

## MULTI-SCALE VARIATION IN FINE-ROOT BIOMASS IN A TROPICAL RAIN FOREST: A SEVEN-YEAR STUDY

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**Abstract.** Understanding the dependency of ecosystem processes on spatial and temporal scales is crucial in current efforts to model ecosystem responses to global change. Here we present a case of nonlinear interactions between temporal and spatial scales in a high spatial- and temporal-resolution study of fine-root biomass responses to edaphic and climatic variation in a lowland tropical rain forest (La Selva, Costa Rica). The spatiotemporal variation in fine roots in this forest was considerably greater than that for aboveground live biomass and litterfall. Standing stocks of both live and dead fine roots varied strongly during a seven-year period (up to 10-fold) and across two edaphic gradients with different soil nutrient and water variation (up to four-fold). Fine-root biomass decreased with soil fertility and volumetric soil water content, but responses across a landscape gradient (decreasing with total soil P and K and increasing with N:P ratio between two Oxisols with different weathering) differed from those across a topographic gradient in older Oxisols (increasing with total Fe and Al and decreasing with Ca, Mg, and C:N ratio down the slopes). The spatial contrasts across the landscape gradient (but not in the topographic gradient) changed substantially through time, and they, in fact, disappeared entirely by the middle of the study interval. Short-term monitoring of belowground standing biomass could thus lead to important biases when quantifying root responses. The positive time  $\times$  gradient interaction in fine-root biomass across soil types (but not downslope) also indicates nonlinear changes in spatial patterns across temporal scales, so studies on temporal responses also need to be spatially explicit at narrow scales. This interaction also appears to be more complex than previously recognized: semester-averaged fine-root biomass was negatively correlated with soil water content in the preceding semester, but the relationship was restricted to residual Oxisols. To increase the accuracy of global carbon cycle models in the future, a critical complement to observations of ecosystem processes at regional and global scales will be quantifying these processes through multiple years and across the substantial edaphic gradients that typically exist within landscapes.

**Key words:** *aboveground biomass; Costa Rica, La Selva Biological Station; ecological scale; ecological stoichiometry; nitrogen; nutrient ratios; phosphorus; soil fertility gradients; soil moisture; soil nutrients.*

### INTRODUCTION

The strong scale dependency of ecosystem processes is an aspect of ecological science that needs to be investigated more intensively (*sensu* Peterson and Parker 1998). Efforts to model global-change effects on ecosystem productivity will require an understanding of scale dependency. Addressing this need will be challenging for tropical rain forests, where the spatial and temporal resolution and scope of ecosystem studies has been limited (Clark 2004a). Although this biome is estimated to contribute substantially to terrestrial net primary productivity (NPP) on a global scale (~33%;

Field et al. 1998), little is known about how tropical forest productivity changes across landscapes and through time. Productivity estimates that do not factor in spatiotemporal variation can be highly inaccurate. This is particularly true in those cases where belowground production is known to be affected by local edaphic variation. Because nutrient limitation acts directly on fine-root demography (Eissenstat and Yanai 1997), changes in fine-root biomass may track changes in nutrient availability at higher fidelity than aboveground responses.

A better knowledge of the spatiotemporal patterns of belowground responses is needed to project the responses of forest carbon (C) cycling to global change. Several lines of evidence suggest that most of the extra C fixed under elevated [CO<sub>2</sub>] may flow belowground (Norby et al. 2004), and that a large proportion may be used in fine-root biomass production (Hamilton et al. 2002). Nonetheless, belowground processes still are less studied

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than aboveground C cycling, and the resolution of the available data on fine-root dynamics is low (Norby and Jackson 2000). A recent global inventory of fine-root productivity data (Gill and Jackson 2000) included only 5 short-term studies on tropical rain forest sites (only two of those in wet forests), compared to >25 studies in temperate broadleaf forests.

Globally, fine roots have been estimated to account for about 33% of NPP (Jackson et al. 1997) and ~50% of NPP in forest ecosystems (Vogt et al. 1996), although they are estimated to be <3% of terrestrial biomass (Jackson et al. 1997). Allocation to fine roots represents a large C cost to the plant as well as an important C source to the soil. The size of belowground C stocks is relevant for global C budgets, especially in habitats with greater C allocation belowground, such as grasslands, some tropical forests (Vogt et al. 1986), and habitats with limited soil resources (Caldwell and Richards 1986). Modeling responses of terrestrial ecosystems to global change could thus benefit greatly from a better characterization of fine-root stocks and dynamics (Norby and Jackson 2000, Woodward and Osborne 2000).

Efforts in last few decades have concentrated on assessing responses of fine-root allocation to soil fertility variation (Nadelhoffer 2000). Applying the concept of functional balance (*sensu* Thornley 1976) to belowground foraging in forest ecosystems (Santantonio 1990, Eissenstat and Yanai 1997) suggests that relative allocation belowground should increase in low-resource environments. Existing evidence from sequential harvest of fine-root biomass indicates lower standing biomass under high N availability (Keyes and Grier 1981, Alexander and Fairley 1983, Vogt et al. 1983, Nadelhoffer et al. 1985, Nadelhoffer 2000). Nonetheless, confirming this response in diverse ecosystems and across natural fertility gradients has been a difficult task. Besides technical limitations in the estimation of belowground allocation (Gill and Jackson 2000), there are problems in data interpretation. These have produced discrepancies in reported patterns of standing fine-root biomass and have complicated comparisons across diverse ecosystems (Burton et al. 2000, Norby and Jackson 2000). Because plants differ in belowground strategies for resource acquisition, total belowground C allocation may vary independently of nutrient availability even if relative allocation to fine-root biomass decreases at high resources (Zak and Pregitzer 1998). The limited data from tropical forests indicate increasing aboveground biomass (Laurance et al. 1999) and decreasing fine-root biomass with greater nutrient availability (Gower 1987, Cavelier 1992, Ostertag 1998, 2001, Maycock and Congdon 2000, Powers et al. 2005), suggesting far greater effects of fertility on allocation patterns. Because none of the root studies quantified aboveground biomass, however, it has not been possible to determine the relation of these changes in fine-root biomass to patterns of overall biomass allocation.

In addition, dichotomizing fertile and infertile soil conditions is overly simplistic (Ostertag 2001). The multifactorial nature of soil fertility in field settings complicates assessments of the relation between belowground C allocation and particular nutrients. Most studies have focused on responses to N availability (considered a limiting soil nutrient in many terrestrial ecosystems), but less is known about allocation responses to other nutrients that may be more limiting (such as phosphorus), especially in tropical forests (Vitousek 1984, 2004), but also some temperate rain forests that also undergo rapid soil development (Richardson et al. 2004). Most reviews of belowground allocation data have derived relations based on disparate field data from very different regions and ecosystems. The predominant paradigm is that fine-root biomass increases with decreasing soil fertility, both within (Gower 1987) and among forests (Maycock and Congdon 2000, Powers et al. 2005). There has been no in-depth study, however, of the relation of belowground allocation across multidimensional gradients within a single ecosystem type. By comparing fine-root responses across differing nutrient gradients within the same landscape, it may be possible to assess how consistent are the effects of single nutrients.

Finally, fine-root responses to fertility at any site are likely to be affected by climatic variation. Model predictions suggest that the degree of nutrient limitation can shift with climatic fluctuations (Vitousek and Field 2001). Interactions between spatial and temporal variation can mask patterns of belowground allocation in response to nutrients. Therefore temporal variation at different scales needs to be factored into studies of spatial variation. Although some degree of temporal variation in fine roots has been documented in short-term studies in tropical rain forests (Cavelier et al. 1999, Silver et al. 2005), few studies have quantified root biomass over a prolonged period in order to assess interannual variation. Further, most tropical fine-root studies are from seasonal forests (*cf.* Kummerow et al. 1990); information from wet tropical forests is scarce.

We present here findings from a long-term study in a tropical rain forest (La Selva Biological Station, in northeastern Costa Rica) where standing stocks of fine roots were quantified across strong multidimensional nutrient gradients through the seven-year period from 1997 through 2004, as part of an ongoing study of forest carbon cycling (the "CARBONO" Project). Within the old-growth forest landscape at La Selva, the large edaphic variation in soil elements (approximately two- to threefold range in total soil stocks of phosphorus (P), potassium (K), calcium (Ca), manganese (Mn), iron (Fe), and aluminum (Al)) allows us to assess responses of fine-root biomass to a large portion of the range of soil element conditions spanned by lowland tropical forests (Vitousek 1984, Raich et al. 1996, Chadwick et al. 1999, Vitousek 2004). CARBONO Project measurements of aboveground biomass across La Selva's major

edaphic gradients (Clark and Clark 2000; D. B. Clark, *unpublished data*) also enable us to quantify relative biomass allocation to fine roots.

Although the forest at La Selva has limited seasonality (temperature, precipitation), tree growth has shown strong interannual variation associated with inter-year differences in annual temperatures (Clark et al. 2003). Changes in soil moisture have also been related to substantial forest belowground responses, such as soil respiration (Schwendenmann and Veldkamp 2006). The landscape at La Selva also presents a multidimensional fertility gradient: soil nutrient levels and water content strongly vary across edaphic gradients in flat terrain (younger vs. older Oxisols) and they also vary across a topographic position (slope crest, mid slope, and slope base) in the older Oxisols. This allows investigating responses to variation in soil nutrient and water content at multiple spatial scales. Finally, at La Selva, landscape-wide variation in soil P and cations is greater than that of soil N (three- to 19-fold vs. two-fold, respectively; D. B. Clark, E. Veldkamp, and J. Mackensen, *unpublished data*), enabling us to test responses to nutrients that are now thought to be more often limiting in tropical forests (Vitousek 1984, Raich et al. 1996, Chadwick et al. 1999, McGroddy et al. 2004, Vitousek 2004).

In this study we use La Selva's multidimensional fertility gradients and extensive long-term data to: (1) determine the relationship between edaphic variation and fine-root stocks at different spatial scales; (2) investigate in particular the relation of fine-root biomass to the variation in soil P across a complex landscape; (3) test for an interaction between the temporal and spatial scales of variation in fine-root stocks; and (4) elucidate the association of environmental variables and temporal variation across space, in particular the role of soil water as a factor affecting soil mineral–fine-root relationships. We hypothesize that: (1) lower soil fertility is associated with greater fine-root biomass at all spatial scales; (2) fine-root biomass is strongly negatively related to soil P stocks; (3) temporal patterns differ across the spatial (edaphic) variation; and (4) soil water content, an additional environmental factor that varies across La Selva's edaphic gradients, can explain this divergence.

## METHODS

### *Study site*

The study site was old-growth forest at the La Selva Biological Station (Organization for Tropical Studies, OTS) in the Atlantic lowlands of Costa Rica. The forest is classified as Tropical Wet Forest in the Holdridge Life-Zone system (Hartshorn and Hammel 1994). Mean annual rainfall is ~4000 mm and mean annual temperature is 26°C (Sanford et al. 1994). La Selva is on the footslopes of Barva Volcano, the source of basaltic lava flows (one aged at  $\sim 1.2 \times 10^6$  yr, Alvarado 1990) that dominate the landscape. Soils on these lava flows (locally termed Residual soils) are deeply weath-

ered clays (augering showed that on stable geomorphological units, saprolite occurs at a depth of 5–6 m) with low pH (4.0 in the top 0.1 m, increasing slightly to 4.5 at a depth of 1–2 m), low effective cation exchange capacity (ECEC: 9.5  $\text{cmol}_c/\text{kg}$  in the top 0.1 m, decreasing to 2.5  $\text{cmol}_c/\text{kg}$  at a depth of 1–2 m), low base saturation (16% in the top 0.1 m, decreasing to 9% at a depth of 1–2 m), low base exchange capacity ( $< 16 \text{ cmol}_c/\text{kg}$  clay), low silica:sesquioxide ratio, low activity of clays, and low content of weatherable mineral (Veldkamp et al. 2003). Although previously described as Ultisols (Sollins et al. 1994), these soils were more recently classified as Oxisols (Typic Haploperox) based on multiple characteristics (Kleber et al. 2007). Close to the major rivers are Old Alluvial terraces, Pleistocene river terraces previously classified as Inceptisols (Sollins et al. 1994) but now considered to be Typic Haploperox similar to the Residual soils but considerably younger (Kleber et al. 2007). These depositional soils are deeply weathered clay soils, typically with strongly weathered coarse material at a depth of 3 m, with low ECEC (7.7  $\text{cmol}_c/\text{kg}$  in the top 0.1 m, decreasing to 4.2  $\text{cmol}_c/\text{kg}$  at a depth of 1–2 m), and with low base saturation (17% in the top 0.1 m, decreasing to 8% at a depth of 1–2 m; Veldkamp et al. 2003). Recent soil mineralogical analyses (Kleber et al. 2007) showed that both the Residual and Old Alluvial soils contain large amounts of the clay minerals kaolinite, halloysite, and gibbsite and some goethite and magnetite but lack 2:1 phyllosilicates. Hematites were only detected in the Residual soils. The forest at La Selva is dominated by a tree legume, *Pentaclethra macroloba*, comprising about one third of the forest biomass, similarly distributed across both edaphic gradients (Clark and Clark 2000). The rest of the tree species ( $> 250$ ) are found in substantially lower densities. Palm species, representing a total of one fourth of the stems (and  $\sim 5$ –10% of the biomass; Clark and Clark 2000) are dominated by three species: *Welfia regia*, *Socratea exorrhiza*, and *Iriartea deltoidea* (Clark et al. 1999).

We monitored fine-root stocks in the CARBONO plots, a network of eighteen 0.5-ha plots (each  $50 \times 100$  m) that were sited across the main edaphic gradients in the La Selva old growth to enable landscape-scale assessment of C stocks and fluxes (see Appendix A). The plots were sited in a replicated, nonbiased design using the La Selva GIS topographic coverage and the soil coverage from Clark et al. (1998). Six plots were located within each of the three dominant edaphic conditions: Old Alluvial terraces (A plots), Residual Soil plateaus (L plots), and Residual Soil slopes (P plots). Soil units were blocked to produce approximately equal sample intensity within each unit. Two scales of edaphic contrast could be made with this plot network: (1) the landscape-wide fertility gradient (Old Alluvial terraces vs. Residual Soil plateaus); and (2) the topographic gradient of local catenas (slope crest, mid slope, and slope base within the Residual Soil slope plots).

### *Soil elements*

The soils of the CARBONO plots were sampled and characterized chemically in 1998 (total C, N, P, cations, Fe, Mn, Al, pH) by E. Veldkamp, J. Mackensen, and D. B. Clark, *unpublished data*. Soil analyses are described in Appendix B. Bulk samples from six cores per depth (0–10 cm, 10–30 cm, 30–50 cm, 50–100 cm), regularly spaced across each plot, were taken in each Old Alluvial terrace and Residual Soil plateau plot; bulked samples from six cores per depth, regularly spaced across each of the three slope positions, were taken from each Residual Soil slope plot. We calculated soil element stocks for each depth by multiplying element concentrations by soil bulk density. Bulk density was determined (Veldkamp et al. 2003) for the two soil types as mean values from each depth in pits adjacent to three plots on each soil (Old Alluvial terrace and Residual Soil plateau; for the Residual Soil slope plots we used Residual Soil plateau bulk density values).

### *Soil moisture and climate*

In situ soil moisture data correspond to a simultaneous study undertaken in the same CARBONO plots (Schwendenmann 2002, Schwendenmann et al. 2003, Schwendenmann and Veldkamp 2006) where soil moisture data were collected every two weeks with permanently installed frequency domain reflectometry (FDR) sensors (Model CS615, Campbell Scientific, Logan, Utah, USA) in soil pits across the landscape gradient (one soil pit per each of three plots per soil type). The sensors were installed horizontally at depths of 5, 20, and 40 cm. Readings were calibrated by the Three-Phase Mixing Model developed by Veldkamp and O'Brien (2000) for La Selva soils. We used porosity coefficient values of 0.696 for Old Alluvial terrace plots and 0.717 for Residual Soil plateau and slope plots, respectively. A soil depth-integrated moisture value was calculated for the 0–50 cm interval by averaging single depth readings at 5 cm (0–10 cm interval), 20 cm (10–30 cm interval), and 40 cm (30–50 cm interval). Data of monthly precipitation, and daily maximum, mean, and minimum air temperatures were collected from the La Selva weather station (OTS, *unpublished data*).

### *Root sampling*

Fine roots were sampled an average of 3–4 times per year ( $N = 25$  sample dates; Appendix C) during the period from October 1997 to April 2004. At each date, a 0–50 cm deep soil core was taken with an AMS Percussion Soil Core Sampler (inner diameter 47.4 mm; AMS, American Falls, Idaho, USA) at six regularly spaced sample points within each CARBONO plot. Cores were taken at a predetermined distance and compass bearing from each of six pre-selected plot grid posts. If a sample point coincided with a tree, a large coarse root, or coarse woody debris, it was shifted the minimum distance needed to avoid the obstruction. In

each of the six Residual Soil slope plots, this sampling design provided two cores from each of three topographic levels (slope crest, mid slope, slope base). On 14 sample dates (Appendix C) in three Old Alluvial terrace plots (A1, A4, A6) and in three Residual Soil plateau plots (L1, L4, L6), at 10 cm from the site of each of the 0–50 cm depth cores, we collected an additional core divided by depth layer (0–20 cm, 20–50 cm). Fine-root vertical distribution was further explored with a single sampling of the top 1 m of soil by 10 cm depth layers (six cores per plot, one Old Alluvial terrace plot, A4, and one Residual Soil plateau plot, L4). All cores were stored in the refrigerator (4–5°C) for a period ranging from two weeks to three months (maximum of six months) before root processing.

### *Root sample processing*

*Root extraction.*—Roots were extracted from soil cores using a device designed for La Selva's high clay, wet soils. Variable-speed electric drills in a fixed frame were fitted with paint-stirring attachments extending down into two-gallon (~7.6 L) pails. One soil core was placed in each pail and water was added to fill the pail two thirds full. The drill speed was set to create a vortex down nearly to the bottom of the pail, but with no spillage, and the sample was stirred for 20 min. No dispersant was added to the slurry and cores were not pre-soaked. After stirring, the pail contents were poured through a U.S. Standard Series No. 45 sieve (0.355-mm mesh). Roots were removed with fine forceps from the material in the sieve, were washed to remove any soil, and were maintained moist through sorting.

*Root sorting and weighing.*—Roots were divided into two diameter classes (<2 mm, and 2 to <5 mm; larger roots were discarded) using a dial calipers and were further divided into live and dead. Roots were considered dead if brown or black to the center and crumbling or lacking flexibility; they were considered live if they maintained structure and flexibility and had a white fibrous center (some palm roots are dark). The sorted roots were dried at 65°C and repeatedly weighed until they reached stable mass ( $\pm 0.001$  g).

### *Biomass allocation to fine roots*

We determined relative fine-root biomass allocation per year for each CARBONO plot by dividing the total estimated aboveground biomass by the mean of live fine-root biomass during that period. Annual measurement years of CARBONO plots extend from 1 October to 30 September. Mean annual estimated aboveground live biomass, based on diameters of all live trees >10 cm diameter (D. B. Clark and D. A. Clark, *unpublished data*), was calculated as the average of the estimated aboveground live biomass at the beginning and at the end of each measurement year. Mean annual live fine-root (0 to <5 mm diameter; 0–50 cm depth) biomass for each plot was calculated by averaging data from all sampling dates in that measurement year.

### Data analysis

Our data are from two edaphic gradients: the across-landscape gradient, using the 12 CARBONO plots on relatively flat terrain (six Old Alluvial terrace, six Residual Soil plateau); and the topographic gradient (three slope positions within each of the six Residual Soil slope plots). Fine-root biomass was calculated as the mean of six replicate soil cores per plot (landscape-wide gradient) and as the mean of two soil cores per slope position within each of the six Residual Soil slope plots. All analyses were performed with JMP Data Analysis Software (Version 4.0.4, SAS 2000).

*Root methods assessment.*—To test the consistency of root sampling, sorting, and weighing procedures, we used linear regression to compare fine-root biomass between the standard cores (0–50 cm depth) and simultaneous split-depth (0–20 and 20–50 cm) cores (fine-root biomass summed across these two subcores). For this comparison we used six plots (three Residual Soil plateau plots, three Old Alluvial terrace plots) and 14 sampling dates (Appendix C).

*Soil element stocks.*—Differences across the landscape and topographic gradients and by soil depth were tested with two-way ANOVA. Variables were transformed (square root, logarithmic, and Box-Cox transformations) as necessary to meet ANOVA assumptions of normal distribution of residuals (Kolmogorov-Smirnov-Lillifor test) and variance equality (Bartlett's test; Sall and Lehman 1996).

*Fine-root biomass.*—Using different data sets, we used independent ANOVA tests to detect effects of soil type (Old Alluvial terrace plots, Residual Soil plateau plots), slope position (crest, mid slope, or base within the Residual Soil slope plots), and soil depth (0–20 cm, 20–50 cm) on fine-root biomass (means from all sampling dates: two diameter classes, live or dead). The simultaneous effects of space (edaphic gradients) and time (year, semester) on fine-root biomass (all live or dead and diameter classes) were analyzed by a repeated-measures split-plot ANOVA (univariate ANOVA; von Ende 1993), using the annual and semester-based averages of fine-root biomass as time variables. Multivariate repeated-measures analyses (MANOVA; von Ende 1993, Espeleta and Donovan 2002) were not appropriate for this data set because of the numerous sampling dates. The sphericity condition was met for the univariate tests (using the Mauchly criterion, Sall and Lehman 1996). To better understand temporal patterns, we grouped data by year and semester (January–June, July–December), treated these as within-subject effects in the ANOVA, and also evaluated the interaction terms. Annual averages corresponded to the mean of all sampling dates within the period from 1 August to 31 December; semester averages corresponded to the period from 1 August to 31 December (Semester 1) and from 1 January to 31 July (Semester 2).

*Fine-root biomass allocation per year.*—A repeated-measures split-plot ANOVA tested the effects of space

(only the landscape gradient) and time (only year effects) on the total estimated aboveground live biomass and the relative fine-root biomass allocation per year (annual interval extended from 1 October to 30 September).

*Relationships of soil elements and root stocks.*—We used pairwise Pearson correlation and linear regression to relate soil element stocks and fine-root biomass (mean of 25 sampling dates, October 1997–April 2004; four root classes). When necessary, data were transformed to meet assumptions of normal distribution of residuals and variance equality.

*Relationships of environmental factors and root stocks.*—We used pairwise Pearson correlation and linear regression to relate air temperatures (daily mean, maximum, and minimum), rainfall and soil moisture (percentage soil water content at 5, 20, 40, and 0–50 cm, measured with the FDR soil moisture sensors), and fine-root biomass. Input data were calculated as semester averages (fine-root biomass, temperatures, and soil moisture) and sums (rainfall) for either simultaneous semesters or one semester lag period in fine-root biomass (semesters extended from 1 August to 31 December and from 1 January to 31 July). When necessary, data were transformed to meet assumptions of normal distribution of residuals and variance equality.

*Power analysis.*—We used power analysis to estimate the relationship between sample size and statistical power to detect a significant trend across the temporal variation in live fine-root (<2 mm diameter) biomass. We used the power analysis function in the JMP ANOVA test, which computed the following parameters: alpha (significance level = 0.05), delta (raw effect size), and sigma (standard error of the residual error in the model). We produced curves of sample size vs. statistical power and interpolated sample size values. We judged an optimal sample size should yield power  $\geq 0.90$ .

## RESULTS

### Edaphic variation in fine-root biomass

In this tropical rain forest landscape, fine-root biomass exhibited strong spatial variation at the two scales studied: (1) across soil types (landscape-wide gradient: Residual Soil plateau plots, Old Alluvial terrace plots); and (2) down the catenas (topographic gradient in Residual Soil slope plots). These contrasting gradients showed marked variation in different sets of soil elements and in soil water content. The changes in fine-root biomass were highly associated with spatial variation of particular elements, in a way specific to each gradient. Fine-root biomass in Residual Soils was also associated with intra-annual variation in soil water content.

*Landscape-wide variation in fine roots.*—The seven-year mean biomass of live fine roots at a depth of 0–50 cm was 48% (<2 mm diameter) to 42% (2 to <5 mm diameter) greater in the Residual Soil plateau plots than in the (more fertile) Old Alluvial terrace plots (Table 1). In strong contrast, however, long-term mean stocks of

TABLE 1. Mean (SE) fine-root biomass (Mg/ha; 0–50 cm depth) for four fine-root classes and the necromass proportion (dead : live ratio) across landscape-wide gradients in the old-growth forest at La Selva Biological Station, Costa Rica.

Soil depth, root class	Biomass of fine roots <2 mm diameter (Mg/ha)					Biomass of fine roots 2 to <5 mm (Mg/ha)				
	Old Alluvial terrace soil	Residual soil	<i>F</i>	df	<i>P</i>	Old Alluvial terrace soils	Residual soil	<i>F</i>	df	<i>P</i>
Landscape gradient										
Soil 0–20 cm										
Live roots	0.74 (0.06)	1.20 (0.12)	11.0458	1, 4	0.0293	0.51 (0.03)	0.80 (0.07)	15.6731	1, 4	0.0167
Dead roots	0.11 (0.01)	0.15 (0.02)	2.9801	1, 4	0.1594	0.08 (0.01)	0.12 (0.01)	6.4803	1, 4	0.0636
Dead : live	0.14 (0.01)	0.13 (0.01)	1.6517	1, 4	0.2681	0.15 (0.02)	0.15 (0.02)	0.0031	1, 4	0.9581
Soil 20–50 cm										
Live roots	0.31 (0.02)	0.37 (0.01)	7.3695	1, 4	0.0533	0.27 (0.04)	0.31 (0.10)	0.1350	1, 4	0.7319
Dead roots	0.06 (0.01)	0.06 (0.01)	0.0682	1, 4	0.8069	0.03 (0.01)	0.04 (0.02)	0.1525	1, 4	0.7161
Dead : live	0.19 (0.03)	0.17 (0.02)	0.0349	1, 4	0.5686	0.14 (0.04)	0.24 (0.19)	0.2964	1, 4	0.6151
Soil 0–50 cm										
Live roots	1.08 (0.13)	1.60 (0.08)	12.8834	1, 10	0.0049	0.76 (0.07)	1.08 (0.04)	14.3218	1, 10	0.0036
Dead roots	0.17 (0.01)	0.20 (0.02)	4.3086	1, 10	0.0647	0.18 (0.02)	0.20 (0.02)	0.1457	1, 10	0.7107
Dead : live	0.17 (0.02)	0.15 (0.01)	0.8694	1, 10	0.3731	0.14 (0.02)	0.20 (0.09)	0.3541	1, 10	0.5650

Notes: Data are seven-year means (entire cores, 25 sampling dates: split cores, depths 0–20 cm and 20–50 cm, 14 dates) over the period October 1997–April 2004.  $N = 6$  plots per soil type for entire cores, and  $N = 3$  plots per soil type for split cores. Differences were analyzed by one-way ANOVA.

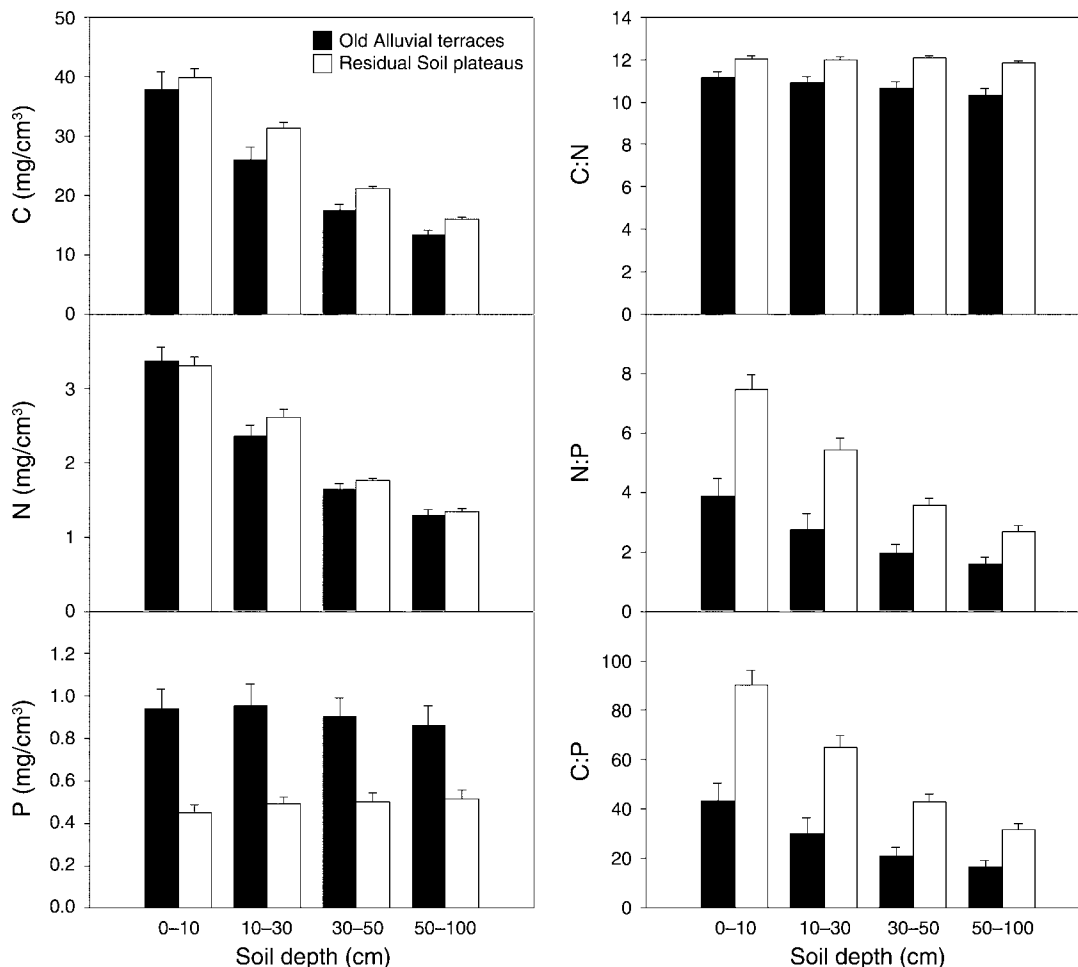


FIG. 1. Contrasting soil element stocks (total stocks) and mass-based nutrient ratios to 1 m depth between the two dominant upland soil types at La Selva Biological Station, Costa Rica (Residual Soil plateaus, open bars; Old Alluvial terraces, solid bars). Data are means (+SE) of six plots per soil type. The effects of soil type and depth on the nutrient stocks were analyzed by two-way ANOVA (see Table 2).

dead fine roots (both size classes) did not differ between the soil types (Table 1). The marked between-soil contrast in live-root biomass matched the strong difference in soil element content between these soil types (Fig. 1, Table 2). The Residual Soil plateaus (0–100 cm depth) had significantly less P, K, Ca, and Mn, greater levels of C and Fe, and higher C:N, C:P, and N:P ratios. The soils did not differ, however, in total N, Mg, or Al.

When evaluated across the landscape-wide gradient (all 12 nonslope plots), the seven-year mean biomass of live <2 mm roots was negatively correlated with total soil P, K and Mn and positively correlated with C, N, C:N, N:P, and Fe (Table 3). The relationship with total soil P was notably the strongest, as seen also in the very strong correlation with soil N:P (Fig. 2a). No relationship was observed with soil Ca, Mg, or Al (Table 3). The live roots 2 to <5 mm diameter showed similar, but somewhat weaker, soil element associations. Long-term mean biomass of dead fine roots showed also less association with soil elements and, contrary to live roots, these relationships varied with root diameter. The

biomass of dead roots <2 mm was negatively correlated with soil P and K and positively correlated with soil C:N and N:P ratios. In contrast, the biomass of the coarser dead roots (2 to <5 mm diameter) was negatively correlated with soil Ca and the Ca:Mg ratio and was unrelated to the other soil characteristics (Table 3).

*Topographic variation in fine roots.*—Within the Residual Soil slope plots, there was a strong downslope gradient in fine-root biomass (Table 4). Long-term (seven years) mean biomass of live fine roots (both diameter classes) was lowest in slope bases, intermediate at mid slope, and highest on the slope crests. In parallel to the landscape-wide variation in soil fertility across flat terrain, soil nutrients varied significantly with slope position (Fig. 3, Table 2). However, this fertility gradient was qualitatively different: while variation in P and K was less than at the landscape scale, it was greater for C, N, Ca, Mg, and Al. As at the landscape scale, the topographic soil gradient involved strong variation in Fe, Mn, and C:N and N:P ratios. Compared to slope crests, slope bases had lower C, N, C:N and N:P, Fe, and Al, and greater soil P, K, Ca, Mg, and Mn

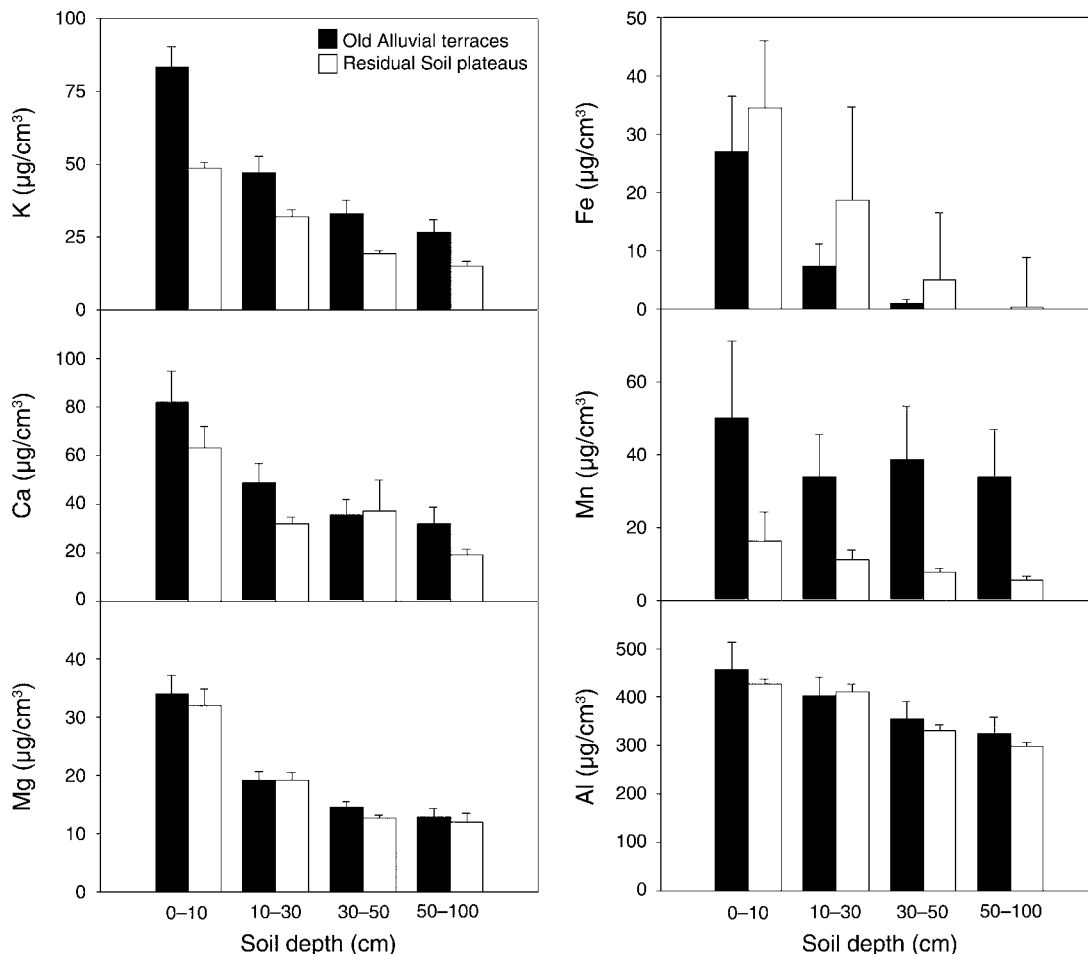


FIG. 1. Continued.

TABLE 2. Depth-specific variation in nutrient stocks and stoichiometry across the two edaphic gradients: landscape-wide and topographic.

Element	Units	Landscape gradient factor						Topographic gradient factor					
		Soil type		Depth		Soil type × depth		Slope position		Depth		Slope position × depth	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
C	mg/cm <sup>3</sup>	18.08	0.0001	73.35	<0.0001	1.49	0.2308	15.46	<0.0001	70.45	<0.0001	0.47	0.8293
N	mg/cm <sup>3</sup>	2.43	0.1268	107.66	<0.0001	0.58	0.6302	10.85	0.0001	80.57	<0.0001	0.56	0.7632
P	mg/cm <sup>3</sup>	79.32	<0.0001	0.10	0.9586	0.55	0.6542	5.08	0.0092	0.89	0.4539	0.03	0.9999
K	μg/cm <sup>3</sup>	40.29	<0.0001	46.83	<0.0001	3.34	0.0286	4.18	0.0200	81.55	<0.0001	0.55	0.7650
Ca	μg/cm <sup>3</sup>	5.15	0.0287	14.19	<0.0001	0.45	0.7209	30.72	<0.0001	27.84	<0.0001	0.24	0.9615
Mg	μg/cm <sup>3</sup>	0.71	0.4041	50.34	<0.0001	0.10	0.9577	12.72	<0.0001	37.31	<0.0001	0.55	0.7685
Fe	μg/cm <sup>3</sup>	14.22	0.0005	30.88	<0.0001	1.52	0.2245	17.80	<0.0001	43.01	<0.0001	1.00	0.4322
Mn	μg/cm <sup>3</sup>	10.43	0.0025	1.05	0.3816	0.16	0.9212	28.18	<0.0001	1.65	0.1885	0.27	0.9506
Al	μg/cm <sup>3</sup>	0.69	0.4104	7.30	0.0005	0.17	0.9186	20.25	<0.0001	11.42	<0.0001	0.42	0.8598
C:N	ratio	56.65	<0.0001	1.85	0.1529	0.98	0.4102	26.38	<0.0001	4.54	0.0062	0.89	0.5102
N:P	ratio	64.05	<0.0001	30.39	<0.0001	4.01	0.0138	8.39	0.0006	20.78	<0.0001	0.26	0.9530
C:P	ratio	73.87	<0.0001	29.11	<0.0001	4.08	0.0128	10.48	0.0001	20.71	<0.0001	0.27	0.9490

Notes: The effects of depth (0–10 cm, 10–30 cm, 30–50 cm, 50–100 cm) and soil type (Old Alluvial terraces, Residual Soil plateaus) or slope position (crest, mid slope, base) on nutrient stocks (Figs. 1 and 3) were analyzed by two-way ANOVAs. For all landscape gradient analyses *df* = 1, 10, and for all topography gradient analyses *df* = 2, 15.

(Fig. 3). Fine-root biomass closely paralleled these fertility changes across slope positions. In contrast to patterns at the landscape scale, however, the associations between elements and root biomass differed between live and dead roots and between root diameter

classes (Table 3). The biomass of live roots <2 mm diameter (Fig. 2b) was significantly negatively correlated with soil Ca, Mg, and Mn, and positively correlated with C, N, C:N, Fe, and Al, but was not associated with levels of soil P and K. For coarser live roots (2 to <5

TABLE 3. Pearson's correlation coefficients (*r*) between soil chemical variables and four fine-root biomass classes at 0–50 cm soil depth for two edaphic gradients across old-growth forest landscape at La Selva, Costa Rica.

Element mass or ratio	Live fine roots				Dead fine roots			
	<2 mm diameter		2 to <5 mm diameter		<2 mm diameter		2 to <5 mm diameter	
	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>	<i>r</i>	<i>P</i>
Landscape gradient								
C	0.762	0.0390	0.716	0.0088	0.441	0.1516	0.339	0.2809
N	0.659	0.0197	0.630	0.0283	0.239	0.4545	0.403	0.1941
P	–0.899	0.0001	–0.848	0.0005	–0.690	0.0129	–0.428	0.1648
K	–0.749	0.0051	–0.647	0.0229	–0.616	0.0330	–0.407	0.1889
Ca	–0.521	0.0822	–0.565	0.0588	–0.224	0.4847	–0.621	0.0313
Mg	0.052	0.8726	–0.046	0.8874	–0.224	0.4840	0.156	0.6289
Fe	0.659	0.0198	0.637	0.0260	0.229	0.4748	0.551	0.0631
Mn	–0.700	0.0113	–0.594	0.0418	–0.447	0.1449	–0.502	0.0967
Al	0.368	0.2396	0.273	0.3903	–0.018	0.9566	0.524	0.0804
C:N ratio	0.749	0.0050	0.683	0.0144	0.619	0.0317	0.214	0.5041
N:P ratio	0.947	0.0000	0.889	0.0001	0.756	0.0044	0.368	0.2390
C:P ratio	0.939	<0.0001	0.880	0.0002	0.760	0.0041	0.332	0.2918
Ca:Mg ratio	–0.557	0.0599	–0.545	0.0670	–0.136	0.6739	–0.750	0.0049
Topography gradient								
C	0.606	0.0077	0.502	0.0339	0.598	0.0087	0.513	0.0293
N	0.535	0.0221	0.409	0.0919	0.562	0.0151	0.441	0.0672
P	–0.400	0.0998	–0.493	0.0377	–0.602	0.0082	–0.208	0.4082
K	–0.233	0.3530	–0.382	0.1178	–0.197	0.4342	–0.366	0.1358
Ca	–0.588	0.0102	–0.491	0.0386	–0.324	0.1903	–0.481	0.0434
Mg	–0.576	0.0124	–0.405	0.0958	–0.287	0.2474	–0.530	0.0236
Fe	0.664	0.0027	0.561	0.0154	0.508	0.0315	0.493	0.0376
Mn	–0.561	0.0155	–0.681	0.0019	–0.496	0.0362	–0.570	0.0136
Al	0.740	0.0004	0.597	0.0089	0.515	0.0287	0.461	0.0542
C:N ratio	0.688	0.0016	0.718	0.0008	0.604	0.0080	0.650	0.0035
N:P ratio	0.472	0.0478	0.422	0.0810	0.570	0.0136	0.232	0.3534
C:P ratio	0.509	0.0311	0.459	0.0552	0.583	0.0111	0.269	0.2803
Ca:Mg ratio	–0.509	0.0311	–0.535	0.0222	–0.395	0.1044	–0.390	0.1098

Notes: *N* = 12 plots (landscape gradient) and 18 plot × slope position combinations (topographic gradient). Measurement units for C, N, and P are Mg/ha; for the rest of the elements units are kg/ha. Values of *P* < 0.05 are considered significant.



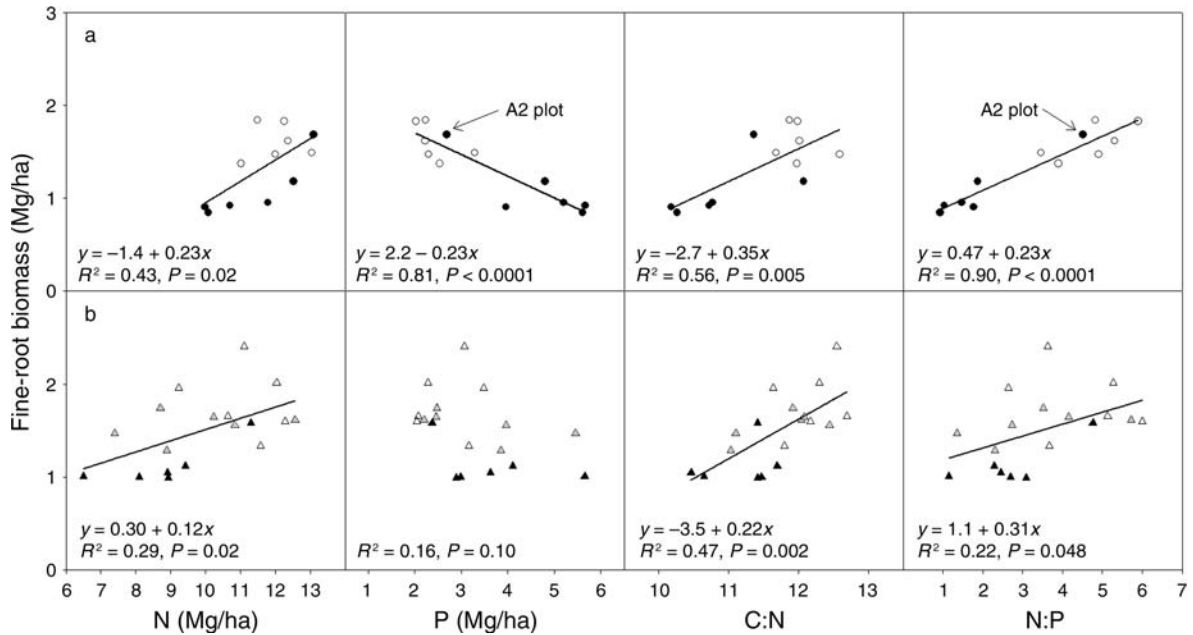


FIG. 2. Relationship between stocks of live fine roots <2 mm diameter and soil chemical characteristics (total N, total P, and ratios of C:N and N:P) at 0–50 cm depth, across contrasting edaphic gradients at La Selva. Data correspond to: (a) a landscape-wide gradient across six Old Alluvial terrace plots (solid circles) and six Residual Soil plateau plots (open circles); and (b) a topographic gradient across three slope positions: slope crest (open triangles), mid slope (gray triangles), and slope base (solid triangles) in the six Residual Soil slope plots. The arrow denotes a plot (A2) in the landscape-wide gradient that shows intermediate soil type characteristics.

mm diameter), mean biomass was negatively correlated with soil P, but the strongest relationship was with C:N ( $r = 0.72, P < 0.008$ ). The biomass of dead <2 mm roots was negatively correlated with total soil P and Mn, and positively correlated with soil C, N, C:N, and N:P, Fe, and Al. Very different patterns were observed with the stocks of larger dead fine roots (2 to <5 mm), which were negatively correlated with soil Ca, Mg, and Mn, and positively correlated only with soil C:N ratio.

*Spatial variation in soil moisture.*—Paralleling the landscape differences in soil element concentrations, soil water content differed between soil types across the study period (Fig. 4). The topsoil (5 and 20 cm depth) water content was lower in Residual Soil plateaus than in Old Alluvial terraces, especially through the first years of the record (Fig. 4a) and during periods of low rainfall (Fig. 4b); these differences disappeared at deeper soil layers (e.g., 40 cm, Fig. 4a).

#### Temporal variation in fine-root biomass

Over the seven-year study period the standing stocks of live and dead fine roots showed notable, complex changes through time (Figs. 5 and 6). Temporal effects were significant across both edaphic gradients and for all fine-root classes (Table 5A, B). There were large multiyear trends as well as substantial shorter term variation in fine-root biomass. The overall temporal change (25 dates) was much larger than the spatial variation seen at any time across the edaphic gradients.

The dynamics in fine-root stocks differed between the soil types and among slope positions, between soil depths, and among fine-root classes.

*Live roots, diameter <2 mm.*—The remarkable temporal variation in these smaller roots is shown by calculating the difference between maximum and minimum standing stocks within sites (Table 6). Over the total seven-year study period, the within-site biomass range averaged 2.5 Mg/ha for the twelve plots of the landscape gradient and 4.5 Mg/ha for the 18 plot  $\times$  slope position combinations of the topographic gradient. These through-time ranges were much larger than the corresponding across-site ranges on each gradient. Within-year (between-semester) variation contributed substantially to the overall temporal variation. Both among- and within-year biomass ranges were greater for the topographic gradient than for the landscape-wide gradient.

Through the first five years, stocks of live <2 mm roots in both types of Residual Soil plots showed a remarkable progressive decline to only 28% of initial levels, followed by a partial recovery (returning to 60% of initial levels) during the following two years (Residual Soil plateau plots, Fig. 5). In the more fertile Old Alluvial terrace plots, the biomass of live <2 mm roots showed similar long-term changes, but not as pronounced (a multiple-year decrease to 43% of initial levels, followed by recuperation of 67% of the initial biomass; Fig. 5).

TABLE 4. Mean (with SE in parentheses) fine-root biomass (Mg/ha; 0–50 cm depth) for four fine-root classes and the necromass proportion (dead : live ratio) across topographic edaphic gradients in the old-growth forest at La Selva Biological Station, Costa Rica.

Root class	Biomass of fine roots <2 mm diameter (Mg/ha)				<i>F</i>	df	<i>P</i>
	Slope crest	Mid slope	Slope base				
Topographic gradient, residual soil 0–50 cm							
Live roots	1.83 (0.15)a	1.55 (0.06)a	1.13 (0.09)b	10.3223	2, 15	0.0015	
Dead roots	0.24 (0.02)a	0.19 (0.02)a	0.17 (0.02)b	4.1920	2, 15	0.0358	
Dead : live	0.14 (0.01)NS	0.12 (0.01)	0.14 (0.01)	1.4380	2, 15	0.2683	

Notes: Data are seven-year means (entire cores, 25 sampling dates) over the period October 1997–April 2004.  $N = 6$  plots per slope position. Differences were analyzed by one-way ANOVA. Means were compared across the topographic positions by a post hoc Tukey hsd multiple comparisons test. Different letters indicate significant differences at  $P < 0.05$ .

Across both gradients, the stocks of <2 mm live roots varied significantly at two temporal scales (Table 5A, B): among years and between semesters, with a general trend of higher biomass in the July–December semester of each year (usually higher rainfall) than in the following January–June. On the landscape gradient there were also significant interactions between spatial and temporal effects (Table 5A) and the among-year and

between-semester pattern was strongest in the Residual Soil plateaus (Table 5A). In contrast, on the topographic gradient we did not observe any interaction of space and any of the two temporal scales (among years and between semesters; Table 5B).

*Live roots, 2 to <5 mm diameter.*—The stocks of these larger fine roots varied substantially, but more erratically, through the study period (Figs. 5 and 6), with the

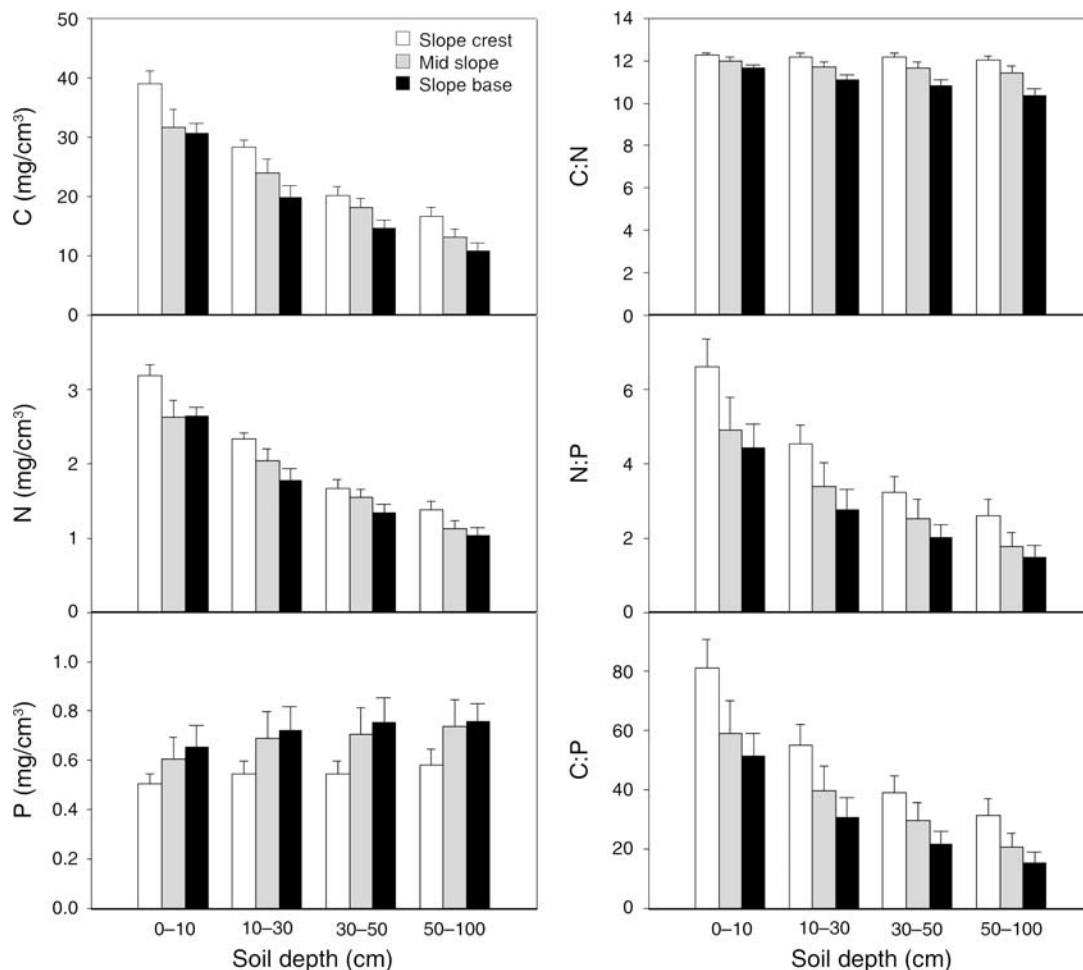


FIG. 3. Soil element stocks (total stocks) and mass-based nutrient ratios to 1 m depth along the topographic gradient at La Selva. Data are means (+SE) of six Residual Soil slope plots per slope position (slope crest, open bars; mid slope, gray bars; slope base, solid bars). The effects of slope position and depth on nutrient stocks were analyzed by two-way ANOVA (see Table 2).

TABLE 4. Extended.

Biomass of fine roots 2 to <5 mm (Mg/ha)					
Slope crest	Mid slope	Slope base	<i>F</i>	df	<i>P</i>
1.31 (0.10)a	1.15 (0.18)ab	0.76 (0.09)c	6.5430	2, 15	0.0091
0.26 (0.04)a	0.24 (0.04)a	0.12 (0.02)b	4.7520	2, 15	0.0252
0.15 (0.02)NS	0.22 (0.03)	0.20 (0.03)	1.4499	2, 15	0.2657

topographic gradient showing greater temporal variation. The maximum biomass over the seven years (mean of six plots per soil type) was 4.8 times the observed minimum on the Residual Soil plateaus, while the corresponding ratio was 3.6 on the Old Alluvial terraces. On the Residual Soil slopes these ratios were much larger: 10.1 (slope crests), 10.2 (mid slopes), and 11.9 (slope bases). The live biomass of these larger roots varied significantly among years on both gradients and by semester across the landscape gradient; neither gradient showed a space × time interaction (Table 5A, B).

The temporal changes in these larger roots varied edaphically. In the Residual Soil plots, live biomass of this root class generally paralleled the trends shown by <2 mm roots. A long-term decline from 1997 to early 2002 was followed by a two-year partial recovery (Residual Soil plateau plots, Fig. 5; Residual Soil slope plots, Appendix D). At times, however, the two Residual Soil plot types (plateau, slope) differed markedly in the dynamics and stocks of these 2 to <5 mm roots. Although during the 1997–1998 mega-Niño (from October 1997 to mid-1998) in both plot types the live

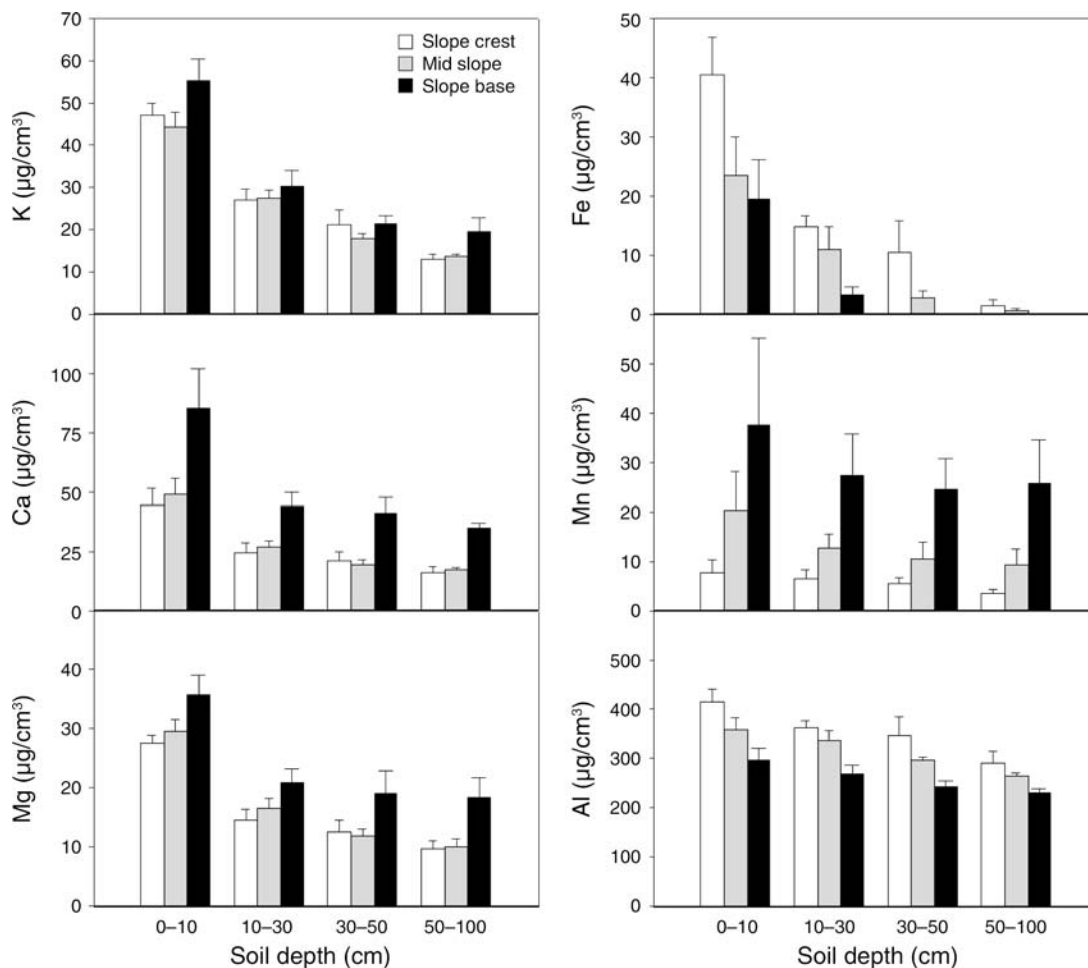


FIG. 3. Continued.

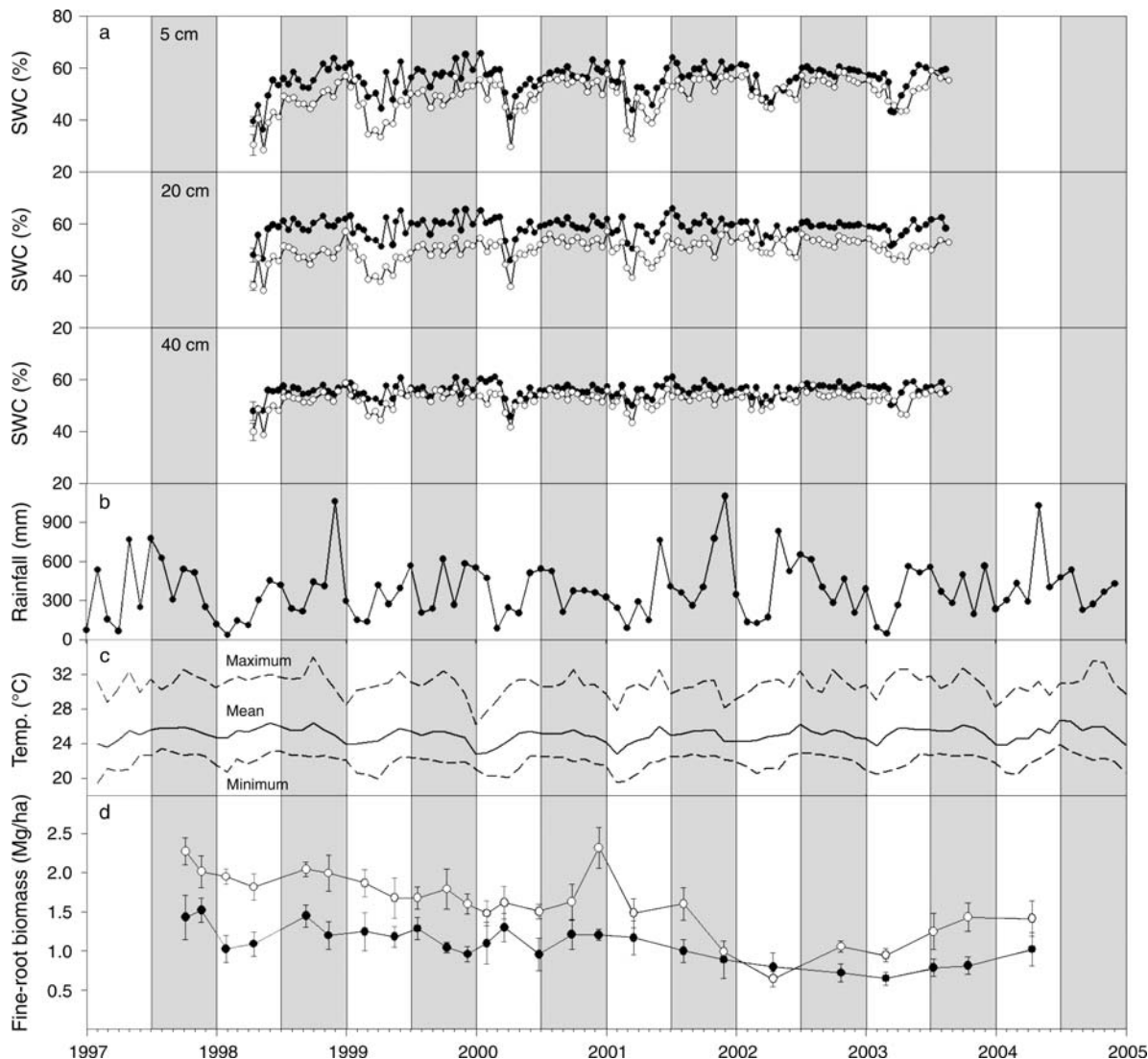


FIG. 4. Relationship between soil moisture and climatic variables (1997–2005) and fine-root stocks across the landscape gradient. (a) Mean volumetric soil moisture content (SWC) at five soil depths (from Schwendenmann and Veldkamp [2006]; bars are pooled SE). (b) Monthly rainfall and (c) daily maximum, mean, and minimum air temperatures at La Selva Biological Station (OTS, unpublished data). (d) Live fine-root biomass (mean  $\pm$  SE) for roots of  $<2$  mm diameter and depth of 0–50 cm in six Residual Soil plateau plots (open circles) and six Old Alluvial terrace plots (solid circles). The open and gray backgrounds indicate the first (January–June, drier) and second (July–December, wetter) semesters, respectively.

biomass first declined by  $\sim 50\%$  and then sharply increased, with the recovery occurring months later on the plateaus than on the slopes. Further, during much of 2003 the plateaus maintained notably greater live biomass than did the slopes. In the Old Alluvial terrace plots, the live biomass of these roots had a different temporal pattern (Fig. 5); erratic variation over the first three years, then a decline to a nearly constant level through the last 2.5 years.

*Dead fine roots.*—The temporal dynamics of dead fine-root biomass contrasted strongly with those for live roots. In all edaphic conditions, stocks of  $<2$  mm dead roots remained relatively constant and low through

much of the seven-year period, but with two- to threefold peaks in 1998 and 2000 (Figs. 5 and 6). There was significant interannual variation on both gradients (Table 5A, B). The landscape gradient also showed significant semester-scale variation (Table 5A), dominated by the large peak in necromass of  $<2$  mm roots in the first semester (January–June) of 1998, a period of lower than average rainfall and soil water content (Fig. 4a, b). Contrary to the live roots, the stocks of dead  $<2$  mm roots showed no space  $\times$  time interactions (Table 5A, B).

The biomass of dead roots 2 to  $<5$  mm, although of similar magnitude to that of the dead  $<2$  mm roots, varied more in time (Figs. 5 and 6). A very large peak in

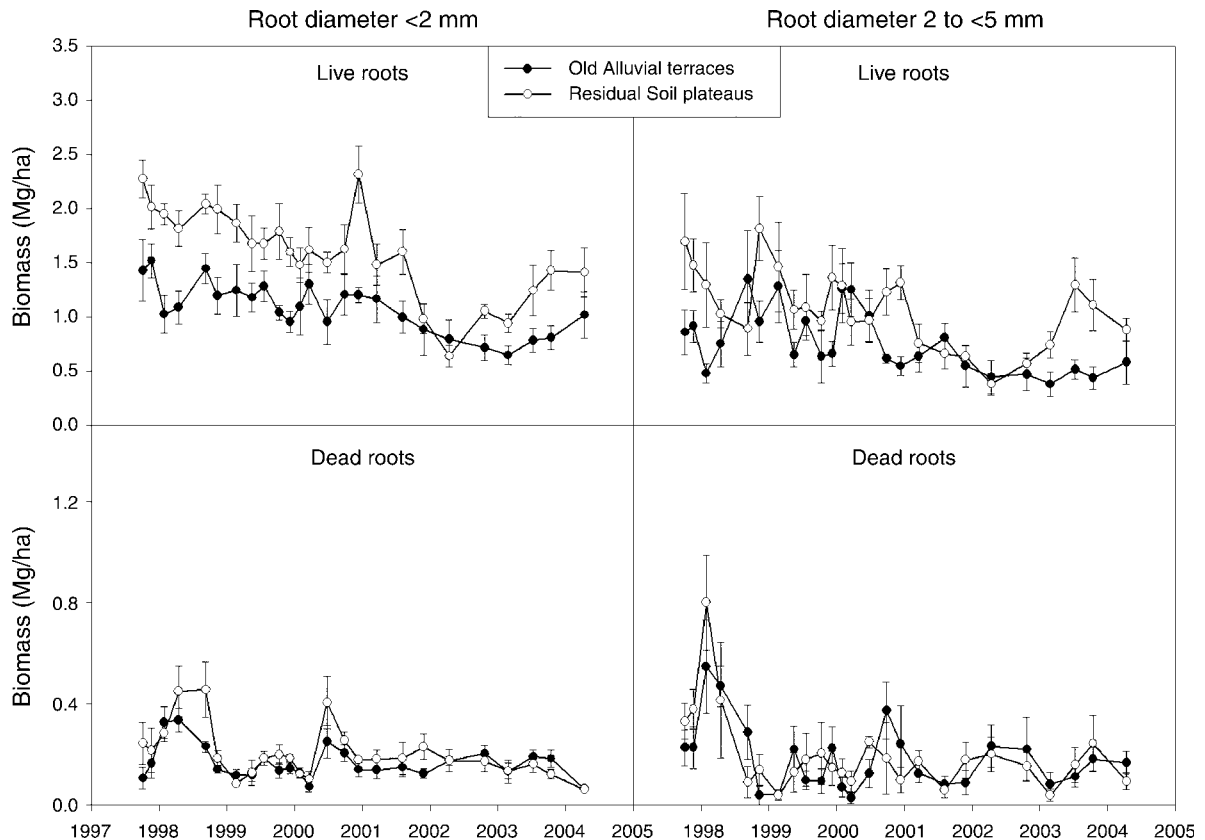


Fig. 5. Long-term temporal variation in fine-root biomass across the old-growth landscape at La Selva. Data are the mean ( $\pm$ SE) of six plots per soil type (Old Alluvial terraces and Residual Soil plateaus) at each of 25 sampling dates.

early 1998 (the mega-Niño drier season) was followed by lesser peaks in different years in certain plot types (2000/2001, Old Alluvial terraces; 2002, Residual Soil slope plots). On the slopes, the temporal dynamics of these larger dead roots differed among slope positions (Fig. 6). In early 1998 there was a very large biomass peak at slope crests, a lower peak at mid slope, and no appreciable increase at slope bases. The 2002 biomass peak was only on the slope crests.

#### *Temporal variation in soil moisture and climate*

Similar to the  $<2$ -mm live root biomass (Fig. 5), the differences in soil water content between the two soil types (Fig. 4a) strongly varied in time. We also observed a concomitant multiyear convergence in topsoil water content by 2002 (Fig. 4a, d).

Temporal patterns of fine-root biomass were explained by soil moisture content across the landscape-wide gradient (Fig. 7b;  $r = -0.74$ ,  $P < 0.0001$ ). Semester-based mean fine-root biomass (live and dead) was strongly and negatively related to percentage soil moisture of the preceding semester, but weaker correlations were observed with simultaneous soil moisture data (Table 7; see Appendix E for a complete table showing the Pearson correlation coefficient matrix). Soil moisture vs. fine-root biomass relationships were only

observed in Residual plateaus, but not in Old Alluvial terraces (Fig. 7a, b) which spanned narrow ranges of soil moisture at different soil depths. Additionally, climate variables (rainfall and daily maximum, minimum, and mean air temperature) were poorly correlated with fine-root biomass, except from maximum air temperatures ( $T_{\max}$ ) that showed some positive correlation ( $r = 0.58$ ,  $P = 0.029$ ) with the biomass of coarser ( $<5$  mm diameter) dead roots in the same semester (Table 7).

#### *Fine-root biomass patterns with soil depth*

Stocks of fine roots strongly decreased with soil depth. The split-depth samples (0–20 cm and 20–50 cm; Fig. 8) showed greater biomass and greater spatiotemporal variation of live and dead fine roots at the surface. The between-soil difference in fine-root biomass was restricted to the topsoil (0–20 cm depth; Table 1). Higher resolution (10 cm interval) depth sampling (one plot/soil type; Fig. 9) also showed this pattern; only in the top 20 cm did the Residual Soil plateau plot show greater live fine-root biomass than the Old Alluvial terrace plot. For both root diameter classes, live biomass declined faster with depth in the Residual Soil plots (10 cm profiles, Fig. 9; split-depth samples, Table 1 and Fig. 8). The Residual Soil plateau plots usually showed substantially more dead-root biomass in the top 20 cm than the Old

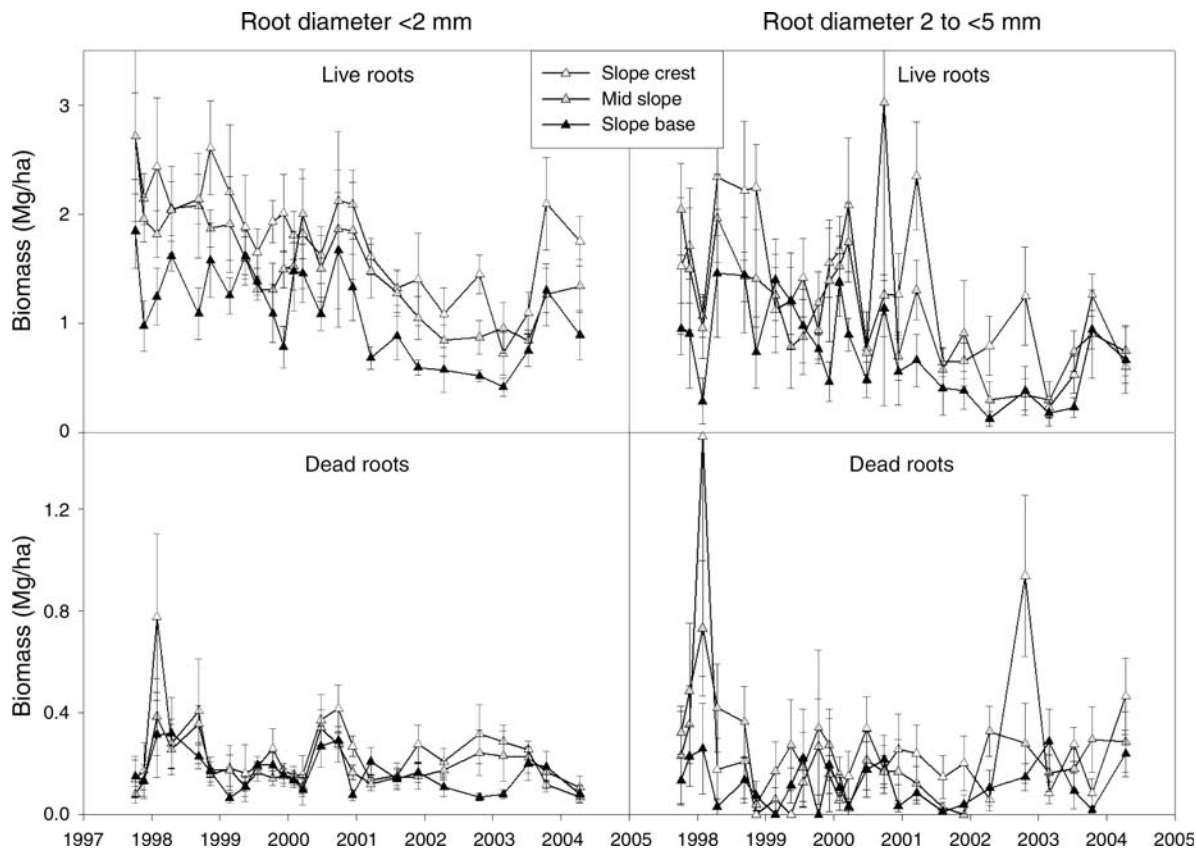


FIG. 6. Long-term temporal variation in fine-root biomass, live and dead, across the topographic gradient in Residual Soil slope plots at La Selva. Data are the means ( $\pm$ SE) of six plots per slope position level (slope crest, mid slope, slope base) at each of 25 sampling dates between 1997 and 2005.

Alluvial terrace plots, but a notable reversal occurred in late 2003 (Fig. 8).

Soil moisture and elements also varied with soil depth. The Residual Soil plateaus showed lower soil water content than the Old Alluvial terraces to 5 and 20 cm depth, but not in the deeper soil layers (Fig. 4a). In both soil types, the temporal variation in soil water content was greatest close to the soil surface (0–10 cm depth), and progressively decreased with depth (Fig. 4a). Nearly all measured elements (C, N, K, Ca, Mg, Fe, Al) decreased markedly with soil depth; the notable exceptions were P and Mn, which showed no significant change over the top meter of soil (Table 2). Soil K stocks and C:P and N:P ratios showed significant soil type  $\times$  depth interactions (Table 2) on the landscape-wide gradient; the between-soil differences in these factors were larger closer to the surface (Fig. 1).

#### *Sampling methods and power to detect patterns*

Comparison of root-biomass data from the 0–50 cm cores and the independent split cores (0–20 and 20–50 cm depth classes) revealed high consistency between the two sampling methods (Fig. 10). This demonstrates the reliability of the fine-root biomass data and validates the observed spatial and temporal patterns.

Power analysis (Fig. 11) on the biomass data for live  $<2$  mm roots showed that many sequential samples would be needed to resolve the spatial patterns we detected. For comparing soil types, the required least significant number (LSN) of sampling dates was 9, and the optimal number,  $N$ , (for statistical power  $>0.9$ ) was 18 (Fig. 11a); for comparing slope positions, the LSN exceeded 6 and  $N$  was 10 sampling dates (Fig. 11b).

#### *Shifting biomass allocation to fine roots*

Relative allocation of biomass to fine roots (the ratio between  $<5$  mm live root biomass and estimated aboveground biomass) varied both in space and time (Table 8, Fig. 12). As seen earlier (cf. Fig. 5), live fine-root biomass was initially greater on the Residual Soils but gradually declined, approaching that of the Old Alluvial terraces late in the record, and then partially recovering in the last years. Over the seven years, estimated aboveground biomass was marginally significantly greater on the Old Alluvial terraces than on the Residual Soil plateaus (Fig. 12a). The net result of these trends was initially higher relative biomass allocation to fine roots on the Residual Soil plateaus than on the Old Alluvial terraces, followed by long-term convergence between soil types, and then a partial recuperation of the

TABLE 5. Repeated-measures split-plot ANOVA of spatial and temporal effects on fine-root biomass (0–50 cm depth) in the La Selva, Costa Rica, old-growth forest.

Source	df	Live roots				Dead roots			
		Diameter <2 mm		Diameter 2 to <5 mm		Diameter <2 mm		Diameter 2 to <5 mm	
		F	P	F	P	F	P	F	P
A) Landscape-wide comparison									
Between subjects									
Soil type	1, 10	9.67	0.0111	13.44	0.0043	2.84	0.1229	0.00	0.9951
Plots within soil type	10, 130	12.13	<0.0001	1.11	0.3626	1.47	0.1567	0.62	0.7973
Within subjects									
Year	6, 130	32.57	<0.0001	11.70	<0.0001	9.06	<0.0001	12.10	<0.0001
Semester	1, 130	16.45	0.0001	5.08	0.0259	4.93	0.0281	0.03	0.8718
Year × semester	6, 130	2.84	0.0125	1.45	0.2004	11.08	<0.0001	4.32	0.0005
Soil type × year	6, 130	3.65	0.0022	2.10	0.0569	1.37	0.2307	1.09	0.3703
Soil type × semester	1, 130	4.93	0.0281	1.85	0.1764	1.18	0.2804	0.01	0.9373
Soil type × year × semester	6, 130	1.06	0.3886	0.99	0.4320	1.37	0.2328	0.85	0.5344
B) Topographic comparison									
Between subjects									
Slope position	2, 3	42.50	0.0063	16.66	0.0237	7.94	0.0633	6.96	0.0747
Plots within slope position	3, 207	0.84	0.4719	0.75	0.5207	2.23	0.0861	0.66	0.5771
Within subjects									
Year	6, 207	26.45	<0.0001	16.63	<0.0001	2.35	0.0342	5.33	<0.0001
Semester	1, 207	7.61	0.0063	2.74	0.0993	0.82	0.3651	0.14	0.7102
Year × semester	6, 207	2.01	0.0654	1.45	0.1972	7.79	<0.0001	2.68	0.0159
Slope position × year	12, 207	0.27	0.9934	0.67	0.7758	1.31	0.2170	1.13	0.3400
Slope position × semester	2, 207	0.95	0.3873	0.12	0.8890	0.02	0.9815	0.63	0.5343
Slope position × year × semester	12, 207	0.93	0.5188	1.15	0.3246	0.70	0.7491	2.27	0.0101

Notes: The data for this table are shown in Figs. 5 and 6. Spatial (between-subjects) effects are shown independently for: (A) landscape-wide comparison between two soil types on similar topography, and (B) topographic comparison among three slope positions. Temporal (within subjects) effects tested mean differences between years ( $N=7$ ) and semesters ( $N=2$  per year), starting in the second semester of 1997 and ending in the first semester of 2004. A separate test was performed for each fine-root class. Data for live, <2mm diameter roots were normally distributed and not transformed. Data for all remaining root classes were normalized by logarithmic transformation. Values of  $P < 0.05$  are considered significant.

initial contrast (Fig. 12c). Although estimated above-ground biomass did not show a significant year effect (Table 8), the relative biomass allocation to fine roots did, reflecting the large temporal changes in fine-root biomass (Table 5A). There were also significant time × soil type interaction effects in both variables (Tables 5A and 8).

#### Raw data files

Raw data of fine-root biomass across all spatial and temporal scales is available in Appendices G to K, and

complete data of soil element stocks is available in Appendix L.

#### DISCUSSION

Studies of tropical forest belowground biomass across large geographic scales (Maycock and Congden 2000, Powers et al. 2005) have revealed strong spatial patterns associated with edaphic variation. Our data from the lowland tropical rain forest at La Selva, Costa Rica, confirm the existence of analogous gradients in fine-root biomass that are associated with fertility variation

TABLE 6. Spatial and temporal variation in biomass of live fine roots &lt;2 mm in diameter for each edaphic gradient in the La Selva, Costa Rica, old-growth forest.

Gradient	Spatial variation		Temporal variation			
	N	Mean (SE)	N	All dates	Among years	Within years
				Mean (SE)	Mean (SE)	Mean (SE)
Landscape wide	25	1.59 (0.06)	12	2.54 (0.18)	0.93 (0.09)	0.69 (0.06)
Topographic	25	2.87 (0.24)	18	4.48 (0.60)	1.48 (0.12)	1.23 (0.09)

Notes: For spatial variation we report the mean (with SE in parentheses) across 25 sampling dates of the range in fine-root biomass (the difference between maximum and minimum biomass in Mg/ha). For temporal variation we report the mean (with SE in parentheses) range in fine-root biomass across the following temporal ranges: (a) across all 25 dates (all dates); (b) among the seven years (among years, i.e., the range among mean biomass values at each of seven years); and (c) between semesters (within years).

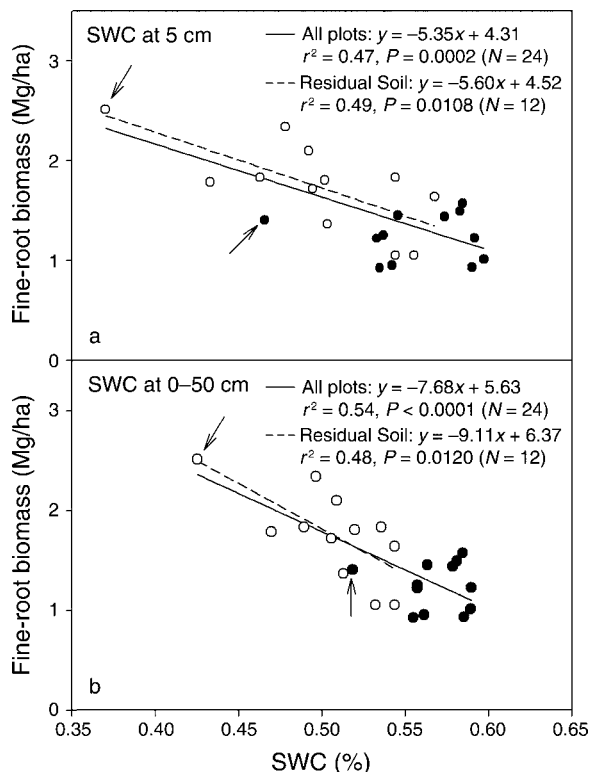


FIG. 7. Relationship between total fine-root biomass (Mg/ha, soil depth 0–50 cm, live + dead, diameter <2 mm) and preceding mean soil water content (SWC, %) at (a) 5 cm and (b) 0–50 cm soil depth. Each data point corresponds to the mean fine-root biomass and SWC over each semester (2–4 samplings per semester for fine-root biomass and measurements every two weeks for SWC) from 1998 to 2004 for Residual Soil plateau plots (open circles) and Old Alluvial terrace plots (solid circles). Arrows indicate soil moisture data of the 1998 ENSO (El Niño Southern Oscillation) dry period and fine-root biomass of the following semester for both soil types. Lines are linear regressions.

within a single tropical forest (i.e., lower fine-root biomass and greater soil fertility). As hypothesized, soil phosphorus was negatively related to fine-root biomass, but this relationship was not general to all soil gradients. We quantified the long-term (seven-year) variation in fine-root stocks across an edaphically stratified set of replicated plots and found strong nonlinear space  $\times$  time interactions across two spatial scales (landscape and topographic) and among live and dead fine-root classes. Our data show that the divergent temporal patterns in fine-root biomass that we found between the major soil types were associated with soil-specific variation in soil water content. Our findings demonstrate that within-landscape variation in tropical forest ecosystem processes can be as large as that found across large geographic scales, and that temporal changes in these same processes, both within and among years, can equal or exceed the spatial variation. With a power analysis of our data (Fig. 11), we estimated that a minimum of nine and six sampling dates are required to capture the spatial patterns in fine-root biomass that we detected across the landscape-wide and topographic gradients, respectively. Such series of sequential root data are scarce in the forest literature. The strong spatiotemporal variation in fine-root biomass that we documented at La Selva points to the potential importance of belowground processes in the responses of forests to large-scale change, and highlights a need for more intensive as well as long-term research on these processes.

#### *Spatial patterns and relationships with soil fertility*

Fine-root biomass was strongly associated with changes in soil element levels down catenas and across soil types within this lowland tropical rain forest. An inverse relationship between fine-root biomass and soil nutrient availability in lowland tropical forests was originally proposed by Vitousek and Sanford (1986). Other research (Vitousek et al. 2003, and references therein) has extensively documented ecosystem respons-

TABLE 7. Significant ( $P < 0.05$ ) Pearson's correlation coefficients between climatic variables ( $T_{\max}$ , daily maximum temperature;  $T_{\min}$ , daily minimum temperature), soil water content (%), and the biomass (0–50 cm soil depth) of different fine root classes (landscape-wide gradient only).

Soil type and root status and diameter	Current semester		Previous semester			
	Temperature ( $^{\circ}\text{C}$ )		Soil water content (%)			
	$T_{\max}$	$T_{\min}$	5 cm	20 cm	40 cm	0–50 cm
Old Alluvial terrace						
Dead, <5 mm	0.582	0.573				
Residual plateaus						
Live, <2 mm			-0.597	-0.613	NS	-0.584
Dead, <2 mm			-0.712	-0.595	-0.866	-0.733
Live + dead, <2 mm			-0.703	-0.695	-0.621	-0.696

Notes: Fine-root biomass and environmental correlations were tested on simultaneous semesters and with a time lag in fine-root biomass of one semester. Each data point was the mean of three plots per soil type. For a complete correlations matrix including rainfall and mean daily temperature (current and previous semester) see Appendix E.



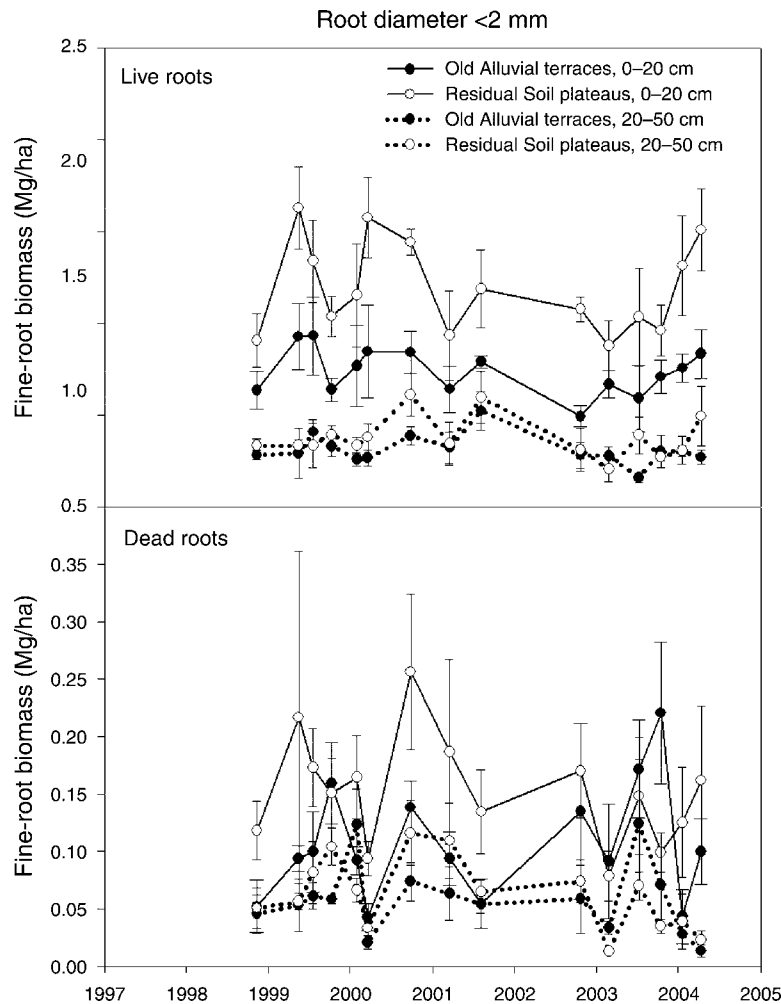


FIG. 8. Long-term variation in stocks of live fine roots  $<2$  mm diameter across the landscape-wide gradient and at two different soil depths: 0–20 cm (solid line) and 20–50 cm (dotted line). Data are means ( $\pm$ SE) from three Old Alluvial terrace plots (solid circles) and three Residual Soil plateau plots (open circles) at each of 14 sampling dates.

es to the variation in fertility down tropical mountain slopes. In this study we found significant within-forest variation in belowground biomass at much smaller scales: between younger and older Oxisols in the landscape-wide gradient (maximum distance between the most separated plots =  $<2.5$  km; Appendix A); and across the approximately 50 m from slope crests to slope bases on the topographic gradient. Fine-root biomass strongly declined with increasing fertility across both gradients (Table 3, Fig. 2). Opposite patterns in aboveground biomass and in fine-root stocks produced large differences between soil types in the relative biomass allocation to fine roots (Fig. 12), suggesting that allocation patterns can be strongly affected by within-landscape levels of variation in fertility. Because this landscape is dominated by a single tree species (*Pentaclethra macroloba*) and three palm species (*Welfia regia*, *Socratea exorrhiza*, and *Iriartea deltoidea*) while the rest of species tend to occur in very low densities, we

believe that belowground spatial patterns reflect more the differences in edaphic conditions than in species composition. A plastic response involving a reduction in belowground allocation is in line with functional balance theory (sensu Thornley 1976; revised by Santantonio 1990) and the so-called “differential allocation” hypothesis (sensu Gower et al. 1992, Haynes and Gower 1995, Ruess et al. 1996). However, contrasting evidence is also presented by Reich et al. (1998), Joslin et al. (2000), and Carter et al. (2004).

The associations between local soil nutrient levels and fine-root biomass (Table 3) were stronger with live roots, particularly those  $<2$  mm. An exception in the landscape-wide gradient was the strong negative relationship between the biomass of dead fine roots (2 to  $<5$  mm diameter) and soil Ca and Ca:Mg ratio. A role of Ca in accelerating root decomposition was hypothesized by Silver and Miya (2001) based on the global relationship they found between root [Ca] and decomposition rates.

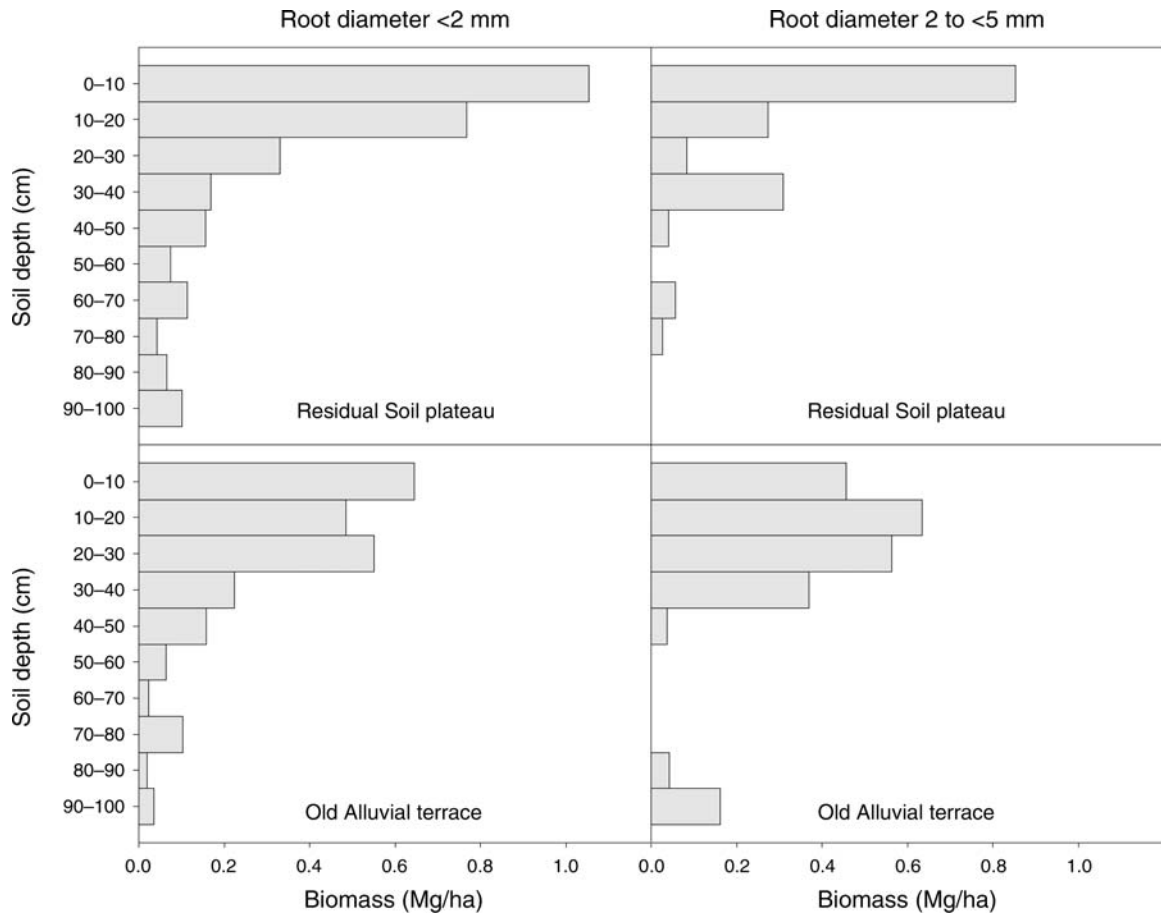


FIG. 9. Vertical distribution, by biomass and diameter, of live fine roots in the top 1 m of soil in the two soil types of the landscape-wide gradient. Data are means of six cores at each depth from one Residual Soil plateau plot (L4) and one Old Alluvial terrace plot (A4), sampled on 19 July 2001.

Although our landscape-wide data for dead fine roots 2 to <5 mm diameter are consistent with this hypothesis, counterevidence from both gradients (Table 3) is the lack of association with soil Ca and Ca:Mg ratio for dead <2 mm roots, and the uniformly negative correlations with both factors shown by live roots (both size classes).

Previous studies in tropical lowland forests indicated inverse relationships of fine-root biomass and P and Ca availability (Gower 1987). Although we observed a clear overall biomass decline with increasing soil fertility, the four fine-root classes (live or dead, and <2 mm or 2 to <5 mm) on each gradient showed diverse relationships with individual soil elements (Table 3). The strongest overall association with the seven-year mean biomass values from any gradient was with total soil P; very high negative correlations were shown by live roots across the landscape gradient (<2 mm:  $r = -0.85$ ,  $P < 0.001$ ,  $N = 12$ ; 2 to <5 mm:  $r = -0.90$ ,  $P < 0.001$ ,  $N = 12$ ). Other studies have found a negative relation between soil P levels and fine-root biomass among or within tropical forests (see La Selva Recent Alluvium vs. "Arboleda"

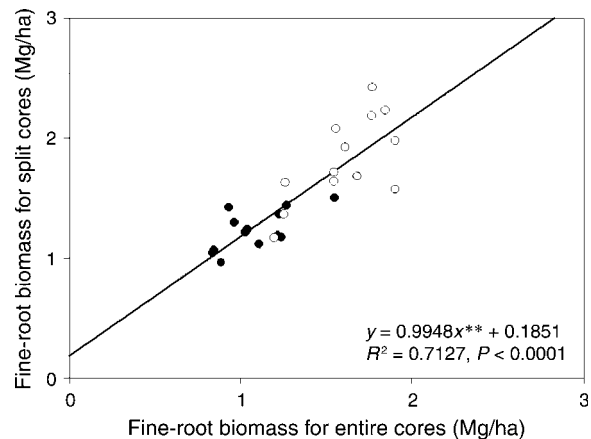


FIG. 10. Total biomass (live + dead) of <2 mm diameter fine roots at 0–50 cm depth as measured by two independent samplings at 12 dates during 1999–2003. The regression relates data from root samples collected with an entire core or a split core (0–20 cm and 20–50 cm) at the same dates (means from three Old Alluvial terrace plots [solid circles] and three Residual Soil plateau plots [open circles]). The significance of the regression equation is  $P < 0.01$  (\*\*). The  $b$  parameter of the equation (intercept = 0.1851) is not significant.

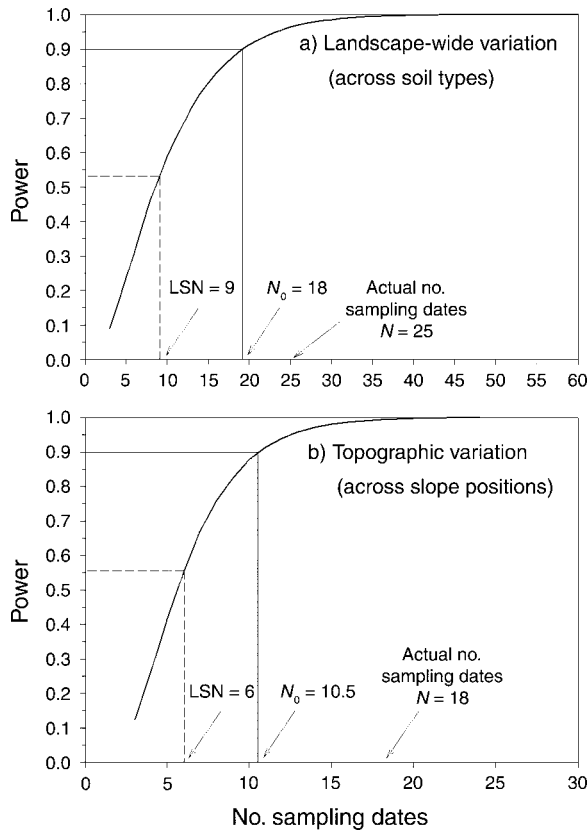


FIG. 11. Power analysis of fine-root biomass data (live roots, diameter <2 mm) across the two La Selva edaphic gradients: (a) landscape-wide and (b) topographic. Interpolated values in the curve represent the optimal number of sampling dates ( $N_0$ ; the sample size for a power value of 0.9), and the minimum number of sampling dates to achieve a power value of >0.5 (least significant number, LSN).

[Old Alluvium] sites in Gower 1987; Hawaiian montane forests in Ostertag 2001; four neotropical forests, including La Selva, in Powers et al. 2005). Across the landscape-wide gradient of the present study, live fine-root biomass on both La Selva gradients was also

significantly negatively related to soil K and Mn levels, indicating potentially multiple nutrient limitations. Less general negative associations existed between the stocks of some dead fine-root classes and the cations K and Ca. In contrast, the biomass of both live and dead fine-roots increased with increasing soil C, N, C:N, C:P, Fe, and on the topographic gradient, Al.

The consistently positive relation we found between the biomass of live fine roots and total soil N (Table 3) is notable, given the opposite trend in most temperate forests (Zak and Pregitzer 1998, Nadelhoffer 2000). At La Selva the within-forest variation in other soil nutrients (P, cations, Mn) was greater than for soil N, so it is likely that N availability does not drive the strong across-landscape variation in fine-root stocks.

Most prior findings from tropical forests on well-developed soils have also failed to find evidence of N limitation. Gower (1987, at La Selva) and Ostertag (2001, in Hawaiian montane forests) found little to no response by fine-root biomass to natural and artificial N gradients. Two global-scale meta-analyses of foliar chemistry (McGroddy et al. 2004, Reich and Oleksyn 2004) point to P rather than N limitation in tropical forests. At La Selva, average N:P values during the first two years of this study (1997–1999) were just below tropical rain forest values (26–29 vs. 28) indicating P limitation (Wood et al. 2005). However, N limitation or colimitation can certainly occur, particularly on young tropical soils (cf. Vitousek 2004). Indeed, in our study at La Selva, fine-root biomass was more strongly correlated with soil N:P than with total soil P (Table 3), and also better explains vertical variation (see section about depth patterns), suggesting a shift in the relative degrees of N and P limitation with degree of weathering across the soil age gradient (cf. Walker and Syers 1976, Richardson et al. 2004, Vitousek 2004). In our study, this was evident even in the relatively narrow gradient of old-alluvial to residual Oxisols. This shift in nutrient limitation can be reflected not only in litter stoichiometry (McGroddy et al. 2004) and potential feedbacks on nutrient cycles (sensu, Schade et al. 2005), but also in

TABLE 8. Repeated-measures split-plot ANOVA of spatial and temporal effects on estimated live aboveground biomass (D. B. Clark and D. A. Clark, unpublished data) and relative biomass allocation to live fine roots <5 mm diameter (0–50 cm depth) in the La Selva old-growth forest.

Source	df	Estimated aboveground biomass		Fine roots : aboveground biomass	
		F	P	F	P
Between subjects					
Soil type	1, 10	5.15	0.0466	11.49	0.0069
Plots within soil types	10, 60	76.59	<0.0001	14.28	<0.0001
Within subjects					
Year	6, 60	0.65	0.6929	25.99	<0.0001
Soil type × year	6, 60	3.04	0.0116	3.96	0.0021

Notes: Spatial (between-subjects) effects comprised landscape-wide and topographic gradients. Temporal (within-subjects) effects tested mean differences among years ( $N = 7$ ), from 1 October 1997 to 30 September 2004. Data were normally distributed and not transformed prior to analysis. Values of  $P < 0.05$  are considered significant.

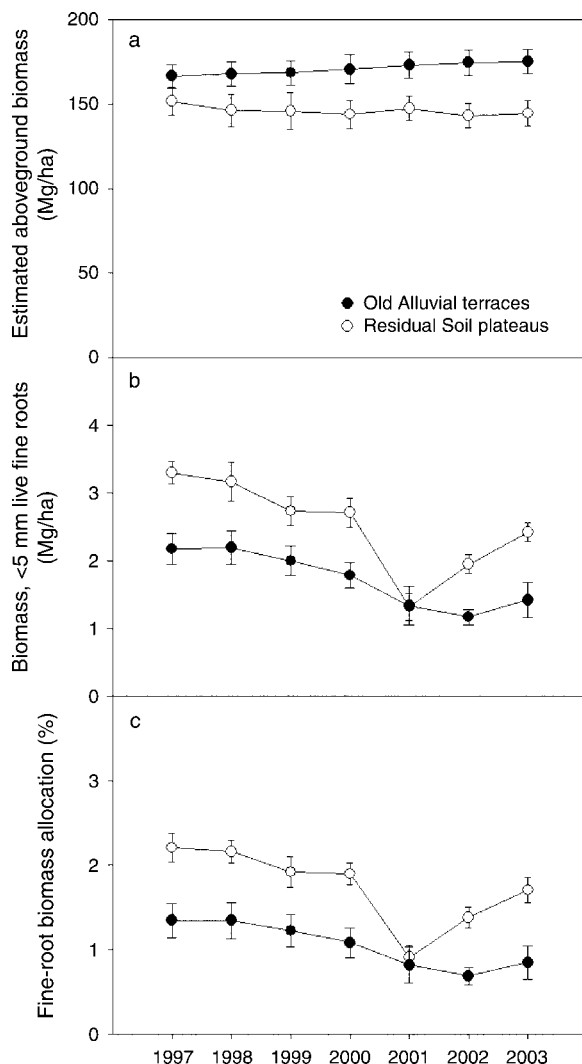


FIG. 12. Variation in biomass allocation to fine roots among years (from 1 October to 30 September) and across the landscape gradient: Residual Soil plateaus (open circles) and Old Alluvial terraces (solid circles). Data are means ( $\pm$ SE) from six plots per soil type: (a) estimated aboveground biomass; (b) biomass of live <5 mm diameter roots (0–50 cm depth); (c) biomass allocation to fine roots, percentage (biomass of live <5 mm fine roots divided by estimated aboveground biomass). The statistical analysis of the differences between soil types and of temporal effects in panels (a) and (b) is shown in Table 8. Year ( $x$ -axis) shows the year that starts each annual measurement.

shifts in belowground allocation (*sensu*, Jordan 1985, Haynes and Gower 1995).

The differing relationships with soil nutrients shown in our study by different fine-root classes (live or dead, <2 mm, 2 to <5 mm) and between the landscape-wide and topographic gradients (Table 3, Fig. 2) point to complex processes underlying the spatial heterogeneity in fine-root biomass. Such complex root responses to soil fertility have been found in other biomes and are widely acknowledged in the root ecological literature (Nadelhoffer 2000). For tropical rain forests, however,

there have been only a handful of studies of fine-root responses to within-landscape soil variation (Gower 1987, Ostertag 2001, Powers et al. 2005, Silver et al. 2005). Our two-gradient comparison at La Selva revealed differing fine-root responses at contrasting spatial scales within the same forest. Down the catenas within the Residual Soil slope plots, fine-root stocks exhibited a weaker association with the variation in soil P and N:P ratio than was shown by fine roots across the landscape-wide gradient. For other soil elements, the strong correlations shown by particular fine-root classes were restricted to one of the gradients (e.g., <2 mm live roots and soil K on the landscape gradient,  $r = -0.75$ ,  $P = 0.005$ ,  $N = 12$ ; <2 mm live roots and soil Al on the topographic gradient,  $r = +0.74$ ,  $P < 0.001$ ,  $N = 18$ ; in each case, corresponding correlations on the other gradient were not significant).

The correlations of fine-root biomass with many soil elements at La Selva (Table 3) could indicate colimitation by multiple nutrients, or they could simply be the result of strong covariation of elements across each study gradient. The latter seems to be the case for elements that covary across the gradients, such as P and K, and C and N, that showed strong pair-wise correlations across the landscape gradient ( $r = +0.91$ ,  $P < 0.001$ , and  $r = +0.93$ ,  $P < 0.001$ ; Appendix F). Nonetheless, some element pairs that were strongly associated with fine-root biomass, such as Mn and P or Mn and K, showed poor pair-wise correlations (Mn and P,  $r = +0.52$ ,  $P = 0.081$ ; Mn and K,  $r = +0.46$ ,  $P = 0.129$ ), suggesting a more independent role of Mn in controlling fine-root dynamics. Although decreased fine-root biomass at high Mn can be related to toxicity effects, in highly weathered tropical soils such as Oxisols total Mn content is often low and Mn deficiencies are common (Marschner 1995). Other groups of elements that were similarly associated with fine-root biomass across the slope gradient (such as C and N, and Ca and Mg) also seemed to vary independently, based on the poor pair-wise correlations: C vs. Ca or Mg, and N vs. Ca or Mg all had  $P > 0.3$  (Appendix F). These element interrelationships showed, however, strong spatial explicitness. Landscape-wide P–K relationships fade away at the topographical scale, and new element associations emerge, such as C and N, and Ca and Mg, all strongly related to fine-root stocks. This supports the notion of multiple nutrient colimitation syndromes that are specific to each soil genetic gradient, causing fine-root dynamics to be controlled simultaneously by diverse soil elements in this complex landscape. Because fine-root biomass increased with increasing Fe and Al (across slopes) and Fe (landscape wide), toxic effects of Fe and Al in fine roots should be discounted. Both Al and Fe are known to increase in highly weathered tropical soils and it is unlikely Fe would limit fine-root biomass. In general, the range of variation in P, K, and Mn (landscape-wide) and C, N, Ca, Mg, and Mn (across slopes) was far greater than that of Fe and Al

(landscape) and Al (topographic), suggesting also that these elements had less control on fine-root dynamics. Therefore, it is possible these Fe and Al correlations are the result of covariance with other limiting soil elements in the soil matrix as a consequence of either alluvial (landscape-wide) or colluvial (topographic) pedological gradients. The question of what specific feature(s) of this within-landscape soil heterogeneity drives the variation in fine-root biomass will still require future experimentation to resolve. Regardless of its cause(s), we now have identified within the La Selva landscape surprisingly strong gradients of variation in fine-root stocks that are highly predictable from soil properties.

Soil nutrients covary differentially with soil development (Vitousek 2004), and our two edaphic gradients (landscape wide and topographic) represent different types of soil development. In soil chronosequences spanning static surfaces across several soil orders, available cations decrease rapidly as young soils (Andisols) age and remain low in old soils (Ultisols, Oxisols; Vitousek 2004). In contrast, P loss lags behind due to the incorporation of P into secondary materials that weather later in soil development (Walker and Syers 1976, Chadwick et al. 1999). The differences in total soil P and K across the static surfaces of the La Selva landscape-wide gradient indicate later stages of soil development. In contrast, the changes in soil Ca and Mg down the slopes reflect more recent pedogenesis. As on Hawaii's older slopes (Vitousek et al. 2003), cation enrichment down the Residual Soil slopes may be linked to fluvial erosion processes that create gradients between remaining constructional surfaces (slope crests), eroded slopes (mid slopes) and depositional surfaces (slope bases). These processes produce a fertility matrix in old sloped soils, as in early soil formation (Vitousek et al. 2003). Recent data with strontium (Sr) isotopes at La Selva (Porder et al. 2006) also supports this idea of nutrient inputs in lower slopes via erosion of weathered soils. Our belowground data further demonstrate that the erosion of La Selva's old (oxisol) surfaces produces a fine-scale mosaic of juxtaposed slope positions and flat surfaces that differ significantly in fine-root biomass.

#### *Temporal patterns in fine-root biomass*

Our seven-year study has produced the first belowground data set for tropical forests that is of sufficiently long duration and intensity to assess the variation in fine-root stocks within and among years. We found substantial temporal variation in fine-root biomass in the La Selva forest. The changes through time within plots and slope positions were much greater than the biomass variation at any time across the strong within-forest fertility gradients (Table 6).

*Intra-annual variation.*—By sampling two to four times each year we were able to detect subannual changes in live fine-root biomass on both gradients. This short-term variation was stronger on the less fertile (and often drier; Fig. 4) Residual Soil. The within-year range

in mean biomass of live <2 mm roots (0–50 cm depth) reached 1.0 Mg/ha on both the Residual Soil plateaus and the Residual Soil slopes. Surprisingly, this level of intra-year variation in fine-root biomass at La Selva equals that reported from the drier and more strongly seasonal forest at Barro Colorado Island, Panama (up to 1 Mg/ha biomass changes in wet–dry transitions; Cavaleri et al. 1999). On the Old Alluvial terraces, in contrast, the maximum within-year range we observed in the biomass of live <2 mm roots was 0.5 Mg/ha.

Besides soil fertility controls on fine-root stocks, our results indicate potential interactions with soil water dynamics that are site specific. Other studies (Cavaleri et al. 1999, Green et al. 2005), including a previous study of La Selva's alluvial soils (Sanford 1989), reported reductions of fine-root biomass during the dry season. In wet tropical forests the variation in fine-root stocks may be driven more by climatic variation than by plant phenology (cf. Kummerow et al. 1990). In our investigation on Residual soils we found a negative relationship between semester-averaged fine-root biomass and preceding soil water content (Fig. 7), more similar to the negative or null effect on fine-root biomass when irrigation has been used to eliminate seasonal drought (see Joslin et al. 2000 for temperate forests; Yavitt and Wright 2001 for a seasonal tropical forest). Our six-month lag period did not differ much from the 16–18 week delayed response of litter P to precipitation (Wood et al. 2005), and suggests that fine-root stocks can vary at the same scale of nutrient cycles in this forest (i.e., changes in rainfall and subsequent leaf litter production and decomposition trigger fine-root responses that ultimately feed back on subsequent leaf litter nutrient concentrations; see conceptual diagram in Fig. 13). The semester-scale variation of fine-root biomass and soil moisture at La Selva also differed between the two soil types (Fig. 7); compared to the Old Alluvial terraces, the Residual Soil plateaus showed more pronounced within-year changes in fine-root biomass, possibly linked to the stronger dry season declines in soil moisture on this soil (Figs. 4a, b and 13). Previous studies on leaf and litter chemistry also indicated greater response of leaf N:P to preceding rainfall in Residual than in Old Alluvial soils, indicative of more pronounced P limitation in the former (Wood et al. 2005).

*Annual-scale and multiyear variation.*—Our seven-year record enables a first assessment of changes in fine-root stocks across many years within a tropical forest. Prior belowground biomass studies in this biome have covered much shorter time spans (see Kummerow et al. [1990] for a one-year study of a Mexican dry forest; Beard et al. [2005] studied Puerto Rican montane hurricane forest during two separate two- to three-year periods; Roderstein et al. [2005] shows results of a one-year Ecuadorian montane forest study; and see Silver et al. [2005] for a two-year Brazilian Amazon moist forest study).

The interannual variation in fine-root biomass at La Selva was surprisingly large and it showed clear long-

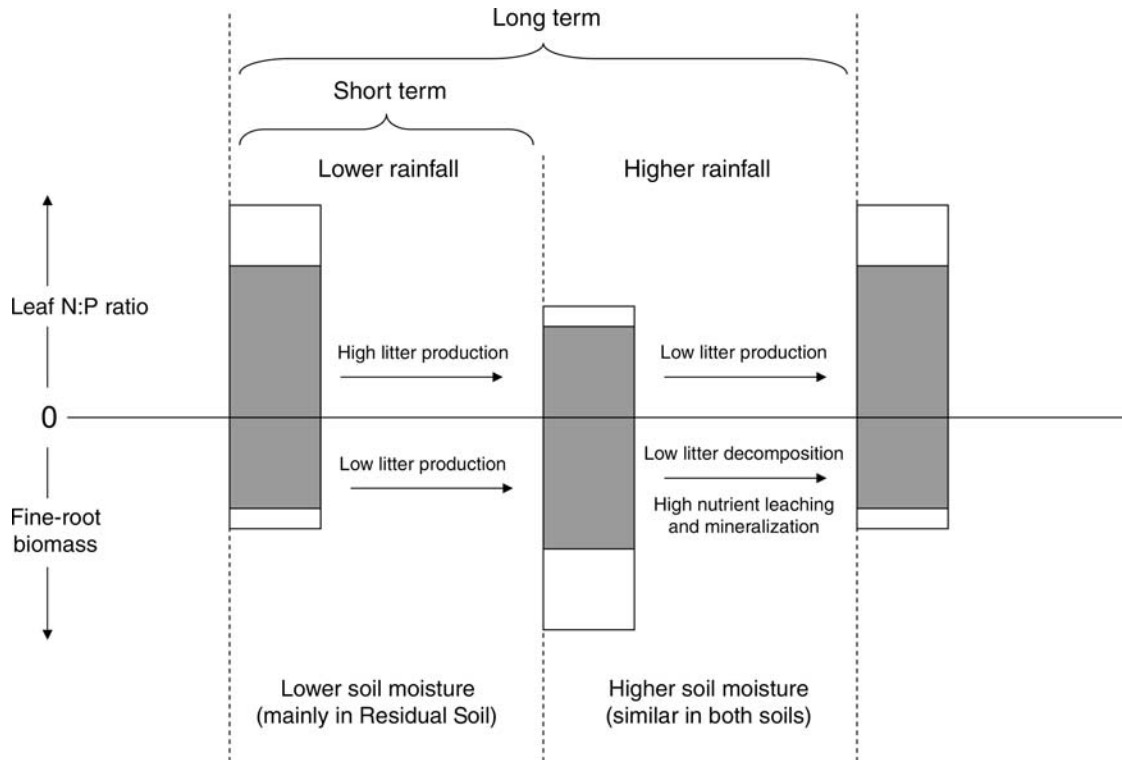


FIG. 13. Proposed integration of belowground responses (soil moisture and fine-root biomass) and aboveground responses (leaf chemistry, leaf litter production) at short- and long-term scales and across the edaphic gradient of La Selva (gray bars, Old Alluvial terraces; open bars, Residual Soil plateaus). The diagram complements a previous aboveground model by Wood et al. (2005), where short-term changes in leaf litter chemistry were linked to rainfall, via soil moisture effects on nutrient uptake and leaching, whereas long-term patterns were attributed to nutrient pulses as the decomposition of litter changes seasonally. Our results indicate that fine-root dynamics are tightly linked to long-term cycles and that increases in fine-root biomass (live and dead) with preceding low soil moisture can be explained indirectly by this mechanism.

term patterns. In the Residual Soil plateau (Fig. 5) and Residual Soil slope plots (Fig. 6), fine-root biomass underwent a dramatic progressive decline between 1997 and 2002: both converged with levels on the Old Alluvial terraces, and then partially recovered in the final two years. Time courses of long-term measurements in the CARBONO plots of soil moisture (Fig. 4a, b) and soil respiration (Schwendenmann et al. 2003, Schwendenmann and Veldkamp 2006) show similar between-soil temporal patterns, giving further support to a link between long-term variation across this landscape in soil water, fine-root stocks, and soil respiration.

These long-term records of fine-root stocks show strong space  $\times$  time interactions. The temporal variation in live fine-root biomass was more pronounced on the Residual Soil plateaus than on the Old Alluvial terraces, and peaks and minima for live (but not dead) roots exhibited different timings in each soil type (Fig. 5). On the Residual Soil catenas, live and dead fine-root biomass showed much more temporal variation on the slope crests than at lower slope positions (Fig. 6).

Fine-root biomass can show long-lasting effects from strong disturbances or climatic events. For example, in a

montane forest in Puerto Rico, reduced levels of fine-root biomass over a two-year period were attributed to a strong drought that occurred years before (Beard et al. 2005). At La Selva, the occurrence of the 1997–1998 mega-Niño in the first year of our study may have produced some of the big temporal signals we saw in fine-root biomass. This event at La Selva brought record low tree growth (Clark et al. 2003). Measurements in the CARBONO plots revealed unprecedented tree mortality, elevated leaf litterfall, and higher coarse woody debris inputs in that year (D. B. Clark and D. A. Clark, *unpublished data*), together with greater litter N:P values (Wood et al. 2005). Our fine-root biomass data (Figs. 5 and 6) indicate both a notable peak in dead fine roots (both size classes) in all edaphic conditions in early 1998 (a period of notably low rainfall and soil moisture; Fig. 4a, b), and a long-term decline in live biomass after that year. Ecosystem processes may also show multiyear cycles involving nutrient-cycle feedbacks, as hypothesized by Côté et al. (2003) to explain the temporal variation in root and aboveground biomass production they found in a temperate forest. Simultaneous studies under shorter periods (Schwendenmann et al. 2003,

Wood et al. 2005) and similar periods (Schwendenmann and Veldkamp 2006) suggest that La Selva's wet forest is subjected to environmental variation on a supra-annual basis (Fig. 13). In the future, integrated analysis of a longer time series of the CARBONO plot measurements of climatic factors, soil nutrients, and other C-cycle components should enable us to identify the key drivers of the substantial temporal variation we have found in fine-root stocks at La Selva.

#### *Fine-root stocks and soil moisture*

Although soil water content (SWC) was unvaryingly high (>50%) in the deeper layers of both soil types, seasonal (dry season) drawdowns were evident on both soil types in the more superficial soil layers where fine-root biomass was concentrated, and these decreases were greater on the Residual Soil (Fig. 4a). The minimum SWC levels measured during our study on the Old Alluvial terraces and Residual Soil plateaus, respectively, were 36.1% and 27.8% at 5 cm depth (corresponding to  $-0.26$  MPa and  $-1.67$  MPa using water retention curves developed by Schwendenmann et al. [2003] for both soil types). Water availability to plant roots can become limiting at these levels. The between-soil differences in SWC (Fig. 4a, b, Table 5) could be explained by differences in soil texture and structure (greater clay content and lower bulk density of the Residual Soil; Veldkamp et al. 2003), and greater water uptake by the greater fine-root biomass in the Residual Soil plateaus than in the Old Alluvial terraces (cf. Fig. 5). Differential soil drying across the La Selva landscape, particularly in periods of lower rainfall (such in the dry period of the 1998 El Niño Southern Oscillation) may account for the spatial  $\times$  temporal interactions of fine-root biomass and SWC at both inter- and intra-annual scales.

#### *Depth patterns of fine roots (landscape gradient only)*

On both soil types of the landscape-wide gradient (Old Alluvial terraces, Residual Soil plateaus) live fine-root biomass dropped rapidly with soil depth (Figs. 8 and 9), as has been documented before at La Selva (Raich 1980, Veldkamp et al. 2003), in tropical Australian forests (Maycock and Congden 2000), and across forests globally (Schenk and Jackson 2002). Approximately 70% of the live fine-root biomass in the top 50 cm of soil was at 0–20 cm depth (both soils; Table 1).

The strong overall differences in live fine-root stocks between soil types were confined to the top soil layer (Table 1), as were the large between-soil differences in dead fine-root stocks that occurred at many sample dates (Fig. 8). Although most nutrient stocks and ratios showed significant decreases with soil depth (except from P and Mn in both gradients; Table 2, Figs. 1 and 3), only three soil element indices exhibited a soil type  $\times$  depth interaction (soil K stocks, N:P, C:P; Table 2). Two of these indices (K and N:P) showed also strong

correlations with fine-root stocks, indicating that landscape-wide differences in K and P availability (relative to N) decrease with soil depth in a pattern parallel to spatial and vertical variation in fine roots. These relationships support the existence of a tight interrelation of soil nutrient stocks and stoichiometry with fine-root biomass across the landscape of La Selva, analogous to global patterns described by Jobbágy and Jackson (2001). In addition, the very similar time series of changes shown by fine-root stocks at the two soil depths (0–20, 20–50 cm; Fig. 8) indicate that a dominant controller(s) of fine-root biomass—whether direct climatic effects on the roots themselves, indirect effects of temporally varying tree C allocation, or some other factor(s)—affects root stocks uniformly down through the top 50 cm of soil.

#### *Fine-root stocks vs. demography*

As explained by Zak and Pregitzer (1998), lower relative biomass of fine roots with higher fertility could result from alternative permutations of fine-root demographic responses to increasing nutrients: (1) lower production and constant mortality, (2) greater mortality and constant production, or (3) greater increases in mortality than in production. Although fine-root demographic data are not yet available from La Selva (three years of root images are currently being analyzed from 72 CARBONO plot minirhizotrons; J. Espeleta, *unpublished data*), some preliminary inferences can be made from the patterns in fine-root stocks. Recent studies comparing tree species demography with root ingrowth cores in Residual Soils of La Selva (Valverde-Barrantes et al. 2006) indicate that fine-root accumulation can be controlled more by fine-root production rather than mortality. This observation is consistent also across the two La Selva edaphic gradients of our study, because live fine-root stocks were much more strongly associated with the spatial variation in soil elements than was fine-root necromass. The contribution of dead roots to total fine-root biomass was also small and varied little across depth (0–20, 20–50 cm), soil types, and slope positions (12–17%; Table 1). These numbers are similar to necromass proportions in tree plots at La Selva (Valverde-Barrantes et al. 2006), but strongly contrast with those found by Silver et al. (2005) for fine roots in a much drier Amazonian forest, where stocks were dominated by necromass (up to 80% of total fine-root biomass at 0–10 cm depth) and where the only edaphic responses were detected in dead fine roots. La Selva's much smaller fine-root necromass stocks over the entire landscape are likely due to higher root decomposition rates in this wetter forest (cf. Gholz et al. 2000). Although fine-root necromass did not vary edaphically at La Selva (Table 5A, B) it showed pronounced temporal variations during our seven-year study period (Figs. 5, 6, and 8), suggesting effects of climatic variation on root death and/or decomposition rates.

*Fine-root stocks across tropical forests*

The total fine-root stocks recorded in our study are among the lowest of any report in tropical forests. Mean fine-root biomass (<2 mm diameter) reached a maximum of 1.5 Mg/ha in Old Alluvial plots, and 2.3 Mg/ha in Residual plots. Maximum fine-root stocks by topographic level in Residual Soil slopes ranged from 2.7 Mg/ha in slope crests to 1.8 Mg/ha in slope bases. Considering only fine roots (<2 mm diameter) of both life classes (live + dead) and in the top soil (0–20 cm), our results are far below the range reported for lowland and premontane rain forests for the top 15 cm of soil (1.4 to 10.4 Mg C/ha; Lawson et al. 1970, Klinge 1975, Raich 1980, Berish 1982, Berish and Ewel 1988, Sanford 1989, Cavellier 1992, Silver and Vogt 1993, Green et al. 2005, Powers et al. 2005). In our study encompassing a larger sampling period, standing biomass of fine roots (live and dead) reached lower values. Topsoil (0–20 cm depth) fine-root biomass of our landscape gradient averaged 0.8–1.3 Mg/ha (Table 1), but the proportion of dead roots was still low, and decreased from deeper (20–50 cm) to more shallow (0–20 cm) soil depths (~18–12%, respectively). For the 0–50 cm depth, total stocks reached 1.2–1.8 Mg/ha across the topographic and landscape gradients. In contrast, Silver et al. (2005) reported greater fine-root (<2 mm) biomass only in the topsoil (0–10 cm) of Amazonian soils (2–3 Mg/ha), with a surprisingly high proportion of dead roots (up to 80% of total fine-root biomass). Dissimilar patterns among regions in the proportion of life classes suggest that local soil conditions may have specific effects on selected fine-root demographic functions (i.e., production, mortality, and decomposition rates). In a comparison across four neotropical forests, Powers et al. (2005) found a large-scale association between site fertility and standing fine-root biomass. Forests with very infertile soils like Oxisols of Cocha Cashu (Peru) and Km 41 (Manaus, Brazil) had the highest belowground allocation to fine roots (up to 10 Mg/ha).

The Oxisols at La Selva are comparably more fertile and have lower seasonality compared to these other forests, and total standing fine-root biomass was the lowest of all recorded. The magnitude of variation in belowground allocation associated with the differences in fertility at this large scale was greater than differences across fertility gradients at each site in Powers et al. (2005). Contrary to the results of the present study and of Gower (1987), soil fertility in Powers et al. (2005) did not appear to be strongly associated to standing fine-root biomass within La Selva, perhaps due to a lower spatial and temporal resolution.

The marked spatiotemporal variation in fine-root stocks in this study confirms that local edaphic gradients in tropical forests can lead to belowground allocation gradients similar to those observed in regional comparisons. At La Selva we found that a difference of ~50% and ~60% in live fine-root biomass across the landscape-wide and topographic gradients, respectively, was

associated with less variation in soil nutrient levels than across tropical forests as a whole (e.g., up to 9-, 76-, 27-, 16-fold variation in soil P, K, Ca, and Mg across four neotropical forests, associated with a threefold range in fine-root stocks; Powers et al. 2005). Previous studies of topographic and pedogenetical sequences in the Hawaiian islands (Vitousek et al. 2003) proposed that fine-scale variation overlaid the coarser gradients associated with soil age and climatic variation. The high spatial and temporal resolution of our study allowed us to demonstrate that two different scales of fertility variation (landscape wide and topographic) can overlay within a single tropical forest and still produce strong differentiation in belowground allocation, even for the same soil order and without major shifts in vegetation composition.

*Conclusions*

Our finding of significant space  $\times$  time interactions in fine-root stock dynamics indicates a combined effect of short- and long-term climatic variation (even in this wet tropical rain forest) and within-landscape edaphic variation. Fine-root biomass varied differently through the seven-year period along the landscape-wide and topographic gradients within this forest. This study is the first to measure fine-root stocks for a sufficiently long period to allow elucidation of such complex, nonlinear variation in fine-root biomass within a tropical forest. Our results demonstrate that explicitly structuring sampling across the important gradients within a forest and maintaining high sampling intensity through several to many years can greatly deepen understanding of belowground allocation. Assessing simultaneously the responses to edaphic and climatic variation is crucial, because the interaction of temporal and spatial heterogeneity can lead to shifts in nutrient limitation across the landscape. We propose that site-specific nutrient variation can be governed by differences in soil water content affecting nutrient acquisition (as in model predictions of ecosystem nitrogen limitation as affected by climate variability [Vitousek and Field 2001], and in models of phosphorus diffusion to the root affected by soil water content and path tortuosity [Nye and Tinker 1977]) and litter production and chemistry (Wood et al. 2005). Differences in nutrient acquisition should in turn feed back on nutrient cycles (Fig. 13). Nonlinear space  $\times$  time coupling in the variation of fine-root stocks, as we found at La Selva, indicates strong sensitivity of belowground carbon and nutrient cycles to shifting ecological scales, and supports the need to explore ecosystem responses to global change at finer resolution and over longer time spans than is generally recognized.

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#### APPENDIX A

A map of La Selva Biological Station showing the location of 18 CARBONO plots in the different soil gradients (*Ecological Archives* M077-012-A1).

#### APPENDIX B

A list of methods and equipment used for soil chemical analysis (*Ecological Archives* M077-012-A2).

#### APPENDIX C

A table showing the number of fine-root samplings per soil gradient, depth, and date (*Ecological Archives* M077-012-A3).

#### APPENDIX D

Graphs showing how fine-root biomass compares between Residual Soil plateaus and slopes during the seven-year study period (*Ecological Archives* M077-012-A4).

#### APPENDIX E

Pearson's correlation coefficients of environmental variables and fine-root biomass (*Ecological Archives* M077-012-A5).

#### APPENDIX F

Pearson's correlation coefficients of soil element contents in landscape-wide and topographic gradients (*Ecological Archives* M077-012-A6).

#### APPENDIX G

Raw data file (in tabular form) fine-root biomass (live, <2 mm diameter) across all sampling dates and replicate sites (*Ecological Archives* M077-012-A7).

#### APPENDIX H

Raw data file (in tabular form) of fine-root biomass (dead, <2 mm diameter) across all sampling dates and replicate sites (*Ecological Archives* M077-012-A8).

**APPENDIX I**

Raw data file (in tabular form) of fine-root biomass (live, 2–5 mm diameter) across all sampling dates and replicate sites (*Ecological Archives* M077-012-A9).

**APPENDIX J**

Raw data file (in tabular form) of fine-root biomass (dead, 2–5 mm diameter) across all sampling dates and replicate sites (*Ecological Archives* M077-012-A10).

**APPENDIX K**

Raw data file (in tabular form) of fine-root biomass from split cores by life and diameter category, soil depth, and across all sampling dates and replicate sites (*Ecological Archives* M077-012-A11).

**APPENDIX L**

Raw data file (in tabular form) of soil element contents by depth, gradient, and site (*Ecological Archives* M077-012-A12).