



Contrasting Predictors of Fern versus Angiosperm Decomposition in a Common Garden

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ABSTRACT

We evaluated differences in the rates and correlates of decomposition among 32 fern and angiosperm litter types collected in Hawai'i. Leptosporangiate ferns were separated into groups based on phylogeny: 'polypod' ferns, a monophyletic clade of ferns that diversified in the Cretaceous, and all other ('non-polypod') ferns that diversified earlier. We measured initial litter chemistry (nutrients and carbon chemistry), and mass loss and nitrogen (N), phosphorus (P), and calcium (Ca) of litter tissue during a 1-yr incubation in a common garden. Nutrient concentrations and carbon (C) chemistry differed significantly among litter types, and litter turnover (k -values) ranged from 0.29 to 8.31. Decomposition rates were more closely correlated with nutrient concentration than is typically observed. Lignin:N was the best predictor of decomposition across all litter types combined; however, among plant groups different predictors of decomposition were important. Nitrogen and P concentrations best predicted fern decomposition, whereas C chemistry, particularly lignin concentration, was more important for angiosperm (monocot and dicot) decomposition. Among native plants, non-polypod ferns decomposed significantly more slowly than both polypod ferns and angiosperms. Contrary to our hypothesis, fern litter did not decompose more slowly than angiosperm litter overall. Nutrient dynamics in litter were affected by initial litter concentration more than phylogeny; low-nutrient litter immobilized more nutrients than high-nutrient litter. Systematic differences in rates of decomposition, and the importance of nutrients in predicting fern decomposition, imply that changes in species composition within ferns and between ferns and angiosperms could influence the functioning of ecosystems where ferns are important forest components.

Key words: calcium; Hawai'i; lignin; nitrogen; phosphorus; phylogeny; pteridophytes; tropical wet forest.

FERNS COMPRIZE A NEARLY UBIQUITOUS AND OFTEN DOMINANT GROUP of understory plants in many forests. Tree ferns are important subcanopy plants in many tropical and subtropical forests and some cool temperate rainforests (Tanner 1977, Enright & Ogden 1987). Bracken (*Pteridium aquilinum*) is one of the most widespread, ecologically important, and best-studied fern species (Watt 1976, Tempel 1981, Cooper-Driver 1990, Marrs *et al.* 2000). Gleichenioid ferns (*Dicranopteris linearis* and *D. pectinatus*; Cohen *et al.* 1995, Walker *et al.* 1996, Russell *et al.* 1998) form monospecific thickets on many islands and some continental areas, and water ferns (*Azolla* and *Salvinia*) have been known to transform the ecosystems they invade (Thomas 1981, Hill & Cilliers 1999, Rivera *et al.* 2000, Adams *et al.* 2002). Ferns are particularly important on the Hawaiian Islands (Palmer 2003), where many different genera dominate the understories, and occasionally overstories, of sites across the broad range of Hawaiian environments. Some of these ferns, including *Dicranopteris* spp. and the tree ferns (*Cibotium* spp.) are particularly important, contributing to stand-level productivity and nutrient cycling in far greater proportion than their often-substantial biomass (Vitousek *et al.* 1995, Raich *et al.* 1997, Russell *et al.* 1998).

Most extant ferns are within a monophyletic clade of 'polypod' ferns, which are closely related to each other and diversified concurrently with the rise of angiosperms (Pryer *et al.* 2004, Schneider *et al.* 2004). These ferns are mainly terrestrial, ground-layer ferns (including bracken), although a few species are short tree ferns. In contrast, *Cibotium* and other larger tree ferns, *Dicranopteris* and other gleichenioid ferns, and water ferns are instead within a grade of 'non-polypod' ferns. Non-polypod ferns have unique foliar stoichiometry, with much lower cation concentrations than

other groups of plants in Hawai'i, the Caribbean, and New Zealand (Tanner 1977, Enright & Ogden 1987, Amatangelo & Vitousek 2008). Soluble and insoluble polyphenolic compounds are abundant in ferns in general, and in non-polypod ferns in particular (Enright & Ogden 1987, Russell & Vitousek 1997). These two fern groups coexist in forests in tropical, subtropical, and southern hemisphere temperate rainforests, whereas northern temperate forests typically lack terrestrial non-polypod ferns.

Comparative studies consistently demonstrate that fern leaves decompose slowly relative to other litter types, particularly dicots, although differences in decomposition rates between fern groups have not been explicitly tested. In Hawai'i, *Cibotium*, *Dicranopteris*, *Elaphoglossum crassicaule*, and *Diplazium sandwichianum* leaves decompose more slowly than angiosperm leaves (Russell & Vitousek 1997, Scowcroft 1997, Allison & Vitousek 2004b). Outside Hawai'i, a variety of studies have observed similar patterns, including studies on *Cyathea* and *Dicksonia* tree ferns, water ferns, bracken, and others (Enright & Ogden 1987, Frankland 1998, Perez-Harguindeguy *et al.* 2000, Wardle *et al.* 2002, Quested *et al.* 2003, Dearden & Wardle 2008). However, in the current literature standard predictors of decomposition such as lignin and lignin:N have been inconsistent in describing fern decomposition, particularly when experiments have included non-polypod ferns. While bracken fern decomposes no more slowly than would be expected based on its litter chemistry, (Hendricks *et al.* 2002, Trofymow *et al.* 2002), decomposition of the Hawaiian non-polypod ferns *Cibotium* and *Dicranopteris* is slow not merely in comparison to angiosperms, but in comparison to expectations based upon aspects of their tissue chemistry (N, P, lignin, polyphenols) (Scowcroft 1997; Allison & Vitousek 2004a, b).

Extending decomposition experiments to a broader range of litter types across phylogenetic groups could help determine the

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extent to which fern decomposition is controlled by the same litter chemistry factors as more commonly studied angiosperms, and whether controlling factors differ among fern groups. In this study, we evaluate the rates and the regulation of decomposition across a large pool of non-polypod ferns, polypod ferns, and angiosperms. We hypothesize that increased nutrient content will correlate positively with decomposition rates and nutrient release when evaluated across a large number of species. We also hypothesize that non-polypod fern litter will decompose more slowly than that of polypod ferns, and ferns in general will decompose more slowly than that of angiosperm litter due to distinct nutrient and carbon chemistry.

METHODS

We selected a total of 32 litter types; we attempted to encompass a large range of predicted litter decomposability, while also selecting species that are abundant and potentially (or demonstrably) important to ecosystem function in Hawaiian forest ecosystems. Twenty litter types were ferns, ten each of which were polypod and non-polypod ferns. Among polypod ferns, we focused on the locally dominant native species *Elaphoglossum crassicaule*, *Elaphoglossum parvisquamum*, *Diplazium sandwichianum* (from two sites), *Athyrium microphyllum*, *Nephrolepis cordifolia*, *Pneumatopteris sandwicensis*, *Microlepia strigosa*, *Dryopteris wallichiana*, and *Sadleria pallida*. Among the ten non-polypod ferns we included the native tree ferns *Cibotium glaucum* (from two sites) and *Cibotium menziesii*, and the native gleichenioid ferns *Dicranopteris linearis* (from two sites), *Sticherus owhyensis*, and *Diplopterygium pinnatum*. Additionally, we included the non-native tree ferns *Cyathea contaminiens* and *Sphaeropteris cooperi* var. Brentwood, and the non-native climbing fern *Lygodium japonicum*. Non-native litter types are necessary to represent the range of leaf types and decomposability in modern Hawai'i, as non-native litter has been shown to decompose more quickly than native litter (Allison & Vitousek 2004b). For comparison with ferns, we chose 11 angiosperm litter types, eight of which were dicots—four dominant canopy species (native *Metrosideros polymorpha* (two sites), *Cheirodendron trigynum* (from two sites), *Ilex anomala*, and *Acacia koa*) and two understory species (native *Vaccinium calycinum* and nonnative *Tibouchina urvilleana*). We also included three monocots (the native palm *Pritchardia beccariana* and grass *Isachne distichophylla* and non-native grass *Andropogon virginianus*) and one non-native conifer (*Pinus caribaea*).

We collected litter in March 2005 from multiple sites on the islands of Hawai'i and Kaua'i. Where possible, we collected litter from at least one representative from each of the major plant groups at each site. Five species (*C. trigynum*, *C. glaucum*, *D. linearis*, *M. polymorpha*, *D. sandwichianum*) were collected from both a relatively N and P rich (150 ky old Kohala) and poor (2.1 ky old Olaa) site on Hawai'i island (Crews *et al.* 1995). These five species are known to have a particularly wide range of decomposition constants and litter chemistry (Thompson & Vitousek 1997, Allison & Vitousek 2004b), and we collected them from sites with varying environmental nutrient availability to increase the range of litter

chemistry included in our experiment. Litter was collected by harvesting recently fallen angiosperm and senesced fern leaves. Canopy species were collected by the placement of window-screen on the forest floor, with collections weekly. As native fern litter does not abscise, we cut recently senesced leaves from the plants. Each litter type was air-dried, homogenized, and subsamples were oven-dried at 65°C for fresh/dry weight conversion and initial chemistry. Fiberglass window screen 1-mm mesh bags were filled with 2 g of a litter type.

Litter bags were deployed on top of the existing litter layer under a closed-canopy *Hibiscus tiliaceus* forest on the North Hilo Coast of Hawai'i Island at 135 meters asl (19°34' N, 155°17' W), with mean annual precipitation and temperature of 3000 mm and 22.7°C, respectively. Five bags of each litter type were collected in July of 2005 and March of 2006, after 3 mo and 1 yr of decomposition. After rinsing with deionized water to remove soil particles, litter was oven-dried at 60°C, weighed, and ground to 40 mesh.

Subsamples of initial litter were analyzed for nutrient content and carbon chemistry (Table 1). Triplicates of 4–6 mg of each litter type were combusted and analyzed on a Carlo Erba NA 1500 elemental analyzer for nitrogen (N) determination. Cation digests (P, Ca, K, Mg, Al) were performed by wet ashing of samples in nitric acid and hydrogen peroxide; extracts were filtered and analyzed on a thermo scientific inductively coupled plasma spectrometer (ICP) (Jones *et al.* 1991). Subsamples were sent to the Marine Science Department analysis lab at the University of Hawai'i, Hilo for Si analysis; samples were dry-ashed in a muffle furnace, followed by hydrofluoric acid digestion and ICP analysis. Initial carbon chemistry was analyzed at the Natural Resources Research Institute, University of Minnesota, Duluth, using a modified sequential acid digestion procedure (McClaugerty *et al.* 1985, Ryan *et al.* 1990). Carbon compounds included non-polar extractives (fats, waxes, chlorophyll), lignin, soluble polyphenols (tannin), water-soluble fraction (simple sugars, amino acids), acid-soluble fraction (polysaccharides, protein, nucleic acids), water-soluble polysaccharides (glucose equivalents—simple sugars), and acid-soluble polysaccharides (glucose equivalents—primarily cellulose and starch). Nitrogen and cation analyses were also performed on decomposed litter.

STATISTICAL ANALYSES.—Turnover times (*k*-values) were calculated for each litter type by fitting the data with a negative exponential decay model, using linear regressions of ln-transformed proportions of initial mass remaining against time.

To test for significant differences between each group in litter chemistry and decomposition rates, we used Tukey's honestly significantly different (HSD) test preceded by a one-way ANOVA on log-transformed data. We excluded the conifer from these analyses and separated native and non-native non-polypod ferns.

We used pairwise correlations (Pearson's *r*) to determine the factors that explained significant variation among species' decomposition rates. We considered initial nutrient and carbon chemistry litter properties we measured (Table 1), and ratios of N:P, lignin to nutrients, and lignin:ash due to successful correlation of that variable in the literature. Variables were log-transformed as necessary before analysis.

TABLE 1. Means and SEs of initial litter nutrient and carbon chemistry and k-values for five phylogenetic groups of plants decomposed at a common site, and significance between groups from Tukey's HSD test (excluding the conifer).

Litter property	Plant Group					
	Native non-polypod	Non-native non-polypod	Polypod ferns	Dicots	Monocots	Conifers
Ferns	Ferns					
N (%)	0.94 (0.14) ^{ab}	1.90 (0.44) ^a	1.38 (0.27) ^a	0.75 (0.11) ^{ab}	0.44 (0.08) ^b	0.60
P (%)	0.04 (0.01) ^a	0.18 (0.04) ^b	0.09 (0.01) ^b	0.04 (0.01) ^a	0.02 (0.01) ^a	0.04
Ca (%)	0.29 (0.05) ^{ab}	0.54 (0.11) ^{ac}	1.11 (0.18) ^c	1.44 (0.27) ^c	0.15 (0.12) ^b	0.36
Mg (%)	0.14 (0.06) ^{ab}	0.36 (0.08) ^{ac}	0.66 (0.13) ^c	0.38 (0.05) ^{ac}	0.09 (0.06) ^b	0.06
K (%)	0.13 (0.05) ^{ab}	0.28 (0.09) ^{ac}	0.67 (0.16) ^c	0.35 (0.10) ^{ac}	0.04 (0.01) ^b	0.04
Si (%)	1.81 (0.94) ^a	2.45 (1.17) ^a	2.83 (1.22) ^a	0.13 (0.05) ^b	3.86 (2.12) ^a	1.32
Al (%)	0.61 (0.28) ^a	0.33 (0.17) ^{ab}	0.04 (0.03) ^{ab}	0.09 (0.09) ^b	0.002 (0.002) ^{ab}	0.02
Lignin (%)	32.8 (1.87) ^a	25.3 (4.62) ^{ab}	25.5 (2.77) ^{ab}	18.3 (2.36) ^b	19.5 (2.39) ^{ab}	38.3
Tannin (%)	4.32 (0.54) ^{ab}	3.68 (1.24) ^{ab}	7.45 (1.91) ^{ab}	10.2 (1.23) ^b	1.86 (0.19) ^a	1.59
Ash (%)	6.87 (1.86) ^a	9.68 (2.16)	11.6 (2.54) ^a	6.46 (0.96) ^a	10.6 (4.62) ^a	4.06
NPE (%)	5.57 (0.56) ^a	5.89 (1.54) ^a	5.31 (0.59) ^a	6.91 (0.78) ^a	4.32 (0.92) ^a	7.31
WS (%)	18.8 (1.26) ^a	23.4 (4.29) ^{ab}	24.7 (3.76) ^{ab}	38.9 (3.21) ^b	13.8 (2.07) ^a	12.7
AS (%)	42.8 (2.34) ^{ab}	45.4 (2.43) ^{abc}	44.4 (2.12) ^a	35.9 (1.58) ^b	62.4 (3.30) ^c	41.7
WSPoly (%)	6.09 (0.65) ^a	6.20 (1.44) ^a	6.10 (1.34) ^a	11.0 (1.34) ^a	4.44 (2.32) ^b	3.86
ASPoly (%)	24.8 (1.65) ^{ab}	22.8 (1.49) ^{ab}	25.1 (2.36) ^b	20.6 (1.89) ^a	48.4 (5.22) ^b	30.5
Lignin:N	38.0 (3.8) ^a	13.3 (1.55) ^c	22.5 (4.2) ^{bc}	26.4 (4.1) ^{abc}	45.2 (2.2) ^{ab}	63.0
k-value	0.51 (0.08) ^a	5.90 (1.43) ^b	1.42 (0.27) ^b	1.99 (0.65) ^b	1.24 (0.71) ^{ab}	0.36

Different letters indicate significant differences between groups. NPE = non-polar extractives, WS = water-soluble compounds, AS = acid-soluble compounds, WS Poly = water-soluble polysaccharides, AS Poly = acid-soluble polysaccharides.

We used paired *t*-tests to evaluate significant differences in nutrient content and carbon compounds contained in the fresh litter of the five species collected at two sites, and performed one-way ANOVAs on the amount of mass remaining in the litter bags at 3 and 12 mo of those ten litter types with site of origin as a fixed effect.

We calculated the effects of litter type and initial nutrient concentration on nutrient release and immobilization during decomposition by analyzing all litter types together, and then clustering litter types into four categories of initial nutrient content ranging from 'poor' to 'high', *sensu* Parton *et al.* (2007). Litter types were grouped separately into poor, low, medium, and high categories for each nutrient analyzed (N, P, and Ca). The proportion of a nutrient remaining in a litter bag was calculated using the equation (final nutrient concentration*final mass)/(initial nutrient concentration*initial mass). We then regressed nutrient remaining on mass lost for all litter types and each category, and determined if the data had a significant linear fit ($P < 0.05$) or polynomial fit (if x^2 term $P < 0.05$). A polynomial fit may occur if nutrient accumulation occurs prior to nutrient release.

RESULTS

Phylogenetic groups differed significantly in most initial litter properties investigated (Table 1). Monocots consistently had the lowest

initial nutrient concentration (N, P, Ca, Mg, and K), low amounts of water-soluble compounds and tannins, but high Si concentrations. In contrast, dicots had large amounts of water-soluble compounds and tannins, and low Si concentrations. Ferns had high concentrations of lignin, N, P, and Al, and non-polypod ferns generally had low cation concentrations. Overall, non-native non-polypod ferns had nutrient characteristics more similar to polypod ferns than native non-polypod ferns. Lignin:N was lowest in polypod ferns, and highest in monocots and the conifer.

DECOMPOSITION DYNAMICS.—Litter *k*-values varied across litter types studied, ranging from 0.292 to 8.314 after 1 yr of decomposition (Table S1). Fern litter types were both the fastest and slowest to decompose; as a result, there were no significant differences between fern and angiosperm decomposition across all litter types. Lignin:N was the single best correlate of decomposition across all litter groups ($r = -0.687$) (Table 2; Fig. 1). Within angiosperms, decomposition was most related to carbon chemistry, lignin:ash, and lignin were both well correlated with *k*-values ($r = -0.951$ and $r = -0.943$, respectively). In contrast, P concentration was the best correlate for all ferns combined ($r = 0.779$), although lignin:N was nearly as good ($r = -0.720$). Variables for non-polypod and polypod ferns analyzed separately demonstrated that polypod fern decomposition was most related to N concentration ($r = 0.911$; Table 2). In contrast, non-polypod fern decomposition was more related to P concentration ($r = 0.888$).

TABLE 2. Initial litter properties that were significantly correlated ($P < 0.05$) with decomposition k -values (\ln) for litter types decomposed in a common site.

	All species (32)	Native species (25)	All angiosperms (11)	Native angiosperms (9)	All ferns (20)	Native ferns (17)	Polypod ferns (10)	Non-polypod ferns (10)
Lignin	-0.417	-0.460	-0.943	-0.951				
Lignin:N	-0.687	-0.667			-0.720	-0.762	-0.785	-0.843
Lignin:P	-0.571	-0.467			-0.673	-0.516		-0.848
Lignin:Ash	-0.386	-0.444	-0.951	-0.957				-0.651
Lignin:Mg	-0.379	-0.499						
Lignin:Ca		-0.525				-0.492		
N	0.372				0.699	0.801	0.911	0.635
P	0.384				0.779	0.621		0.888
Ca		0.458				0.470		0.668
Mg		0.413						0.849
N:P								-0.666
WS Poly								-0.642

All polypod ferns were native, and no litter properties were significantly correlated with the decomposition of the seven native non-polypod fern litter types. Litter properties were log-transformed when necessary for assumption of normality. WS Poly = percent water-soluble polysaccharides.

We performed the same set of analyses including native species only. Decomposition constants were generally slower, ranging from 0.293 to 5.150 (Table S1). The range and median k -values for most groups were similar, except that of the non-polypod fern group, for which the largest k among native species was 0.832. As a result, native non-polypod ferns decomposed more slowly than dicots and polypod ferns (Table 1). Best correlates of decomposition within categories were similar to those including non-native species. However, Ca and Mg and those elements' ratios with lignin were significantly

correlated with decomposition rates across all native species and native ferns (Table 2).

NUTRIENT ANALYSES.—Dynamics of N, P, and Ca were analyzed in all litter types during decomposition. Across all litter types, the proportion of initial Ca remaining was not correlated with mass lost, proportion P was significantly linearly negatively correlated ($P < 0.0001$, $R^2 = 0.20$), as was proportion N ($P < 0.0001$; $R^2 = 0.71$). All 32 litter types were also clustered into categories based on initial nutrient content (increasing initial nutrient content toward bottom panels), and proportion of initial litter nutrient remaining was plotted against mass remaining within each category (Fig. 2). Monocots and the conifer clustered in the poor and low nutrient categories (top panels) for N, P, and Ca whereas dicots were more evenly distributed across categories. Non-polypod ferns often appeared in the poor and low categories, whereas polypod ferns were almost exclusively clustered in the medium and high categories. The relationship between the percentage of mass lost and the proportion of the initial nutrient content remaining became tighter, with a slope approaching 1:1, as initial nutrient content of the leaves increased. The relationship between N remaining and mass remaining was better fit by a polynomial regression in the poor-N category, indicating N immobilization during initial decomposition (Figs. 2A, D, G, and J). Medium and high N-categories exhibited a linear relationship close to 1:1 between N remaining and mass loss. All regression lines were significant ($P < 0.05$).

P dynamics were more variable; there was a weaker but significant negative linear relationship between P remaining and mass lost in low, medium, and high P categories, and a significant polynomial relationship in the most P poor species (Figs. 2B, E, H, and K). There was a large range in P remaining at the three-month litter collection compared to other nutrients—Independent of initial P content, some species lost P quickly during initial decomposition,

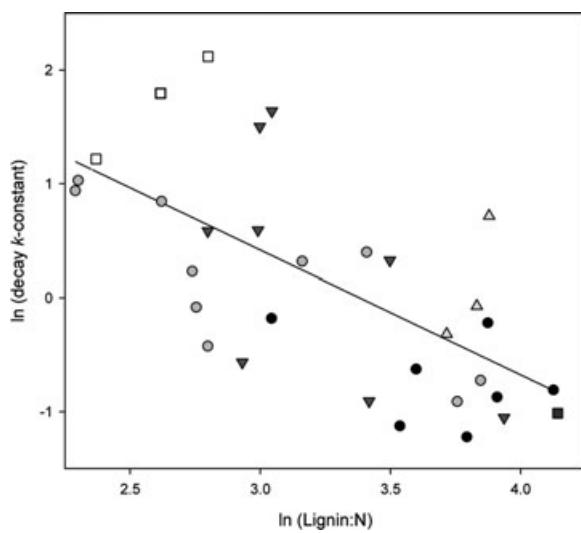


FIGURE 1. Initial lignin:N of 32 litter types regressed against litter turnover times (k -values) calculated after 1 yr of decomposition in a common site. $R^2 = 0.471$; $P < 0.0001$. Dark circles = native non-polypod ferns; light circles = polypod ferns; dark triangles = dicots; light triangles = monocots; dark square = conifer; white squares = non-native non-polypod ferns.

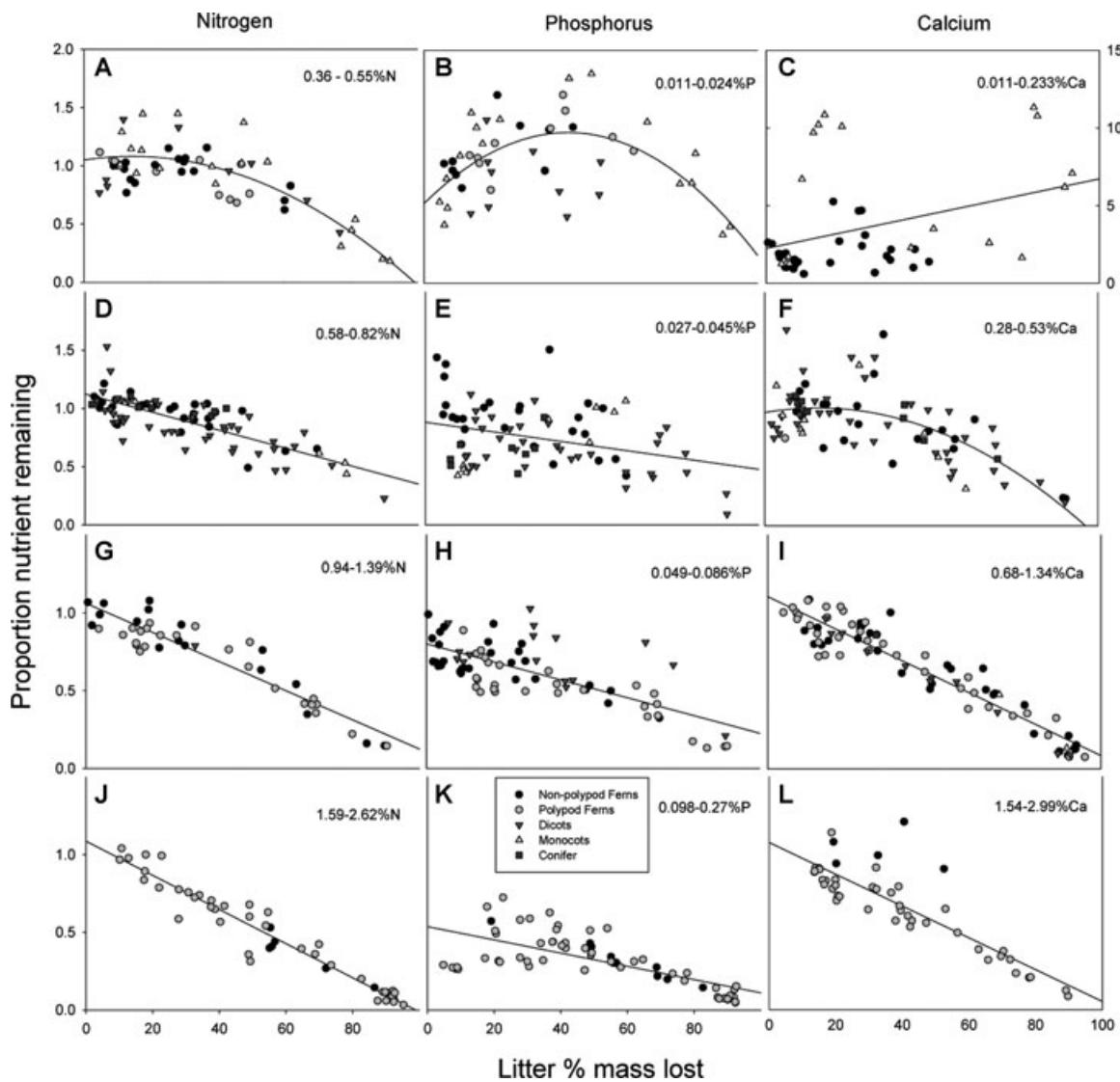


FIGURE 2. Proportion of N, P, and Ca remaining in litter correlated with percent mass lost in individual bags of 32 litter types decomposed in a common garden for 1 yr. Litter types were clustered into four groups based on initial nutrient concentration (separately for each nutrient), including poor (panels A–C), low (panels D–F), medium (panels G–I), and high (panels J–L) initial nutrient concentration. Ranges are indicated in the upper right of each panel. Lines indicate significant linear regressions, or polynomial regressions where the χ^2 term was significant. Axes are consistent across rows except for panel C. Dark circles = non-polypod ferns; light circles = polypod ferns; dark triangles = dicots; light triangles = monocots; solid square = conifer.

and then accumulated P after initial losses. Additionally, there were distinct phylogenetic patterns within categories for P; very-low and low-P non-polypod ferns immobilized more P than polypod ferns, angiosperms or the conifer during initial decomposition.

Ca content increased as mass was lost in the nutrient-poor Ca group, indicative of Ca immobilization. This relationship switched to a negative one and became tighter and closer to 1:1 in more Ca-rich categories (Figs. 2C, F, I, and L). We observed Ca immobilization up to 10× initial levels in two monocot species and up to 5× initial levels in two non-polypod fern species. In contrast, immobilization of Ca only reached 1.5× initial levels in the higher-initial-Ca categories.

INFLUENCE OF SITE OF ORIGIN ON CHEMISTRY AND DECOMPOSITION.—The five species collected at both a nutrient-rich site and a poor site differed significantly in initial nutrient concentrations, but not in carbon chemistry. Litter collected from more nutrient-rich site had significantly higher N ($P < 0.05$) and marginally higher P and lower carbon ($P < 0.10$) than litter collected at the poorer site. Lignin:N was lower in litter collected at the richer site for the three more slowly decomposing species (*M. polymorpha*, *D. linearis*, *C. glaucum*), and not different for the two other species (Table 3). In contrast, lignin:P was lower at that site for *M. polymorpha* and the two easily decomposable species (*C. trigynum* and *D. sandwichianum*), but was higher for

TABLE 3. Initial litter parameters, mean percent mass remaining \pm SE after 3 and 12 mo, and k-values calculated after 1 yr of decomposition for five species collected from both low- (2.1 ky) and high-nutrient (150 ky) sites and decomposed in a common site.

Species	2.1 ky litter					150 ky litter				
	Lig:N	Lig:P	3 m	12 m	k	Lig:N	Lig:P	3 m	12 m	k
<i>C. trigynum</i>	20	300	56 \pm 2	1 \pm 0.1	4.5	21	274	24 \pm 9**	0.5 \pm 0.1**	5.2
<i>D. sandwichianum</i>	10	220	77 \pm 3	7 \pm 1	2.8	10	140	60 \pm 3**	8 \pm 1	2.5
<i>M. polymorpha</i>	51	720	90 \pm 1	69 \pm 2	0.35	30	447	87 \pm 1*	67 \pm 7	0.40
<i>D. linearis</i>	62	820	87 \pm 1	64 \pm 5	0.44	50	1310	91 \pm 1*	66 \pm 4	0.42
<i>C. glaucum</i>	44	664	96 \pm 0.5	75 \pm 3	0.29	34	692	97 \pm 1	73 \pm 2	0.32

Significant effects of site of collection on a species' mass remaining at 3 or 12 mo are indicated in the 150 ky litter column * $P < 0.05$, ** $P < 0.001$. *C. trigynum* and *M. polymorpha* are dicots, *D. sandwichianum* is a polypod fern, and *C. glaucum* and *D. linearis* are non-polypod ferns.

the non-polypod ferns. Site of origin was a significant factor in litter mass remaining at 3 mo for four of the five species (all but *C. glaucum*), but was only a significant factor for one species (*C. trigynum*) at 12 mo.

DISCUSSION

We observed similar average rates of decomposition in ferns and angiosperms, contrary to our hypotheses. Most studies of decomposition and nutrient release have focused on ferns that dominate multiple sites; these often are non-polypod ferns or bracken fern (a 'basal' polypod; Schneider *et al.* 2004). Although polypod ferns are locally dominant, they have not received as much study by ecosystem ecologists. Polypod ferns share high specific leaf areas and relatively high nutrient contents with dicots; these similarities may contribute to similar decomposition rates. In agreement with our hypotheses, native non-polypod ferns decomposed more slowly than other groups of plants. Non-polypod ferns evolved prior to the diversification of angiosperms, often in inhospitable, nutrient-poor environments where many of them are found today (Galtier & Phillips 1996, Page 2002). Native litter is relatively high in Si and low in macronutrient cations, and has a low specific leaf area (Allison & Vitousek 2004b, Amatangelo & Vitousek 2008)—all of which can contribute to slow decomposition. However, non-native non-polypod ferns were among the most fast-decomposing species analyzed here. Invasive species in Hawaiian systems often decompose more quickly than native plants (Allison & Vitousek 2004b). Two of the non-native non-polypod ferns analyzed here are naturalized and spreading aggressively, while the third (*C. contaminans*) shares many characteristics with the invader *S. cooperi* and is volunteering in the tropical botanical gardens where it currently resides (K. Amatangelo, pers. obs.).

A predictor that integrates both carbon and nutrient factors, lignin:N, was the best correlate of k-values across all the species in our study. At sites with similar rainfall to ours, other researchers have found that markers of carbon chemistry—including water-soluble compounds, lignin:ash, phenolics, and lignin—were the best predictor across litter types that included both ferns and di-

cots (Scowcroft 1997, Wardle *et al.* 2002, Allison & Vitousek 2004b, Shiels 2006). Even so, using those predictors Scowcroft (1997) found that decomposition of the one non-polypod fern in his study fell far below his lignin:ash regression line. Here, native non-polypod ferns also fall below the lignin:N-based prediction, though to a lesser extent. In contrast, monocots all rise above the line, indicating faster decomposition than the lignin:N model predicted, despite their low N and P. One factor that may account for phylogenetic differences is biochemical variation within broad categories of carbon chemistry. In particular, there are different types of lignin; monocots consist primarily of the syringol-type, whereas ferns may be primarily composed of the more recalcitrant guiacol-type lignin found in gymnosperms, as the same lignin-production pathway is used in ferns and gymnosperms (Opsahl & Benner 1995, Ros *et al.* 2007).

When considered separately, decomposition rates of ferns and angiosperms were correlated with different factors. Angiosperm decomposition was correlated with carbon chemistry—consistent with observations of dicot decomposition in New Zealand (Wardle *et al.* 2002). Despite their relatively high N and P concentrations, nutrients were the best correlates of decomposition among ferns. The other study we know of that looked at fern decomposition separately from other litter types found it to be most related to lignin:N and lignin:P (Wardle *et al.* 2002). In our study, non-polypod fern decomposition was best correlated with P, largely because quickly decomposing exotic non-polypod ferns had much higher concentrations of that element. Low-P native non-polypod ferns immobilized substantial quantities of P during decomposition. In contrast, P did not correlate with decomposition dynamics of polypod ferns, and that generally high-P group rapidly mineralized large quantities of P. P-rich plants often hold up to 85–95 percent of their total P as easily leachable inorganic forms in vacuoles (Bielecki 1973).

Why would nutrients be better correlates of fern litter decomposition here than in other studies? This study included litter that encompassed a greater range of variability in quality than other studies that compared both fern and angiosperm litter. We included litter types with greater than five-fold variation in lignin concentration, compared to less than four-fold (and down to 2.2-fold) variation in other studies (Scowcroft 1997, Allison & Vitousek 2004a).

Similarly, we included litter with greater differences in N and P concentration (Scowcroft 1997, Allison & Vitousek 2004a). As a result, our study more than doubled the initial variation in nutrient concentration from previous work. Selecting species that more fully encompass the existing range in litter quality can more accurately determine correlates of decomposition across sites of varying nutrient availability and species with differing biochemistry.

In addition to N and P, Ca and Mg were correlated with decomposition in this experiment, and Ca particularly among native plants. Both monocots and non-polypod ferns have significantly lower concentrations of Ca in litter than dicots and polypod ferns. Very low Ca could affect decomposition in several ways. At the community level, fungi and many soil fauna require relatively large amounts of Ca (Silver & Miya 2001, Reich *et al.* 2005, Hobbie *et al.* 2006). Suppression of fungal growth on low-Ca fern litter could reduce the production of fungal oxidases and peroxidases, and so slow the decomposition of recalcitrant organic C—which is abundant in those species with low Ca (Kirk & Farrell 1987). This is consistent with Scowcroft's (1997) observation of Ca immobilization during the decomposition of *Cibotium* but not angiosperm litter. We too observed significant Ca immobilization in low-Ca species (up to 10× initial nutrient contents), and deviation from a 1:1 line of Ca remaining with mass lost in low-Ca litter types. Because fungal hyphae are responsible for nutrient translocation into high C:nutrient litter (Wells & Boddy 1995, Frey *et al.* 2000), limitation of fungi by Ca could exacerbate micro-scale limitation by N or P in high lignin:nutrient litter.

Decomposition dynamics of five fern and angiosperm species collected from both high and low N and P sites support a hypothesis of nutrient control of decomposition initially and carbon control later during decomposition (Hoorens *et al.* 2003, Gartner & Cardon 2004). Species collected from high and low N and P sites, which varied primarily in litter nutrient content and carbon:nutrient ratios, had significantly different mass loss only at 3 mo. As a result, litter turnover times calculated after 1 yr were only 10 percent faster for N and P-rich litter.

Although this broad survey of fern species demonstrates that on average ferns in Hawai'i do not decompose more slowly than angiosperms in litter bags on the ground, all Hawaiian fern species have marcescent (non-abscising) leaves and stems. As such, initial decomposition occurs above ground in environments that reduce soil-litter contact and could reduce decomposition rates (but see Maheswaran & Gunatilleke 1988, Russell & Vitousek 1997, Dearden & Wardle 2008). The site of litter decomposition is likely to play a significant role in decomposition dynamics, increasing differences in decomposition rates and regulation between plant groups.

Unique predictors of fern and angiosperm decomposition, combined with nutrient accumulation and release patterns, suggest potential differences in the control and timing of decomposition among phylogenetic groups. Different fern types could have distinct impacts on the functioning of ecosystems. The relative importance of phylogenetic groups can shift due to both natural (succession) and human-influenced (plant and animal invasion, selective removal of species) factors in forests. In forests where native

non-polypod ferns are important, replacement with many of the groups studied in this experiment, including dicots, polypod ferns, or even non-native non-polypod ferns, could substantially alter the rate of nutrient cycling, particularly of limiting elements such as N and P, in those systems.

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SUPPORTING INFORMATION

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

TABLE S1. Litter turnover times (k-values) calculated after decomposition in a common site for 1 yr.

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