Effects of Earthworms on Slopewash, Surface Runoff, and Fine-Litter Transport on a Humid-Tropical Forested Hillslope in Eastern Puerto Rico

By Matthew C. Larsen, Zhigang Liu, and Xiaoming Zou

Chapter G of

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Contents

Figures

Table

Abbreviations Used in This Report

cm	centimeter
cm s^{-1}	centimeters per second
g m^{-2}	grams per square meter
h	hour
kg ha^{-1}	kilograms per hectare
kg m^{-2} yr^{-1}	kilograms per square meter per year
m	meter
m^2	square meter
mm	millimeter
mm 1,000 yr^{-1}	millimeters per thousand years
r^2	correlation coefficient
t ha yr^{-1}	metric tons per hectare per year

Conversion Factors

Multiply	By	To obtain
	Length	
millimeter (mm)	0.03937	inch (in.)
centimeter (cm)	0.3937	inch (in.)
meter (m)	3.281	foot (ft)
	Area	
square meter (m^2)	10.76	square foot (ft^2)
	Flow rate	
centimeters per second (cm s^{-1})	0.3937	inches per second (in. s^{-1})
millimeters per 1,000 years (mm 1,000 yr^{-1})	0.03937	inches per year (in. 1,000 yr^{-1})
	Other	
grams per square meter (g m^{-2})	8.922	pounds per acre (lb $acre^{-1}$)
kilograms per hectare (g ha^{-1})	0.8922	pounds per acre (lb $acre^{-1}$)
kilograms per square meter per year (kg m^{-2} yr^{-1})	1.843	pounds per square yard per year (lb yd^{-2} yr^{-1})

Effects of Earthworms on Slopewash, Surface Runoff, and Fine-Litter Transport on a Humid-Tropical Forested Hillslope in Eastern Puerto Rico

By Matthew C. Larsen,[1] Zhigang Liu,[2] and Xiaoming Zou[2, 3]

Abstract

Rainfall, slopewash (the erosion of soil particles), surface runoff, and fine-litter transport were measured in tropical wet forest on a hillslope in the Luquillo Experimental Forest, Puerto Rico, from February 1998 until April 2000. Slopewash data were collected using Gerlach troughs at eight plots, each 2 square meters in area. Earthworms were excluded by electroshocking from four randomly selected plots. The other four (control) plots were undisturbed. During the experiment, earthworm population in the electroshocked plots was reduced by 91 percent. At the end of the experiment, the electroshocked plots had 13 percent of earthworms by count and 6 percent by biomass as compared with the control plots.

Rainfall during the sampling period (793 days) was 9,143 millimeters. Mean and maximum rainfall by sampling period (mean of 16 days) were 189 and 563 millimeters, respectively. Surface runoff averaged 0.6 millimeters and 1.2 millimeters by sampling period for the control and experimental plots, equal to 0.25 and 0.48 percent of mean rainfall, respectively. Disturbance of the soil environment by removal of earthworms doubled runoff and increased the transport (erosion) of soil and organic material by a factor of 4.4. When earthworms were removed, the erosion of mineral soil (soil mass left after ashing) and the transport of fine litter were increased by a factor of 5.3 and 3.4, respectively. It is assumed that increased runoff is a function of reduced soil porosity, resulting from decreased burrowing and reworking of the soil in the absence of earthworms. The background, or undisturbed, downslope transport of soil, as determined from the control plots, was 51 kilograms per hectare and the “disturbance” rate, determined from the experimental plots, was 261 kilograms per hectare. The background rate for downslope transport of fine litter was 71 kilograms per hectare and the disturbance rate was 246 kilograms per hectare. Data from this study indicate that the reduction in soil macrofauna population, in this case, earthworms, plays a key role in increasing runoff and soil erosion and, therefore, has important implications for forest and water management.

Introduction

The hydrological role of tropical forests as compared with deforested landscapes has been a source of considerable controversy during the past century because forests, although they are recognized to have many benefits, such as carbon storage, biodiversity, and landscape aesthetics, almost universally consume more water than deforested landscapes (Bruijnzeel, 2004; Jackson and others, 2005). In seasonal-climate regions, this excess consumption of water can be mitigated if pedogenic processes characteristic of forests promote sufficient infiltration such that groundwater reserves under forests exceed those under deforested landscapes—the “sponge effect” of Bruijnzeel (2004).

One characteristic of forested environments is macroporosity and soil structure created by burrowing animals. We examined the generation of macroporosity by earthworms in forests of eastern Puerto Rico. Eastern Puerto Rico represents an excellent setting for such an experiment because it hosts fewer types of burrowing organisms than mainland tropical forests, where burrowing mammals, leaf-cutter ants, and cicadas are common. Earthworms at the Puerto Rico site can easily be excluded using electroshock techniques.

Soil erosion is a widespread problem in the humid tropics (Douglas, 1967; Haantjens, 1969; Lal, 1990; Nooren and others, 1995). Rates of soil erosion are high in part because of abundant, deep, highly weathered regolith and soils typical of the warm, moist environment and high rainfall intensity associated with convective storms and tropical disturbances such as hurricanes (Ruxton, 1967; Hastenrath, 1991; Reading and others, 1995). The rate of soil erosion is influenced by the character, abundance, and decomposition of plant litter, which is, in turn, strongly affected by soil fauna, including

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earthworms (Hazelhoff and others, 1981; Haria, 1995; Chauvel and others, 1999; Heneghan and others, 1999; Lavelle and others, 1999; Liu and Zou, 2002; Six and others, 2004).

Land degradation has been defined as a substantial decrease in either or both of an area's biological productivity or usefulness due to human interference (Johnson and Lewis, 1995). One aspect of landscape degradation is increased runoff, which in disturbed environments has been thought to be largely a function of such factors as soil compaction, loss of the soil A horizon, loss of vegetative cover, decreased evapotranspiration, and decreased leaf litter (Johnson and Lewis, 1995). In contrast, the burrowing of earthworms increases soil porosity, resulting in greater rainfall infiltration. As they burrow, earthworms exert pressure on surrounding soil and deposit mucus on the burrow walls; additionally, the burrow walls may be lined with oriented clays (Six and others, 2004). These two features of earthworm burrows can provide stable, efficient conduits of near-surface throughflow. Earthworms ingest organic and inorganic materials that are mixed in the gut and excreted as a cast (Six and others, 2004). Deposition of surface casts on the ground surface creates surface roughness, which can itself reduce rainfall runoff and soil erosion (Le Bayon and Binet, 2001). Additionally, field observations by the authors and others (Le Bayon and Binet, 2001) indicate that earthworm casts, if abundant, can increase soil surface area at the microtopographic scale. The comminuting, feeding, burrowing, and casting activities of earthworms regulate soil processes and are well recognized for their influence on the decomposition of plant materials (Darwin, 1892; Lee, 1985). Darwin (1892) was the first to quantify the geomorphic work accomplished by earthworms, calculating that in Staffordshire, England, they brought to the soil surface 1.7 kilograms per square meter per year (kg m^{-2} yr^{-1}) (17 metric tons per hectare per year (t ha^{-1} yr^{-1})) of dry earth. Chauvel and others (1999) estimated that earthworms in a humid-tropical area of Brazil produced 100 metric tons per hectare per year of casts.

Earthworms generally represent the greatest portion of macrofauna biomass in moist and wet tropical forests (Camilo and Zou, 2001). In tropical wet forest in the Luquillo Experimental Forest, eastern Puerto Rico, earthworms compose as much as one third of the fauna biomass (Odum and Pigeon, 1970). In agroecosystems, Parmelee and others (1990) showed that earthworms increase plant litter decomposition rates by 20 to 50 percent. This substantial effect is reduced in disturbed landscapes or when forests are converted to other uses such as pasture (Liu and Zou, 2002). Where natural forest in Puerto Rico was replaced by Caribbean pine and mahogany plantations, earthworm richness and density were shown to be reduced by half, possibly as a result of differences in soil water content, soil pH, organic matter content, and nutrient availability associated with the quantity and quality of litter inputs (González and others, 1996; Liu and Zou, 2002). Exclusion of tropical earthworms *P. corethrurus* in the study forest was associated with a reduction in soil respiration rates (Liu and Zou, 2002)

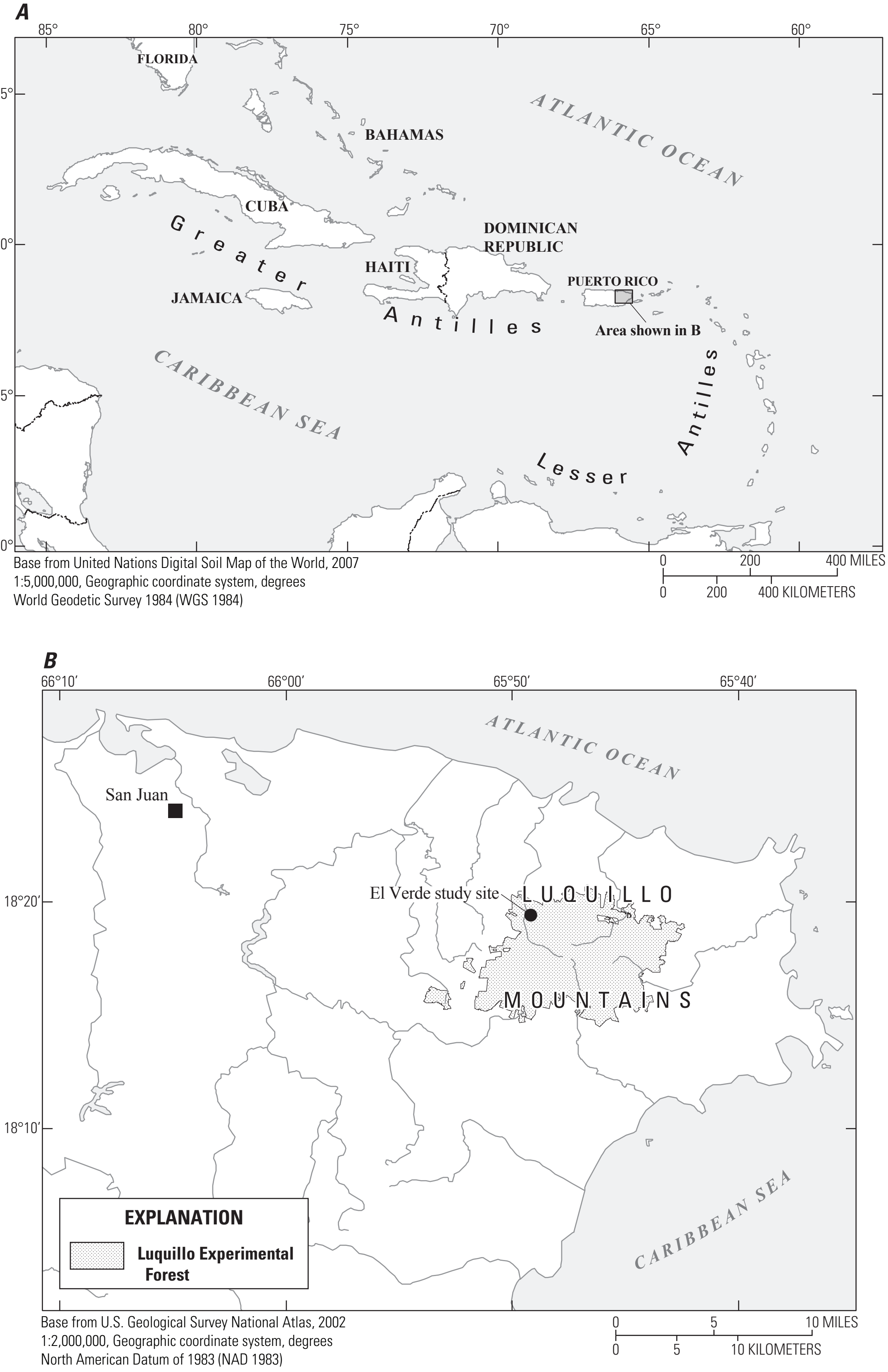
Purpose and Scope

Soil fauna populations are known to be affected by land use change, but the ecological consequences of changing soil fauna have not been extensively evaluated in tropical ecosystems (Blanchart and others, 1997). Nonetheless, many studies demonstrate that tropical soil macrofauna speed the decomposition of plant litter (Bouché, 1977; Chauvel and others, 1999; Heneghan and others, 1999; González and Seastedt, 2001). The published literature describing the role of soil macrofauna in soil erosion and runoff processes in the humid tropics is limited (Baidgett and others, 2001). Because human population pressure on the natural environment has increased substantially in the humid tropics in recent decades, baseline studies are needed to better understand these process and to improve land-management practices (Johnson and Lewis, 1995; Grau and others, 2003).

In an effort to quantify the association of earthworms with several basic physical soil and hydrological processes, in the present study we asked the following questions: do earthworms affect slopewash, the amount of surface rainfall runoff, and the transport of fine litter? A simple field experiment was designed to measure these quantities.

Site Description

A gentle hillslope 350 meters (m) above sea level, sloping 10° to the northwest (azimuth 310°) in the El Verde section of the Luquillo Experimental Forest (18° 20′ N., 66° 49′ W.) was selected for the experiment (fig. 1). The site is classified as tropical wet forest (Ewel and Whitmore, 1973) and is dominated by tabonuco trees (*Dacryodes excelsa*), a broad-leafed evergreen (fig. 2). Mean monthly temperature ranges from 20.8 to 24.4°C (Brown and others, 1983). Mean annual rainfall is 3,536 millimeters (mm), and it was 4,035 mm during the study period (Schaefer and Melendez, 2001). Mean daily rainfall was 12 mm during the study period; maximum daily rainfall was 160 mm, recorded on April 16, 1998, in association with a local convective storm. The soil is classified as a deep, moderately well-drained Oxisol with a high clay content (89 percent; Soil Survey Staff, 1995). Surficial soil is highly permeable, and little rainfall becomes surface runoff; Larsen and others (1999) reported runoff values of 0.2 to 0.5 percent of monthly rainfall and soil infiltration rates of 0.001 centimeters per second (cm s^{-1}) to 0.46 cm s^{-1} in the Luquillo Experimental Forest. Vegetation covers 80 percent of the forest, and a layer of leaf litter several centimeters thick covers the soil surface (fig. 2). The mean fresh weight of earthworms in the forest is 25 grams per square meter (g m^{-2}), and earthworm density ranges from 32 to 137 m^{-2}; the mean is 89 worms per square meter (Liu and Zou, 2002). Earthworms are dominated by nonendemic species *P. corethrurus* and *Amynthas rodericensis,* but the native species *Estherella gates* also is present (Zou and González, 1997; González and others, 1999). In mature forest, *P. corethrurus* is the most abundant species, but biomass



Base from United Nations Digital Soil Map of the World, 2007
1:5,000,000, Geographic coordinate system, degrees
World Geodetic Survey 1984 (WGS 1984)

Base from U.S. Geological Survey National Atlas, 2002
1:2,000,000, Geographic coordinate system, degrees
North American Datum of 1983 (NAD 1983)

Figure 1. Location of Puerto Rico and study area, eastern Puerto Rico.

Figure 2. Study site, El Verde, eastern Puerto Rico, 1998. *A*, tabonuco forest; *B*, one of eight 2-square-meter measurement plots prior to installation of Gerlach trough at downslope end; *C*, understory; and *D*, closeup of forest floor and litter layer. In *D*, note worm castings (w), fine rootlets (f), and small anthills (a); scale in inches (top) and centimeters.

of native earthworms is higher (Zou and González 1997; Sanchez and others, 2003). Earthworms are not highly active during the relative dry season between January and April.

In general, three morphoecological groups of earthworms are described by Bouché (1977): epigeic species, anecic species, and endogeic species. Epigeic species inhabit the litter layer of forest soils above the mineral soil surface and have little effect on soil structure. Anecic species form a network of burrows that penetrate deep into the mineral soil, feed on decayed surface litter, and transport organic material from the surface into their burrows. Endogeic species live in mineral soil horizons and feed on soil enriched with organic matter. *P. corethrurus* and *E. gates* are endogeic species and *A. rodericensis* is an anecic species.

Preparation and Observation of Study Plots

A forested hillslope at the El Verde study site was sampled from February 26, 1998, to April 28, 2000 (fig. 1). Eight rectilinear plots each 2 square meters (m^2) in area (1 m wide, 2 m long) were bounded along their margins with plastic sheeting attached to steel rods for 26 months. The plastic sheets were buried to a depth of 0.5 m; 0.15 m was exposed above the surface to prevent runoff and earthworms from crossing the plot boundaries. Earthworms were removed from four of these plots by electroshocking, by using a 240 volt alternating electrical current (supplied by a portable generator) to bring earthworms to the surface. Once at the surface, earthworms were removed by hand. Each of the four plots from which earthworms were removed was treated with the electrical current for 1.5 hours (h) every 3 months. Electroshocking is an effective technique for removing earthworms; it has been shown to result in minimal soil disturbance and no appreciable effects on microarthropods and nematodes, and it does not persist in the soil, unlike chemicals that can affect soil's biological properties (Blair and others, 1995). At the end of the 26-month experiment, a 0.25- by 0.25-m quadrant in the center of each of the eight plots was excavated to a depth of 0.5 m, and all earthworms were removed and sorted for counting and weighing in a laboratory.

At the start and end of the experiment, Liu and Zou (2002) collected soil samples from six cores (19 mm in diameter) in each plot. They determined soil bulk density by oven-drying at 105°C for 48 h and soil pH by using a 1:1 mixture of soil and deionized water (Liu and Zou, 2002).

Surface-water runoff and slopewash were trapped at the downslope end of each plot by using Gerlach troughs (Gellis and others, 1999; Larsen and others, 1999). A Gerlach trough is a sediment trap designed to retain soil particles, organic material, and surface runoff transported downslope by gravity (Young, 1960; Gerlach, 1967). The Gerlach troughs were fabricated with materials available from a standard hardware store, using a plastic section of household rain gutter with a hinged metal lid to prevent direct interception of rainfall, rainsplash-transported sediment, and direct litterfall (fig. 3). A rectangular metal strip was attached to the upslope side of the trough and imbedded in the soil to allow slopewash, surface runoff, and fine litter to enter the trough. A 13-mm-diameter plastic tube connected the side of the trough to a 20-liter closed bucket anchored downslope to allow excess runoff and fine sediment to be trapped. Regular sampling of each trap included scooping out sediment and fine litter caught in the trough and measuring the volume of the water-sediment mixture in the buckets. Runoff for each of the eight plots was defined as the total volume of water in the Gerlach trough and 20-liter bucket, divided by the 2-m^2 drainage area. Slopewash samples were collected from each Gerlach trough on average every 16 days (range 8 to 34 days), oven dried at 100°C for 24 h, weighed, then ashed at 550°C for 1 h, and reweighed to determine loss on ignition. Average daily flux of material was calculated for the total mass of oven-dried soil and organic material; for the total mass of mineral soil (soil mass left after ashing); and for the total mass of organic material, defined as the portion of oven-dried soil and organic material that was lost on ignition. Daily rainfall data were collected at the El Verde field station, located approximately 0.4 kilometers south of the study site (Schaefer and Melendez, 2001). Rainfall data were expressed as average daily amounts for each sampling period. All data were expressed as totals for the study period; as mean, median, and maximum by sampling period; and as time series and scatter plots. Least-squares linear regression models (Helsel and Hirsch, 2002) were developed for each data set with model confidence limits set at 95 percent and number of samples (n)=50.

Data Characteristics and Limitations

Although Gerlach troughs provide an inexpensive means for quantifying surface runoff and slopewash, their limitations should be noted. Occasional decoupling of the Gerlach troughs from the soil resulted in the diversion of slopewash and runoff and undermeasurement of the sample. Reseating the trough sometimes resulted in a temporary increase in the mass of soil particles and organic debris transported into the trough. The use of bounded plots for Gerlach troughs defines the contributing area, in this study, 2 m^2 each, but ultimately the contributing area for each trough is controlled by such factors as the soil heterogeneity, intensity of a rainstorm, antecedent soil moisture, and the subsequent surface runoff. The uncertainty of these factors increases scatter in the data. Odum and others (1970) measured an average of five rainfall events per day in their study of climate in the Luquillo Experimental Forest. The difficulty of sampling at the end of every rainfall event prevented the precise determination of the relation between rainfall, runoff, and transport of soil and organic material.

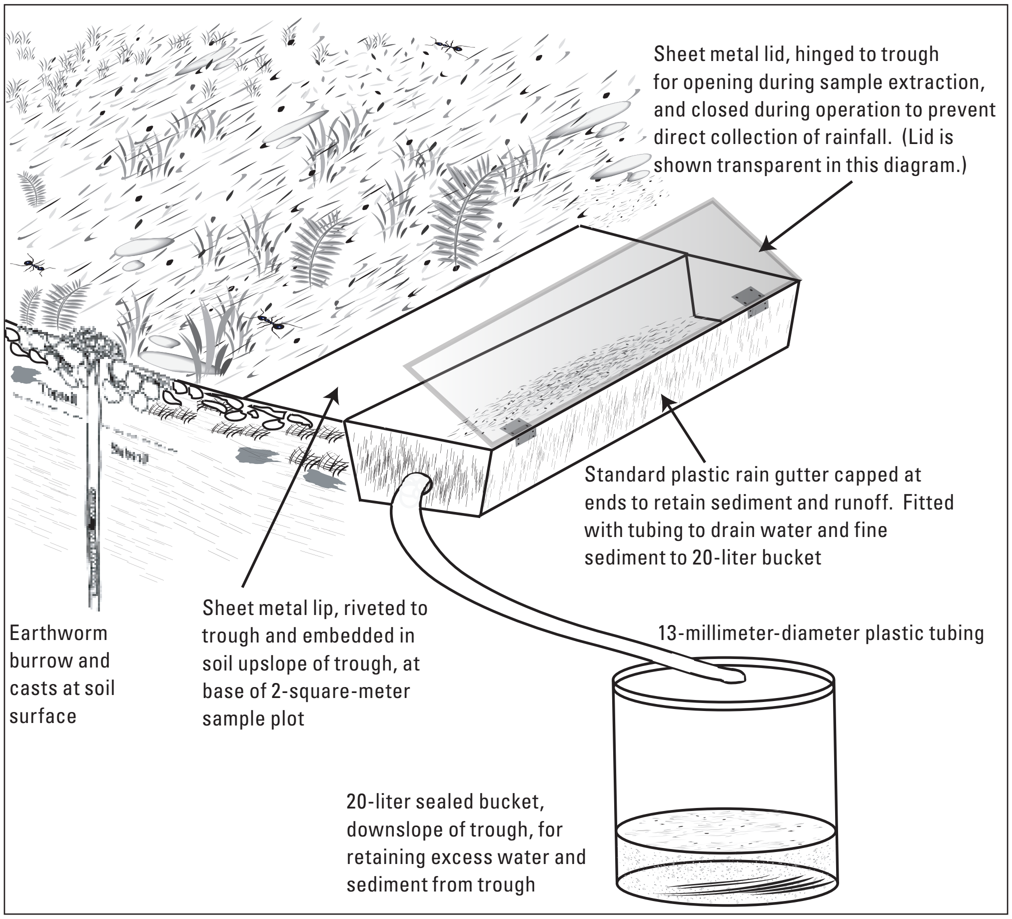


Figure 3. Idealized soil cross section and Gerlach trough showing hinged lid, which covers trough to prevent direct interception of rainfall and permits removal of sediment and water during sampling. Sheet metal lip embedded in soil upslope of trough allows soil particles, debris, and runoff to enter trough. Plastic tubing and bucket are attached downslope to collect overflow water and sediment from trough.

Effects of Earthworms on Slopewash, Surface Runoff, and Fine-Litter Transport

Earthworm population in the experimental (electroshocked) plots was reduced by 91 percent by the end of the 26-month experiment, compared with the population prior to shocking. When the experiment was terminated, the electroshocked plots had 13 percent of earthworms by count and 6 percent by biomass as compared with the control plots (Liu and Zou, 2002). Electroshocking had no effect on soil bulk density or pH (Liu and Zou, 2002).

A total of 9,423 mm of rainfall was recorded during the 793-day study period (table 1). Mean and maximum rainfall by sampling period (mean of 16 days) were 189 and 563 mm, respectively. Runoff averaged 0.6 mm and 1.2 mm by sampling period for the control and experimental plots, respectively. The mean runoff (calculated using the runoff percent for each of the 50 sample periods) was 0.25 percent and 0.48 percent of rainfall for the control and experimental plots, respectively (table 1). Runoff from the control plots was nearly identical to earlier results using Gerlach troughs in other parts of the study area (Larsen and others, 1999), where runoff was 0.2 percent of rainfall on the same soil type in an undisturbed setting but with steeper slopes. Comparable runoff data were obtained by Chandler and Walter (1988) at tropical upland watersheds in Leyte, Philippines, where surface hydrologic response of forest, tilled land, slash and mulch, and pasture were compared; the forested site had the lowest annual runoff—less than 3 percent of rainfall.

At the El Verde site, time series of rainfall and runoff show generally increased runoff from the experimental plots compared with runoff from the control plots throughout the

Table 1. Rainfall, runoff, and transported material by sampling period, El Verde, eastern Puerto Rico.

[transported material, grams transported from each 2×2-meter plot; 50 sampling periods with a mean of 16 days each; g, gram; mm, millimeter; SD, standard deviation]

	Sampling period (days)	Rainfall (mm)	Mean runoff (mm)		Runoff (percent of rainfall)		Mean soil and organic material (g)		Mean mineral soil (g)		Mean organic material portion (g)	
			Control	Experimental	Control	Experimental	Control	Experimental	Control	Experimental	Control	Experimental
Mean	16	189	0.6	1.2	0.25	0.48	1.1	4.6	0.40	2.30	0.60	2.20
Median	15	167	0.2	0.5	0.03	0.16	0.7	3.5	0.30	1.00	0.40	1.70
Maximum	34	563	4.8	6.6	1.22	2.07	5.9	36.1	3.10	27.00	2.80	9.10
Minimum	8	1.3	0.0	0.0	0.0	0.0	0.2	0.7	0.05	0.25	0.03	0.35
SD	4.0	143	1.0	1.6	0.20	0.40	1.1	5.7	0.50	4.40	0.70	1.70
Total	793	9,423	31	59	0.33	0.62	53	231	22[1]	114[1]	31[1]	107[1]

[1] Totals for mean mineral soil and mean organic portion do not sum to soil and organic material because data are missing in one sample set.

experiment (fig. 4*A*). This tendency is also indicated by the greater slope, 0.0099 as compared with 0.0065, of the curves representing the dependency of runoff on rainfall (fig. 4*B*). The approximately two-fold difference in runoff between the experimental and control plots increased slightly as daily rainfall increased (fig. 4*B*). As expected, daily rainfall was a reasonably good predictor of runoff; the least-squares linear regression models had correlation coefficient (r^2) values of 0.67 and 0.60, respectively, for the experimental and control plots. In this and each of the other data sets that were analyzed, r^2 values were greater for the experimental plots, suggesting that the absence of earthworms reduces some of the natural heterogeneity in the hydrological response to rainfall. Soil fauna such as earthworms and termites can substantially increase rates of infiltration through soil by creating macropores and channels during their feeding and burrowing activities (Baidgett and others, 2001). Removal of earthworms reduces porosity and eliminates earthworm casting activity, resulting in more microtopographic uniformity and a reduction of total surface area of the soil surface.

Daily rainfall and daily transported soil and organic material expressed as a time series showed a clear difference between the experimental and control plots (fig. 5*A*). Transport of total soil and organic material from the experimental plots was 4.4 times as great as from the control plots, totaling 231 and 53 g, respectively, for the duration of the experiment (table 1). Shuster and others (2002) also reported increased transport of soil in an experiment in which earthworm populations were reduced in a tilled corn agroecosystem; they attributed the increase in sediment flux to incorporated residue levels, reduction of the earthworm population, and reduced macropore and midden density. In our experiment, mean transport of total soil and organic material was 4.6 and 1.1 g per sampling period, respectively, from the experimental and control plots. The transport of soil and organic material from the experimental plots was variable, but it showed a general correlation with rainfall (slope, 0.018 and r^2 value, 0.35 (fig. 5*B*). Control plots showed no correlation with rainfall, presumably because of their greater heterogeneity in hydrologic response as noted above.

Chauvel and others (1999) also reported increased soil erosion in tropical pastures by *P. corethrurus* owing to surface casting associated with soil compaction due to cattle grazing. At El Verde, the background, undisturbed downslope transport of soil, as determined from the control plots, was 51 kilograms per hectare (kg ha^{-1}) and the "disturbance" rate, determined from the experimental plots, was 261 kg ha^{-1}. The background rate for downslope transport of fine litter was 71 kg ha^{-1} and the disturbance rate was 246 kg ha^{-1}.

On steep hillslopes, earthworm casts may become detached and roll downslope, possibly contributing to net soil erosion (Larsen and others, 1999). However, when earthworm casts are dried or aged, they become quite stable (Shipitalo and Protz, 1988), and on a gentle slope such as the one studied here, casting activity in and of itself was not observed to contribute directly to net downslope movement of soil, at least by movement of detached casts.

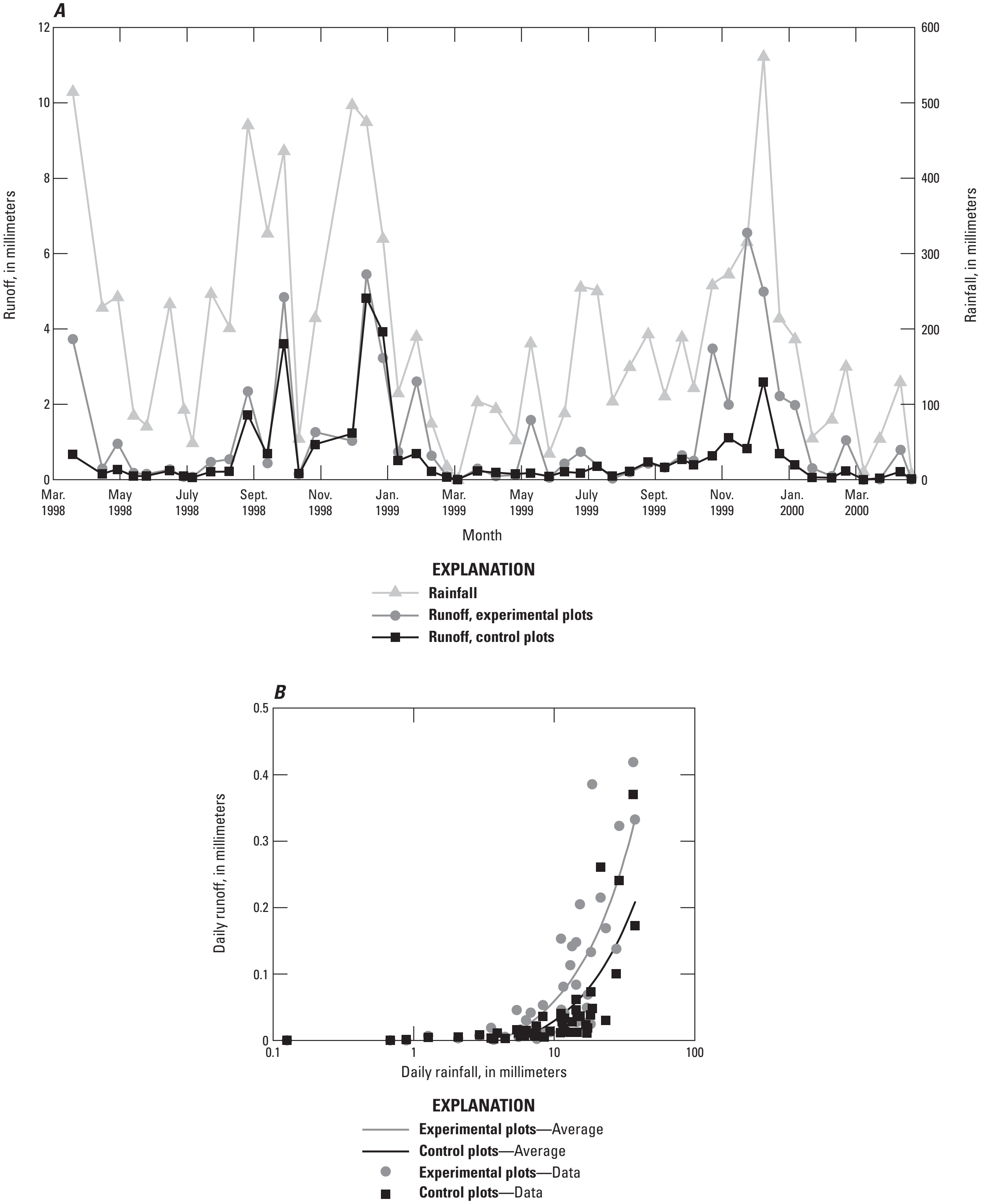


Figure 4. Rainfall and runoff per sampling period (mean of 16 days) at control and experimental plots, El Verde, eastern Puerto Rico. *A*, Time series; *B*, Scatterplot (control: daily runoff = 0.0065 • daily rainfall – 0.0353, correlation coefficient (r^2) = 0.60; experimental: daily runoff = 0.0099 • daily rainfall – 0.0407, r^2 = 0.67).

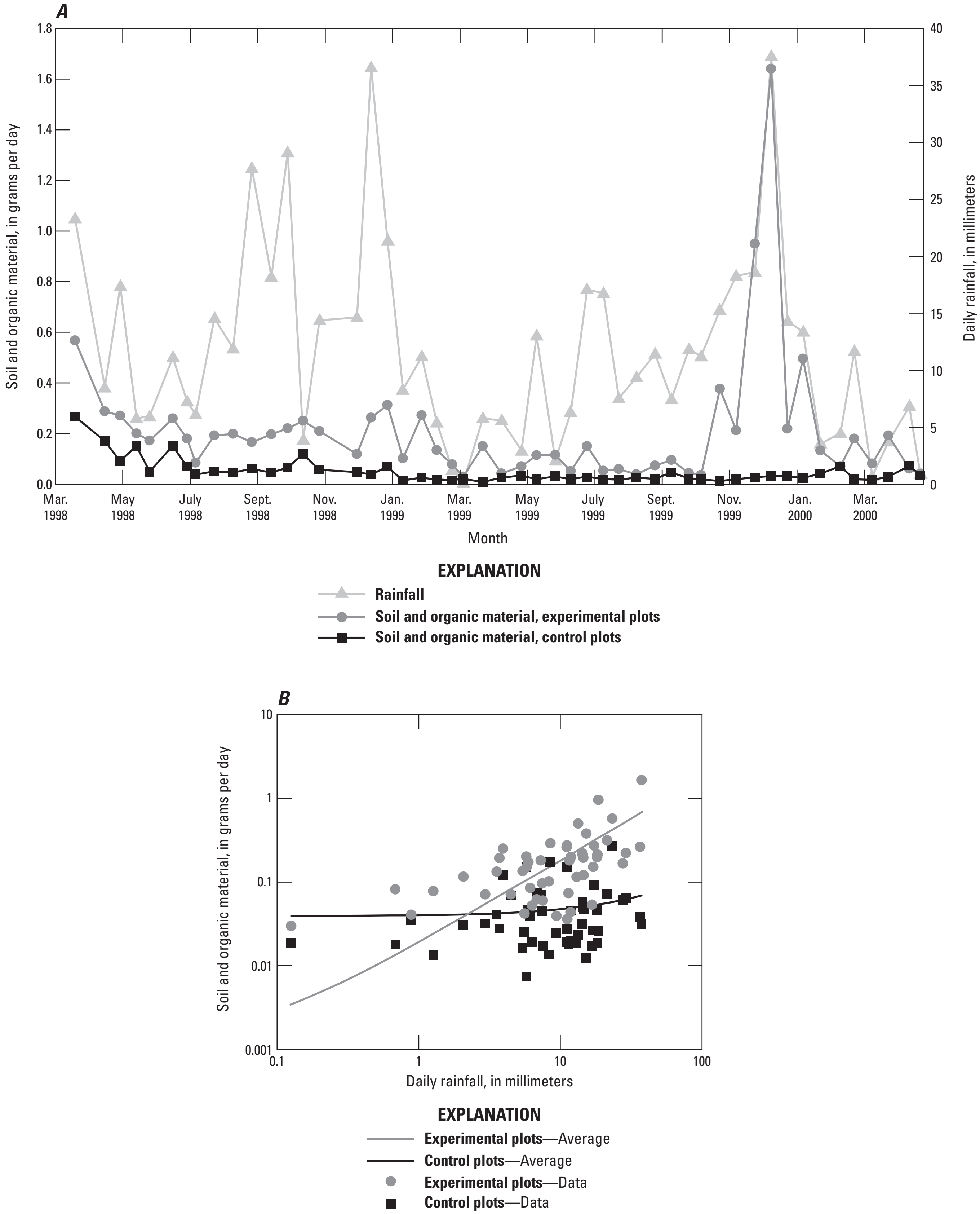


Figure 5. Daily rainfall and transported soil and organic matter at control and experimental plots, El Verde, eastern Puerto Rico. *A*, Time series; *B*, Scatterplot (control: soil and organic material = 0.0008 • daily rainfall + 0.0391, correlation coefficient (r^2) = 0.02; experimental: soil and organic material = 0.018 • daily rainfall + 0.0012, r^2 = 0.35).

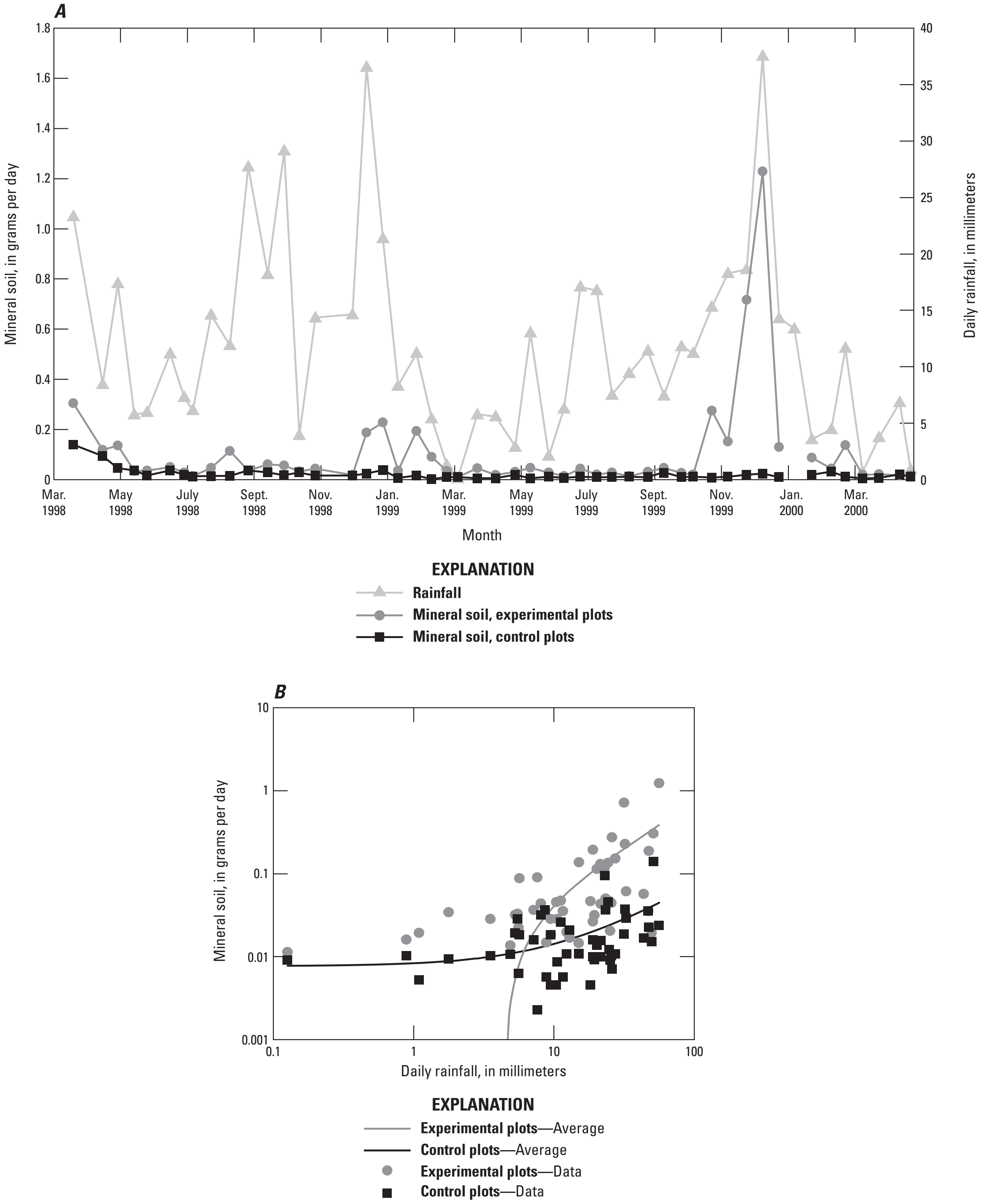


Figure 6. Daily rainfall and transported soil and transported mineral soil at control and experimental plots, El Verde, eastern Puerto Rico. *A*, Time series; *B*, Scatterplot (control: mineral soil = 7 x 10^{-5} • daily rainfall + 0.0077, correlation coefficient (r^2) = 0.17; experimental: mineral soil = 0.0007 • daily rainfall – 0.0335, r^2 = 0.28).

Earthworm casts on the soil surface may mitigate soil erosion by increasing surface roughness (Le Bayon and Binet, 2001). Additionally, field observations by the authors indicate that earthworm casts, if abundant, increase soil surface area at the microtopographic scale. The increased surface area can be estimated by calculating the area of the one half of a spherical cast that is exposed to direct rainfall and summing the surface area of all casts per square meter. The worm castings shown in figure 2*D* are roughly spherical and on the order of 1 centimeter (cm) in diameter. Using an estimate of a single 1-cm cast produced by each of the average of 89 earthworms per square meter, the increase in surface area would be 280 cm^2, approximately 3 percent of a 1-m^2 area. At another humid-tropical site, Henrot and Brussaard (1997) describe *P. corethrurus* surface casts up to 3 cm thick. The increase in surface area at this site would be approximately 840 cm^2, or approximately 8 percent of a square meter. These effects of casting would be expected to reduce runoff and enhance infiltration during low- to moderate-intensity rainfall.

The pattern of daily rainfall and daily transport of mineral soil was comparable to that of total soil and organic material (figs. 5*A*, 6*A*). The transport of mineral soil was 5.2 times as great from the experimental plots as from the control plots, totaling 114 and 22 g, respectively, for the duration of the experiment (table 1). Mean transport of mineral soil was 2.3 and 0.4 g per sampling period, respectively, from the experimental and control plots. The least-squares linear regression models developed for daily transport of mineral soil as compared with daily rainfall had r^2 values that were similar to those developed for the total soil and organic material (figs. 5*B*, 6*B*). Transport of organic material was calculated using a residual value (loss on ignition), so the magnitude and frequency of mineral-soil transport was similar to that discussed above (see fig. 5) for total-soil and organic-material transport (fig. 7). On average, organic-material transport from the experimental plots was 46 percent of the total material collected, compared with 59 percent in the case of the control plots (table 1).

The three-fold increase in fine litter trapped in Gerlach troughs at the experimental plots likely reflects the greater availability of fine litter—the result of a decrease in fine-litter decomposition associated with the lowered earthworm population (Liu and Zou, 2002). The relatively lower rate of fine-litter export in the control plots may also be due to the gluing effect of earthworm casts (Chauvel and others, 1999). Shipitalo and Protz (1988) report that clay minerals and organic material become encrusted with mucus when they are mixed in the earthworm gut, contributing to microaggregate (cast) formation. It is possible that the bonding of cast material may also inhibit litter transport downslope.

The results of our study at El Verde indicate that the reduction of earthworm populations in a managed tropical forest with moderate-gradient hillslopes can substantially increase soil erosion, from a background rate (defined by the control plots) of 51 kg ha^{-1} to the disturbance rate (defined by the experimental plots) of 261 kg ha^{-1}. These rates of soil erosion are equal to a background surface-lowering rate of 9 millimeters per thousand years (mm 1,000 yr^{-1}) and a disturbance surface-lowering rate of 48 mm 1,000 yr^{-1}. The background rate for downslope transport of fine litter was 71 kg ha^{-1} and the disturbance rate was 246 kg ha^{-1}. The increased mass of soil and fine litter moving downslope may be temporarily sequestered in local swales or depressions on the hillslope as well as at the footslope; however, no measurements were made to test this assumption. In the highly dissected Luquillo Experimental Forest, however, upland hillslopes have limited flood plain or other low-gradient surfaces. As a result, most of the soil and fine litter is presumed to be delivered to ephemeral and perennial channels, where it is easily entrained and incorporated by streamflow into the suspended-sediment load.

The effect of reduced earthworm population on hillslope hydrology is evident in the runoff rate, which more than doubled in the plots within which earthworm populations were reduced (table 1). If extended across a landscape, this association indicates that in areas where widespread changes in land use also markedly reduce earthworm population, streamflow peaks may be greater and may rise and fall more quickly in response to storms. Such earthworm reduction may increase downstream channel scour and flash-flood risk. Additionally, lower rates of rainfall infiltration (more than a 50 percent decline) in areas where earthworm populations have been greatly reduced would be expected to diminish soil moisture and groundwater recharge. Although we were not able to measure rates of infiltration below the rooting depth of 15 to 30 cm (Brown and others, 1983), earthworm burrows in the mineral horizon would serve to divert near-surface flow (in the meaning used by Elsenbeer, 2001; see fig. 2 in chapter E of this report) into deeper groundwater where it would contribute to higher dry-season base flow. This possibility is a potential area for future research. It is clear that the effects of reducing earthworm population on hydrologic and soil properties could be substantial in the montane humid tropics, where effective management of these critical natural resources is often a challenging task (Larsen, 2000; Bruijnzeel, 2004).

Summary and Conclusions

Disturbance of the soil environment by removal of earthworms doubled runoff and increased the erosion of soil and downslope transport of fine litter. This doubling can be attributed to two factors: reduced soil porosity resulting from decreased burrowing and reworking of the soil, and decreased soil surface area and surface roughness from a reduction in earthworm casting activity. Earthworm casts increase soil surface area and roughness at the microtopographic scale, thereby reducing runoff, at least during light- to moderate-intensity rainfall. Increased runoff in disturbed environments has been thought to be largely a function of such factors as soil compaction, loss of the soil A horizon, loss of vegetative cover, decreased evapotranspiration, and decreased leaf litter. In

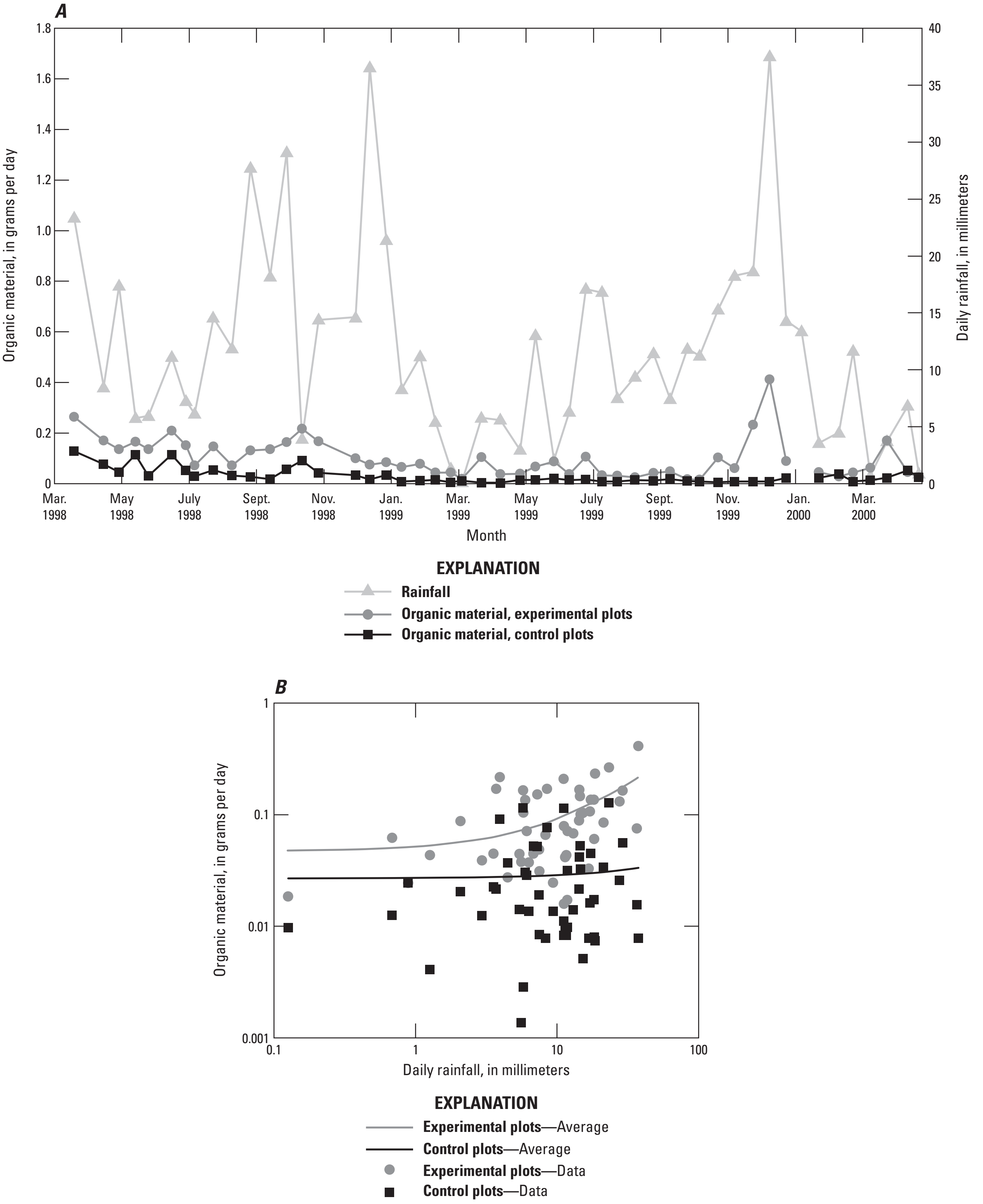


Figure 7. Daily rainfall and transported soil and transported organic material at control and experimental plots, El Verde, eastern Puerto Rico. *A*, Time series; *B*, Scatterplot (control: organic material = 0.0002 • daily rainfall + 0.0269, correlation coefficient (r^2) = 0.003; experimental: organic material = 0.0045 • daily rainfall + 0.0471, r^2 = 0.25).

the Luquillo Experimental Forest, and presumably in similar humid tropical forests, a decrease in burrowing soil macrofauna should be added to this list.

Land degradation has been defined as a substantial decrease in either or both of an area's biological productivity or usefulness due to human interference. Anthropogenic reduction in earthworm population, whether intentional (as in this experiment) or unplanned (as the result of the disturbance of soil or vegetative cover) is a form of land degradation that has unanticipated consequences. The data from this study indicate that the reduction in soil macrofauna population, in this case earthworms, can substantially alter soil physical properties, resulting in the degradational processes of markedly reduced rainfall infiltration, increased runoff, and increased soil erosion. As land and ecosystem management strategies become increasingly complex, improved understanding of the role of macrofauna on soil and water resources is needed.

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