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Fine Root Dynamics in a Subtropical Wet Forest Following Hurricane Disturbance in Puerto Rico[1]

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ABSTRACT

Fine root dynamics were evaluated at four sites in a subtropical wet forest in Puerto Rico over a period of 13 months following disturbance by Hurricane Hugo in September 1989. Live fine root standing stocks (to a depth of 10 cm) declined to zero over a three month period after the hurricane and fluctuated greatly thereafter. Maximum fine root biomass (49 g/m^2) occurred in June 1990. Dead root standing stocks (mean 423 g/m^2) were relatively constant through the study period. Recovery of fine roots following the initial hurricane-related mortality appears to be a slow process, regulated at least initially by environmental factors such as precipitation.

RESUMEN

Se evaluó la dinámica de raíces finas en cuatro localidades de un bosque húmedo subtropical en Puerto Rico durante un período de 13 meses luego de la perturbación ocasionada por el huracán Hugo en septiembre de 1989. La cantidad presente de raíces finas (a una profundidad de 10 cm) disminuyó a cero en un período de tres meses luego del huracán y luego de esto tuvo grandes fluctuaciones. La biomasa máxima de raíces finas (49 g/m^2) ocurrió en junio de 1990. La cantidad presente de raíces muertas (promedio 423 g/m^2) fue relativamente constante durante el período de estudio. La recuperación de las raíces finas luego de la mortalidad inicial relacionada con el huracán parece ser un proceso lento, regulado, al menos inicialmente, por factores ambientales como la precipitación.

During the past 30 years numerous studies have examined spatial and temporal patterns of fine root biomass in a variety of tropical forest ecosystems (Greenland & Kowal 1960, Klinge 1973, Huttell 1975, Stark & Jordan 1978, Klinge & Herrera 1978, Berish 1982, Raich 1983, Gower 1987, Sanford 1989, Cuevas *et al.* 1991). However, we are not aware of any previous tropical forest studies that have focused on the influence of natural disturbance on fine root dynamics and its implications for ecosystem structure and function. Large-scale natural disturbances may have profound effects on root dynamics, as suggested by studies of wind-exposed subalpine spruce-fir forests in the northeastern United States, where physical damage to tree root systems has been linked to extensive wave mortality (Harrington 1986, Marchand *et al.* 1986).

In September 1989 Hurricane Hugo caused extensive canopy defoliation and associated nutrient losses from vegetation of the Luquillo Experimental Forest in Puerto Rico (Scatena & Larsen 1991, Walker 1991). In heavily damaged areas, nutrient transfers to the forest floor amounted to more than one year's normal annual litterfall input (Lodge *et al.* 1991). Root uptake of nutrients may therefore be important for rapid regrowth of vegetation and also for limiting leaching losses from the forest ecosystem. In this study we followed posthurricane fine root dynamics in the litter and surface soils at four subtropical wet forest sites.

STUDY SITE AND METHODS

The study was conducted in the El Verde research area (see map in Scatena & Larsen 1991) of the Luquillo Experimental Forest in northeastern Puerto Rico (18°20′N, 65°49′W). The general topography is mountainous with deeply dissected drainages and steep northeast- and southwest-facing slopes. Mean annual precipitation is 392 cm, distributed evenly over the year except for a somewhat drier period from January to April. In most years rainfall exceeds 20 cm in all months; the site is therefore classified as nonseasonal. Soils of the El Verde site are predominantly upland Ultisols, which are mostly well-drained clays and silty clay loams (Edmisten 1970). The site lies within the Holdridge's subtropical wet

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forest life zone and the tabonuco forest-type (Ewel & Whitmore 1973).

In August 1989, a total of twelve 20 × 20 m plots were established at four locations (blocks) in the Sonodora, Prieta, and Toronja watersheds of the El Verde research area at elevations ranging from 300 to 500 m. These plots formed the lower end of a larger elevational gradient study examining the influences of variation in climate, soil fertility, and genome on productivity and postdisturbance recovery processes. Each of the four blocks included one replicate of each of the following treatments: control; one-time removal of all leaf litter and woody debris (hurricane inputs and prehurricane litter standing stocks); and addition of inorganic fertilizers, applied at 3-month intervals at an annual rate of 300 kg/ha N, 100 kg/ha P, 100 kg/ha K, 8 kg/ha B, 15.4 kg/ha Cu, 2.2 kg/ha Fe, 25 kg/ha Mn, 26 kg/ha Zn, and 19 kg/ha Mg. Plots were located on slopes in such a way as to preclude the possibility of surface and subsurface water flow between plots.

A prehurricane census of all trees >2 m in height within the interior 100 m zone of each of the experimental plots indicated important differences in tree species composition, tree density, and stem basal area (an index of tree aboveground biomass) among plots, both within and among blocks. The number of tree species ranged from 5 to 16 per plot (median 8.5); tree density ranged from 0.06 to 0.64 stems m^{-2} (median 0.25 m^{-2}); and stem basal area ranged from 10.4 to 94.9 m^2 ha^{-1} (median 23.6 m^2 ha^{-1}). The dominant tree species occurring in the experimental plots were *Dacryodes excelsa* Vahl, *Manilkara bidentata* (A. DC.) A. Chev., *Matayba domingensis* (DC.) Radlk., *Buchenavia capitata* (Vahl) Eichl., *Drypetes glauca* Vahl, and *Inga fagifolia* (L.) Willd. These species comprised, respectively, 30.4, 18.9, 8.1, 5.1, 4.6, and 4.5 percent of the total basal area across all plots. Hurricane damage varied considerably within the experimental area (Walker 1991) and included defoliation, branch loss, and uprooting.

Beginning in mid-October 1989 (*ca* one month after the hurricane), core samples were taken at 60 d intervals to a soil depth of 10 cm (plus litter layers) using 5.1 cm diameter plastic (PVC) tubes. While sampling to greater depths would have yielded more accurate measures of total fine root mass in the forest, we estimate that sampling to 10 cm depth yielded approximately two-thirds of the total fine root mass. Lugo (in press) reported that root density, mass of fine root <1 mm diameter, and total root mass in the 0–10 cm horizon at El Verde comprised 65, 60, and 87 percent, respectively, of the total recovered to a depth of 60 cm. Sample locations were randomly selected within a central 100 m^2 subplot of each 20 × 20 m plot. During the first sampling period (October 1989) the number of samples per plot ranged from 5 to 13; in December 1989, 10 samples were taken in each plot, and from February 1990 onward, sample size remained constant at 8 per plot. Sample cores were sealed in plastic bags in the field and transferred to the laboratory within 5 hr of collection, where they were stored at 0–5°C for a period of 2 to 21 d before sorting. The length of time samples were stored within this 21 d period was found to have no effect on either total root mass or the proportion of live and dead roots recovered from sample cores.

Prior to sorting, the plastic cores were immersed in a water-filled beaker placed in an ultrasonic cleaner bath at room temperature for a period of up to 90 minutes. This technique minimized root damage and was found to greatly facilitate the process of removing clay adhering to root surfaces. Root samples were then washed through a series of sieves (0.18 to 2.00 mm mesh), and separated according to size (<3 mm, ≥3 mm diameter), and physiological status (live *versus* dead) using morphological criteria (color, texture, elasticity, and friability) developed previously for work at this site; characteristics of dead roots were confirmed by microscopy on hand-sectioned samples (D. J. Lodge, pers. obs.; E. Cuevas, pers. comm.). Fine roots were defined as those <3 mm diameter due to the presence of a high proportion of magnolioid roots with terminal branch diameters of 1 to 3 mm for several of the common species at this site (D. J. Lodge, pers. obs.). Subsamples were dried at 70°C to a constant mass for conversion of total fresh mass to dry mass equivalents.

The dry masses per volumetric sample for both live and dead fine roots (<3 mm) were expressed per unit area (g/m^2 at 0–10 cm soil depth). Mean live and dead fine root mass was calculated for each plot; treatment means were calculated using plot means. While within-plot and treatment mean values were not normally distributed, a square root transformation normalized the treatment means. A two-way analysis of variance (ANOVA) without replication showed no significant differences among treatments ($P = 0.99$ and $P = 0.25$ for live and dead roots, respectively) and no time by treatment interaction ($P = 0.95$). Therefore, treatment means were used as replicates in a one-way ANOVA to compare fine root mass standing stocks over time. The Bonferroni procedure with an overall 0.05 significance level (Neter *et al.* 1985) was used to compare fine root mass means between successive sampling dates.

RESULTS AND DISCUSSION

Throughout the study period, fine root standing stocks fluctuated greatly among plots and between sampling dates, regardless of experimental treatments. Total (live plus dead) fine root standing stocks in the upper 10 cm during the study period averaged 423 g/m^2 (SE = 20). While it is difficult to directly compare these results with those from other tropical forest studies because of differences in the definition of root size classes and sampling depth, these data appear to fall within the range obtained in other studies of secondary forest sites in the Luquillo Experimental Forest (Cuevas *et al.* 1991; Lugo, in press), and in premontane forest sites in Costa Rica (Berish 1982, Raich 1983, Gower 1987).

In late October 1989, approximately 4 weeks after hurricane Hugo, standing stocks of live fine roots were extremely low, with treatment means ranging from 0 to 2 g/m^2 (Fig. 1a). Two months later, in December 1989, live fine root mass was reduced to zero in all experimental plots.

The virtual absence of live fine roots in surface soil and litter during this period may have profoundly reduced the ability of trees to absorb nutrients released from aboveground hurricane litterfall (Lodge *et al.* 1991) and may help to explain observed changes in stream water chemistry in these watersheds following the hurricane. For example, the temporary disappearance of nitrate from stream water for several weeks immediately after the storm (C. Asbury & F. N. Scatena, pers. comm.) may have resulted from microbial immobilization that was possibly stimulated by an increase in the mass of dead roots with a high lignin-to-nutrient ratio (Cuevas *et al.* 1991). The subsequent massive increase in stream water nitrate concentrations beginning several weeks after the hurricane (C. Asbury & F. N. Scatena, pers. comm.), and the increased soil denitrification (Steudler *et al.* 1991) may have been exacerbated by reduced plant uptake of mineralized soil nitrogen.

Over the succeeding 10 months live root standing stocks fluctuated considerably with peaks in February (29 g/m^2; SE = 4) and June 1990 (49 g/m^2; SE = 9). Increases in live root mass were significant at the 95 percent confidence level between December 1989 and February 1990, and between April and June 1990 (as indicated by Bonferroni contrasts, Neter *et al.* 1985). Following each of these peaks, sharp declines were noted, with means of 13 g/m^2 (SE = 7) and 16 g/m^2 (SE = 1) in April and August 1990, respectively. The decline in live root mass between June and August 1990 was significant ($P < 0.05$), but the decline between February and April 1990 was only suggestive ($P < 0.1$; Fig. 1a).

The data in Figure 1a suggest that live root mass may fluctuate more through time in the litter removal treatment than in the other treatments, but the interaction of treatment with time was not significant due to high within-treatment variances ($P = 0.95$). The soil environment in the litter removal treatment may have been less buffered from environmental fluctuations than in the other treatments, possibly contributing to fluctuations in live root mass. For example, mean temperatures at the surface of the litter in control plots at this site two months after the hurricane ranged from 19.5 to

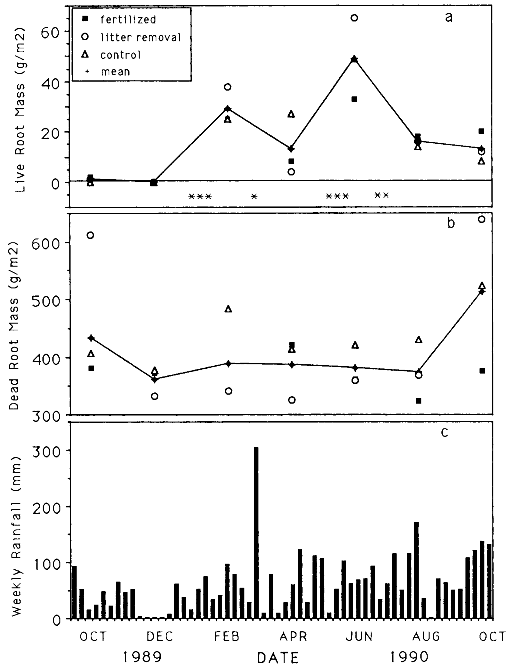

FIGURE 1. Fine root mass in surface litter and soil horizons (soil to 10 cm depth) and weekly rainfall distribution in a mature subtropical wet forest at El Verde, Puerto Rico, during a 13-month period following Hurricane Hugo. (a) Mass of live roots <3 mm diameter. (b) Mass of dead roots <3 mm diameter. (c) Weekly rainfall at the El Verde field station. Statistical differences in live fine root mass between successive sampling dates are denoted as: *** $P < 0.01$; ** $P < 0.05$, and * $P < 0.10$.

46°C; whereas, mean temperatures at the litter–mineral soil interface only ranged between 19.3 and 33.1°C (C. Blanton, pers. comm.).

Live root standing stocks remained very low throughout the study period, averaging 17.3 g/m^2 (SE = 6.4), and comprised between 0 (December 1989) and 11 (June 1990) percent of total fine root mass. These values are considerably lower than those reported by Cuevas *et al.* (1991) in a study of an undisturbed secondary site in the Luquillo Experimental Forest, in which live roots comprised approximately 40 percent of the total fine root mass (1050 g/m^2, to 30 cm depth). These data suggest that more than one year may be required for the recovery of shallow live root standing stocks to pre-hurricane levels. Dead root standing stocks were fairly constant throughout the study period with overall mean values ranging from a low of 361 g/m^2 (SE = 14) in December 1989 to a high of 513 g/m^2 (SE = 76) in October 1990 (Fig. 1b).

Three important factors—physical disturbance, moisture stress, and changes in nonstructural carbohydrate reserves—may have contributed to the paucity of live fine roots in surface soil and litter during the three months following Hurricane Hugo and to the subsequent fluctuations in live root standing stocks. Physical disturbance of tree root systems caused by the swaying and, in some cases, partial uprooting of canopy trees could have contributed to fine root death during and immediately after the hurricane. Many severed or damaged roots were seen at El Verde after the hurricane (D. J. Lodge, pers. obs.). Extensive root damage and mortality resulting from physical stress on root systems has previously been observed in wind-exposed subalpine spruce–fir forests in the northeastern United States (Harrington 1986, Marchand *et al.* 1986).

The three months following the hurricane had exceptionally low rainfall (Fig. 1c), which may have precluded the rapid regrowth of fine roots. Between 20 November and 28 December 1989 total rainfall at El Verde was 1.57 cm. In spite of extensive canopy defoliation and assumed reductions in soil water loss via transpiration, a sharp decline in soil moisture was noted between 20 October and 28 December 1989 (Steudler *et al.* 1991). Lack of adequate soil moisture during this period may have precluded new root growth and resulted in the mortality of most of the fine surface roots. The drought was followed by an increasingly wet period through late February 1990, a somewhat dry period during late March and early April, and more or less constant rainfall thereafter (Fig. 1c). The first flush of new fine roots of *Dacryodes excelsa* and *Drypetes glauca* occurred in early January of 1990 (D. J. Lodge, pers. obs.), coinciding with increased rainfall.

We hypothesize that the fluctuations in live root standing stocks between December 1989 and June 1990 are, at least in part, a reflection of changing moisture conditions in the surface soils and litter in this forest. However, the significant decline in live root mass after June 1990 does not appear to be related to moisture, as rainfall was relatively high and constant during this period. The observed fluctuations in live fine root mass may also be linked to changes in total nonstructural carbohydrate (TNC) reserves (Singh & Srivastava 1986). Most of the TNC stored in coarse roots may have been utilized in the first and second flushes of fine root growth. Depletion of coarse root TNC could have contributed to subsequent declines in live fine root production and mass after June 1990.

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