

## Drought and Irrigation Effects on Fine Root Dynamics in a Tropical Moist Forest, Panama<sup>1</sup>

Joseph B. Yavitt

Department of Natural Resources, Fernow Hall, Cornell University, Ithaca, New York 14853, U.S.A.

and

S. Joseph Wright

Smithsonian Tropical Research Institute, Apartado 2072, Balboa, Republic of Panamá

---

### ABSTRACT

Seasonal drought in tropical moist forest may be the cue for fine root death and turnover, and it may signal root growth deeper to access subsurface water and (or) nutrients. We examined these predictions by measuring fine root biomass (<2 mm diam.) and the timing of root growth and disappearance in an old growth tropical moist forest on Barro Colorado Island (BCI), Republic of Panama, in the fifth year of a dry season irrigation experiment. Irrigated soil had greater available P concentrations; however, a more pronounced effect was less stable soil aggregates causing higher bulk density. Irrigation did not affect fine root biomass. Mean ( $\pm$ SE) biomass between 0 and 30 cm was  $372 \pm 63$  g/m<sup>2</sup> within control versus  $286 \pm 39$  g/m<sup>2</sup> within irrigated plots. Mean biomass between 45 and 75 cm was  $74 \pm 7$  g/m<sup>2</sup> within control versus  $62 \pm 7$  g/m<sup>2</sup> within irrigated plots. Dead roots were less than eight percent of the total. We characterized root growth using in-growth screens (1.7 mm mesh) installed between 0 and 15 cm. Root density in the screens peaked soon after the rains began in the control plots but during the dry season in the irrigated plots. Very few dead roots accumulated in the screens, with no differences seasonally or among treatments. We developed a model to estimate birth and death rates of fine roots using root densities in the in-growth screens and the disappearance of roots laced into screens and incubated *in situ*. Inferred root birth rates were greatest in the early part of the wet season in control plots and in the dry season in irrigated plots. Inferred mortality rates of fine roots less than four months old were reduced by irrigation, but this was offset by much greater disappearance of six- to eight-month-old roots in the irrigated plots. Although irrigation altered the timing of root growth and mortality, roots did not grow year-round in the always-wet soil. Therefore, soil water availability was an important cue for root growth, but an inherent seasonal cycle remained. Fine roots died continuously throughout the year and disappeared quickly.

---

### RESUMEN

La sequía estacional en los bosques húmedo tropicales podría ser la señal que promueve la muerte y recambio de las raíces y su crecimiento hacia zonas más profundas del suelo para acceder a fuentes de agua subterránea y/o a nutrientes. Para examinar estas predicciones medimos la biomasa de raíces finas (diámetro <2 mm) y la cronología de su crecimiento y desaparición durante el quinto año de un experimento de irrigación de la época secas en un bosque húmedo tropical maduro de la Isla de Barro Colorado (IBC) en la República de Panamá. El suelo que fue irrigado tuvo mayores concentraciones de fósforo disponible. Sin embargo, fue más notable fue la presencia de agregados de suelo menos estables que dieron lugar a una mayor densidad del suelo. La irrigación no afectó la biomasa de raíces finas. Entre 0 y 30 cm de profundidad el promedio ( $\pm$  error estándar) de la biomasa de raíces fue  $372 \pm 63$  g/m<sup>2</sup> en las parcelas control y  $286 \pm 39$  g/m<sup>2</sup> en las parcelas irrigadas. Entre 45 y 75 cm estos valores fueron  $74 \pm 7$  g/m<sup>2</sup> en las parcelas control y  $62 \pm 7$  g/m<sup>2</sup> en las parcelas irrigadas. Las raíces muertas representaron menos del 8 por ciento de la biomasa total de raíces. Para caracterizar el crecimiento de las raíces, utilizamos mallas de crecimiento (ojo de malla = 1.7 mm) instaladas entre 0 y 15 cm de profundidad. En las parcelas de control la densidad de raíces en las mallas alcanzó sus valores máximos inmediatamente después del inicio de las lluvias; por el contrario, las máximas densidades de raíces en las parcelas irrigadas se observaron durante la época seca. El número de raíces muertas que encontramos en las mallas fue muy bajo y no varió entre las estaciones, ni entre los tratamientos. Para estimar las tasas de producción y mortalidad de raíces finas desarrollamos un modelo que utiliza la densidad de raíces en las mallas de crecimiento y la desaparición de raíces atadas a las mallas e incubadas *in situ*. Las tasas de producción de raíces que calculamos alcanzaron sus valores máximos al inicio de la época lluviosa en las parcelas de control y durante la época seca en las parcelas irrigadas. La irrigación redujo la mortalidad calculada de las raíces finas de menos de cuatro meses de edad, pero este cambio fue compensado por una mayor tasa de desaparición de las raíces de seis a ocho meses en las parcelas irrigadas. A pesar de que la irrigación alteró la cronología del crecimiento y mortalidad de las raíces, éstas no crecieron a lo largo de todo el año en el suelo con humedad permanentem de las parcelas irrigadas. Por lo tanto, la disponibilidad de agua en el suelo fue una señal importante para el crecimiento de las raíces, pero se

---

<sup>1</sup> Received 25 July 1999; revision accepted 11 July 2000.

mantuvo un ciclo estacional intrínseco. Las raíces finas murieron continuamente a lo largo del año y desaparecieron rápidamente.

*Key words:* fine root demography; forest irrigation; Panama; root growth; soil aggregates; soil fertility; tropical moist forest.

LIKE OTHER PLANT ORGANS, FINE ROOTS are born, they age, and they die (Eissenstat & Yanai 1997). Because these processes occur below ground, our understanding of their dynamics and control by soil conditions (*e.g.*, temperature, moisture, and structure) versus resource levels (*e.g.*, inorganic nutrient availability and supply of photosynthate) versus other factors (*e.g.*, grazing) is very limited. Clearly, we need more detailed studies of fine root dynamics, especially in tropical forests, to understand the consequences of root life span for plant growth and productivity, plant competition, and carbon (C) flow and nutrient cycling (Eissenstat & Yanai 1997).

In theory, fine roots should grow and live longer in resource-rich parts of the soil because tissue can be maintained more cheaply (in terms of C for respiration) than growing new roots. When conditions and/or resource levels fluctuate, growth should peak under the most favorable conditions. Shedding of fine roots, however, may not be necessary under unfavorable conditions if reductions in maintenance respiration can match reductions in water and nutrient uptake (Kosol & Eissenstat 1994).

In northern hardwood forests, the birth of new roots peaks in early spring soon after leaf flush in the canopy (Burke & Raynal 1994, Fahey & Hughes 1994, Hendrick & Pregitzer 1996). Hence, growth coincides with seasonal increases in both soil temperature and gross photosynthesis. In more northern taiga forests, however, maximum root growth lags behind leaf flush by several weeks (Ruess *et al.* 1998) until the soil warms to the temperature optimum for root growth (Steele *et al.* 1997). This pattern, combined with the finding that root mortality occurs primarily in the winter (Ruess *et al.* 1998), indicates that soil temperature is a strong cue for root dynamics in northern systems (Hendrick & Pregitzer 1997). Temperature control, however, seems unlikely in tropical forests. Rather, studies of forest in which rainfall is highly seasonal have shown that roots grow mostly in the rainy season (Kavanagh & Kellman 1992, Lopez *et al.* 1998) and die during the dry season (Srivastava *et al.* 1986, Kummerow *et al.* 1990). Although these patterns suggest direct control by soil water availability, growth also coincides with leaf flush in the canopy and a very sharp increase in soil nutri-

ent availability as the rains begin (Singh *et al.* 1989, Roy & Singh 1995), which may be the ultimate cues. Other important factors during drought include the inability to penetrate the hard clay soil (Cavelier 1992, Carvalheiro & Nepstad 1996) and the need to grow deeper into the soil to access subsurface moisture (Hinckley *et al.* 1983, Dickmann *et al.* 1996). While soil conditions and leaf flush are the conspicuous controls of fine root dynamics, no less important are subtle factors such as grazing both above ground (Ruess *et al.* 1998) and below ground (Stanton *et al.* 1981), about which very little is known.

We examined fine root dynamics as part of a dry season irrigation experiment on Barro Colorado Island (BCI), Republic of Panama, in which two 2.25 ha plots of old growth tropical moist forest were irrigated during the four-month dry season for five contiguous years. Two 2.25 ha control plots had ambient soil water levels. Within the control plots, we expected fine root growth to peak soon after the rains begin and root mortality to peak in the dry season. If true, this would not necessarily mean direct control by soil moisture availability because the onset of rains also causes a confounding pulse in soil nutrient availability, although less than in dry tropical forest (Yavitt & Wright 1996), and a peak in canopy leaf flush (Wright & Cornejo 1990). Dry season irrigation, however, had several effects that helped us understand root dynamics. (1) It alleviated drought stress and prevented soil drying and hardening; (2) it increased, but slightly, the pulse in soil nutrient availability (Yavitt & Wright 1996); and (3) it had no effect on leaf flush in the canopy (Wright & Cornejo 1990), although it affected phenology of some understory shrubs (Wright 1991) and had strong effects on growth of herbs (Fisher *et al.* 1991). Therefore, finding root growth during the dry season in irrigated plots would allow us to reject the hypothesis that the pulse in soil nutrient availability and/or leaf flush in the canopy are the ultimate cues.

We also examined whether five contiguous years of dry season irrigation altered soil fertility and soil structure. Yavitt and Wright (1996) measured only nutrient availability in the surface soil (0–15 cm depth), not throughout the soil profile. Therefore, we examined soil nutrient concentrations to 1 m depth in control and irrigated plots.

Kursar *et al.* (1995) found lower soil oxygen concentrations within the irrigated plots, suggesting less soil aeration. We hypothesized that drying helped increase the stability of soil aggregates (Utom & Dexter 1982, Epshteyn *et al.* 1987), and thus the loss of aggregate stability in the irrigated plots contributed to lower aeration.

We studied fine root dynamics using an *in situ*, in-growth screen method that Fahey and Hughes (1994) developed as an inexpensive and efficient way to quantify fine root growth. The method measures community-level root dynamics averaged across species. To ensure that these averages were representative, our design included a large number of randomly located replicates. We extended the method to include the disappearance of fine roots that we laced into screens and then incubated *in situ*. We used the data in a model to infer birth and death rates of fine roots. We also analyzed our data in the model of Santantonio and Grace (1987) that estimates mean life span from the masses of live and dead fine roots.

## MATERIALS AND METHODS

**STUDY SITE.**—Barro Colorado Island (9°9'N, 79°51'W) has a tropical monsoon climate under the Köppen system of climatic classification and supports tropical moist forest in the Holdridge Life Zone System (Holdridge & Budowski 1956). Ten percent of the canopy tree species are dry season deciduous (Croat 1978). Mean monthly maximum temperatures at 1 m in the forest understory vary just 1°C from 22.4 in January to 23.4°C in June (Windsor 1990). Annual precipitation is 2620 mm. A predictable four-month dry season begins in December and ends in April, with just 84 mm of rain between 1 January and 31 March (Windsor 1990). Litterfall peaks early in the dry season during December, remains high through April, and falls by 50 percent to low wet season levels from May to November (Wright & Cornejo 1990).

The irrigation experiment was conducted in forest established on a well drained Alfisol (Yavitt *et al.* 1993) derived from volcanoclastic sandstone (Johnsson & Stallard 1989). The mineral soil is rich in Ca, Mg, and S but poor in K and P. The soil has 40 percent clay content, 35 percent silt content, and 25 percent sand content between 0 and 15 cm depth (Yavitt *et al.* 1993).

Irrigation occurred throughout each dry season from 1986 through 1990. We used water drawn from Gatun Lake and delivered by sprinklers mounted 1.8 m above the ground, arranged in a

hexagonal array at 15 m intervals. Each point, except plot borders, would have received irrigation water from three or more sprinklers, except for interception by the vegetation. The irrigation schedule was modified continuously to maintain soil water potentials (20 cm depth) above  $-0.03$  MPa compared to levels as low as  $-1.5$  MPa in the control plots during the dry season (Wright 1991). On average, irrigation deposited 30 mm of water per week in each irrigated plot (Wright 1991).

The irrigation treatment did not cause a confounding fertilization effect because solute concentrations in Gatun Lake are exceedingly low (Gonzalez *et al.* 1975). The weekly influx in irrigation was 45 mg Ca/m<sup>2</sup>, 7.5 mg Mg/m<sup>2</sup>, 15 mg K/m<sup>2</sup>, 45 mg N/m<sup>2</sup>, and 1.5 mg P/m<sup>2</sup>.

**SOIL CHARACTERISTICS.**—Between 18 and 27 February 1990, we opened five pits in each plot ( $N = 20$ ). The sites were chosen using random numbers and a 15 m × 15 m coordinated grid across the central 120 m × 120 m of each plot. Pit depth was 1 m unless saprolite was encountered sooner. Four soil samples (2.5 cm diam. × 15 cm long) were collected from each face inside each pit at the following depths (when possible): 1, 5, 10, 15, 25, 35, 45, 55, 75, and 95 cm. We bulked samples taken from each face, giving us four replicate samples from each depth in each pit.

One sample from each depth was used to estimate initial moisture content (drying at 105°C) and bulk density as dry mass of known collection volume. We used a second sample to estimate soil bulk density another way by applying Archimedes' principle to determine volume of soil clods covered with saran (Blake & Hartge 1986). We examined two clods per sample ( $N = 1120$ ). We measured the mass and volume of clods twice: once field-moist and again after oven-drying at 105°C. We also measured the stability of soil of aggregates using a modification of the technique described by Strickland *et al.* (1988). We did not measure the amount of aggregation (*i.e.*, the pyrophosphate treatment), but we did measure the breakdown of aggregates in water and in sodium oxalate, as prescribed. We also measured loss on ignition for soil (minus roots) by heating for 4.5 hours at 450°C. We examined triplicates per sample.

We used the third sample from each depth to estimate soil chemical concentrations. Base cations (Ca, Mg, K, and Na) and aluminum (Al) were extracted from a separate 5 g sample of fresh soil using 50 ml of 1 mol/liter NH<sub>4</sub>Cl for 12 hours. Nitrogen (NH<sub>4</sub>, NO<sub>3</sub>) was extracted from a sepa-

rate 5 g sample of fresh soil using 50 ml of 2 mol/liter KCl. Phosphorus was extracted from a separate 1 g sample of fresh soil using 7 ml of an acid fluoride solution (Olsen & Sommers 1982).

We used the fourth sample from each depth to estimate fine root biomass. Roots (<2 mm diam.) were separated from soil by washing over 500  $\mu$ m screens and hand-sorting material. All roots and root fragments were classified as "live" or "dead" based on gross morphology and condition. Dead roots were brittle and dark. Roots were dried for 48 hours at 60°C and weighed to  $\pm 0.1$  mg.

**ROOT DYNAMICS.**—Although in-growth screens provide an inexpensive method to assess fine root dynamics, the method requires several assumptions. One is the effect of root severing during installation, which is inevitable; however, we detected periods of very rapid growth in screens installed two, four, and eight months before the growth episode (see below), suggesting little disturbance associated with screen installation. Another potential problem is that fine roots may grow, die, and disappear before the screen is excavated, which would underestimate the growth rate. Therefore, we made measurements at two- and four-month intervals after installation. Although the age of a root affects mortality rates (Clarkson *et al.* 1968), we assumed mortality was constant for "cohorts" of roots that differed in age by no more than two months. We also modified the method to include "disappearance screens" in which we laced a known number of roots in the screen, then incubated the screen *in situ*. After incubation, we removed these screens with utmost care to ensure no contacts were lost by the excavation process, and we used the data to correct for intersections lost from the in-growth screens.

We chose six locations in each plot using random numbers and the 15  $\times$  15 m coordinated grid in the central 120  $\times$  120 m area of each plot in December 1988, and we used these locations repeatedly throughout the study. Pieces of nylon-coated, fiberglass screen (1.7 mm mesh; 5 cm wide) were inserted into slits (15 cm deep) made *in situ* with a sharp, straightedge tool on eight different dates. Ten screens were installed at each location on 15 December 1988 and ten more on 7 September 1989. Four additional screens were installed at each location on 3 March 1989, 28 April 1989, 30 June 1989, 13 November 1989, 15 December 1989, and 13 February 1990. At two-month intervals after installation, two screens from each set were analyzed *in situ* by excavating soil from one

side of the screen and by recording roots passing through the screen in one of three diameter classes: <1 mm, 1–2 mm, and >2 mm. Roots were classified as live or dead based on gross morphology, dead roots being brittle and dark in color. A total of 1056 in-growth screens were censused.

The disappearance screens were assembled starting one week before installation of the in-growth screens. We collected soil near the study area and picked fine roots from it by hand. Random subsamples of roots were used to determine initial moisture and ash content. The remaining roots were air-dried for one day and brushed free of mineral soil. Eight 7 cm segments (<2 mm diam. and weighed to  $\pm 0.1$  mg) were sewn or laced into each disappearance screen, and the initial number of root–screen intersections was recorded ( $I_1 = 33.9 \pm 4.7$ ;  $\bar{x} \pm$  SD). Four of these screens were installed along with each in-growth screen on each installation date. Two screens were excavated at each location two and four months after installation, and the final number of root–screen intersections was recorded ( $I_2$  or  $I_4$ ). Root disappearance rates were estimated as the proportion of root contacts lost in the appropriate time interval [*i.e.*, for four months:  $1 - (I_4/I_1)$ ]. Roots initially sewn into the screens were easily distinguishable upon excavation because they still passed through the screens multiple times. A total of 384 disappearance screens were censused.

Birth rates and mortality rates of roots were inferred from the harvesting of in-growth and disappearance screens after two or four months. Let the relative number of live and dead roots at time  $t$  be  $L_t$  and  $D_t$ , respectively, where  $t$  refers to the two or four-month harvest. Also, let the disappearance rate of roots be  $v_t$ , the birth rate be  $b_t$ , and the mortality rate be  $m_t$ . Then,

$$L_t = (L_{t-1} + b_{t-1,t}) \cdot (1 - m_{t-1,t}) \quad \text{and} \quad (1a)$$

$$D_t = (L_{t-1} + b_{t-1,t}) \cdot m_{t-1,t} + D_{t-1} \cdot (1 - v_{t-1,t}). \quad (1b)$$

$L_2$ ,  $L_4$ ,  $D_2$ , and  $D_4$  were measured directly, and the equations were solved for  $b$  and  $m$ . Assumptions implicit to this model are considered in the Discussion.

**STATISTICAL ANALYSES.**—Within-location averages of all data were used for statistical analyses, resulting in 10 or 12 replicate values ( $N = 5$  or 6 per plot) for each variable in each treatment (control and irrigated). We used repeated measures analysis of variance (ANOVA) to test effect of treatment and

depth on soil characteristics. Depth was a fixed repeated measure or within-subjects effect. Treatment was a fixed between-subjects effect, and plot was a random effect nested within treatment. We also used repeated measures ANOVA to test effects of treatment and date on the number of roots alive at two months, alive at four months, and dead at four months after screen installation, and the proportion of roots lost after four months. Date was a fixed repeated measure or within-subjects effect. *Post hoc* tests based on single treatments were used to evaluate significant interactions between treatment and installation dates. All analyses were performed with SYSTAT 8.0.

## RESULTS

**SOIL CHARACTERISTICS.**—Several soil characteristics differed significantly among irrigated and control plots (Fig. 1; Table 1). Since sampling occurred in the dry season, gravimetric soil water content was nearly invariant down the profile in the control plots, whereas it was 40 percent greater at the surface within the irrigated plots. Soil bulk density was greater at the surface than depth in the control plots, but surprisingly, it was significantly greater below 35 cm depth in the irrigated plots. Soil aggregates in the top 35 cm of the irrigated plots were significantly less stable (*i.e.*, more fine particles dislodged by shaking) in the water shake than aggregates from control plots. There was no significant effect of irrigation on aggregate stability measured in the sodium oxalate shake.

Concentrations of inorganic soil nutrients were consistently greater in irrigated than control plots, although the trend was statistically significant only for  $\text{PO}_4$  (Fig. 2; Table 1). Most of the treatment differences occurred between 45 and 90 cm.

Fine root biomass did not differ significantly among irrigated and control plots (Fig. 3; Table 1). Biomass in the upper 30 cm of the soil averaged ( $\bar{x} \pm \text{SE}$ ;  $N = 10$ )  $372 \pm 63 \text{ g/m}^2$  in the control versus  $286 \pm 39 \text{ g/m}^2$  in the irrigated plots. Between 45 and 95 cm, biomass was  $74 \pm 7 \text{ g/m}^2$  in the control versus  $62 \pm 7 \text{ g/m}^2$  in the irrigated plots. The proportion of dead root biomass was very low (7.7% in the control plots and 5% in the irrigated plots) and did not differ significantly among treatments.

**FINE ROOT DYNAMICS.**—More than 90 percent of the roots passing through the in-growth screens installed in December 1988 and again in September 1989 were live (Fig. 4) and less than 1 mm in

diameter (Fig. 5) ten months after installation. In both sets, fine root density peaked about six months after installation and declined after that. The decline was significantly greater in the irrigated than control plots, so that fine root density did not differ among treatments after ten months. Likewise, mean values were similar for the screens installed in December 1988 (0.19 root/cm<sup>2</sup>) versus September 1989 (0.16 root/cm<sup>2</sup>).

We found that fine root density was about twice as high in the irrigated than control plots during the dry season, whereas no treatment effect occurred during the wet season (Fig. 6). In the control plots, fine root density was 0.128 root/cm<sup>2</sup> after two months and 0.165 root/cm<sup>2</sup> after four months of the wet season compared to 0.063 root/cm<sup>2</sup> after two months and 0.102 root/cm<sup>2</sup> after four months of the dry season. In the irrigated plots, fine root density averaged 0.169 root/cm<sup>2</sup> after two months and 0.270 root/cm<sup>2</sup> after four months of the dry season, compared to 0.058 root/cm<sup>2</sup> for growth that occurred during the wet season.

As noted in Figure 4, fine root density peaked several months after screen installation, suggesting that rates of root growth and mortality reached a balance. The time interval until peak root density differed between seasons, however, as root intersections continued to increase for a longer duration during seasons associated with high root growth rates. For example, fine root density after two months of the wet season was similar to fine root densities after ten months (0.16 and 0.13 root/cm<sup>2</sup> vs. 0.19 and 0.16 root/cm<sup>2</sup>, respectively; Figs. 4 and 6). For four of the eight sets of screens, the fine root density was similar at two versus four months after screen installation ( $P > 0.4$ ; *post hoc* tests based on a three-factor ANOVA). Therefore, the ratio of live root densities at two and four months approached unity for each of these four installation dates (bottom panel in Fig. 6); however, fine root densities continued to increase when the interval fell during a season associated with high root growth (*i.e.*, dry to wet transition in control plots; dry season in irrigated plots; Fig. 6). Hence, steady state values were approached within two months of screen installation, except during the early wet season in the control plots, and in the dry season under irrigation.

The density of dead roots was just 0.012 root/cm<sup>2</sup> and did not differ among treatments or among sample dates (data not shown; Table 2). The disappearance screens showed that 90 percent of the initial root contacts remained after two months

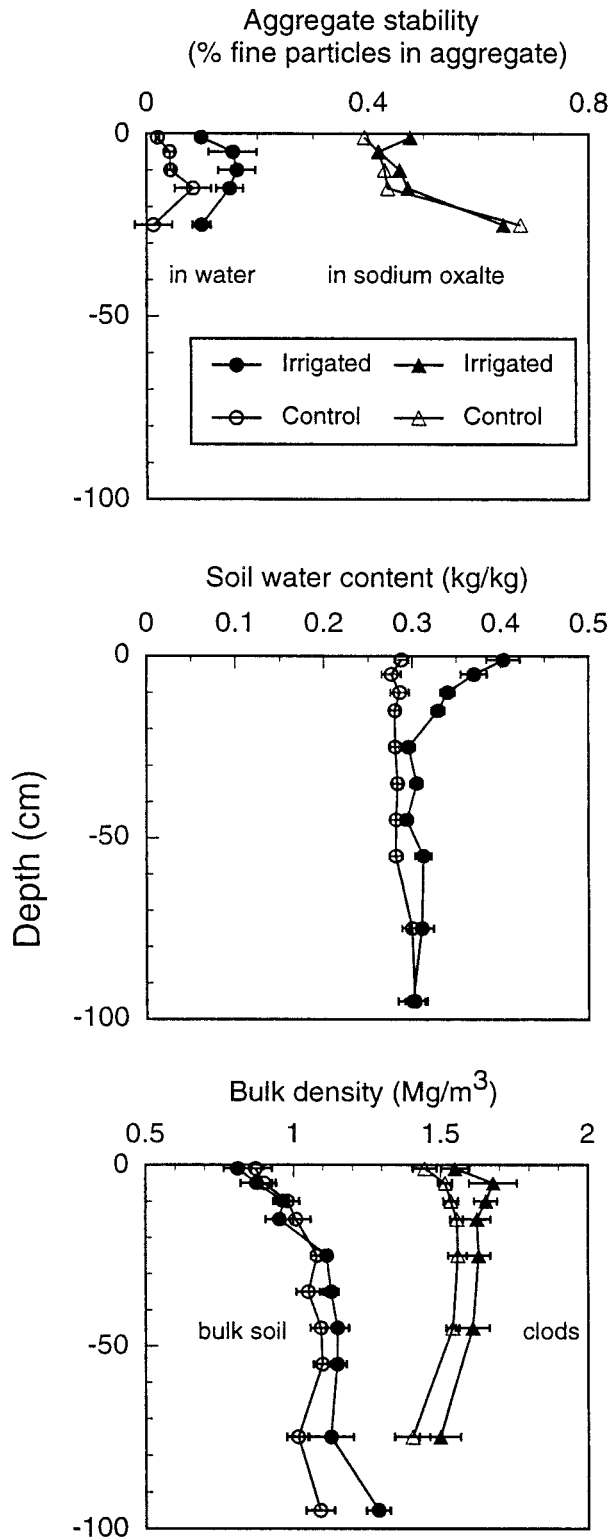


FIGURE 1. Soil physical characteristics in control and irrigated plots sampled during the dry season in February 1990. Symbols are  $\bar{x} \pm 1$  SE.

TABLE 1. F-values in the repeated measures ANOVA for gravimetric soil water content, aggregate stability in water, density of bulk soil and soil clods, exchangeable soil chemical concentration, and fine root biomass. Repeated measures occurred on depth in each soil pit to 35 cm depth. Fixed levels of treatment were irrigated and control. Random effects of plot nested within treatments have been pooled with the appropriate error. Error df were 90 for soil physical characteristics and fine root biomass, and 36 for soil chemical characteristics. Significance (\*) was  $P < 0.05/18$ .

Source	df	Water	Agg. stab.	Bulk den.	Clod den.
Treatment	1	45.8	10.5*	11.4*	25.3*
Depth	5	19.3*	3.8	9.7*	6.7
Depth × TMT	5	16.3*	1.0	18.5*	1.0
Source	df	NH <sub>4</sub> <sup>+</sup>	NO <sub>3</sub> <sup>-</sup>	PO <sub>4</sub> <sup>3+</sup>	Al <sup>3+</sup>
Treatment	1	3.3	1.0	10.5*	1.0
Depth	2	10.9*	37.6*	22.8*	11.0*
Depth × TMT	2	2.9	1.0	1.0	1.1
Source	df	Ca <sup>2+</sup>	Mg <sup>2+</sup>	K <sup>+</sup>	Na <sup>+</sup>
Treatment	1	1.0	1.0	1.4	2.0
Depth	2	4.3	1.0	6.5	1.4
Depth × TMT	2	1.0	1.0	1.0	1.8
Source	df	Total root bio.	Dead root bio.		
Treatment	1	1.1	1.1		
Depth	5	19.6*	7.4*		
Depth × TMT	5	0.7	0.1		

(Fig. 7), and there was no difference among treatments. After four months, however, the disappearance of root–screen contacts differed significantly among treatments, averaging 29 percent in the irrigated plots and 19 percent in the control plots (Table 2).

From equation (1), we determined that irrigation altered the seasonality of inferred root birth rates (top panel in Fig. 8; Table 2). In control plots, inferred birth rates averaged 0.177 root/cm<sup>2</sup> for the sample in place during the dry to wet season transition (the second sample in Fig. 8) and just 0.050 root/cm<sup>2</sup> during the remainder of the year. In contrast, in irrigated plots, inferred birth rates averaged 0.145 root/cm<sup>2</sup> for the three dry season samples and the one sample in place during the wet to dry season transition (the first and fifth through seventh samples in the top panel of Fig. 8). After that, inferred birth rates were just 0.028 root/cm<sup>2</sup> during the remainder of the year. Dry season irrigation reduced inferred root mortality rates of roots less than four months old, which averaged 4.4 percent in the irrigated plots and 10.5 percent in the control plots (bottom panel in Fig. 8; Table 2).

## DISCUSSION

The reason for collecting and analyzing soil samples in February 1990 was to examine how five contiguous years of dry season irrigation affected

chemical and physical properties. Our results indicated that irrigation leached very little inorganic chemical elements into the subsoil. Only available P showed significantly greater concentrations in irrigated than control plots; however, P is essentially immobile in old clay soil (Walker & Syers 1976). Rather, our results suggested that irrigation caused fine soil particles to dislodge from soil aggregates in the surface soil and move downward to fill soil air spaces in the subsoil. Therefore, P moved as a particulate rather than as a solute. The results also supported the hypothesis that periodic drying increased the stability of soil aggregates (Utomo & Dexter 1982, Epshteyn *et al.* 1987). Stable soil aggregates are necessary to create soil air spaces that give the good drainage property to soil with a high clay (*i.e.*, very small particle size) content. Apparently, the soil had enough shrink–swell clay in it (Uehara & Gillman 1981) to affect soil aggregate stability upon drying.

The net effect of the changes in soil characteristics, including the somewhat greater concentrations of Al in irrigated plots (Fig. 2), would have impeded (not promoted) greater fine root biomass. For example, studies in tropical forests have shown negative relationships between fine root biomass and (1) available P concentrations (Gower 1987, Cavelier 1992, Maycock & Congdon 2000), (2) harder, denser soil (Carvalho & Nepstad 1996), and (3) concentrations of Al (Hirano & Hijii

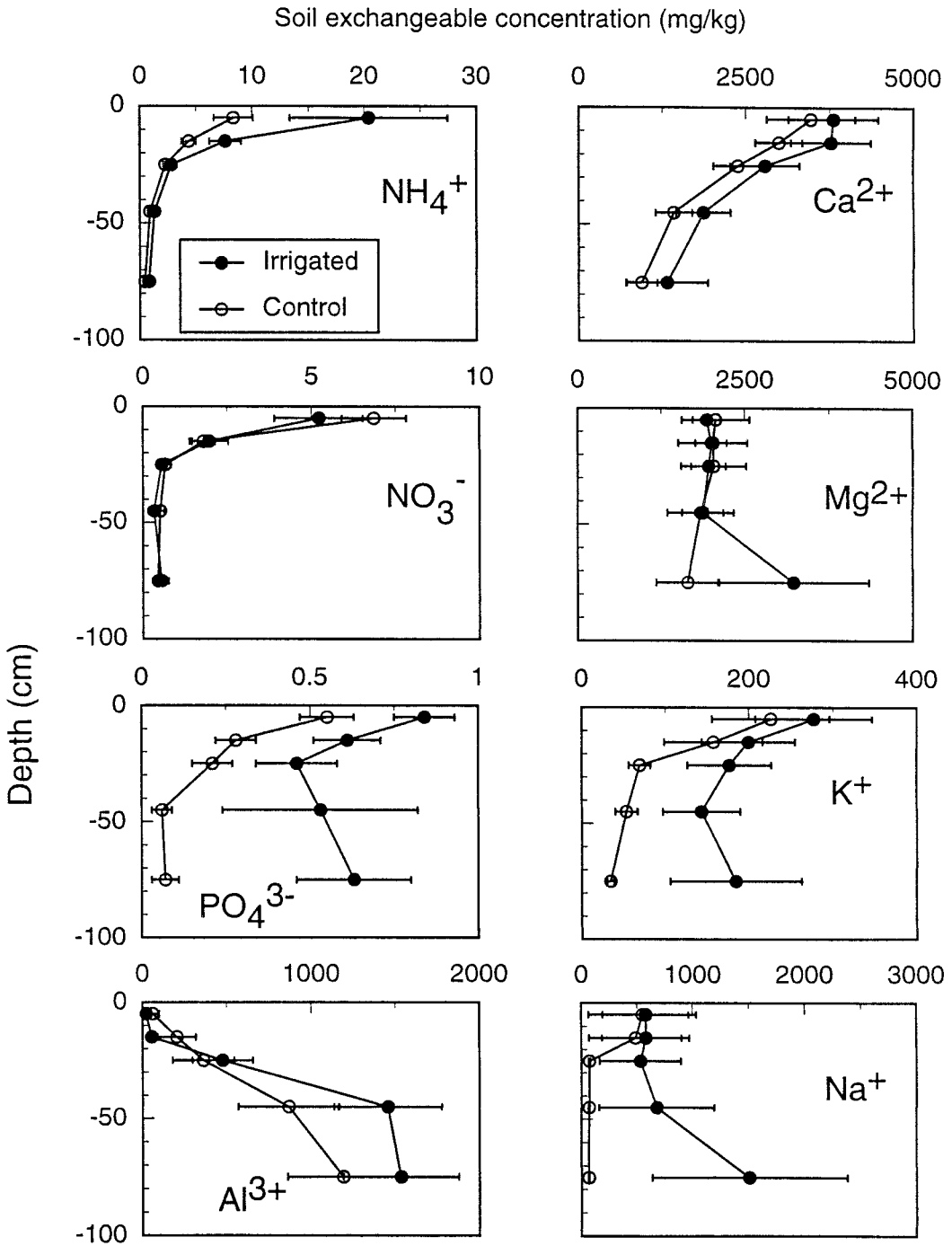


FIGURE 2. Soil chemical characteristics in control and irrigated plots sampled during the dry season in February 1990. Symbols are  $\bar{x} \pm 1$  SE.



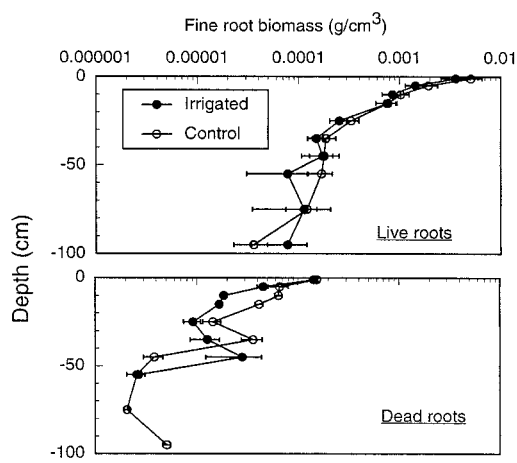


FIGURE 3. Biomass of live and dead fine roots in control and irrigated plots sampled during the dry season in February 1990. Symbols are  $\bar{x} \pm 1$  SE.

1998). Therefore, our result of no statistical difference in fine root biomass throughout the soil profile in irrigated and control plots was consistent with these patterns. In contrast, Cavelier *et al.* (1999) reported significantly greater fine root biomass in the surface soil of the irrigated plots during the fourth year of the experiment. That treatment difference, however, occurred in March during the dry season, and it may have been short-lived.

Nevertheless, it was somewhat surprising to find that fine roots penetrated more than 1 m deep in the irrigated plots, given no soil water limitation in the top 25 cm of the soil. This suggests that

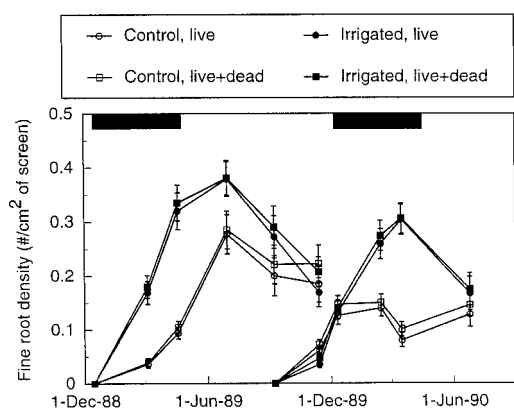


FIGURE 4. The density of living and living plus dead roots for in-growth screens installed on 15 December 1988 and 7 September 1989, and excavated and censused ca 2, 4, 6, 8, and 10 months later. Symbols are  $\bar{x} \pm 1$  SE. Dark bar denotes dry season.

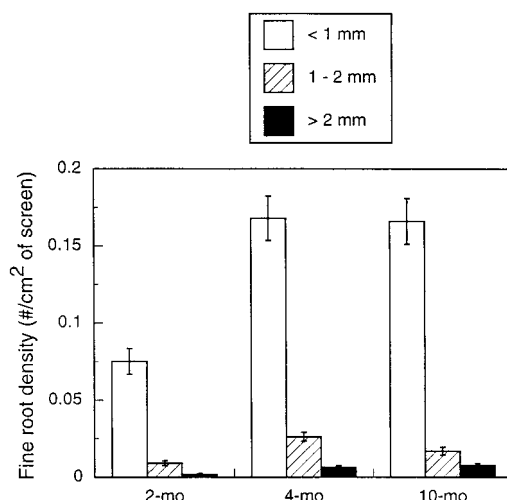


FIGURE 5. The density of fine roots in three diameter classes in in-growth screens excavated 2, 4, and 10 months after installation. Bars represent  $\bar{x} \pm 1$  SE.

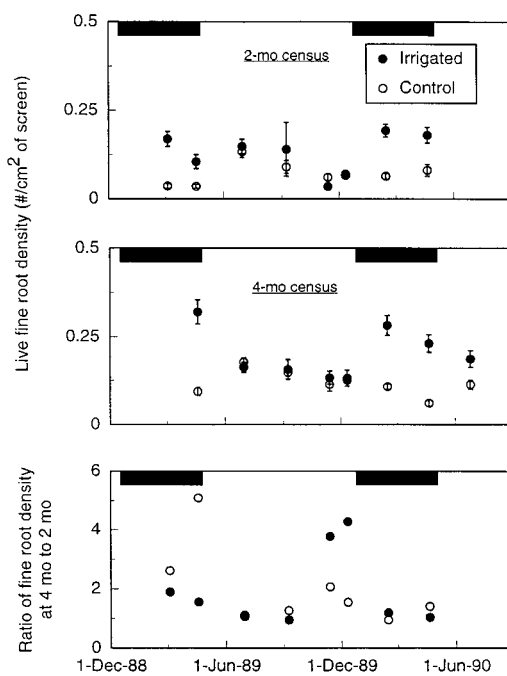


FIGURE 6. The density of live roots for screens censused 2 months after installation (top panel) and 4 months after installation (middle panel) and their ratio (bottom panel) in control and irrigated plots. Symbols are  $\bar{x} \pm 1$  SE. Dark bar denotes dry season.

TABLE 2. F-values and significance levels in the repeated measures ANOVA for root growth into in situ screens. Dependent variables for six separate analyses were the density of roots alive at 2 months, alive at 4 months, and dead at 4 months after screen installation, the proportion of dead root contacts lost after 4 months, and the birth rate (number/cm<sup>2</sup>/2 mo) and death rate (proportion/2 mo) of roots inferred from a simple model of root dynamics (equation 1). Repeated measures occurred on the date of screen installation. The fixed levels of treatment were irrigated and control. The random effects of plot nested within treatments were pooled, with the appropriate error term (see Results).

Source of variation	Root density (no./cm <sup>2</sup> )			Root dynamics		
	Alive 2 mo	Alive 4 mo	Dead 4 mo	Lost (no.)	Birth	Death
Between subjects						
Treatment	47.4**	38.9**	3.8	14.3*	1.3	9.1*
Within subjects						
Date	7.2**	3.0	1.9	1.8	4.5*	2.6
Date × TMT	6.7**	7.9**	1.1	1.1	4.0*	1.5

\*  $P < 0.05/18$ .

\*\*  $P < 0.01/18$ .

deep fine roots behaved independently of the surface soil environment and/or plant water status (Hendrick & Pregitzer 1997). This agrees with other studies showing that deep roots behaved independently in irrigation experiments (Axelsson & Axelsson 1986, Joslin & Wolfe 1998), although the study of Joslin and Wolfe (1998) is notable because they found a treatment effect when water was diverted from, rather than added to, soil.

Fine root biomass in the top 30 cm of the soil was similar to the 280 g/m<sup>2</sup> that Cavelier (1992) measured for secondary forest close to BCI. In contrast, Jackson *et al.* (1997) have summarized estimates of fine root biomass for ecosystems world-

wide and reported an average of 570 g/m<sup>2</sup> for tropical forests. Cavelier (1992) argued that the low value for BCI reflected the relatively high soil nutrient availability (Yavitt *et al.* 1993), favoring less C allocated below ground with (presumably) more C allocated above ground to compete for light. Our data indicated another difference. We found essentially no dead roots, despite dead root biomass being 40–60 percent of the total in most forest

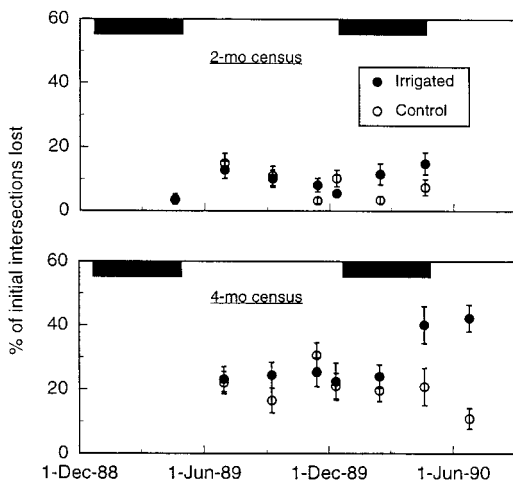


FIGURE 7. The proportion of root–screen contacts lost 2 months (top panel) and 4 months (bottom panel) after installation in control and irrigated plots. Symbols are  $\bar{x} \pm 1$  SE. Dark bar denotes dry season.

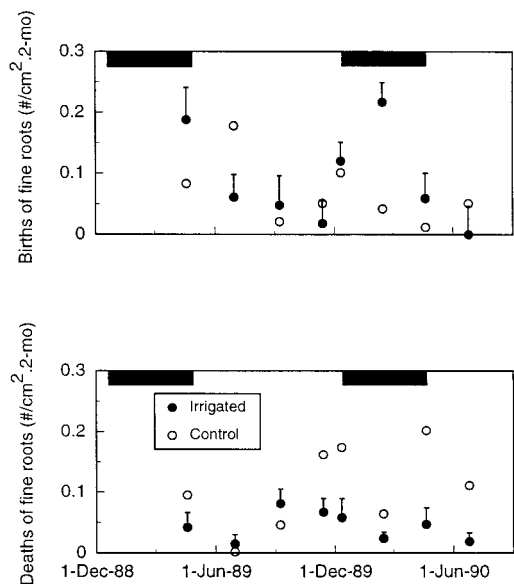


FIGURE 8. Root birth rates (top panel) and death rates (bottom panel) inferred from equation 1 using parameters determined for screens interred for 2 and 4 months. Symbols represent means. For clarity, the positive SE is presented for just one treatment.

ecosystems (Jackson *et al.* 1997 and references cited therein). Even studies in tropical deciduous and wet forests have found 30–50 percent dead root biomass (Kummerow *et al.* 1990, Silver & Vogt 1993). We suggest that fine roots either decomposed rapidly or disappeared completely through grazing, which prevented their accumulation as dead roots.

The very rapid disappearance of fine roots was evident in the two sets of in-growth screens in which we tracked root dynamics for ten months (Fig. 4). In both cases, fine root density increased to a peak then declined sharply. The increase reflected that births exceeded disappearance; however, the only way for fine root density to decrease after peak density was for root disappearance to surpass birth of new roots. The complete disappearance of fine roots has been reported in studies of other forest ecosystems that followed individual roots through time using either a video camera (Hendrick & Pregitzer 1992, Ruess *et al.* 1998) or in-growth screens (Fahey & Hughes 1994). In temperate and boreal forest, disappearance occurred mostly during the winter (Hendrick & Pregitzer 1993, Fahey & Hughes 1994, Ruess *et al.* 1998), whereas we found the phenomenon year-round.

The suggestion that grazing of live roots accounted for disappearance is inviting, although we have no direct evidence. This may be confirmed in the future when video cameras catch a grazer in action. In the past, however, root decomposition (actually mass loss) has been estimated by lacing root fragments into screens or placing them in mesh bags, then incubating in the soil (*e.g.*, McLaugherty *et al.* 1982, Fahey *et al.* 1988, Ostertag & Hobbie 1999). Fahey (1992), however, has shown the flaws in this method because it underestimated mass loss rates in every case, as decomposition rates were too slow to account for measured biomass of dead fine roots. Indeed, we measured the mass of root fragments before and after two- and four-month incubation in the soil in our disappearance screens (although we do not show the mass loss data and perpetuate the flawed technique). We found mass loss of 50 percent after two months but only 10 percent more between two and four months. These values are too slow to account for the rapid root disappearance shown in Figure 4 and the small biomass of dead roots *in situ*. Therefore, roots either decay faster if not removed from the soil disrupting root-decomposer connections, or they are lost to grazing.

Our data showed that root dynamics varied seasonally. Under ambient soil water regime, root

growth was rapid during the first half of the wet season and much lower during the remainder of the year. Therefore, growth coincided with the onset of the rainy season, leaf flush in the canopy (Wright & Cornejo 1990), and a pulse in soil N and soil P availability (Yavitt & Wright 1996). It did not coincide with the period of high fruit production among understory fleshy-fruited plants that peaked at the transition between the wet season and dry season (Foster 1982, Poulin *et al.* 1999). Seasonal variation in root growth has been reported in many forests despite seemingly favorable environmental conditions during other times of the year (*e.g.*, Teskey & Hinckley 1981, Kuhns *et al.* 1985, Burke & Raynal 1994). Indeed, Lopez *et al.* (1998) reported one of the few cases in which fine root growth occurred year-round, although with seasonally variable rates. Overall, root growth displays a remarkable, inherent timing that is thought to be linked to the availability of photosynthate. Lynch (1995) argued that this phenology overrides the environment and that root growth shows little plastic response to fluctuations in soil resource availability; however, studies finding different seasonal growth patterns in different years, when leaf flush does not vary (Cote *et al.* 1998), challenge this notion.

Our irrigation experiment also showed that root dynamics responded to soil watering when the canopy did not, and thus root dynamics were uncoupled from canopy phenology. This agrees with findings from other irrigation experiments (Katterer *et al.* 1995, Dickmann *et al.* 1996), as well as with Persson *et al.*'s (1995) finding that forced drought caused a redistribution of live fine roots deeper in the soil and more dead fine roots at the surface. Apparently, canopy phenology is set by phylogeny (Wright & Calderon 1995), or the cue is atmospheric (*e.g.*, humidity or cloudiness) rather than from the soil. In our case, root growth during the dry season in the irrigated plots could have been from shrubs and herbs that responded to the treatment (Fisher *et al.* 1991, Wright 1991).

The demographic model allowed us to estimate birth rates and mortality rates of fine roots. There are three assumptions in the model (represented by equation 1) that need clarification. First, the model involved discrete time intervals, while root dynamics occur continuously. Estimates derived from the model were averaged over the time intervals  $t - 1$ ,  $t$ . Therefore, the time intervals should be short and chosen such that conditions within each interval are homogeneous for root dynamics. In addition, time intervals should be short enough to minimize

root aging and growth in size during the time interval. The problems posed by differences in root age and size are developed further below. The second assumption implicit to equations 1 is that no root can grow, die, and disappear in a single time interval. This assumption will bias estimates of root growth and mortality rates downward unless time intervals are short enough that the assumption is true. The third class of assumptions implicit to equation 1 is that all live roots have the same season-dependent mortality rates and all roots have the same season-dependent disappearance rates. We discuss this assumption with respect to mortality, but the same arguments apply to the disappearance of dead roots. The assumption of equal season-dependent mortality rates obfuscates differences among species, size, and age of a root. We will treat these three sources of variation separately.

The size or diameter of a root affects its growth and mortality rates. In theory, fine roots maximize water and nutrient acquisition by minimizing root diameter, maximizing specific root length, and living longer (Eissenstat & Yanai 1997). This source of error is maximal for roots less than 1 mm in diameter. Therefore, expanding the root-dynamic model to include multiple diameter classes is warranted.

The key findings of the model, in context with our other findings, were as follows. We found slightly greater fine root biomass in the control than in the irrigated plots during the middle of the dry season, which indicated no large treatment effect on fine root biomass. On the other hand, the growth rate of fine roots was clearly greater in irrigated than in control plots (Fig. 6). Therefore, irrigation must have reduced the longevity of fine roots born in the surface soil in order to maintain similar biomass; however, there was no difference in dead root biomass or in the depth distribution of fine roots among treatments. This does not seem logical, especially since the model suggested that irrigation reduced fine root mortality rates (Fig. 8). Our interpretation of these findings is that the birth rate of fine roots was significantly greater under irrigation only during selected seasons (*i.e.*, the dry season). Although we did not see increased mortality of fine roots that reached the age of four months during the dry season in the irrigated plots, there was a huge mortality of six- to eight-month-old roots in the irrigated plots (Fig. 4). Therefore, irrigation did increase fine root mortality for slightly older roots than we studied using the model dynamically.

This can be analyzed another way using the model of Santantonio and Grace (1987) in which measurements of live and dead fine root biomass are state variables. Enough roots must be “produced” and “turned over” to maintain the observed biomass pools. The model assumes that mass loss is the only way for roots to disappear, and it can be used to estimate fine root production and mortality on a dry weight basis. We ran the model for three time steps: dry season, first part of the wet season, and second part of the wet season. Given that we measured live root and dead root biomass only in the dry season, we increased the values two-fold for the first part of the wet season following the seasonal pattern found by Cavelier (1989). Fine root biomass did not differ between the second part of the wet season and the dry season (Cavelier 1989). We had season-specific decay rates from the present study (data not shown). The model predicted a fine root production of 300 g/m<sup>2</sup>/yr in the control plots and 330 g/m<sup>2</sup>/yr in the irrigated plots. Consequently, dividing fine root biomass by production yielded root longevity of 1.14 yr in the control and 0.82 yr under irrigation. These values are much larger than Cavelier’s (1989) estimate of 0.67 yr measured directly as fine root biomass and production in in-growth cores at a site very close to ours. The Santantonio and Grace (1987) model, however, probably overestimates longevity in this case because BCI soil has so little dead root biomass and mass loss rates are underestimated, as argued above.

Low fine root longevity suggested that plants “waste” C constructing, but not maintaining, fine roots. This is surprising given the relatively large C cost to construct new roots. Even in the control plots, fine root biomass peaked when water and nutrient levels were optimal at the time the rains began, but biomass decreased after that and roots lived less than one year. Fine roots are energetically expensive tissues to construct, and thus it is perplexing why plants seemingly do not allocate C to defense. Apparently, the plants are able to “waste” the NPP on the production of fine roots because of abundant soil nutrient resources.

## ACKNOWLEDGMENTS

We thank Elena Cedeno, Mirna Samaniego, and Milton Garcia for infinite hours of fieldwork. David Clark, Tim Fahey, Ruth Yanai, and an anonymous reviewer provided very helpful comments. Research support was provided by the Environmental Studies Program of the Smithsonian Institution.

## LITERATURE CITED

- AXELSSON, E., AND B. AXELSSON. 1986. Changes in carbon allocation patterns in spruce and pine trees following irrigation and fertilization. *Tree Physiol.* 2: 189–204.
- BLAKE, G. R., AND K. H. HARTGE. 1986. Bulk density. *In* A. Klute (Ed.). *Methods of soil analysis*, part 1, pp. 363–375. American Society of Agronomy, Madison, Wisconsin.
- BURKE, M. K., AND D. J. RAYNAL. 1994. Fine root growth phenology, production and turnover in a northern hardwood forest ecosystem. *Plant Soil* 162: 135–146.
- CARVALHEIRO, K., DE O., AND D. C. NEPSTAD. 1996. Deep soil heterogeneity and fine root distribution in forests and pastures of eastern Amazonia. *Plant Soil* 182: 279–285.
- CAVELIER, J. 1989. Root biomass production and the effect of fertilization in two tropical rain forests. Ph.D. dissertation. University of Cambridge, Cambridge, England. 116 pp.
- . 1992. Fine-root biomass and soil properties in a semideciduous and a lower montane rain forest in Panama. *Plant Soil* 142: 187–201.
- , S. J. WRIGHT, AND J. SANTAMARIA. 1999. Effects of irrigation on litterfall, fine root biomass and production in a semideciduous lowland forest in Panama. *Plant Soil* 211: 207–213.
- CLARKSON, D. T., J. SANDERSON, AND R. S. RUSSELL. 1968. Ion uptake and root age. *Nature* 220: 805–806.
- COTE, B., W. H. HENDERSHOT, J. W. FYLES, A. G. ROY, R. BRADLEY, P. M. BIRON, AND F. COURCHESNE. 1998. The phenology of fine root growth in a maple-dominated ecosystem: relationships with some soil properties. *Plant Soil* 201: 59–69.
- CROAT, T. B. 1978. *Flora of Barro Colorado Island*. Stanford University Press, Stanford, California. 943 pp.
- DICKMANN, D. I., P. V. NGUYEN, AND K. S. PREGITZER. 1996. Effects of irrigation and coppicing on above-ground growth, physiology, and fine-root dynamics of two field-grown hybrid poplar clones. *For. Ecol. Manage.* 80: 163–174.
- EISSENSTAT, D. M., AND R. D. YANAI. 1997. The ecology of root lifespan. *Adv. Ecol. Res.* 27: 1–60.
- EPSHTEYN, S. M., V. F. UTKAYEVA, AND A. I. MOSOLOVA. 1987. Effect of the drying of artificial soil aggregates on their stability. *Sov. Soil Sci.* 19: 59–65.
- FAHEY, T. J. 1992. Mycorrhizae and forest ecosystems. *Mycorrhiza* 1: 83–89.
- , AND J. W. HUGHES. 1994. Fine root dynamics in a northern hardwood forest ecosystem, Hubbard Brook Experimental Forest, NH. *J. Ecol.* 82: 533–548.
- , P. MOU, AND M. A. ARTHUR. 1988. Root decomposition and nutrient flux following whole-tree harvest of northern hardwood forest. *For. Sci.* 34: 744–768.
- FISHER, B., H. F. HOWE, AND S. J. WRIGHT. 1991. Survival and growth of *Viola surinamensis* seedlings: water augmentation in gap and understory. *Oecologia* 86: 292–297.
- FOSTER, R. B. 1982. The seasonal rhythm of fruit fall on Barro Colorado Island. *In* E. G. Leigh Jr., A. S. Rand, and D. M. Windsor (Eds.). *The ecology of a tropical forest*, pp. 151–172. Smithsonian Institution Press, Washington, DC.
- GONZALEZ, A., G. ALVARADO-DUFREE, AND C. T. DIAZ. 1975. Canal Zone water quality study, final report. Water and Laboratories Branch, Panama Canal Company, Canal Zone, Panama.
- GOWER, S. T. 1987. Relations between mineral nutrient availability and fine root biomass in two Costa Rican tropical wet forests: a hypothesis. *Biotropica* 19: 171–175.
- HENDRICK, R. L., AND K. S. PREGITZER. 1992. The demography of fine roots in a northern hardwood forest. *Ecology* 73: 1094–1104.
- , AND ———. 1993. Patterns of fine root mortality in two sugar maple forests. *Nature* 361: 59–61.
- , AND ———. 1996. Temporal and depth-related patterns of fine root dynamics in northern hardwood forests. *J. Ecol.* 84: 167–176.
- , AND ———. 1997. The relationship between fine root demography and the soil environment in northern hardwood forests. *Ecoscience* 4: 99–105.
- HINCKLEY, T. M., F. DUHME, A. R. HINCKLEY, AND H. RICHTER. 1983. Drought relations of shrub species: assessment of the mechanisms of drought resistance. *Oecologia* 59: 344–350.
- HIRANO, Y., AND N. HIJII. 1998. Effects of low pH and aluminum on root morphology of Japanese red cedar saplings. *Environ. Pollut.* 101: 339–347.
- HOLDRIDGE, I. R., AND G. BUDOWSKI. 1956. Report of an ecological survey of the Republic of Panama. *Caribb. For.* 17: 92–101.
- JACKSON, R. B., H. A. MOONEY, AND E.-D. SCHULZE. 1997. A global budget for fine root biomass, surface area, and nutrient contents. *Proc. Natl. Acad. Sci. USA.* 94: 7362–7366.
- JOHNSSON, M. J., AND R. F. STALLARD. 1989. Physiographic controls on the composition of sediments derived from volcanic and sedimentary terrains on Barro Colorado Island, Panama. *J. Sediment Petrol.* 59: 768–781.
- JOSLIN, J. D., AND M. H. WOLFE. 1998. Impacts of water input manipulations on fine root production and mortality in a mature hardwood forest. *Plant Soil* 204: 165–174.
- KATTERER, T., A. FABIAO, M. MADEIRA, C. RIBEIRO, AND E. STEEN. 1995. Fine-root dynamics, soil-moisture and soil carbon content in a *Eucalyptus globulus* plantation under different irrigation and fertilization regimes. *For. Ecol. Manage.* 74: 1–12.

- KAVANAGH, T., AND M. KELLMAN. 1992. Seasonal pattern of fine root proliferation in a tropical dry forest. *Biotropica* 24: 157–165.
- KOSOL, K. R., AND D. M. EISSENSTAT. 1994. The fate of surface roots of citrus seedlings in dry soil. *J. Exp. Bot.* 45: 1639–1645.
- KUHNS, M. R., H. E. GARRETT, R. O. TESKEY, AND T. M. HINCKLEY. 1985. Root growth of black walnut trees related to soil temperature, soil water potential and leaf water potential. *For. Sci.* 31: 617–629.
- KUMMEROW, J., J. CASTILLANOS, M. MAAS, AND A. LARIGAUDERIE. 1990. Production of fine roots and the seasonality of their growth in a Mexican deciduous dry forest. *Vegetatio* 90: 73–80.
- KURSAR, T. A., S. J. WRIGHT, AND R. RADULOVICH. 1995. The effects of the rainy season and irrigation on soil water and oxygen in a seasonal forest in Panama. *J. Trop. Ecol.* 11: 497–516.
- LOPEZ, B., S. SABATE, AND C. GARCIA. 1998. Fine root dynamics in a Mediterranean forest: effects of drought and stem density. *Tree Physiol.* 18: 601–606.
- LYNCH, J. 1995. Root architecture and plant productivity. *Plant Physiol.* 109: 7–13.
- MAYCOCK, C. R., AND R. A. CONGDON. 2000. Fine root biomass and soil N and P in north Queensland rain forest. *Biotropica* 32: 185–190.
- MCCLAUGHERTY, C. A., J. D. ABER, AND J. M. MELILLO. 1982. The role of fine roots in the organic matter and nitrogen budgets of two forested ecosystems. *Ecology* 63: 1481–1490.
- OLSEN, S. R., AND L. E. SOMMERS. 1982. Phosphorus. *In* A. L. Page (Ed.). *Methods of soil analysis, part 2*, pp. 403–430. Agronomy Society of America, Madison, Wisconsin.
- OSTERTAG, R., AND S. E. HOBBI. 1999. Early stages of root and leaf decomposition in Hawaiian forests: Effects of nutrient availability. *Oecologia* 121: 564–573.
- PERSSON, H., Y. VON FIRCKS, H. MAJDI, AND L. O. NILSSON. 1995. Root distribution in a Norway spruce (*Picea abies* (L.) Karst.) stand subjected to drought and ammonium-sulphate application. *Plant Soil* 168–169: 161–165.
- POULIN B., S. J. WRIGHT, G. LEFEBVRE, AND O. CALDERON. 1999. Interspecific synchrony and asynchrony in the fruiting phenologies of congeneric bird-dispersed plants in Panama. *J. Trop. Ecol.* 15: 213–227.
- ROY, S., AND J. S. SINGH. 1995. Seasonal and spatial dynamics of plant-available N and P pools and N-mineralization in relation to fine roots in dry tropical forest habitat. *Soil Biol. Biochem.* 27: 33–40.
- RUESS, R. W., R. L. HENDRICK, AND J. P. BRYANT. 1998. Regulation of fine root dynamics by mammalian browsers in early successional Alaskan taiga forest. *Ecology* 79: 2706–2720.
- SANTANTONIO, D., AND J. C. GRACE. 1987. Estimating fine-root production and turnover from biomass and decomposition data: a comparative-flow model. *Can. J. For. Res.* 17: 900–908.
- SILVER, W. L., AND K. A. VOGT. 1993. Fine root dynamics following single and multiple disturbances in a subtropical wet forest ecosystem. *J. Ecol.* 81: 729–738.
- SINGH, J. S., A. S. RAGHUBANSHI, R. S. SINGH, AND S. C. SRIVASTAVA. 1989. Microbial biomass acts as a source of plant nutrients in dry tropical forest and savanna. *Nature* 338: 449–450.
- SRIVASTAVA, S. K., K. P. SINGH, AND R. S. UPADHYAY. 1986. Fine root growth dynamics in teak (*Tectona grandis* Linn. F.). *Can. J. For. Res.* 16: 1360–1364.
- STANTON, N. L., M. ALLEN, AND M. CAMPION. 1981. The effect of the pesticide carbofuran on soil organisms and root and shoot production in shortgrass prairie. *J. Appl. Ecol.* 18: 417–431.
- STEELE, S. J., S. T. GOWER, J. G. VOGEL, AND J. M. NORMAN. 1997. Root mass, net primary production and turnover in aspen, jack pine and black spruce forests in Saskatchewan and Manitoba, Canada. *Tree Physiol.* 17: 577–587.
- STRICKLAND, T. C., P. SOLLINS, D. S. SCHIMEL, AND E. A. KERLE. 1988. Aggregation and aggregate stability in forest and range soils. *Soil Sci. Soc. Am. J.* 52: 829–833.
- TESKEY, R. O., AND T. M. HINCKLEY. 1981. Influence of temperature and water potential on root growth of white oak. *Physiol. Plant* 52: 362–369.
- UEHARA, G., AND G. GILLMAN. 1981. *The mineralogy, chemistry, and physics of tropical soils with variable charge clays*. Westview Press, Boulder, Colorado. 170 pp.
- UTOMO, W. H., AND A. R. DEXTER. 1982. Changes in soil aggregate water stability induced by wetting and drying cycles in non-saturated soil. *J. Soil Sci.* 33: 623–637.
- WALKER, T. W., AND J. K. SYERS. 1976. The fate of phosphorus during pedogenesis. *Geoderma* 15: 1–19.
- WINDSOR, D. M. 1990. Climate and moisture availability in a tropical forest, long term records for Barro Colorado Island, Panama. *Smithson. Contrib. Earth Sci.* 29: 1–145.
- WRIGHT S. J. 1991. Seasonal drought and the phenology of understory shrubs in a tropical moist forest. *Ecology* 72: 1643–1657.
- , AND O. CALDERON. 1995. Phylogenetic patterns among tropical flowering phenologies. *J. Ecol.* 83: 937–948.
- , AND F. H. CORNEJO. 1990. Seasonal drought and leaf fall in a tropical forest. *Ecology* 71: 1165–1175.
- YAVITT, J. B., R. K. WIEDER, AND S. J. WRIGHT. 1993. Soil nutrient dynamics in response to irrigation of a Panamanian tropical moist forest. *Biogeochemistry* 19: 1–25.
- , AND S. J. WRIGHT. 1996. Temporal patterns of soil nutrients in a Panamanian moist forest revealed by ion-exchange resin and experimental irrigation. *Plant Soil* 183: 117–129.