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EFFECTS OF NITROGEN AND PHOSPHORUS AVAILABILITY ON FINE-ROOT DYNAMICS IN HAWAIIAN MONTANE FORESTS

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Abstract. Although it is often assumed that root dynamics are similar to leaf dynamics in relation to nutrient availability, this hypothesis is rarely tested. Using sequential soil coring and a decomposition experiment, patterns of fine-root (<2 mm diameter) biomass, belowground net primary productivity, and root turnover rates were examined over a 1-yr period in three sites along a forest chronosequence in the Hawaiian Islands. These sites form a natural fertility gradient but have similar species composition, climate, and geology. The youngest site (300 yr old) was low in N availability, the oldest site (4.1×10^6 yr old) was low in P availability, and the intermediate-aged site (20 000 yr old) was higher in both N and P. The youngest and oldest sites also contained long-term fertilization plots that were fertilized with N or P, or were unfertilized (control).

Along the natural fertility gradient, the oldest site generally differed from the other two sites; this site had the greatest standing stock of live root mass, the greatest root length density, the lowest belowground net primary productivity (BNPP), and the slowest root turnover rate. The 300-yr-old and 20 000-yr-old sites were similar in all of these variables, except that root turnover was slightly faster at the 300-yr-old site. The response of fine roots to fertilization was consistent with the response along the natural fertility gradient. Despite N limitation to aboveground growth at the 300-yr-old site, fertilization had small effects on root variables, with the only significant effects being a small increase in the standing stock of live root biomass in N-fertilized plots and an increase in root tissue P concentrations in P-fertilized plots. In contrast, fertilization at the 4.1×10^6 yr-old site altered root dynamics more than fertilization at the 300-yr-old site. In the P-fertilized plots, P concentrations increased, BNPP tended to be greater, and root turnover rates increased. These results suggest that root dynamics differ dramatically between ecosystems low in N and ecosystems low in P, even though each system is regarded as ''infertile.'' N availability had a smaller effect on root dynamics than did P availability, suggesting that the simple dichotomy between fertile and infertile sites that is often evoked to explain plant characteristics may be unjustified.

Key words: *belowground net primary productivity; fertilizer treatment; fine roots; Hawaii;* Metrosideros polymorpha*; montane forests; N availability; nutrient limitation; P availability; productivity; root dynamics; turnover.*

INTRODUCTION

Availability of mineral nutrients is a key factor controlling forest productivity. Interest in understanding the relationship between soil fertility and plant growth has therefore led to the development of classification schemes linking plant characteristics to soil fertility (e.g., Monk 1966, Grime 1979, Chapin 1980, Chabot and Hicks 1982, Coley et al. 1985, Tilman 1988). These generalizations are based on the economic analogy that tissue- or plant-level traits are directly related to construction costs and resource return times (e.g., Chapin 1980). Tissues that are expensive to build because of a scarcity of mineral nutrients or slow acquisition of carbon should be long-lived because it will take longer for them to return the resources spent in constructing them to the plant. Consequently, plants growing on infertile sites often have long-lived leaves with low carbon-gaining capacities. Conversely, plants on fertile sites often have leaf tissues that require a shorter time period before the resources spent in building them are returned to the plant.

Although factors other than nutrient availability affect leaf dynamics, many studies have demonstrated that leaf turnover rates increase as nutrient availability increases (e.g., Chabot and Hicks 1982, Reich et al. 1992, Bargali and Singh 1993). These generalizations also have been applied to roots, and it is often assumed that fine roots will exhibit responses similar to those of leaves in relation to nutrient availability (see Chapin 1980: Fig. 2). If fine roots behave as leaves, then in-

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TABLE 1. Belowground processes along natural fertility gradients.

Location, ecosystem	Method	Fine-root diameter (mm)	New root production	Standing stock	Root-to-shoot ratio	Root mortality	Root turnover rate	Source†
Venezuela, tierra firme forest	soil coring; root screens	NG	F < I	F < I	F > I	···	F < I	1
Tennessee, USA, hardwood forest	soil coring; root screens	NG	F < I	F < I	F > I	···	F < I	1
Washington, USA, coniferous forest	soil coring; observation windows	<2	F < I	F < I	F < I	F < I	F < I	2
Wisconsin, USA, hardwood and coniferous forest stands	N-budgeting	<3	F > I	F < I	···	···	F > I	3
Wisconsin and Massachusetts, USA, hardwood and coniferous forest stands	N-budgeting; soil coring	<3	F > I	F < I	···	···	F > I	4
Costa Rica, tropical wet forest	soil coring	<1	···	F < I	···	···	···	5
Washington, USA, mixed conifer and hardwood forest stands	soil coring	<2	···	F < I	···	···	···	6
Venezuela, tierra firme forest, caatinga, bana	various	NG	···	F < I	F < I	···	···	7
Mexico, tropical deciduous forest	soil coring	<2	···	F < I	···	···	···	8
Panama, semi-deciduous and lower montane rain forest	soil coring	<2	···	F < I	···	···	···	9
Ethiopia, juniper, eucalypt, and cupressus plantations	ingrowth cores	<2	F > I	···	···	···	···	10
Saskatchewan and Manitoba, Canada, boreal forest	minirhizotron	<2	F < I	F = I	···	···	···	11
	ingrowth cores	<2	F = I	F = I	···	···	···	11
Costa Rica, tropical wet forest	soil coring	<2	···	F < I	···	···	···	12

Note: Abbreviations are: F = root measurement at the more fertile site(s), I = root measurement at the less fertile site(s), NG = not given.

† References are: 1, Jordan and Escalante (1980); 2, Keyes and Grier (1981); 3, Nadelhoffer et al. (1985); 4, Aber et al. (1985); 5, Gower (1987); 6, Vogt et al. (1987); 7, Medina and Cuevas (1989); 8, Kellman (1990); 9, Cavelier (1992); 10, Michelsen et al. (1993); 11, Steele et al. (1997); 12, Ostertag (1998).

creasing nutrient availability should lead to higher belowground net primary productivity (BNPP) and root turnover rates. Few studies, however, have tested this prediction (Hendricks et al. 1993). Rather, studies have focused on measuring static root parameters, such as root-to-shoot biomass ratios or simply root biomass at a given time. Although these biomass measurements are of value, they say little about the mechanisms (i.e., the dynamics of root productivity and longevity) that lead to these static values (Pregitzer et al. 1995).

Root dynamics in relation to nutrient availability can be examined in two ways: along a natural fertility gradient and in response to fertilization. Along natural fertility gradients, plants growing on nutrient-poor sites often have greater root-to-shoot biomass ratios (Table 1), but studies examining root dynamics have found varied results. For example, in a study of 13 temperate hardwood and pine forest sites, fine-root turnover rates were positively related to the N availability of a site (Aber et al. 1985). When species composition is more constant along a soil fertility gradient, however, fine-root turnover does not always increase with increasing nutrient availability (Table 1). In one case, BNPP and root turnover rates were reportedly faster on more infertile soils (Keyes and Grier 1981). These conflicting results regarding fine-root production and turnover rates may not be related to the direct effects of nutrient availability on root growth, but rather may be related to the characteristics of species that tend to inhabit infertile and fertile sites. Because plant species usually replace each other along strong fertility gradients (Chapin et al. 1986), even under similar climatic conditions, the suggestion that plants growing in fertile sites have greater root turnover rates might arise because species typical of nutrient-rich sites tend to have traits associated with fast growth and fast tissue turnover rates.

Examining the effects of fertilization within a site reduces some of the confounding intersite environmental factors and allows for species composition to be held constant. Root responses after fertilization, however, may not be directly comparable to root responses along natural soil fertility gradients, because plants growing at each site may be adapted for the nutrient conditions at that site. Thus, plants may respond to short-term changes in nutrient availability differently due to varied background soil conditions and evolutionary histories (Chapin et al. 1986). Despite

these potential confounding factors, root-to-shoot ratios generally decrease after fertilization (Table 2), analogous to responses on fertile sites (Table 1). Similarly, another index, the root weight ratio (i.e., the ratio of root mass to total plant mass), reportedly decreased with increased nitrogen in 75% of the 206 cases considered in a literature review examining root responses to nutrient availability (Reynolds and D'Antonio 1996). When only root (but not shoot) biomass is measured in both field and species-specific pot studies (for a review, see Friend et al. 1994), there also appears to be an inverse relationship between root biomass and nutrient availability. Root turnover rates, however, have been reported to be both faster and slower after fertilization (Table 2).

To determine if roots behave similarly to leaves in relation to nutrient availability, I investigated root biomass, BNPP, and fine-root turnover rates along a geologic chronosequence in the Hawaiian Islands. The sites in this chronosequence form a soil fertility gradient that varies greatly in nitrogen (N) and phosphorus (P) availability, but where 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 it remains similar in these forests because of the broad ecological ranges of the limited number of tree species in the Hawaiian Islands (Carlquist 1980). I also examined root dynamics within a site in response to manipulation of N and P by fertilization, to account for the fact that the differences in soil ages among the sites interact with other environmental variables besides nutrient availability. Taken together, these two approaches eliminate some factors that are confounding in many studies to address how nutrient availability can influence belowground plant productivity and turnover rates.

METHODS

Study sites and experimental design

Natural fertility gradient.—I compared root production and turnover rates along a natural fertility gradient that consisted of sites differing in soil age and, consequently, in N and P availability (Table 3). 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, has a mean annual rainfall of ~2500 mm, has a mean annual 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, known for its morphological variation, 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), where it tends to form even-aged stands that are subject to synchronous dieback (Mueller-Dombois 1985).

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 200–400 yr old coarse tephra deposits (Crews et al. 1995) overlaying an older pahoehoe (smooth) lava flow (Vitousek et al. 1993). Vegetation at this site is dominated by *Metrosideros*, with a conspicuous tree fern understory/subcanopy of *Cibotium* spp. (Crews et al. 1995). The intermediate-aged site, located in Laupahoehoe State Forest Reserve on the island of Hawai'i, contains 10 000–30 000 yr 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 the 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 4.1×10^6 yr old. Although *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-yr-old site) and by P alone at the oldest site (hereafter 4.1×10^6 yr-old site). The intermediate-aged 20 000-yr-old site is 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 this more fertile site, however, is still limited by nutrients. *Metrosideros* trees increased ANPP 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).

As discussed by Crews et al. (1995), the fact that present-day climatological and topographical conditions are similar among the sites does not imply that identical conditions occurred throughout the development of each system. The oldest site has accumulated more dust that has blown over from Asia; this dust may be a source of base cations and P (Chadwick et al. 1999). Temperatures and elevation were also not constant through time because these islands are undergoing subsidence (Crews et al. 1995). The 4.1×10^6 yr-old site was also hit by hurricanes in 1982 and 1992, but fine-root biomass had recovered to its pre-hurricane levels before the initiation of this study (Herbert et al. 1999).

Fertilized plots.—To examine the effect of fertiliza-

TABLE 2. Effects of fertilization on fine roots.

Location, ecosystem	Method	Elements added	Fine-root diameter
New York, USA, red pine plantation	coring in plots 5 yr after fert.	...	NG
Scotland, sitka spruce	monthly cores for 2 yr	N	<5 mm
Sweden, Scots pine stand	ingrowth cores	N, NPK	<2 mm
Venezuela, tierra firme forest	ingrowth cores	P, Ca	NG
Venezuela, tall caatinga	ingrowth cores	N	...
Venezuela, low bana	ingrowth cores	N, P	...
Panama, semideciduous and lower monane rain forest	coring	NP	<2 mm
Hawaii, USA, tropical montane wet forest	cores taken 15 mo after fert.	N	<2 mm
New Mexico, USA, coniferous forest	cores taken 11 mo after fert.	NPK+	<2 mm
Michigan, USA, old-field seedlings	video camera for 7–14 d	NPK+	NG
Michigan, USA, mixed-hardwood forest	video camera for 82 d	N	NG
New Hampshire, USA, hardwood forest	root screens	NPK+	<2 mm
New Zealand, coniferous sand dune forest	coring	N	<2 mm
Sweden, coniferous forest	coring	N	<1, 2 mm
Wisconsin, USA, red pine plantation	coring	NPK+	<5 mm
Portugal, eucalyptus plantation	minirhizotron for 10 mo	N	<2 mm
Michigan, USA, *Populus* tree cuttings	video camera for 158 d	N	<0.5 mm
Sweden, Norway spruce stand	minirhizotron for 1 yr	N	<2 mm
Sweden, Norway spruce stand	minirhizotron for 1 yr	N	<2 mm
Sweden, Norway spruce stand	minirhizotron for 2 yr	N	<2 mm
California, USA, pine seedlings	minirhizotron for 2 yr	N	<2 mm
Europe, coniferous forest	ingrowth cores	N	≤2 mm
Tasmania, eucalyptus plantations	coring	NP	<1 mm
Sweden and Finland, Norway spruce stand	coring; ingrowth	N	<2 mm
Massachusetts, USA, oak forest, red pine plantation	coring	N	NG

Note: Abbreviations are: NG, not given; fert., fertilization; NPK+, complete fertilizer.

† References are: 1, Farrell and Leaf (1974); 2, Alexander and Fairley (1985); 3, Ahlstrom et al. (1988); 4, Cuevas and Medina (1988); 5, Cavelier (1989); 6, Gower and Vitousek (1989); 7, Gower et al. (1992); 8, Gross et al. (1993); 9, Pregitzer et al. (1993); 10, Fahey and Hughes (1994); 11, Smith et al. (1994); 12, Clemensson-Lindell and Persson (1995); 13, Haynes and Gower (1995); 14, Kätterer et al. (1995); 15, Pregitzer et al. (1995); 16, Majdi and Nylund (1996); 17, Majdi and Kangas (1997); 18, Tingey et al. (1997); 19, Boxman et al. (1998); 20, Misra et al. (1998); 21, Helmisaari and Hallbäcken (1999); 22, Nadelhoffer et al. (1999).

tion on fine-root production and turnover, I compared root dynamics between fertilized and unfertilized plots at both the 300-yr-old and 4.1×10^6 yr-old sites. Long-term factorial fertilization experiments have been ongoing at the 300-yr-old site since October 1985 (Vitousek et al. 1993) and at the 4.1×10^6 yr-old site since March 1991 (Herbert and Fownes 1995). A 15×15 m area of each plot was fertilized semiannually at a rate of 100 $kg \cdot ha^{-1} \cdot yr^{-1}$ of N (half as urea, half as ammonium nitrate) or 100 $kg \cdot ha^{-1} \cdot yr^{-1}$ of P (as triple superphosphate). Unfertilized plots are referred to as controls. There were four plots for each treatment (+ N, + P, and control). I did not examine the effects of fertilization at the 20 000-yr-old site, where trees were fertilized individually rather than in plots.

Annual root productivity and turnover rate

Sequential soil sampling.—To test the hypothesis that root production decreases as nutrient availability increases, fine-root (defined hereafter as <2 mm diameter) biomass and decomposition at all sites were monitored for one year. All of the calculations presented here use only data from fine roots, because soil coring is not an appropriate method for sampling coarse roots (Vogt and Persson 1991). I made comparisons on two levels: among sites (comparing the unfertilized control plots across the three sites) and within sites (comparing the N and P fertilization treatments with control plots at both the 300-yr-old and the 4.1×10^6 yr-old sites). For fine-root production to be estimated, it is necessary to know the change in live-root mass, the change in dead-root mass, and the fine-root decomposition rate. The first two were measured using sequential soil coring, the latter was determined by a root decomposition study using litterbags. I was unable to separate roots by species in the soil cores; thus, the data presented are for the entire plant community.

Sampling depth for the sequential cores varied among the three sites, depending on soil and rooting characteristics. Sampling depth was limited at the 300-yr-old site by the presence of lava at ~35–40 cm. The final sampling depths were chosen based on field observations, previous investigations (Herbert and Fownes 1999), and data from initial cores. At each site, I took cores using a 5 cm diameter corer, separating the cores into 5 cm depth increments, until I reached a depth at which I no longer saw substantial amounts of fine roots. In choosing sampling depths, I tried to encompass ~85% of the fine-root length and biomass of each soil type. The final sampling depths chosen were 20 cm at the 300-yr-old site, 30 cm at the 20 000-yr-old site, and 15 cm at the 4.1×10^6 yr-old site.

TABLE 2. Extended.

New root production	Standing stock	Root-to-shoot ratio	Root mortality	Root turnover rate	Reference†
decrease	···	···	···	···	1
decrease	no change	decrease	···	decrease	2
···	no change in biomass; increase in length	···	···	···	3
increase	···	···	···	···	4
increase	···	···	···	···	4
increase	···	···	···	···	4
decrease	decrease	···	···	···	5
···	decrease	···	···	···	6
decrease	···	···	···	···	7
increase	increase	increase	···	···	8
increase	···	···	···	decrease	9
increase	···	···	···	···	10
···	increase	···	···	···	11
···	decrease	···	···	···	12
decrease or no change	decrease	···	···	decrease	13
···	no change	···	increase	···	14
increase	···	···	···	···	15
decrease (0–20 cm depth)	···	···	increase	increase	16
increase (41–85 cm depth)	···	···	increase	increase	16
decrease	···	···	increase	increase	17
···	···	···	no change	increase	18
···	no change	···	···	···	19
···	no change	···	···	···	20
···	no change	···	···	···	21
···	increase	···	···	···	22

Sequential coring with a 5 cm diameter corer began in late October and early November 1995, and continued at approximately monthly intervals for one year. At the 20 000-yr-old site, there were no pre-existing plots, so I set up four plots in areas of the forest that were unfertilized. A 7.5 × 7.5 m grid consisting of 49 points, each 1 m apart, was set up in each plot. At each sampling date, I randomly chose, without replacement, four of these points; these four cores are considered subreplicates and the plots were treated as replicates in the statistical analysis ($n = 4$).

Each core was homogenized and subsampled for gravimetric soil moisture and for root length and biomass. For root measurements, one-fourth of the core (by mass), was used and these subsamples were frozen until they could be processed; previous tests (R. Ostertag, *unpublished data*) on samples demonstrated that the variation within each one-fourth of a core was much less than the variation between cores. Processing involved washing soil through a 0.5-mm sieve and then placing the resulting material in a tray of deionized water to separate roots from other organic matter. I separated roots (from all depths combined) into live and dead components and quantified length and mass for every core. Root length was determined using the line-intercept method (Newman 1966, Tennant 1975), and mass was determined after drying at 70°C for 48 h. Live and dead roots were distinguished based on texture and color (Vogt and Persson 1991). Live roots were flexible and friable and often a light color (except for fern roots, which were black). In dead roots, the stele often separated from the cortex, or these roots were extremely rigid.

Root decomposition rates were determined by collecting roots from the top 10 cm of soil in each of the four plots per site and fertilizer combination. Live fine roots were selected, washed, dried at 50°C, and cut into 2–5 cm lengths. Roots were then pooled by site and fertilizer combination, and 0.5 g of root material was placed into each litterbag (10 × 10 cm size with 0.3 mm mesh). These bags were then placed back into their site and fertilizer treatment ($n = 4$ plots) of origin and were buried to 10 cm depth at a 45° angle. Four bags from each plot were collected at intervals of 1, 3, 6, 9, and 12 mo, and the roots remaining were dried at 70°C and weighed. Root mass remaining was calculated for each plot by averaging the four bags collected at each time period. Root mass was corrected for residual soil particles by ashing subsamples and calculating mass change on an ash-free dry mass basis. The decomposition rate constant, k, was calculated for each site and fertilizer treatment (and not each individual plot); in all cases, k was best described by a linear decay model (Ostertag and Hobbie 1999).

Calculation of annual fine-root productivity and turnover.—I calculated annual fine-root productivity using a modification of the compartment flow model of Santantonio and Grace (1987). This equilibrium model allows the calculation of mortality and productivity using data on decomposition rate and the standing-stock mass of live and dead roots. The decomposition rate for each sampling interval is used to cal-

TABLE 3. Characteristics of the study sites along the natural fertility gradient. Most numerical values are expressed as means ± 1 SE, followed by sample sizes (*n*), in parentheses, whenever possible.

Characteristics	Study site		
	300 yr	20 000 yr	4.1×10^6 yr
Physical characteristics†			
Site name, island	Thurston, Hawaii	Laupahoehoe, Hawaii	Koke'e, Kauai
Elevation (m)	1176	1170	1134
Soil type	Hydric Dystrandept	Typic Hydrandept	Plinthic Acrudox
Soil characteristics			
In situ resin bags ($\mu g \cdot bag^{-1} \cdot d^{-1}$)†			
NO_3-N	0.22 ± 0.12 (5)	4.25 ± 1.27 (8)	10.20 ± 4.91 (6)
NH_4-N	3.09 ± 1.44 (5)	8.12 ± 2.05 (8)	4.12 ± 2.29 (6)
P	0.20 ± 0.08 (5)	1.21 ± 0.28 (8)	0.41 ± 0.17 (6)
Total nutrients (upper 100 cm mineral soil)‡			
N (g/kg)	0.10 ± 0.03 (7)		0.53 ± 0.04 (4)
P (g/kg)	0.05 ± 0.01 (7)		0.04 ± 0.02 (4)
Gross N mineralization ($mg \cdot m^{-2} \cdot d^{-1}$)‡	195 ± 70 (8)		647 ± 114 (4)
Gross nitrification ($mg \cdot m^{-2} \cdot d^{-1}$)‡	33 ± 9 (8)		112 ± 52 (4)
pH in H_2O†	5.02	3.57	3.99
Plant characteristics			
Mean maximum tree height (m)†	16.5 ± 0.4 (5)	24.7 ± 1.0 (5)	13.7 ± 0.4 (5)
Community basal area (m^2/ha)†	35.8 (81% *Metrosideros*)	33.6 (83% *Metrosideros*)	38.0 (88% *Metrosideros*)
Foliar nutrients§			
N (%)	0.87 ± 0.04	1.42 ± 0.05	0.86 ± 0.04
P (%)	0.060 ± 0.006	0.101 ± 0.006	0.061 ± 0.002
Litterfall†			
N (%)	0.40 ± 0.01	0.80 ± 0.04	0.37 ± 0.015
P (%)	0.026 ± 0.001	0.053 ± 0.003	0.022 ± 0.001
Lignin (%)	25.8 ± 2.2	36.0 ± 0.7	36.7 (bulked sample)
Net primary productivity ($g \cdot m^{-2} \cdot yr^{-1}$)‖			
Leaf	381	430	305
Twig	166	118	107
Stem	506	422	389
Total aboveground	1053	970	801
Root (soil respiration measurements only)	524	634	713
Total	1577 ± 127	1604 ± 87	1514 ± 135

† Data from Crews et al. (1995).
‡ Data from Riley and Vitousek (1995).
§ Foliar nutrients on *Metrosideros polymorpha* leaves (glabrous variety); data from Vitousek et al. (1995).
‖ Data from Herbert and Fownes (1999) and D. Herbert (*personal communication*).

culate the amount of live fine-roots needed to restock the dead fine-root compartment (mortality rate), and the amount of biomass needed to restock the live fine-root compartment (production rate). This model makes the assumption that death and decay are temporally segregated; fine roots that die during one interval do not decompose until the next interval.

I modified this approach slightly because the decomposition equation in the compartment flow model is based on an exponential rate of decay. Fine roots in the forests studied had a linear decay rate over the 12-mo period, perhaps because they were still in the early stages of decomposition. For a linear rate of decay, k (per month) is simply the slope of the relationship between the fraction of roots remaining in the litterbags and time. Therefore, the equation of a linear rate for decomposition is

$$R = 1 - kt \quad (1)$$

where R is the fraction of roots remaining after decomposing for time t. Therefore, $1 - R$ is equal to the fraction of roots that have decomposed over the time interval:

$$1 - R = kt. \quad (2)$$

Substituting this linear rate of decay equation for the exponential equation ($1 - e^{-kt}$) described by Santantonio and Grace (1987) yields a decomposition amount (D):

$$D_j = y_i(1 - e^{-kt}) = y_i(kt) \quad (3)$$

where y_i is the standing-stock mass of dead roots at interval i, and D_j is the decomposition over the interval j.

I therefore used the equation $D_j = y_i(kt)$ to calculate the amount of decomposition over the interval j. This gives the amount of roots decomposed in units of grams per square meter, as y_i is in grams per square meter, k is rate per month, and t is in months. Annual rates of

decomposition were determined by summing the calculations for each sampling interval over the 12-mo period to obtain a decomposition rate (in grams per square meter per year).

To convert these decomposition rates into belowground net primary productivity values, Publicover and Vogt (1993) have demonstrated that productivity calculations can be simplified to

$$\text{BNPP}_{\text{annual}} = (x_{\text{final}} - x_{\text{initial}}) + (y_{\text{final}} - y_{\text{initial}}) + |D_{\text{annual}}| \quad (4)$$

where x_{final} and x_{initial} are the standing-stock mass of live roots at months 12 and 1, respectively; y_{final} and y_{initial} are the standing-stock mass of dead roots at months 12 and 1, respectively; and D_{annual} is the amount of roots decomposed annually (in grams per square meter per year).

I used this approach to calculate annual belowground net primary productivity (BNPP) for every plot. Standing-stock values used were determined for each plot. The k values used were based on values calculated for each site and fertilizer treatment; because k was linear, a monthly k value was calculated by dividing the annual value by 12. For added rigor, I only considered changes in root mass (data log-transformed) between months 1 and 12 when they are significantly different, an approach recommended by many authors to eliminate adding random sampling error (e.g., Vogt et al. 1986, Publicover and Vogt 1993). I determined whether standing stocks of live and dead root mass changed with time using a repeated-measures ANOVA model, with data from all of the sampling periods, to determine significance. As pointed out by Publicover and Vogt (1993), an ANOVA of variance on all dates is more appropriate than a pairwise t test between the first and last sampling dates; if the ANOVA is significant, then the first and last dates are compared by a multiple-comparison test. No plots had any significant differences in live or dead mass between month 1 and month 12; therefore, productivity was calculated as the annual sum of each month's decomposition amount, $y_i(kt)$ (Eq. 3). Because the compartment flow model assumes that roots produced in one interval do not decompose until the next interval, I calculated the amount of roots decomposed for month 12 by assuming the same decomposition constant used previously. This assumption extended the compartment flow model to give a 12-mo annual decomposition amount. Values for BNPP are slightly different than what would be predicted simply by multiplying the standing stock of dead roots by the k constant, because not all sampling intervals were equal. Root turnover rate was calculated as BNPP divided by the standing stock of live roots.

Calculations of BNPP are problematic for any forest, and there remains much debate over which methodology is best (e.g., Vogt et al. 1986, 1998). The compartment flow model was chosen for the calculations because it tends be more accurate than other calculation methods when there are either lack of seasonal differences in root biomass or simultaneous root production and mortality (Publicover and Vogt 1993, Vogt et al. 1998). The limitation of this method is that the BNPP estimates in this study are only as good as the estimates of decomposition rates and the ability to sort live- and dead-root biomass (Publicover and Vogt 1993). The two other common methods of calculating BNPP were developed for situations in which root decomposition has not been measured. The maximum–minimum method calculates production by taking the difference between the maximum and minimum peaks in biomass over the course of the sampling period (BNPP = Δ live mass + Δ dead mass; Vogt and Persson 1991). Because of the lack of seasonal peaks in live or dead fine-root biomass at these study sites, the maximum–minimum method would give a BNPP value of 0 for these three forests. Similarly, estimating BNPP based on summing the positive increments of biomass, rather than just the maximum and the minimum (e.g., Fairley and Alexander 1985), would also yield a BNPP of 0. If significant differences were not considered, BNPP estimates from these study sites would be up to four times higher using the compartment flow model and 10 times higher using the maximum–minimum method; such values are much higher than most in the literature, and are probably overestimates.

Nutrient analysis of fine-root tissue

To determine if the nutrient concentration of fine roots varied among fertilization treatments, between live and dead roots, and among sites, roots were analyzed for total N and P. Although the sites were fertilized semiannually, they were fertilized at different times of the year. The 300-yr-old and 20 000-yr-old sites were fertilized every January and July, and the 4.1×10^6 yr-old site was fertilized every October and April. Nutrient concentrations were determined in both live and dead fine roots collected from the three sites 4 mo after fertilization.

Tissue nutrients were analyzed on oven-dried roots that were pooled from the four subreplicate cores taken in a given plot; hence, all nutrient values represent a plot average ($n = 4$ plots per fertilization treatment per site). These composite samples were ground in a Wiley mill (40-mesh) and were analyzed for total N and P using a peroxide persulfate procedure to acid-digest the samples in a block digester. N and P concentrations were determined with an Alpkem autoanalyzer (Alpkem Corporation, Wilsonville, Oregon, USA) at Stanford University, Stanford, California, USA.

Statistical analysis

Comparisons were made (1) among unfertilized control plots at the three sites along the natural fertility gradient; (2) among the N, P, and control fertilization treatments within the 300-yr-old site; and (3) among

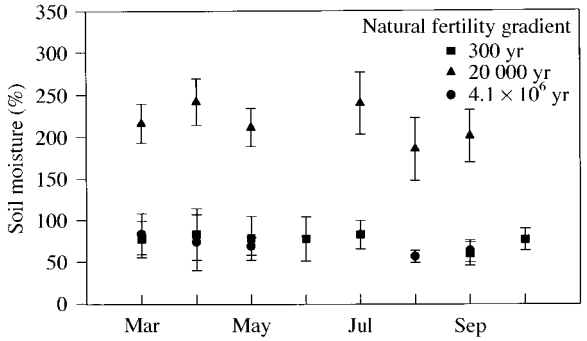

FIG. 1. Gravimetric soil moisture in unfertilized plots (n = 4) among three Hawaiian forest sites that differed in age and fertility. Samples were taken from March to October 1996. Values are means ± 1 SD.

the N, P, and control fertilization treatments within the 4.1 × 10^6 yr-old site. In all analyses, the plots (either fertilized or unfertilized controls) that were set up at each site were treated as true replicates (n = 4). BNPP values were first determined for each plot by the procedure previously described, based on a repeated-measures ANOVA. One-way ANOVA was then used to compare plot-level variables (gravimetric soil moisture, annual fine-root production, annual root turnover rate, annual average of standing-stock mass of live roots, annual average of standing-stock mass of dead roots, and nutrient concentrations); treatment differences were determined by Fisher's LSD test. Whenever necessary, as determined by Bartlett's F test, data were log-transformed (or arcsine-transformed in the case of soil moisture) before analysis to make variances more homogeneous. Nonparametric tests were used when transformation did not make variances equal. Differences in nutrient concentrations among dead and live roots taken from the same plot were compared using a paired t test. Differences among k values in the decomposition experiment were determined by comparing slopes, and multiple comparisons were made with Tukey-Kramer tests (Sokal and Rohlf 1981). Data were analyzed using SYSTAT (SYSTAT 1992), SAS 6.12 (SAS 1997), or JMP 3.1 (SAS 1995).

RESULTS

The natural fertility gradient

Although similar in climate and vegetation, the soils at the 20 000-yr-old site were consistently wetter than those at the other two sites ($F_{2,69}$ = 126.819, P < 0.0001; Fig. 1). In terms of root characteristics, the sites diverged in rooting profiles, but fine roots were

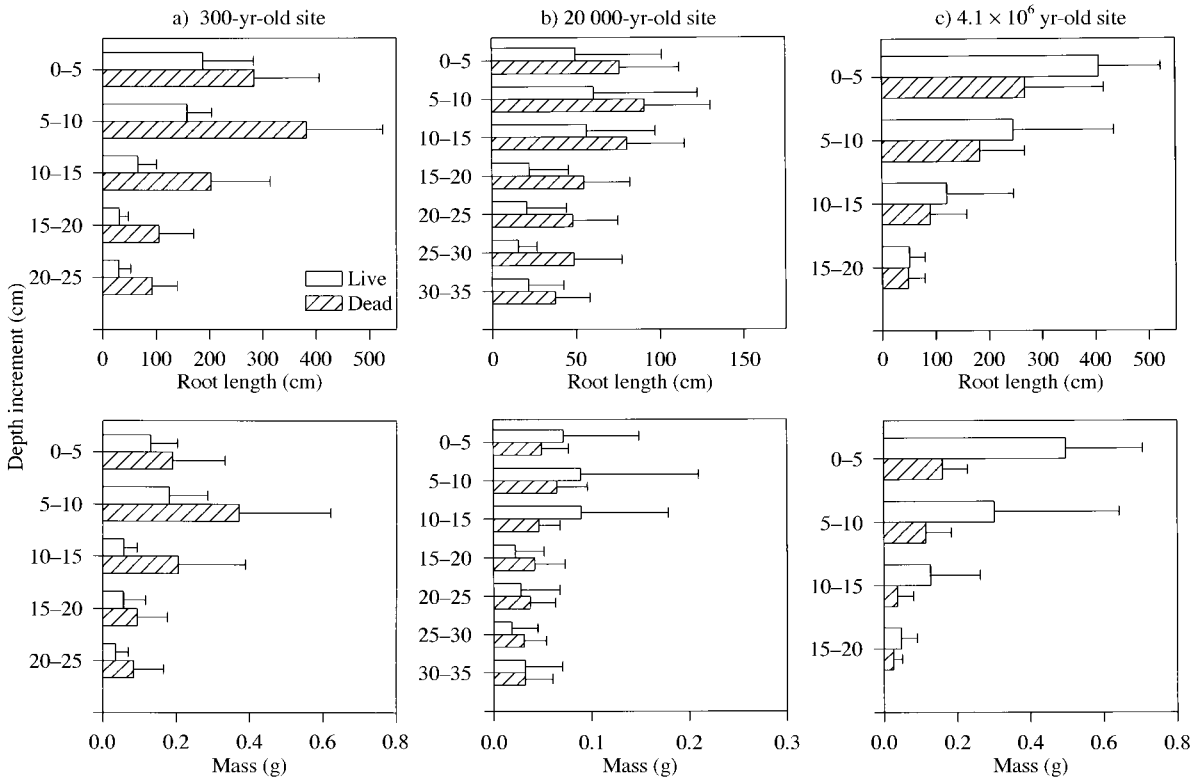

FIG. 2. (a) Length and biomass of fine roots (<2 mm diameter) in the top 25 cm of soil at the 300-yr-old site. Values for all graphs are mean + 1 SD (n = 10 cores). Values are based on a one-time sampling in late 1995 to determine the rooting-depth characteristics at all sites. (b) Length and biomass of fine roots (<2 mm diameter) in the top 35 cm at the 20 000-yr-old site. (c) Length and biomass of fine roots (<2 mm diameter) in the top 20 cm at the 4.1 × 10^6 yr-old site.

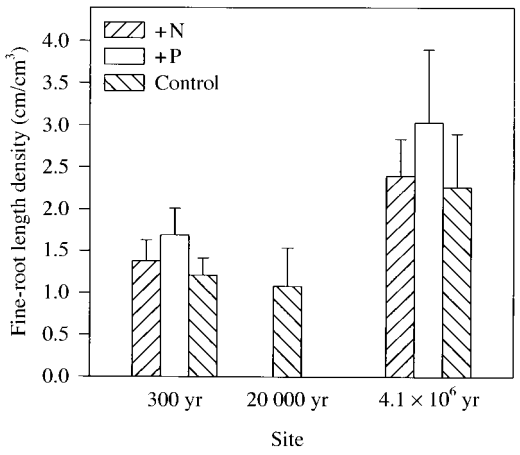

FIG. 3. Mean (+1 SD) root length density in fertilized and unfertilized plots. Each bar represents the average of four replicate plots; plot averages were based on cores taken over the entire 12-mo sampling period (~40 cores).

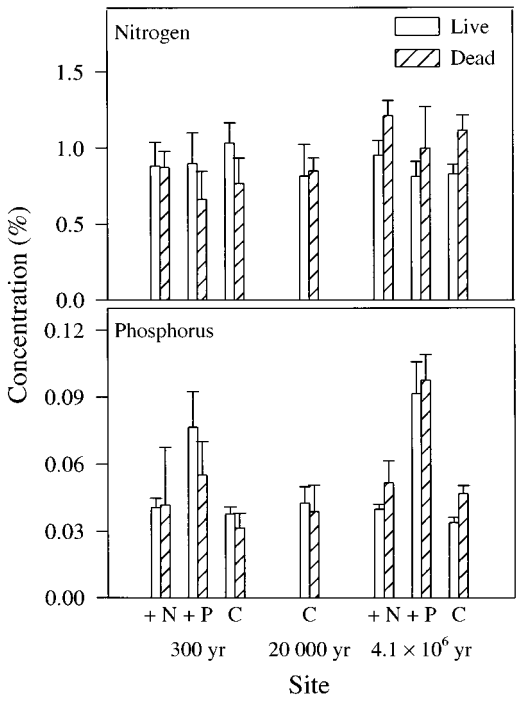

FIG. 4. Nitrogen and phosphorus concentrations of live and dead fine roots under fertilizer treatments (+N or +P) and controls (C). Values represent means + 1 SD (n = 4 plots).

more concentrated in the upper soil layers (Fig. 2) at all three sites. Fine-root length density (centimeters of roots per cubic centimeter of soil) was greatest at the 4.1×10^6 yr-old site, but similar at the 300-yr-old and 20 000-yr-old sites ($F_{2,9} = 7.816$, $P = 0.011$; Fig. 3a). Live roots did not vary in tissue N or P concentration among the three sites and there were no consistent differences between live- and dead-root nutrient concentrations (Fig. 4).

Changes in root mass (Fig. 5a) and length (Fig. 5b) of fine roots were not statistically significant over the course of the annual cycle, underscoring the difficulty of calculating productivity in this system based on seasonal fluctuations in root biomass. In general, live and dead roots mirrored each other, so that dead-root mass or length was low when live mass or length was high. Necromass was often more variable than live mass (Fig. 5a). Although the root mass was not significantly different among months, the 4.1×10^6 yr-old site had wider fluctuations of root mass than the other two sites; this variation may be related to a drought that occurred on this island during the beginning of the study period (R. Harrington, *unpublished data*).

Root parameters that were estimated based on sequential coring demonstrated differences between sites, with the 4.1×10^6 yr-old site usually differing from the other two sites (Table 4). The average standing-stock mass of live fine roots (computed by averaging monthly mean standing stocks over the 12-mo sampling period) was greater at the 4.1×10^6 yr-old site than at the 300-yr-old site, but the 20 000-yr-old site did not differ from the other two sites. The standing-stock mass of dead roots averaged over the 12-mo period did not vary among sites. Belowground net primary productivity (BNPP) of fine roots was lower at the 4.1×10^6 yr-old site than at the other two sites, in part because of lower decomposition rates. The differences in standing stocks of live roots and BNPP caused fine-root turnover rate to be lowest at the 4.1×10^6 yr-old site (Table 4).

Responses to fertilization

At the 300-yr-old site, gravimetric soil moisture did not differ among the fertilization treatments ($F_{2,81} = 0.677$, $P = 0.511$). Root length density tended to be greater in the N- and P-fertilized plots than in control areas, but this effect was not significant ($F_{2,9} = 3.5$, $P = 0.074$; Fig. 3). N concentrations in live roots were similar among fertilization treatments, but P concentrations were significantly greater in the P-fertilized plots ($\chi^2 = 7.9$, $P = 0.019$; Fig. 4). The standing-stock mass of live fine roots was greater in the N-fertilized plots than in control plots, but the P-fertilized plots did not differ from the other two treatments (Table 5). There were no differences among fertilization treatments in the decomposition rates, standing-stock mass of dead roots, BNPP, or root turnover rates (Table 5).

At the 4.1×10^6 yr-old site, soils in the N-fertilized plots were slightly wetter than in the control plots ($F_{2,57} = 3.225$, $P = 0.047$). Root length density did not differ among the fertilization treatments ($F_{2,9} = 1.5$, $P = 0.277$; Fig. 3). N concentrations in live roots were not affected by fertilization treatment; P concentrations were greater in P-fertilized plots ($\chi^2 = 9.6$, $P = 0.008$; Fig. 4). Standing stock of live or dead roots did not differ among the fertilized plots. Decomposition rates were lower in the control plots, and BNPP in the P-

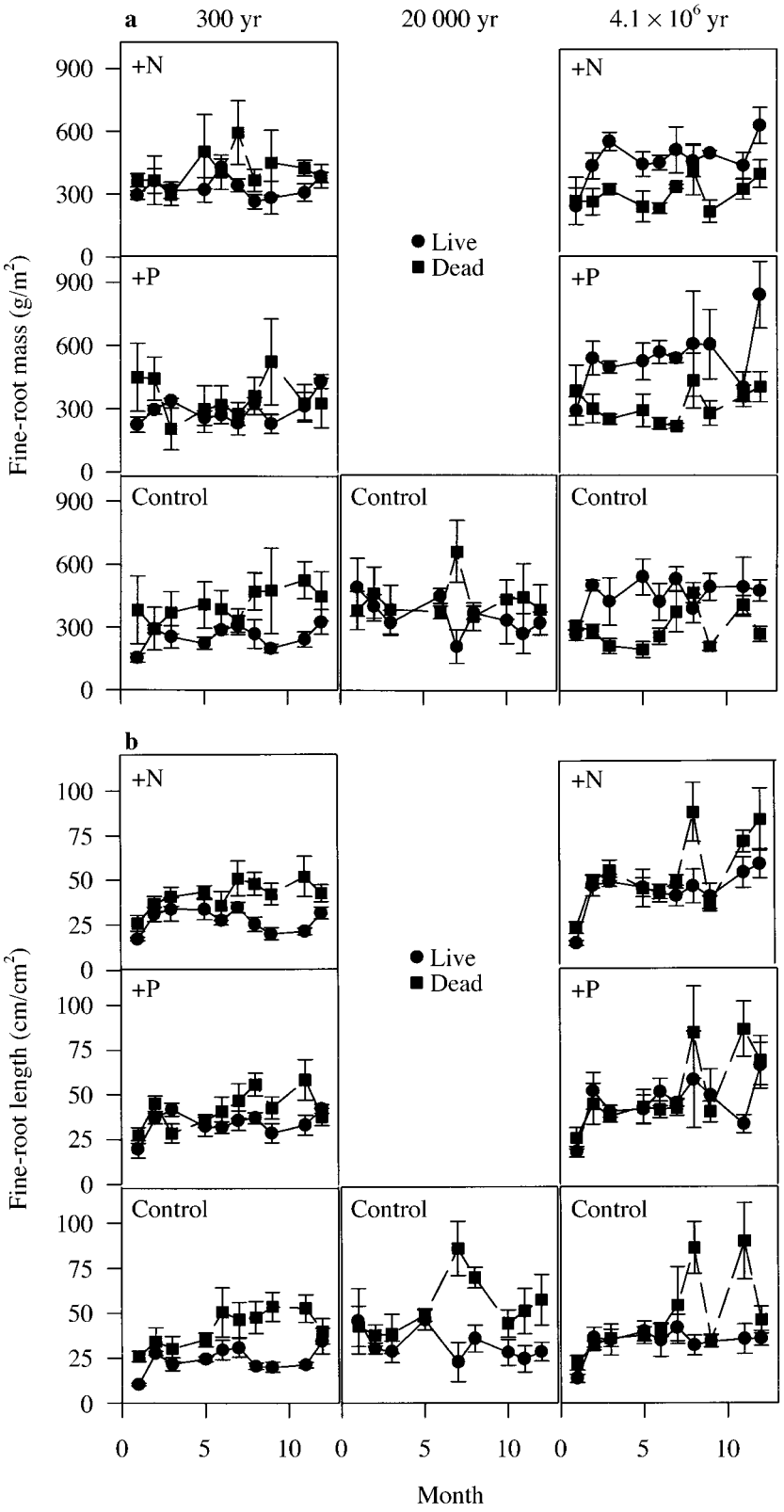

FIG. 5. (a) Monthly mass of fine live and dead roots at the three sites. Sampling began in late October/early November 1995 (month 1) and continued through late September/early October 1996 (month 12). Values are given as standing stock ± 1 SE. Each point represents the average of four replicate plots, and each plot average is based on four subreplicated samples averaged for the plot. (b) Monthly length of fine live and dead roots at the three sites.

TABLE 4. Fine (<2 mm) root dynamics in unfertilized plots (n = 4 plots/site) along the natural fertility gradient.

Site	Standing stock of live roots (g/m^2)	Standing stock of dead roots (g/m^2)	Decomposition rate constant (k) (yr^{-1})	Production rate† (g·m^{-2}·yr^{-1})	Turnover rate† (yr^{-1})
300 yr	257^{a} ± 45	410^{a} ± 175	0.419^{a}	173^{a} ± 83	0.68^{a} ± 0.32
20,000 yr	354^{a,b} ± 119	433^{a} ± 183	0.405^{a,b}	169^{a} ± 72	0.47^{a} ± 0.10
4.1 × 10^6 yr	457^{b} ± 81	302^{a} ± 52	0.261^{b}	75^{b} ± 14	0.16^{b} ± 0.02
df	2, 9	2, 9	2, 12	2, 9	2, 9
F	5.3	0.9	4.6	4.8	9.4
P	0.0297	0.4513	<0.05	0.0384	0.0062

Notes: Values are means ± 1 SD, except for k values, which were determined as the slope of the percentage of mass remaining over time. Different superscript letters within a column indicate statistically significant differences.

† ANOVA on log-transformed data.

fertilized plots tended to be greater (P = 0.0572) than in control plots (Table 5). Because of this increase in BNPP, turnover rates were greatest in P-fertilized plots and lowest in control plots (Table 5).

DISCUSSION

Root characteristics along the natural fertility gradient

Fine-root dynamics differed dramatically between forest ecosystems low in N and ecosystems low in P, even though each system is regarded as ''infertile.'' At these three sites, species composition, climate, and geology were similar, allowing inferences about the effects of soil fertility on root dynamics to be made. Although the 4.1 × 10^6 yr-old site on the island of Kaua'i (low P availability) had lower BNPP and slower root turnover rates than the 20 000-yr-old site, this result was not the case for the 300-yr-old site (low N availability). In most of the belowground processes measured, the 300-yr-old site and the 20 000-yr-old site were similar. The two younger sites had comparable amounts of live and dead standing-stock root mass, root decomposition rates, BNPP, and root turnover rates.

Differences inherent in N and P limitation may be influencing the belowground allocation patterns reported here. In these forests with moderately high root length densities, a new root produced is likely to be competing with other roots for nutrients, but the strength of this competitive interaction is dependent on the ion involved. Nitrate (NO_3) is very mobile in the soil and enters the root through mass flow, which leaves large depletion zones, and its uptake is limited by the surface area of root tissue available for absorption (Nye and Tinker 1977, Cooper 1984). In contrast, phosphate (PO_4) is fairly immobile in the soil and the depletion zones formed are much smaller (Nye and Tinker 1977). PO_4 uptake is also enhanced by the presence of mycorrhizae; its uptake is limited by the rate of diffusion

TABLE 5. Fine (<2 mm) root dynamics at the two infertile sites. Plots (n = 4 plots/site) received N fertilization, P fertilization, or no fertilization (control) at the 300-yr-old and 4.1 × 10^6 yr-old sites.

Treatment	Standing stock of live roots (g/m^2)	Standing stock of dead roots (g/m^2)	Decomposition rate constant (k) (yr^{-1})	Production rate (g·m^{-2}·yr^{-1})	Turnover rate (yr^{-1})
300-yr-old site					
+ Nitrogen	331^{a} ± 34	416^{a} ± 70	0.483^{a}	197^{a} ± 43	0.60^{a} ± 0.13
+ Phosphorus	292^{a,b} ± 20	354^{a} ± 141	0.470^{a}	167^{a} ± 76	0.57^{a} ± 0.24
Control	257^{b} ± 45	410^{a} ± 175	0.419^{a}	173^{a} ± 83	0.68^{a} ± 0.32
df	2, 9	2, 9	2, 12	2, 9	2, 9
F	4.6	0.3	0.27	0.2	0.2
P	0.0429	0.7818	>0.5	0.8113	0.8271
4.1 × 10^6 yr-old site					
+ Nitrogen	467^{a} ± 103	294^{a} ± 47	0.333^{a}	96^{a} ± 15	0.21^{a} ± 0.03
+ Phosphorus	544^{a} ± 147	319^{a} ± 95	0.387^{a}	120^{a} ± 34	0.22^{a} ± 0.02
Control	457^{a} ± 81	302^{a} ± 52	0.261^{b}	75^{a} ± 14	0.16^{b} ± 0.02
df	2, 9	2, 9	2, 12	2, 9	2, 9
F	0.7	0.1	11.8	4.0	6.8
P	0.5210	0.8721	<0.005	0.0572	0.0157

Notes: Values are means ± 1 SD, except for k values, which were determined as the slope of the percentage of mass remaining over time. Different superscript letters within a column indicate statistically significant differences.

to the root or hyphal surface (Nye and Tinker 1977, Cooper 1984, Eissenstat and Yanai 1997).

Although BNPP and root turnover rates were slower when P (rather than N) was the nutrient limiting aboveground growth, other differences among the three sites may contribute to these patterns. For example, differences in root growth among sites may be related to ecotypic differences among conspecific plants. *Metrosideros* is a species with high genetic and morphological variability (Aradhya et al. 1990, Cordell et al. 1998), and trees on the oldest 4.1×10^6 yr-old site on Kaua'i have had a longer time to adapt or acclimate to local conditions than those on the younger sites on the island of Hawai'i. Other site differences that might affect root dynamics include soil texture (Table 3), soil moisture (Fig. 1), root competition for water and nutrients, internal plant demands (i.e., the steepness of the concentration gradient from roots to leaves; Cooper 1984), and mycorrhizal associations. Although the percentage of root length colonized with VA (vesicular-arbuscular) mycorrhizae was low at the 4.1×10^6 yr-old site, mycorrhizal alkaline phosphatase activity was high at this site (Treseder 1998). It has been hypothesized that this enzyme is involved in phosphate transfer from soil to roots by arbuscular mycorrhizal fungi (Tisserant et al. 1993), which suggests that a large fraction of the mycorrhizae that are present at the 4.1×10^6 yr-old site are active in P uptake. If all newly produced roots need to be reinfected, fast turnover rates at the 4.1×10^6 yr-old site may not be advantageous. At present, the mechanisms of infection for VA mycorrhizal species (which comprise ~90% of the endemic Hawaiian flora, including *Metrosideros*; Koske et al. 1992) are poorly understood (Wilcox 1996). However, if the mycorrhizal associations in the 300-yr-old and 4.1×10^6 yr-old ecosystems differ, it may partly explain why P has more of an effect on root growth and turnover rates than does N.

Based on the observed differences in belowground dynamics between the 300-yr-old and 4.1×10^6 yr-old forests, the simple dichotomy between fertile and infertile sites that is often evoked in the literature to explain plant characteristics is probably unjustified. Rather, consideration of whether a site is infertile because of N or P limitation should underlie hypotheses about the patterns of plant productivity and turnover in relation to nutrient availability. Such an approach may help to explain the numerous anomalies in both root (Tables 1 and 2) and leaf studies (e.g., Gower et al. 1993*a*, *b*, Singh et al. 1994). This distinction is important because most of these studies are conducted in temperate zone ecosystems in which N is usually the most limiting nutrient (Hendricks et al. 1993). Furthermore, a variety of other soil and plant variables may co-vary with N and P availability, such that considering all low-nutrient sites together further limits the ability to detect a relationship.

Effects of fertilization on root dynamics

The response of root dynamics to fertilization resembled the patterns along the natural fertility gradient. At the 300-yr-old site, BNPP, root turnover rate, and root tissue N concentrations were not affected by N fertilization, despite its enhancement of tree diameter increments, leaf litterfall rates, and foliar N (Vitousek et al. 1993, Vitousek and Farrington 1997). P fertilization at the 300-yr-old site did increase P concentrations in root tissues, but did not affect any other root variables. In contrast, at the 4.1×10^6 yr-old site, fertilization with P increased root turnover rates and root tissue P, and there was also a trend toward increased BNPP. Therefore, as with the natural fertility gradient, increases in P availability appeared to affect the dynamics of root growth and turnover more strongly than did increases in N availability. N did not appear to enhance root growth at either site, but P did affect root growth and root tissue concentrations.

Although N did not have a large effect on root dynamics in this study, it clearly had effects on root dynamics in other systems, and has been shown to lead to both increases and decreases in the production of new roots after fertilization (Table 2). There may be several reasons for the varied responses. First, long-term effects of fertilization may differ from short-term effects. For example, in a study at the 300-yr-old site conducted 1.5 yr after fertilization, N fertilization was found to decrease standing stocks of live fine-root ($<$ 2 mm) mass (Gower and Vitousek 1989), whereas this study found a small increase. Second, many of these studies examine species' responses to patches of N rather than a community-level response to long-term changes in bulk soil nutrient concentrations. Root responses to nutrient patches are probably not equivalent to root responses to fertilization across entire root systems occupying large soil volumes, although these responses can be useful assays of nutrient limitation (e.g., Raich et al. 1994, Riley and Vitousek 1995). Finally, it may not have been possible to enhance nutrient availability to identical levels on both of these study sites. The 300-yr-old site has been fertilized for a longer amount of time and, therefore, plants at this site may be experiencing lower levels of N limitation than they were during the first several years of fertilization. In addition, soil processes that commonly occur on older tropical soils, such as P fixation (Brady 1990), may maintain P limitation for a longer amount of time than N limitation can be maintained.

Conclusions

Understanding how nutrient availability affects root dynamics is complicated by several factors including (1) methodological differences among studies; (2) comparisons among sites of contrasting fertility that also differ in species composition and other ecosystem properties; (3) correlations of tissue life-span with

many other life-history traits (Chabot and Hicks 1982, Reich et al. 1991, 1992); and (4) disregard for the differences between N and P limitations. Because of these limitations, it is difficult to compare these values across studies. There is also a great deal of error associated with BNPP estimates, regardless of the method used to calculate them. Thus, in this paper, I avoid comparing the BNPP values presented here to other temperate or tropical forests. Instead, I rely on the methodological strength of this study, i.e., relatively constant species composition and climate over a gradient of N and P availability, to make comparisons across sites and fertilization treatments.

Other studies along natural fertility gradients have been conducted in ecosystems in which in was not possible to keep species composition constant; therefore, it has been difficult to evaluate whether patterns in fine-root production and turnover rates may be related more to the characteristics of species that tend to inhabit these ecosystems or to the direct effects of nutrient availability. This study suggests that root dynamics indeed may be related to nutrient availability, but they depend on the nutrient. Nonetheless, in most natural fertility gradients, species change does occur, and relating all patterns of root dynamics to nutrient availability is probably erroneous. For example, within a species, it appears that many of these plant characteristics may be linked; in three grass species in Switzerland, rates of leaf and root turnover were positively correlated (Schläpfer and Ryser 1996). Among these grasses, the species characteristic of more nutrient-rich meadows had faster relative growth rates and faster leaf and root turnover rates than did species characteristic of nutrient-poor meadows. When a species was transplanted into a habitat of different fertility, there was little change in root and leaf turnover rates (Schläpfer and Ryser 1996). Furthermore, tissue turnover rates of roots and leaves were negatively correlated with species-specific traits such as tissue density (Ryser and Lambers 1995, Ryser 1996). Both of these results suggest that rates of tissue turnover may be strongly influenced by a species' life history and not solely by exogenous nutrient supply. Perhaps much of the confusing results in the literature may be ameliorated by considering separately how life history and exogenous nutrient supply can affect plant traits.

Finally, if we assume that, in this study, the ecotypic differences among sites are smaller than species differences, it appears that, both along a natural fertility gradient and in response to fertilization, N availability had a smaller effect on root dynamics (productivity and turnover) than did P availability. Roots therefore do not necessarily behave like leaves in relation to nutrient availability. Leaves tend to respond to increases in nutrient availability by increasing turnover rates (Chapin 1980), but in this study, this response occurred for roots only with P fertilization. Therefore, the processes of root growth and turnover cannot be predicted based only on leaf dynamics. Consideration of whether a site was infertile because of N or P limitation therefore had a strong impact on root dynamics in these Hawaiian montane forests.

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