allow harvests after 4 months (November) and 8 months (March). After collection, the remaining tissue was removed from the bag, dried, and weighed. Litter decay constants (*k*-values) for each species and treatment were generated by fitting mass loss over time to a negative exponential model:

$$M_t = M_o \cdot e^{-kt} \quad (1)$$

where M_t is litter mass at time t in years and M_o is initial litter mass (Olson 1963).

Statistical analysis

Differences in soil, foliar, and litter properties among species and plots were analyzed by one-way ANOVA. Planned post hoc comparisons were analyzed by Tukey's honest significant difference. Decay constants were fit by an exponential model in the regression module of Sigma Plot v.6.10 (SPSS, Chicago, IL, USA). Treatment differences in k -values were analyzed by a three-way ANOVA with species, litter source (from fertilized and unfertilized plots), and plot (fertilized and unfertilized) as main effects. Pearson product-moment correlation coefficients were generated to evaluate the linear association between k -values and litter properties. Data that violated the ANOVA assumptions of normality and homogeneity of variance were rank transformed. Correlations and ANOVA were performed in Statistica v.5.1 (Statsoft, Tulsa, OK, USA).

Results

Soil moisture, pH, inorganic N availability, and rates of N cycling were remarkably similar between plots dominated by *Hedychium* and plots dominated by native trees and tree ferns (Table 1). Nitrification rates were significantly lower in invaded plots, which may suggest that the invasion of *Hedychium* slows down N cycling in these forests.

SLA and foliar N content were higher in *Hedychium* compared to either native species (Table 2). However, *Hedychium* resorbed 60% of total leaf N during leaf senescence, which resulted in relatively low litter N content. In contrast, N resorption from *Cibotium* leaves was very low (~17%), which resulted in high litter N content. N content was lowest in *Metrosideros* litter. Fertilization increased foliar and litter N content in *Cibotium* only. Across species, there was no effect of fertilization on litter C:N ($P > 0.25$ for all comparisons).

Both *Hedychium* and *Cibotium* displayed low litter polyphenol content (Table 2). Concentrations of Folin-reactive polyphenols and tannin were too low to be detected in *Hedychium* litter. In contrast, polyphenol content was high in *Metrosideros* litter. Lignin and protein content was lower in *Hedychium* litter than in litter from either native species. Across species, fertilization did not influence the polyphenol or protein content of litter ($P > 0.10$ for all comparisons).

Overall, there were significant effects of species ($F = 53.5$, $P < 0.001$), litter source ($F = 4.2$, $P = 0.05$; litter from fertilized and unfertilized plots), and plot ($F = 6.9$, $P = 0.01$; litter decomposed in either fertilized or unfertilized plots) on rates of decomposition (Table 2). *Hedychium* litter decomposed faster than litter from either native species, with the slowest rates observed for tree fern (*Cibotium*) litter. Combining data from all three species, litter from fertilized plots decomposed faster than litter from unfertilized plots. However,

Table 1. Soil properties for plots dominated by native species *Metrosideros* and *Cibotium* (uninvaded) and plots dominated by *Hedychium* (invaded).

Forest type	Soil moisture (%)	Soil pH	Soil inorganic N ($\mu\text{g g}^{-1} \text{NO}_3, \text{NH}_4\text{-N}$)	Net mineralization ($\mu\text{g g}^{-1} \text{d}^{-1}$)	Nitrification ($\mu\text{g g}^{-1} \text{d}^{-1}$)
Uninvaded	71 (2) ^a	3.5 (0.3) ^a	2.1 (0.7) ^a	0.008 (0.011) ^a	0.021 (0.006) ^a
Invaded	67 (2) ^a	3.7 (0.1) ^a	2.4 (0.3) ^a	0.012 (0.011) ^a	0.005 (0.003) ^b

Numbers are means and (standard error) for four plots per forest type. Nitrogen mineralization and nitrification rates are from soil incubated in the field for 10 days. Letters denote statistical significance at $P < 0.05$ within each parameter.

within a species, decomposition rates were similar between litter from fertilized and unfertilized plots when decomposed in a common plot (Table 2). Overall, fertilization decreased decomposition rate (plot effect). However, a significant species by soil interaction ($F = 4.13$, $P = 0.02$) likely reflects different effects of fertilization on decomposition of *Hedychium* and *Cibotium* litter relative to *Metrosideros* litter. Decomposition was inhibited most strongly by fertilization in *Hedychium* litter, followed by *Cibotium* litter from unfertilized plots, while decomposition of *Metrosideros* litter and *Cibotium* litter from fertilized plots was not influenced by fertilization. However, when corrected for multiple comparisons across groups, the inhibition of litter decomposition by fertilization was only statistically significant for *Hedychium* litter from fertilized plots (Table 2). Across species and fertilization treatment, decomposition rates (k -values) were negatively correlated with litter lignin content ($r = -0.97$, $P < 0.01$) only.

Discussion

Hedychium displayed high SLA, low litter lignin and overall polyphenol content, and rapid rates of litter decomposition. However, despite high litter quality and rates of litter decomposition, *Hedychium* invasion did not increase N cycling (inorganic N pools, net mineralization) in this montane Hawaiian rainforest. Instead, net nitrification rates, which were four times greater in uninvaded plots relative to invaded plots, suggest that N cycling in the system may be more tightly regulated following invasion. These results contrast with those of Ehrenfeld et al. (2001) and Standish et al. (2004) who found increased N availability and cycling under alien understory species in closed-canopy forests. It is important to note that, in this study, N cycling was only measured over a 10-day period at one time during the year (July). While 10-day soil incubations have been used effectively to demonstrate species-specific effects on soil N dynamics in other studies (e.g., Matson 1990), N cycling can vary seasonally as processes are differentially controlled by litter chemistry and microclimate (e.g., Mack and D'Antonio 2003). N cycling in these closed-canopied forests is not likely limited by microclimate (e.g., low water availability and temperature) during July. I've also made the assumption that, prior

Table 2. Foliar and leaf litter properties for three species where leaves were collected and decomposed in unfertilized (control) and fertilized (NPT) plots.

	SLA (cm ² g ⁻¹)	Foliar N (mg g ⁻¹)	Litter N (mg g ⁻¹)	Litter C:N	N resorption ¹ (%)	k (y ⁻¹) control litter	k (y ⁻¹) NPT litter
<i>Hedychium gardnerianum</i>							
Unfertilized plots	169 (8) ^a	17.1 (0.6) ^{ad}	6.9 (0.4) ^a	63.3 (3.3) ^a	60 ^a	0.71 (0.03) ^a	0.85 (0.12) ^a
Fertilized plots	211 (13) ^b	18.6 (0.8) ^a	7.5 (0.6) ^a	57.9 (3.9) ^a	60 ^a	0.57 (0.04) ^a	0.54 (0.06) ^b
<i>Metrosideros polymorpha</i>							
Unfertilized plots	35 (0.4) ^c	7.1 (0.2) ^b	4.5 (0.2) ^b	108.9 (5.6) ^b	36 ^b	0.38 (0.06) ^b	0.45 (0.05) ^{cd}
Fertilized plots	37 (2) ^c	7.3 (0.2) ^b	4.6 (0.3) ^b	108.8 (6.0) ^b	38 ^b	0.43 (0.02) ^b	0.49 (0.04) ^{bc}
<i>Cibotium glaucum</i>							
Unfertilized plots	96 (9) ^d	13.1 (1.2) ^c	10.7 (0.7) ^c	40.5 (2.4) ^c	18 ^c	0.31 (0.03) ^b	0.34 (0.02) ^{cd}
Fertilized plots	113 (10) ^d	15.8 (1.1) ^d	13.2 (0.8) ^d	34.3 (1.9) ^c	16 ^c	0.24 (0.02) ^b	0.30 (0.04) ^d
	Lignin (%)	Lignin:N	Folin-reactive phenolics (%)	Condensed tannin (%)	Hydrolyzable tannin (%)	Protein (%)	
<i>Hedychium gardnerianum</i>							
Unfertilized plots	14.6 (0.5) ^a	22.0 (2.0) ^{ad}	nd	nd	nd	3.9 (0.7) ^a	
Fertilized plots	13.4 (1.3) ^a	17.9 (0.6) ^a	nd	nd	nd	4.5 (0.8) ^a	
<i>Metrosideros polymorpha</i>							
Unfertilized plots	31.9 (0.5) ^b	71.1 (4.3) ^b	13.7 (2.9) ^a	10.3 (1.8) ^a	11.2 (2.2) ^a	7.4 (0.3) ^b	
Fertilized plots	33.4 (1.3) ^b	74.0 (5.2) ^b	10.2 (2.6) ^b	12.4 (2.7) ^a	10.2 (3.0) ^a	7.6 (0.5) ^b	
<i>Cibotium glaucum</i>							
Unfertilized plots	38.5 (0.7) ^c	36.3 (2.7) ^c	4.6 (1.1) ^c	3.3 (0.3) ^b	1.3 (0.2) ^b	7.1 (0.7) ^{bc}	
Fertilized plots	38.9 (0.7) ^c	29.7 (1.3) ^a	4.3 (1.1) ^c	2.7 (1.3) ^b	4.2 (1.2) ^b	6.5 (0.2) ^c	

Numbers are means and (standard error) from four plots per treatment. Letters denote statistical significance at $P < 0.05$ within each parameter. ¹value uncorrected for whole-leaf mass loss during senescence. nd = not detected.

to invasion, soil properties were similar in invaded and uninvaded plots. Similarities between invaded and uninvaded plots following invasion suggest that *Hedychium* neither selects nor causes sites of markedly different quality.

Lower net nitrification rates in invaded plots and high N resorption from senescing *Hedychium* leaves (Table 2) concur with recent evidence that *Hedychium* invasion may cause N to cycle more tightly within a system. Asner and Vitousek (2005) found lower foliar N in *Metrosideros* stands that had been invaded by *Hedychium* compared to uninvaded stands and attributed this result to greater N uptake by *Hedychium*. High foliar N content of *Hedychium* relative to native species (Table 2) supports this argument. The positive correlation between *Hedychium* abundance and soil N availability (Ostertag and Verville 2002) suggests that *Hedychium* does not preferentially invade N-limited forest.

The effects of *Hedychium* on soil N pools and rates of net mineralization were negligible despite rapid rates of litter decomposition and, presumably, N return to the soil. Rapid decomposition of invasive litter may have a minor influence on soil N cycling if the biomass production of native species is substantially larger than that of invasive species (Chapin et al. 1996; Prescott et al. 2000). The present study was conducted in a dense rainforest where large-statured native trees and tree ferns dominate biomass and litterfall and likely regulate N capture and cycling. One possibility for unaltered N pools and rates of net mineralization in *Hedychium* patches is that rapid rates of *Hedychium* litter decomposition were not large enough to compensate for the relatively low litter N content (Table 2). Alternatively, it is possible that rapid decomposition of *Hedychium* litter increases N return to the soil but that other processes, such as increased microbial immobilization or N uptake by *Hedychium*, consume additional N.

Slower decomposition of *Hedychium* litter in fertilized plots compared to unfertilized plots suggests that a positive feedback between increased soil N availability and rates of litter decomposition may not occur for *Hedychium* in these forests. Fertilization had a smaller influence on *Cibotium* decomposition and no effect on *Metrosideros* decomposition, which is consistent with results from previous work in these plots (Vitousek 1998; Hobbie and Vitousek 2000). It is unclear why fertilization had a greater impact on the decomposition of *Hedychium* litter relative to the native species. Inhibition of litter decomposition by fertilization has been observed in other studies and may be explained by interactions between N and lignin (reviewed in Heal et al. 1997; Berg 2000). However, *Hedychium* has very low lignin content. The inhibition of *Hedychium* decomposition observed in this study contrasts with results of Allison and Vitousek (2004b), who found faster decomposition of *Hedychium* litter in fertilized plots compared to unfertilized plots at a lower elevation site. Because the initial litter quality of *Hedychium* was similar in both studies, the discrepancy between studies suggests that site characteristics (such as soil temperature or substrate age) may mediate the effects of fertilization on soil processes. Few studies have examined the invasion of a single species into

different sites (Ehrenfeld 2003; Hook et al. 2004). This approach may provide insight into the relative importance of species traits and ecosystem characteristics (e.g., native species composition, soil properties) in governing ecosystem responses to invasion.

In conclusion, my results highlight the need for a better understanding of how inter-specific differences in litter chemistry, physiology (e.g., N uptake), and biomass determine the influence of understory plants on soil processes in forests. In particular, the threshold density of invasive species necessary to detect changes in stand-level processes when the invaders differ from native species with respect to qualitative traits (e.g., litter quality, growth rate) is currently unknown (Ehrenfeld 2003). The results from the fertilization experiment suggest that a negative feedback between litter quality and soil N availability may exist over longer timescales due to the negative effect of fertilization on decomposition rate. Monitoring plant and soil properties in forests that vary in the abundance of invasive understory species and time since invasion may be the best approach to determine the influence of understory plants on soil processes in forests.

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