Oecologia (1999) 121:564–573

Rebecca Ostertag · Sarah E. Hobbie

Early stages of root and leaf decomposition in Hawaiian forests: effects of nutrient availability

Received: 30 November 1998 / Accepted: 12 August 1999

Abstract We examined the effects of soil nutrient availability and tissue chemistry on decomposition of both fine roots (<2 mm diameter) and leaves in three sites along a forest chronosequence in the Hawaiian Islands. These sites form a natural fertility gradient, with the youngest and oldest sites having lower nutrient availability than the intermediate-aged site. Nitrogen (N) limits aboveground net primary productivity (ANPP) in the youngest site, while phosphorus (P) limits ANPP in the oldest site. Both root and leaf litter decomposed most slowly in the 4.1-Myear-old site. We also investigated root decomposition in fertilized plots at the youngest and oldest sites; when roots were produced and decomposed in fertilized plots, root decomposition rates increased with N and P additions at the 4.1-Myear-old site. At the 300-year-old site, however, root decomposition rates did not respond to N or P additions. Roots decomposed faster than leaves at the more infertile sites, in part because of lower lignin-to-nitrogen ratios in roots than in leaf litter. Decomposing roots immobilized more nutrients than did decomposing leaves, and may serve an important role in retaining nutrients in these forests.

R. Ostertag (✉)
Department of Botany, University of Florida, Gainesville, FL 32611-8526, USA

S.E. Hobbie
Department of Biological Sciences, Stanford University, Stanford, CA 94305, USA

Present address:
R. Ostertag
Department of Environmental Science Policy and Management, Ecosystem Sciences Division, 151 Hilgard Hall, University of California, Berkeley, CA 94720-3110, USA, e-mail: ostertag@nature.berkeley.edu, Tel.: +1-510-6423874

R. Ostertag
International Institute of Tropical Forestry, USDA Forest Service, Call Box 25000, Rio Piedras, PR 00928, Puerto Rico

S.E. Hobbie
Department of Ecology, Evolution, and Behavior, University of Minnesota, 100 Ecology Building, 1987 Upper Buford Circle, St Paul, MN 55108, USA

Key words Fertilization · Lignin-to-nitrogen ratios · *Metrosideros polymorpha* · Nutrient accumulation · Nutrient limitation

Introduction

Root decomposition is an often ignored, yet potentially important regulator of carbon and nutrient cycling. While many studies have investigated rates of mass and nutrient loss from decaying leaves, and the factors that control these rates, comparable information for roots is lacking for most ecosystems (Bloomfield et al. 1993). Based on leaf decomposition studies, site fertility is hypothesized to be one factor controlling decomposition rates. Under similar climatic conditions, plants growing on nitrogen-rich sites tend to produce leaf litter of higher quality that decomposes more quickly than the leaf litter of plants from nitrogen-poor sites (Gosz 1981). In addition, initial leaf nitrogen (N) concentration often correlates positively with decomposition rate (Melillo et al. 1982; Taylor et al. 1989), at least during the initial stages of decomposition (Berg et al. 1982; Berg and Matzner 1997). Thus, both the exogenous supply of nutrients and the chemical quality of tissue produced may limit the decomposition rates of leaves. Due to the limited data available on root decomposition rates, however, it is unknown whether nutrient availability controls rates of root decomposition analogously.

Despite the evidence that plants on infertile sites have leaves that generally decompose more slowly than those of plants growing on more fertile sites, the influence of soil nutrient availability on decomposition rates of leaves has been challenged by studies in which nutrient supplies were manipulated by fertilization (reviewed by Fog 1988). In these experiments, fertilization increases exogenous nutrient supply and also affects the nutrient concentration of leaf tissues. In some of these investigations, fertilization increased decomposition rates (Salonius 1972; Gill and Lavender 1983; Prescott et al. 1992), which would be expected if decomposition rates were

positively related to nutrient availability. In other cases, fertilization either decreased leaf decomposition rate (Titus and Malcolm 1987; Kemp et al. 1994; Wright and Tietema 1995; Prescott 1995) or had no effect (Staaf 1980; MacKay et al. 1987; Theodorou and Bowen 1990; Šlapokas and Granhall 1991; van Vuuren and van der Eerden 1992; Prescott 1995). Root decomposition in relation to fertilization has only been examined in one study, and results varied with the successional age of the vegetation. On 24- and 36-year-old barrier dune islands in Virginia, root decomposition rates were faster with N addition, but N fertilization had no effect on root decomposition on 120-year-old dunes (Conn and Day 1996).

Comparing within a single species rather than across plant communities, exogenous nutrient supply (particularly N) does not always exert a controlling influence on decomposition rates (Fog 1988). Instead, faster rates of decomposition with increases in nutrient availability may be due to the indirect effect that soil nutrient supply exerts on leaf tissue chemistry. Faster rates of decomposition on more fertile sites may therefore be faster mainly due to the presence of species with more readily decomposable tissues on fertile sites than on infertile sites, an indirect consequence rather than a direct effect of exogenous nutrient supply (Hobbie 1992; Prescott 1995).

To examine the effects of soil nutrient availability and tissue chemistry on decomposition of both roots and leaves, we conducted a study of decomposition rates and nutrient dynamics along a chronosequence in the Hawaiian Islands. The sites in this chronosequence form a soil fertility gradient that varies greatly in N and P availability, but where present climate, geology, and species composition are relatively constant (Crews et al. 1995). In most ecosystems, species composition changes completely over gradients of soil fertility, but due to the broad ecological ranges of tree species in the Hawaiian Islands (Carlquist 1980), the same species dominate across these sites. Additionally, the sites are part of a long-term fertilization experiment (Vitousek and Farrington 1997) that was established to examine nutrient limitations to tree growth.

We describe three experiments aimed at examining (1) how nutrient availability affects decomposition rates of roots, and (2) whether rates of root decomposition are similar to rates of leaf decomposition. Decomposition was measured in unfertilized and fertilized plots at sites across this soil fertility chronosequence. In the first approach, we examined how natural variation in soil age and consequently nutrient availability affected decomposition of leaves and roots by comparing decay rates in unfertilized plots along the chronosequence (a natural fertility gradient). In the second experiment, we assessed whether N or P limited decomposition of roots by comparing rates of root decomposition between unfertilized and fertilized plots. These roots were harvested from both fertilized and unfertilized plots and were placed back in their plot of origin (i.e., *in situ* decomposition). Therefore, roots decomposed in the fertilized plots are affected both by the enhanced nutrient availability in the soil and any effect that such soil nutrient increases may have on the tissue chemistry of roots. To examine the effects of tissue chemistry on root decomposition, we conducted a third experiment in which roots from all sites and fertilizer treatments were placed in a common site. Because roots at the common site were decomposed in the same soil environment, the influence of tissue chemistry on decomposition rates can be isolated. Together, these three experiments highlight the mechanisms by which N and P availability can influence decomposition rates.

Methods

Study sites

Natural fertility gradient

We compared root and leaf decomposition rates along a natural fertility gradient that consisted of sites differing in soil age and consequently, in N- and P-availability (Table 1). These sites are three of six sites described as the "long substrate age gradient" by Crews et al. (1995). Each site has soils derived from volcanic ash, receives a mean annual rainfall of about 2500 mm, has a mean an-

Table 1 Description of the four study sites. Data from Crews et al. (1995) and Riley and Vitousek et al. (1995)

Aboveground growth limitations	Site name	Parent material age (years)	Island	Elevation (m)	Soil type	pH in H_20
Natural fertility gradient						
N-limited	Thurston	300	Hawai'i	1176	Hydric Dystrandept	5.02
Fertile	Laupahoehoe	20,000	Hawai'i	1170	Typic Hydrandept	3.57
P-limited	Koke'e	4,100,000	Kaua'i	1134	Plinthic Acrudox	3.99
Common site						
Undetermined	Ola'a	2100	Hawai'i	1200	Typic Hydrandept	

nual temperature of 16°C, is located between 1122 and 1210 m elevation, and is dominated by *Metrosideros polymorpha* (Myrtaceae) (Crews et al. 1995). This tree species is widespread throughout the Hawaiian Islands (Carlquist 1980). It is the dominant canopy tree in mesic to wet forests and is one of the earliest pioneers on recent lava flows (Aradhya et al. 1990).

The youngest site is adjacent to Thurston Lava Tube in Hawai'i Volcanoes National Park on the island of Hawai'i. The soil at this site consists of 200- to 400-year-old coarse tephra deposits (Crews et al. 1995) overlying an older pahoehoe (smooth) lava flow (Vitousek et al. 1993). Vegetation at this site is dominated by *Metrosideros* with a conspicuous tree fern understory/sub-canopy of *Cibotium* spp. (Crews et al. 1995). The intermediate-aged site, located in Laupahoehoe State Forest Reserve on the island of Hawai'i contains 10,000- to 30,000-year-old tephra deposits from Mauna Kea. *Metrosideros* trees at this site are much larger, with tree ferns and shrubs dominating the understory (Crews et al. 1995). The oldest site is located within Na Pali Kona Forest Reserve on the island of Kaua'i. The substrate is so weathered that it is difficult to determine conclusively whether soils here were derived from tephra or lava, but the parent material has been estimated to be 4.1 Myear. While *Metrosideros* is also dominant here, the trees are considerably shorter and *Cibotium* is almost completely absent from study plots. Other ferns, particularly *Elaphoglossum* spp., are common in the understory (Crews et al. 1995).

Nutrient limitation to aboveground net primary productivity (ANPP) of *Metrosideros* at the three sites has been documented through fertilization experiments (Herbert and Fownes 1995; Vitousek and Farrington 1997). These nutrient addition experiments demonstrated that ANPP was enhanced by N alone at the youngest site (hereafter 300-year-old site) and by P alone at the oldest site (hereafter 4.1-Myear-old site). We consider the intermediate-aged site as the most fertile site because it has trees of the greatest diameter, height, and foliar N and P concentrations (Crews et al. 1995; Vitousek et al. 1995) and it has soils with relatively high levels of both available N and P (Crews et al. 1995). Growth at the 20,000-year-old site, however, is still limited by nutrients. *Metrosideros* trees increased diameter growth when N and P were applied together, but not when they were applied singly; this site is co-limited by these two elements (Vitousek and Farrington 1997).

Fertilized plots

We compared *in situ* rates of root decomposition between N- and P-fertilized and unfertilized plots at both the 300-year-old and 4.1-Myear-old sites to determine the effect of fertilization on decomposition. Roots produced in fertilized plots were placed back into the fertilization treatment in which they were produced. Therefore, roots that were set out for decomposition in fertilized plots were in a relatively more N- or P-rich soil environment, but roots may also have produced more N- or P-rich tissues when growing in these plots. An analogous experiment was not conducted on leaves; leaf decomposition was only measured in the unfertilized control plots along the natural fertility gradient. We also did not do reciprocal transplants in which tissues from fertilized plots were placed into unfertilized plots.

Long-term factorial fertilization experiments have continued at the 300-year-old site since October 1985 (Vitousek et al. 1993) and at the 4.1-Myear-old site since March 1991 (Herbert and Fownes 1995). A 15×15 m area of each plot was fertilized semi-annually at a rate of 100 kg ha^{-1} $year^{-1}$ of N (half as urea, half as ammonium nitrate) or 100 kg ha^{-1} $year^{-1}$ P (as triple superphosphate). We refer to unfertilized plots as controls.

Common site

This common site, in the Ola'a Forest in Hawai'i Volcanoes National Park (island of Hawai'i) was formed over several thousand years by tephra deposits of the Kilauea Volcano and is estimated to be about 2100 years old (Vitousek et al. 1993; Crews et al. 1995). The vegetation is again dominated by *Metrosideros* and *Cibotium* spp., but densities of *Metrosideros* are lower than at the other sites, perhaps due to canopy dieback in this area (Vitousek et al. 1993). This site was chosen as a common site because leaves had relatively fast decomposition rates here (P.M. Vitousek, personal communication). In order to isolate the effect of tissue chemistry on root decomposition, we decomposed at the common site roots produced in control (unfertilized), N-fertilized, and P-fertilized treatments at both the 300-year-old and 4.1-Myear-old sites, along with root material from unfertilized plots from the 20,000-year-old site.

Collection and preparation of leaf and root material

Senesced leaves of *Metrosideros* were collected every 2–4 weeks from litter traps placed throughout each plot. Only whole leaves no longer containing any green areas were selected. Leaves from all four plots within a treatment were homogenized and then redistributed into litterbags. Each 10×10 cm litterbag was made of nylon tent netting (0.3 mm mesh) and was filled with approximately 1.0 g of leaf litter that had been dried at 50°C for 48 h to avoid potential disintegration of total phenolics (Makkar and Singh 1991). This mass was later adjusted to dry mass using a 50°C/70°C dry-mass conversion factor.

Roots were collected from the top 10 cm of soil using a trowel. At each site, an approximately equal amount of live fine (<2 mm in diameter) roots was collected from every plot, and roots collected from plots within a fertilization treatment were then homogenized. Roots were not sorted into species as this could not be done with certainty, but each collection area was dominated by *Metrosideros*. After washing, these roots were dried at 50°C, cut into 2- to 5-cm lengths, and then 0.5 g of formerly live roots was placed into each litterbag.

Experimental set-up

In late January to early February 1996 we placed litterbags in the field. Before placement in the field we arranged litterbags at least 15 cm apart and connected them with string or monofilament so that each "string" of litterbags contained all the bags that would be harvested at a single time point. We arranged the leaf litterbags on top of the soil in a wheel pattern, with the five strings of litterbags radiating out from a central anchoring point. Litterbags that contained roots were also anchored and were buried in the areas between the strings of leaf litterbags (i.e., between the spokes of the wheel). To bury the bags, we sliced down through the soil at a 45° angle to 10 cm depth and then slipped the bag into this incision. Because the incision was not wide, bags had good soil contact, and soil disturbance was minimal.

For the three sites along the natural fertility gradient, each string contained four root litterbags. These four litterbags were sub-replicates used for obtaining an average mass loss per plot; the true replicates were the plots (n=4 per site). For leaves, each string contained also represented one harvest, but there was only one bag per string (i.e., no sub-replicates, n=4 plots). Root litterbags were collected at 1-, 3-, 6-, 9-, and 12-month intervals, while leaf litterbags were collected only after 1, 6, and 12 months. For comparisons between leaves and roots, there were 240 root litterbags (3 sites×4 plots×4 sub-replicates/plot×5 harvests) and 36 leaf litterbags (3 sites×4 plots×3 harvests). An additional 320 root litterbags were placed in fertilized plots at the young and old sites (2 sites×2 fertilization treatments×4 plots×4 sub-replicates/plot×5 harvests) and compared with the root bags described above that contained root material from unfertilized control plots.

At the common site, we established four replicate stations, approximately 5 m apart. Litterbags containing the seven site/fertilizer combinations of root material along one string (i.e., one harvest) were buried at each station. Each litterbag station contained five buried strings radiating out from a central point. Bags were harvested after 1, 3, 6, 9, and 12 months; 140 litterbags were used (7 site/fertilizer combinations×4 replicates×5 harvests).

Processing and chemical analyses of roots and leaves

Samples of roots and leaves to be used for initial chemistry were dried at root 50°C and ground in a Wiley mill (20 mesh for leaves,

40 mesh for roots). Both root and leaf samples were analyzed for initial N and P concentrations using a peroxide persulfate procedure on an Alpkem autoanalyzer at Stanford University. Carbon was separated into its various fractions based on gravimetric mass loss following sequential extractions (Ryan et al. 1989) at the Center for Water and the Environment (Natural Resources Research Institute, University of Minnesota, Duluth, Minn., USA). The carbon fractions measured were nonpolar extractables (NPE), which includes fats, oils, waxes, and chlorophylls; water-soluble (WS), which includes simple sugars, hydroxy phenol groups, amino acids, and other organics; acid-soluble (AS) polysaccharides, which includes cellulose, hemicellulose, and starch; and tannins (soluble polyphenols). The acid-insoluble fraction (primarily lignin) is determined as the difference between the total sample and the sum of the NPE, WS, and AS fractions. Because initial tissue samples were homogenized before placement into litterbags, values for initial chemistry are unreplicated.

At each harvest date, root and leaf litterbags were collected from the field, dried at 70°C, weighed, and analyzed for total N and P; only a few bags were unable to be recovered. Prior to processing, leaf litter was sorted to remove invertebrates, roots, and soil. For root material we carefully tried to extract the roots that were inside the bag but not penetrating the holes of the mesh; the latter we assumed to be ingrowth. The four root litterbags within a plot (the sub-replicates) were pooled, so that all nutrient values represent a plot average (n=4 plots per site or fertilization treatment). For the common site, the four replicates were pooled into one sample for nutrient analysis. The partially decomposed roots were not washed before drying so that the microbial community might remain intact. To correct for residual soil particles on roots, each root sample was ashed in an oven for 4 h at 500°C; all mass and nutrient data for roots are expressed on an ash-free dry mass basis.

Data analysis

We tested whether linear or exponential decay (Wieder and Lang 1982) best fit each root and leaf litter type based on r^2 values. A linear model best described decomposition rates, so we calculated a relative decomposition constant (k, in year^{-1}), as the slope in a linear decay model: $M_t/M_0 = -kt + c$, where M_t is mass (g) at time t, M_0 is initial mass (g) at the beginning of the experiment, t is time (days), and c is a regression constant. The relative decomposition rate constant k was calculated for each site/fertilizer combination and was based on the plot averages of percent mass remaining (n=4 for each time interval).

Differences in relative decomposition rates among the treatments were determined by comparing slopes (Sokal and Rohlf 1981). Using this approach, we were able to test for differences in decomposition rates in several ways: (1) among leaf litter samples along the natural fertility gradient; (2) among fine root samples along the natural fertility gradient; (3) among leaves and roots decomposed at the same site; (4) among roots decomposed in the N-fertilized, P-fertilized, and unfertilized plots; and (5) among roots from the seven site/fertilizer combinations that were decomposed at the common site. Significant differences were identified using Tukey-Kramer multiple comparison tests (Sokal and Rohlf 1981).

Nutrient content (in g nutrient) was calculated by multiplying the mass of the tissue remaining after decomposing in the field (g tissue) by its nutrient concentration (g nutrient g^{-1} tissue). Nutrient contents were then expressed as a percentage of the initial nutrient content in that tissue at the beginning of the experiment. Tissues that accumulated nutrients over time (i.e., >100% N or P) reflect nutrient gain by microbial immobilization, N-fixation, or atmospheric deposition. For simplicity, we refer to any increase in relative nutrient content as accumulation and any decrease as mineralization. We compared differences among treatments at the end of the experiments (12 months) using one-way analysis of variance (ANOVA). All data were transformed using natural logarithms before analysis to increase homogeneity of variances. To determine the effect of initial chemistry on decomposition rate, we used single and multiple regression with k as a dependent variable and various indicators of tissue chemistry as independent variables. All data were analyzed using SYSTAT (SYSTAT 1992) or SAS 6.12 (SAS 1997).

Table 2 Initial chemical characteristics of leaf (*L*) and root (*R*) tissue that was homogenized and placed in the field (abbreviations of each fraction: *NPE* non-polar extractable, *WS* water-soluble, *AS* acid-soluble, *WSG* water-soluble glucose equivalents, *ASG* acid-soluble glucose equivalents). All root values are expressed on an ash-free dry mass basis

Site/Fertilizer combination	NPE(%)		WS(%)		AS(%)		Lignin(%)		Tannin(%)		WSG(%)		ASG(%)		N (mg g^{-1})		P (mg g^{-1})		Lignin:N (g g^{-1})		Lignin:P (g g^{-1})	
	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R	L	R
300 year/N-fert.		8.63		17.49		44.86		29.02		6.73		3.53		30.55		6.11		0.36		48		817
300 year/P-fert.		6.73		17.97		47.70		27.6		5.99		3.51		35.06		4.02		1.13		69		244
300 year/Control	7.99	7.04	17.23	18.30	34.61	47.74	40.17	26.92	7.29	5.45	4.63	4.02	24.35	34.18	3.31	4.17	0.27	0.50	121	65	1488	535
Fertile/Control	4.19	5.99	24.26	18.10	30.82	45.52	40.73	30.38	10.47	9.15	6.09	3.71	21.13	32.71	8.77	4.23	0.51	0.40	46	72	799	753
4.1 Myear/N-fert.		4.85		16.37		44.53		34.24		5.09		3.05		30.29		4.38		0.21		78		1598
4.1 Myear/P-fert.		5.80		15.80		45.65		32.75		5.59		3.09		31.18		5.39		0.91		61		361
4.1 Myear/Control	6.84	6.97	24.84	15.63	26.40	44.73	41.92	32.67	11.31	7.91	7.18	3.19	18.95	30.61	3.67	3.05	0.21	0.22	114	107	1996	1457

Results

Root and leaf chemistry

Roots and leaves differed in initial carbon chemistry and in total N and P (Table 2), and simple correlations indicated that the ratio of lignin to N was a good predictor of the root decomposition rate constant (k) (Table 3). When leaves and roots decomposed *in situ* were considered together, k was best described by a multiple regression where k=–0.001(lignin:N)–0.0001(lignin:P)–0.016(water soluble sugar)+0.612 (R^2=0.91, $F_{3,6}$=20.4, P=0.002). However, consideration of only one variable also led to good predictions of leaf and root decomposition rates, as k was strongly related to both lignin-to-N ratio (R^2=0.72, $F_{1,8}$=20.4, P=0.002) and lignin-to-P ratio (R^2=0.76, $F_{1,8}$=25.6, P=0.001). At the common site, k was best predicted as k=–0.004(lignin:N)–0.028(non-polar extractable)+0.027(tannin)+0.706 (R^2=0.94, $F_{3,3}$=14.6, P=0.027).

Decomposition of leaves and roots along the natural fertility gradient

Within a site, roots decomposed at a faster rate than leaves except at the 20,000-year-old site, where leaves and roots decomposed at a similar rate (Table 4). Leaf decomposition rates were fastest at the 20,000-year-old site and slowest at the 4.1-Myear-old site ($F_{2,6}$=51.4, P<0.001 for leaves); root decomposition rates were fastest at the 300-year-old and 20,000-year-old sites and slowest at the 4.1-Myear-old site ($F_{2,12}$=4.6, P<0.05 for roots; Fig. 1).

Decomposing leaves and roots differed substantially in their nutrient dynamics. The amount of N and P remaining in leaves after 12 months did not differ among the sites and leaves generally showed few changes in relative (Fig. 2) N content or P over time. When the changes in nutrient content, relative to initial nutrient content, were examined, roots accumulated N over time, and after 12 months the roots decomposed at the 4.1-Myear-old site accumulated more N than roots from the other two sites ($F_{2,9}$=43.1, P<0.001; Fig. 2). Roots accumulated P only at the 4.1-Myear-old site ($F_{2,9}$=42.7, P<0.001; Fig. 2).

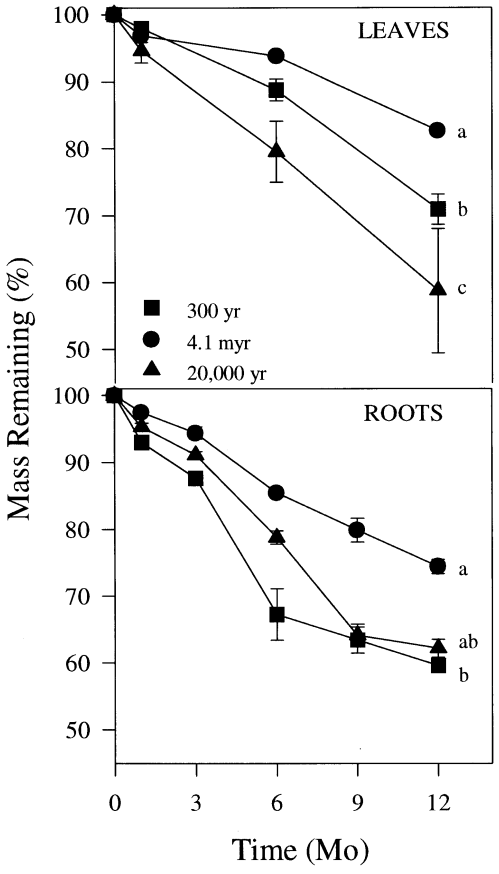


Fig. 1 Percent of mass remaining of leaves and fine roots among the three sites on the natural fertility gradient. *Letters* represent significant differences among slopes using Tukey-Kramer multiple comparison tests

Effects of fertilization on root decomposition rates

The effect of fertilization on root decomposition rate varied between the 300-year-old and 4.1-Myear-old sites (Fig. 3). At the 300-year-old site, fertilization had no effect on decomposition rate. At the 4.1-Myear-old site, fertilization with N or P enhanced decomposition rates relative to the control ($F_{2,12}$=11.8, P<0.005; Fig. 3).

Table 3 Correlations (r) between tissue quality measurements and the decomposition rate constant ($|k|$ in year^{-1}) for roots decomposed *in situ* and for roots decomposed at the common site. Significant correlations are indicated with an *asterisk*. Eleven values were compared to each k constant; therefore the correlation should only be considered significant if P<0.0045 (Bonferroni adjusted significance level)

Tissue quality variable	In situ k constant		Common site k constant	
	r	P	r	P
Acid soluble	0.64	0.048	–0.12	0.806
Acid soluble glucose	0.66	0.039	0.13	0.787
Lignin	–0.72	0.020	–0.32	0.492
Lignin:N	–0.85	0.002 *	–0.74	0.058
Lignin:P	–0.87	0.001 *	–0.39	0.385
N concentration	0.45	0.192	0.62	0.139
Non-polar extractable	0.12	0.744	0.35	0.437
P concentration	0.60	0.070	–0.002	0.997
Tannin	–0.50	0.139	0.22	0.629
Water soluble	–0.32	0.376	0.61	0.150
Water soluble glucose	–0.63	0.053	–0.20	0.666

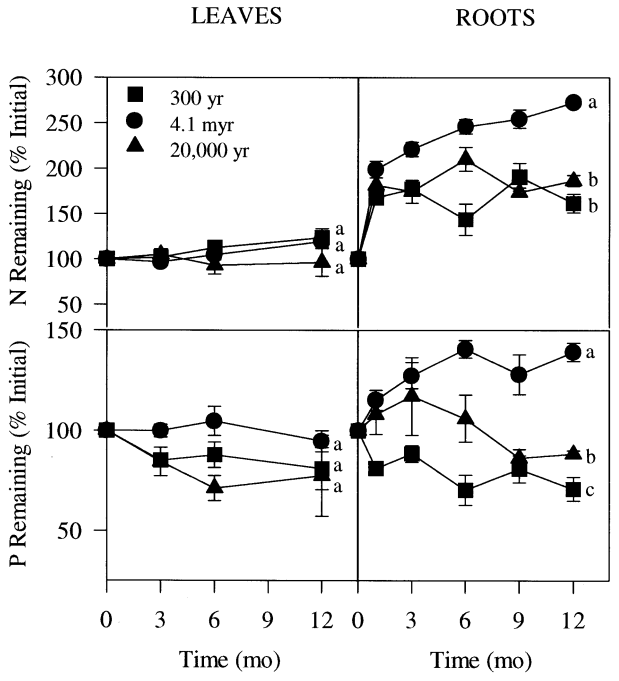


Fig. 2 Nutrient content remaining, relative to initial nutrient content (100 g g^{-1}), in decomposing leaves and fine roots at the three sites along the natural fertility gradient. Leaves and roots were produced and then decomposed in plots that received either N fertilization (*+N*), P fertilization (*+P*), or no fertilization (*control*). Values greater than 100% represent net accumulation, values less than 100% represent net mineralization. *Letters* represent significant differences among means at 12 months using Tukey's HSD multiple comparison tests

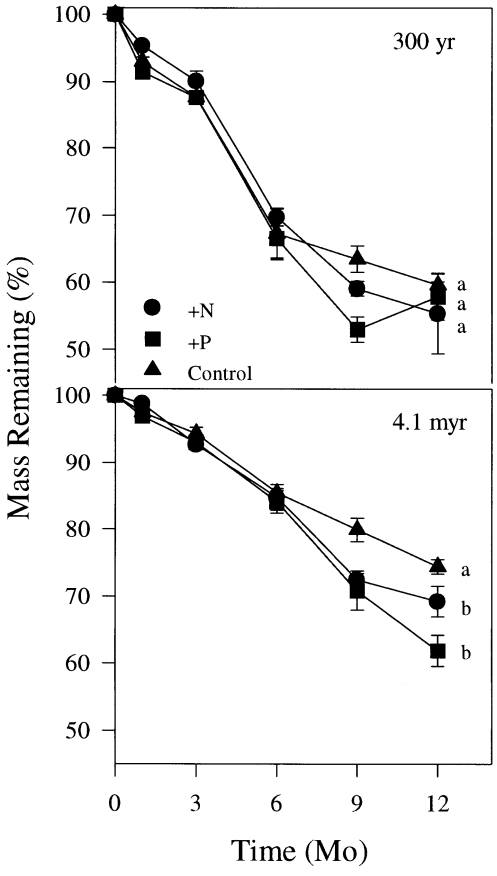


Fig. 3 Percent of mass remaining of fine roots at the 300-year-old site and at the 4.1-Myear-old site. Roots were produced and then decomposed in plots that received either N-fertilization (*+N*), P-fertilization (*+P*), or no fertilization (*control*). *Letters* represent significant differences among slopes using Tukey-Kramer multiple comparison tests

At both sites, fertilization treatment affected loss or gain of N and P in decomposing roots (Fig. 4). Several patterns emerged: (1) roots at both sites accumulated N over time; (2) those roots decomposed in soils fertilized with the limiting nutrient had a smaller increase in relative N content than the other treatments because they had higher initial tissue N concentrations ($F_{2,9}$=11.3, P<0.004 for 300-year-old site; $F_{2,9}$=112.8, P<0.001 for 4.1-Myear-old site; and (3) roots from P-fertilized plots tended to lose P at the sites ($F_{2,9}$=28.9, P<0.001 for 4.1-Myear-old site).

Effects of tissue chemistry on root decomposition

Tissue chemistry had a large influence on decomposition rates of roots. Decomposition rates differed among the seven site/fertilizer combinations of roots placed out in the common site ($F_{6,147}$=12.5, P<0.001) (Fig. 5), but were similar for roots decomposed *in situ* and at the

Table 4 Statistics for determining the best decomposition model. Regression statistics are given for both linear (R^2_L) and exponential (R^2_E) rates of decay. A linear model of decay was chosen to best represent the data; all regressions were significant at $P \leq 0.001$. The k values are the absolute value of the slope of the relationship between mass loss and time (in $year^{-1}$) and are based on a linear model of decay

Site/Fertilizer combination	*In situ* leaves			*In situ* roots			Common site roots		
	k	R^2_L	R^2_E	k	R^2_L	R^2_E	k	R^2_L	R^2_E
300 year/N-fert.				0.483	0.90	0.86	0.438	0.89	0.85
300 year/P-fert.				0.470	0.86	0.84	0.352	0.93	0.92
300 year/Control	0.288	0.94	0.92	0.419	0.89	0.88	0.401	0.84	0.82
Fertile/Control	0.396	0.75	0.62	0.405	0.96	0.95	0.476	0.94	0.94
4.1 Myear/N-fert.				0.333	0.95	0.94	0.365	0.90	0.90
4.1 Myear/P-fert.				0.387	0.95	0.92	0.393	0.93	0.91
4.1 Myear/Control	0.156	0.93	0.93	0.261	0.96	0.96	0.282	0.86	0.85

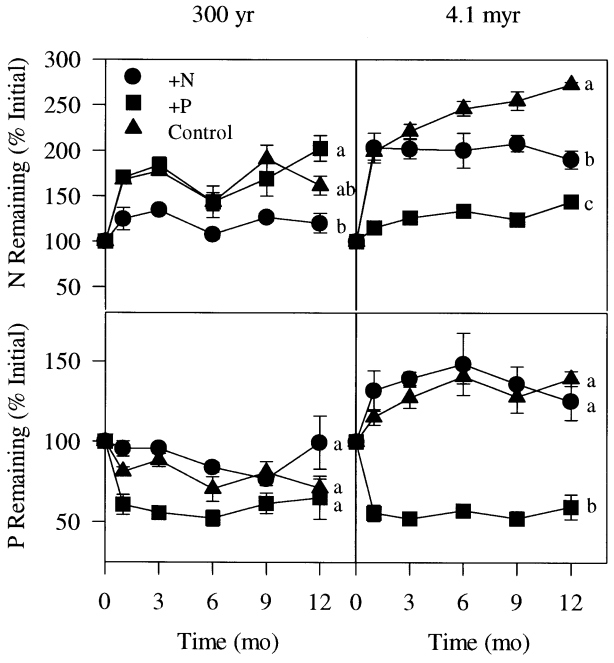
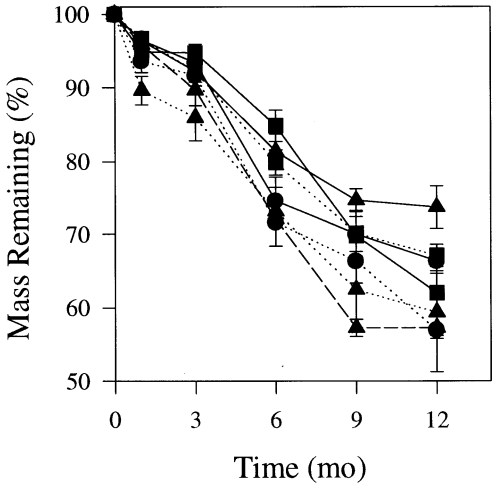


Fig. 4 Nutrient content remaining, relative to initial nutrient content (100 g g^{-1}), in decomposing fine roots at the 300-year-old and 4.1-Myear-old sites. Roots were produced and then decomposed in plots that received either N-fertilization (*+N*), P-fertilization (*+P*), or no fertilization (*control*). Values greater than 100% represent net accumulation, values less than 100% represent net mineralization. *Letters* represent significant differences among means at 12 months using Tukey's HSD multiple comparison tests



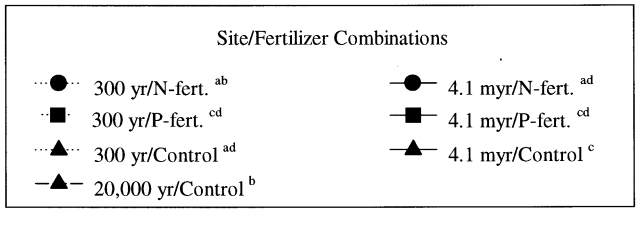
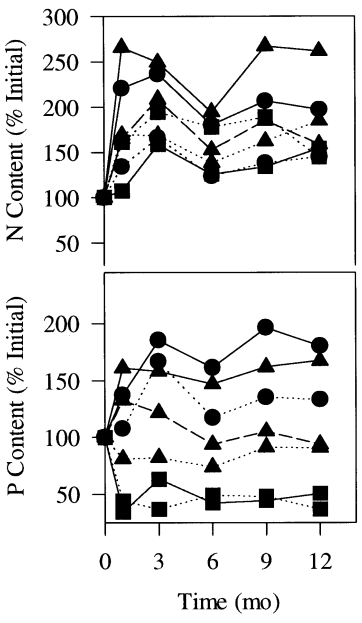


Fig. 5 Percent of mass remaining of fine roots that were taken from all seven site/fertilizer combinations and decomposed at the common site. *Letters* represent significant differences among slopes using Tukey-Kramer multiple comparison tests



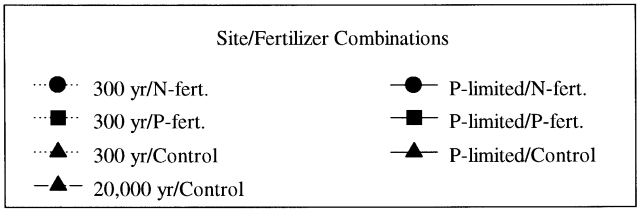


Fig. 6 Nutrient content remaining, relative to initial nutrient content (100 g g^{-1}), in decomposing fine roots at the common site. Values greater than 100% represent net accumulation, values less than 100% represent net mineralization. Each value represents a composite sample from four replicates

common site (Table 4). The relative order of the decomposition rates were also similar to the relative order of roots decomposed *in situ* (Table 4, Fig. 5); these results suggest that tissue chemistry is more important than site effects in determining decomposition rates. Nutrient dynamics of roots at the common site were also consistent with patterns of roots decomposed at their site of origin in terms of N and P gain and loss (Fig. 6).

Discussion

Controls over leaf and root decomposition rates

Roots and leaves that were produced and decomposed in the same site differed in rates of decomposition, nutrient accumulation, and tissue chemistry characteristics. Roots decomposed faster than leaves at two out of the three sites on the natural fertility gradient, and roots tended to have lower lignin-to-nutrient ratios than leaves. Roots also differed from leaves in their nutrient accumulation patterns. Roots increased their relative N content during the decomposition process, while leaves generally expe-

rienced net release. The high levels of N immobilization in roots contrast with the low N immobilization potential of roots in tallgrass prairies (Seastedt et al. 1992), but the occurrence of P release is in agreement with other studies (Seastedt 1988; Conn and Day 1996). The ability of roots to decompose faster than leaves but to retain N may indicate that roots serve an important role in N retention in these forests.

Some of these divergences between leaves and roots in decomposition rate and nutrient dynamics might be explained by the fundamental differences between the two tissue types. The decomposing roots were buried and thus experienced different moisture conditions, different microbial communities, and closer proximity to mineralized nutrients than leaves. For methodological considerations, the roots used in this study were live when collected, while leaves had already senesced, and therefore experienced some nutrient resorption. Preliminary evidence suggests that roots do not retranslocate nutrients before their death (Nambiar 1987; Aerts et al. 1992), and dead roots from these forests did not have any higher total N or P concentrations than live roots (R. Ostertag, unpublished work). In addition, decomposition rates may be influenced by characteristics such as leaf type, sclerophylly, and root diameter class (Berg 1984; McClaugherty et al. 1984; Fahey et al. 1988); *Metrosideros* is fairly sclerophyllous leaf (Cordell et al. 1998).

Despite these inherent differences between leaves and roots, decomposition of both tissue types appears to be related strongly to plant tissue chemistry. When root decomposition and leaf decomposition were compared, fine roots, with their lower lignin-to-N and lignin-to-P ratios, decomposed faster than leaves at the two infertile sites. Thus, tissue chemistry appears to be a good predictor of both leaf and root decomposition rates, although rates of decomposition were not identical between roots decomposed *in situ* and at the common site, suggesting that some site-specific effects also influence decomposition rates. If tissue chemistry is the primary influence of decomposition rates, faster decomposition rates on nutrient-rich sites may be explained by lower lignin-to-nutrient ratios of litter produced by species growing in fertile sites.

In the few studies that have compared fine root and leaf decomposition rates simultaneously, there appears to be no consistent trend in decomposition rates or tissue chemistry. Roots have been reported to decompose faster (Andrén 1987; Seastedt 1988; Seastedt et al. 1992; Hobbie 1996) or slower (Andrén 1987; Aber et al. 1990; Taylor et al. 1991; Bloomfield et al. 1993; van Vuuren et al. 1993; Hobbie 1996) than leaves, and roots and leaves vary in tissue chemistry, particularly percent lignin (Bloomfield et al. 1993; Hobbie 1996). Rates of mass loss reported here for both leaves (Anderson and Swift 1983; Vitousek et al. 1994; Crews et al. 1995) and roots (Bloomfield et al. 1993) were similar to values reported for other montane tropical forests. The decomposition rates and initial chemical characteristics of roots were also consistent with the range of values reported in the limited number of root decomposition studies conducted in forests (e.g., Berg 1984; McClaugherty et al. 1984; Fahey et al. 1988; Aber et al. 1990; Bloomfield et al. 1993; Camiré et al. 1991; Burke and Raynal 1994; Lõhmus and Ivask 1995). Other studies on leaves have also suggested that soil environment did not influence decomposition rates as strongly as tissue chemistry. For example, in Wisconsin hardwood forests in which leaf litter (*Acer saccharum*) was decomposed along a natural fertility gradient (McClaugherty et al. 1985), site effects were found to be negligible. In another study, the amount of inorganic N in the soil beneath leaf litterbags was unrelated to decomposition rate (Hunt et al. 1988). Thus, there is evidence from this and other studies that soil fertility appears to regulate rates of both root and leaf decomposition through its effects on plant tissue chemistry. However, this conclusion must be interpreted with caution because clearly soil nutrient availability is not the only property that varies among the sites on the natural fertility gradient, and site-specific factors such as soil fauna, soil moisture regime, and microbial community composition may also affect decomposition rates (Prescott 1996).

Nutrient limitations to decomposition: effects of soil fertilization

Fertilization had mixed effects on root decomposition and nutrient dynamics of decaying roots. At the 300-year-old site, soil fertilization with N and P had no effect on root decomposition rate, even though it has been demonstrated that N-fertilization increased leaf litterfall rates, total N concentration in litterfall, and diameter growth of *Metrosideros polymorpha* (Vitousek et al. 1993; Vitousek and Farrington 1997). At the 4.1-Myear-old site, roots in plots fertilized with N or P decomposed faster than roots in unfertilized plots. These results suggest that N and P limit root decomposition at the old, 4.1-Myear-old site, but not in the young, 300-year-old soils. The only other study that has examined root decay after N-fertilization found enhanced mass loss on two young dune sites but not on the oldest dune site (Conn and Day 1996).

Nutrient limitation of decomposition is a common interpretation in many leaf decomposition studies whenever mass loss is enhanced after fertilization. In addition, the observation that decaying litter undergoes net immobilization of nutrients is also interpreted as evidence of nutrient limitation (Prescott 1995). Because exogenous nutrients are necessary for immobilization, fertilization should increase net immobilization (Conn and Day 1996). Yet even under circumstances where nutrients have been demonstrated to limit aboveground net primary productivity, fertilization does not always stimulate increased mass loss rates, as evidenced at the 300-year-old site and in a *Pinus radiata* plantation in Australia (Theodorou and Bowen 1990). One reason for this pattern is that fertilization is more likely to increase decom-

position rates when labile carbon compounds are readily available (Fog 1988; Prescott 1995). We suggest that the lack of a decomposition response after fertilization may occur because microbes are limited primarily by appropriate carbon sources rather than by N or P, a hypothesis that has been invoked in several decomposition studies (Salonius 1972; McClaugherty et al. 1985; MacKay et al. 1987; Titus and Malcolm 1987; Prescott et al. 1992). While nutrient availability does influence decomposition in these Hawaiian forests, its effects seem stronger across sites than when nutrient availability is enhanced within a site due to fertilization.

Acknowledgements We thank Jack Ewel, Jack Putz, Peter Vitousek, and Kim Williams for advice on experimental aspects of this study; Peter Vitousek for logistical support of many kinds; and Heraldo Farrington for help in the field. We are grateful to Hawai'i Volcanoes National Park, the state of Hawaii Division of Forestry and Wildlife, and the Department of Parks and Recreation in Kaua'i for providing access to field sites. Lodging and logistical assistance on Kauai was graciously provided by the Joseph Souza Center in Kokee State Park. Doug Turner (Stanford University) provided the N and P analysis and Brad Dewey (University of Minnesota-Duluth) provided carbon fraction analyses. Many helpful comments on this manuscript were made by Nick Comerford, Jack Ewel, Steve Mulkey, Jack Putz, Ted Schuur, Whendee Silver, and Kim Williams. This research was supported by grants to R.O. from the National Science Foundation and the National Geographic Society and a NSF post-doctoral fellowship to S.E.H.

References

Aber JD, Melillo JM, McClaugherty CA (1990) Predicting long-term patterns of mass loss, nitrogen dynamics, and soil organic matter formation from initial fine litter chemistry in temperate forest ecosystems. Can J Bot 68:2201–2208

Aerts RC, Bakker C, De Caluwe H (1992) Root turnover as determinant of the cycling of C, N, and P in a dry heathland ecosystem. Biogeochemistry 15:175–190

Anderson JM, Swift MJ (1983) Decomposition in tropical forests. In: Sutton SL, Whitmore TC, Chadwick AC (eds) Tropical rain forest: ecology and management. Blackwell, Oxford, pp 287–309

Andrén O (1987) Decomposition of shoot and root litter of barley, lucerne, and meadow fescue under field conditions. Swed J Agric Res 17:113–122

Aradhya KM, Mueller-Dombois D, Ranker TA (1990) Genetic evidence for recent and incipient speciation in the evolution of Hawaiian *Metrosideros* (Myrtaceae). Heredity 67:129–138

Berg B (1984) Decomposition of root litter and some factors regulating the process: long-term root litter decomposition in a Scots pine forest. Soil Biol Biochem 16:609–617

Berg B, Matzner E (1997) Effect of N deposition on decomposition of plant litter and soil organic matter in forest systems. Environ Rev 5:1–25

Berg B, Wesson B, Ekbohm G (1982) Nitrogen level and decomposition in Scots pine needle litter. Oikos 38:291–296

Bloomfield J, Vogt KA, Vogt DJ (1993) Decay rate and substrate quality of fine roots and foliage of two tropical tree species in the Luquillo Experimental Forest, Puerto Rico. Plant Soil 150: 233–245

Burke MK, Raynal DJ (1994) Fine root growth, phenology, production, and turnover in a northern hardwood forest ecosystem. Plant Soil 162:135–146

Camiré C, Côté B, Brulotte S (1991) Decomposition of roots of black alder and hybrid poplar in short-rotation plantings: nitrogen and lignin control. Plant Soil 138:123–132

Carlquist S (1980) Hawaii: a natural history. Pacific Tropical Botanical Garden, Hawaii

Conn CE, Day FP (1996) Response of root and cotton strip decay to nitrogen amendment along a barrier island dune chronosequence. Can J Bot 74:276–284

Cordell S, Goldstein D, Mueller-Dombois D, Webb D, Vitousek PM (1998) Physiological and morphological variation in *Metrosideros polymorpha*, a dominant Hawaiian tree species, along an altitudinal gradient: the role of phenotypic plasticity. Oecologia 113:188–196

Crews TE, Kitayama K, Fownes JH, Riley RH, Herbert DH, Mueller-Dombois D, Vitousek PM (1995) Changes in soil phosphorus fractions and ecosystem dynamics across a long chronosequences. Ecology 76:1407–1424

Fahey TJ, Hughes JW, Pu M, Arthur MA (1988) Root decomposition and nutrient flux following whole-tree harvest of northern hardwood forest. For Science 34:744–768

Fog K (1988) The effect of added nitrogen on the rate of decomposition of organic matter. Biol Rev 63:433–462

Gill RS, Lavender DP (1983) Litter decomposition in coastal hemlock stands: impact of nitrogen fertilizers on decay rates. Can J For Res 13:116–121

Gosz JR (1981) Nitrogen cycling in coniferous ecosystems. Clark FE, Rosswall T (eds) Terrestrial nitrogen cycles. Ecological Bulletin, Stockholm, pp 405–426

Herbert DA, Fownes JH (1995) Phosphorus limitation of forest leaf area and net primary production on a highly weathered soil. Biogeochemistry 29:223–235

Hobbie SE (1992) Effects of plant species on nutrient cycling. Trends in Evolution and Ecol 7:336–339

Hobbie SE (1996) Temperature and plant species control over litter decomposition in Alaskan tundra. Ecological Monographs 66:503–522

Hunt HW, Inghan ER, Coleman DC, Elliot ET, Reid CPP (1988) Nitrogen limitation of production and decomposition in prairie, mountain meadow, and pine forest. Ecology 69: 1009–1016

Kemp PR, Waldecker DG, Owensby CE, Reynolds JF, Virginia RA (1994) Effects of elevated CO_2 and nitrogen fertilization pretreatments on decomposition on tallgrass prairie leaf litter. Plant Soil 165:115–127

Lõhmus K, Ivask M (1995) Decomposition and nitrogen dynamics of fine roots of Norway spruce (*Picea abies* (L.) Karst.) at different sites. Plant Soil 168–169:89–94

MacKay WP, Fisher FM, Silva S, Whitford WG (1987) The effects of nitrogen, water, and sulfur amendments on surface litter decomposition in the Chihuahuan Desert. J Arid Environments 12:223–232

Makkar HPS, Singh B (1991) Effect of drying on tannin, fibre, and lignin levels in mature oak (*Quercus incana*) leaves. J the Science of Food and Agriculture 54:323–328

McClaugherty CA, Aber JD, Melillo JM (1984) Decomposition dynamics of fine roots in forested ecosystems. Oikos 42: 378–386

McClaugherty CA, Pastor J, Aber JD, Melillo JM (1985) Forest litter decomposition in relation to soil nitrogen dynamics and litter quality. Ecology 66:266–275

Melillo JM, Aber JD, Muratore JF (1982) Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. Ecology 63:621–626

Mueller-Dombois D (1985) Ohia dieback in Hawaii: 1984 synthesis and evaluation. Pacific Science 39:150–170

Nambiar EKS (1987) Do nutrients retranslocate from fine roots? Can J For Res 17:913–918

Prescott CE (1995) Does nitrogen availability control rates of litter decomposition in forests? Plant Soil 168–169:83–88

Prescott CE (1996) Influence of forest floor type on rates of litter decomposition in microcosms. Soil Biol Biochem 28: 1319–1325

Prescott CE, Corbin JP, Parkinson D (1992) Immobilization and availability of N and P in the forest floors of fertilized Rocky Mountain coniferous forests. Plant Soil 143:1–10

Riley RH, Vitousek PM (1995) Nutrient dynamics and nitrogen trace gas flux during ecosystem development in montane rain forest. Ecology 76:292–304

Ryan MG, Melillo JM, Ricca A (1989) A comparison of methods for determining proximate carbon fractions of forest litter. Can J For Res 20:166–171

Salonius PO (1972) Microbiological response to fertilizer treatments in organic forest soils. Soil Sci 114:12–19

SAS (1997) SAS/STAT software: changes and enhancements through release 6.12. SAS Institute, Cary

Seastedt TR (1988) Mass, nitrogen, and phosphorus dynamics in foliage and root detritus of tallgrass prairie. Ecology 69:59–65

Seastedt TR, Parton WJ, Ojima DS (1992) Mass loss and nitrogen dynamics of decaying litter of grasslands: the apparent low nitrogen immobilization potential of root detritus. Can J Bot 70:384–391

Šlapokas T, Granhall U (1991) Decomposition of litter in fertilized short-rotation forests on a low-humified peat bog. For Ecol Manage 41:143–165

Sokal RR, Rohlf FJ (1981) Biometry. Freeman, San Francisco

Staaf H (1980) Influence of chemical composition, addition of raspberry leaves, and nitrogen supply on the decomposition rate and dynamics of nitrogen and phosphorus in beech litter. Oikos 35:55–62

SYSTAT (1992) SYSTAT: statistics, version 5.02 edn. Systat, Evanston

Taylor BR, Parkinson D, Parsons WFJ (1989) Nitrogen and lignin content as predictors of litter decay rates: a microcosm test. Ecology 70:97–104

Taylor BR, Prescott CE, Parsons WFJ, Parkinson D (1991) Substrate control of litter decomposition in four Rocky Mountain coniferous forests. Can J Bot 69:2242–2250

Theodorou C, Bowen GD (1990) Effects of fertilizer on litterfall and N and P release from decomposing litter in a *Pinus radiata* plantation. For Ecol Manage 32:87–102

Titus BD, Malcolm DC (1987) The effect of fertilization on litter decomposition in clearfelled spruce stands. Plant Soil 100: 297–322

Vitousek PM, Farrington H (1997) Nutrient limitation and soil development: experimental test of a biogeochemical theory. Biogeochemistry 37:63–75

Vitousek PM, Walker LR, Whiteaker LD, Matson PA (1993) Nutrient limitation to plant growth during primary succession in Hawaii Volcanoes National Park. Biogeochemistry 23:197–215

Vitousek PM, Turner DR, Parton WJ, Sanford RL (1994) Litter decomposition on the Mauna Loa environmental matrix, Hawaii: patterns, mechanisms, and models. Ecology 75:418–429

Vitousek PM, Turner DR, Kitayama K (1995) Foliar nutrients during long-term soil development in Hawaiian montane rainforest. Ecology 76:712–720

Vuuren MMI van, Eerden LJ van der (1992) Effects of three rates of atmospheric nitrogen deposition enriched with ^{15}N on litter decomposition in a heathland. Soil Biol Biochem 24:527–532

Vuuren MMI van, Berendse F, Visser W de (1993) Species and site differences in the decomposition of litters and roots from wet heathlands. Can J Bot 71:167–173

Wieder RK, Lang GE (1982) A critique of the analytical methods used in examining decomposition data obtained from litter bags. Ecology 63:1636–1642

Wright RF, Tietema A (1995) Ecosystem response to 9 years of nitrogen addition at Sogndal, Norway. For Ecol Manage 71: 133–142