TABLE 5. Number of foraging maneuvers by foraging substrate at Monteverde. X's indicated impossible combinations.

Foraging substrate	Foraging maneuver				
	glean	snatch	hover	hawk	probe
leaves	7	6		X	
vines				X	
flowers			11	X	
epiphytes				X	
branches	16	7	3	X	
boles	4	1		X	
leaf litter				X	1
dead wood				X	
air	X	X	X	6	X

TABLE 6. Number of foraging maneuvers by foraging substrate at Corcovado. X's indicated impossible combinations.

Foraging substrate	Foraging maneuver				
	glean	snatch	hover	hawk	probe
leaves	24	2	5	X	
vines	2			X	
flowers	3		1	X	11
epiphytes				X	
branches	5			X	1
boles	1	1		X	4
leaf litter	2			X	2
dead wood	2			X	
air	X	X	X	2	X

TABLE 7. Number of foraging maneuvers by foraging substrate at La Selva. X's indicated impossible combinations.

Foraging substrate	Foraging maneuver				
	glean	snatch	hover	hawk	probe
leaves	21	2	3	X	
vines	2			X	
flowers	1			X	7
epiphytes				X	
branches	14	3		X	2
boles				X	7
leaf litter	10			X	4
dead wood	1			X	
air	X	X	X	4	X

TABLE 8. Number of foraging maneuver x foraging substrate combinations observed at each site

Site	Total number of foraging events	Observed number of maneuver x substrate combinations
Palo Verde	39	7
Monteverde	62	10
Corcovado	68	16
La Selva	81	14

A COMPARISON OF SOIL PHYSICAL AND BIOLOGICAL CHARACTERISTICS IN FOUR COSTA RICAN FORESTS.

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Abstract. We compared the physical and biological characteristics of soils in four Costa Rican forests representing four distinct zones of climate, habitat and soil types. We measured air and soil temperature, moisture content, pH and litterfall in sites of primary vegetation. We also measured the responses of soil respiration to additions of sucrose and water to assess degrees of carbon and water limitation to microbes. Palo Verde was characterized by hot, dry, high pH soils with little organic matter accumulation in spite of high seasonal litterfall. Monteverde was characterized by cold, wet soils with moderate pH and a deep organic layer. This site exhibited a strong respiratory response to added water. Corcovado was characterized by highly acidic, red clay soils that had a strong respiratory response to added sucrose. La Selva was characterized by moist deep red clay soils with little organic matter accumulation and a weak respiratory response to added sucrose. These results indicate a great deal of variation in soils of different sites and emphasize the danger of applying any generalizations to tropical forest soils.

Key words: soils, microbial respiration, organic matter, pH, litterfall

INTRODUCTION

Tropical soils have often been generalized as infertile, acidic, highly weathered, having a thin organic layer, and a low retention time for organic matter compared with temperate soils (Kricher 1997). Tropical soils, however, are not homogenous, and such generalizations do not account for variations between different soil types (Vitousek and Sanford 1986). Costa Rican soils vary a great deal across different elevations and habitat types because the soils are of different origins, ages, and under different climatic regimes (Vásquez Morera 1983). We characterized the physical and biological properties of soils from 4 Costa Rican biomes and examined how these properties differ among soil and habitat types (Table 1).

We predicted that a combination of varying climatic patterns and soil types would contribute to differences in physical and biological soil properties between sites: (1) increased precipitation would lead to greater soil moisture; (2) increased soil water and temperature would lead to greater soil respiration; (3) seasonal site differences in leaf fall would lead to different litter input rates; and (4) different soil types would have different pH. We also predicted that differences in temperature, litter fall, and soil moisture would cause carbon to be more limiting to soil microbes in some systems, and water to be more limiting in others. By assessing the physical and biological characteristics of a variety of Costa Rican soil types, we intended to provide an initial database for future projects while critically evaluating the notion of uniformity in tropical soils.

TABLE 1. Habitat type, soil type, and mean annual rainfall of 4 Costa Rican field sites (Janzen 1983).

Field Site	Habitat Type	Soil Type	Mean annual rainfall (mm)
Palo Verde 1	tropical dry forest	residual soils, hilly relief	1000 - 1500
Palo Verde 2	tropical dry forest	poorly drained alluvial soils	1000 - 1500
Monteverde	tropical lower montane rain forest	volcanic ash derived soil	2500 - 3000
Corcovado	tropical premontane wet forest	well drained alluvial soils	3000 - 3800
La Selva	tropical wet forest	poorly drained alluvial soils	4000 +

METHODS

We surveyed characteristics of four Costa Rican forest soils in January and February, 1998. At each site we set up four 400-cm^2 experimental treatment plots: water, sugar, water + sugar and control. We added 1 liter of water to each water treatment and 125 g of sugar to each sugar treatment. We also set three 1-m^2 litter traps of black plastic sheeting secured along the edges with tree limbs we found on the site. After 24 hours we sampled soil from each of our experimental plots and returned these samples to the lab for respiration measurement. We measured soil and air temperature in control plots *in situ* with a Barnant 90 Digital thermometer, measured soil moisture and pH with a Demetra System Soil Tester, and collected all litter that fell into litter traps. We collected 1.5 X 25 cm soil cores at each site for characterization of soil profile structure.

Respiration rates of soil samples were measured in the lab using volumetric respirometers. Respiration flasks containing a bottom layer of soda lime, middle layer of cotton and top layer of soil (each layer ≈ 1.5 cm thick, loosely packed) were capped with a rubber stopper with an inserted graduated pipette. Flasks were placed in a water bath with the pipettes above the water surface to equilibrate for 15 minutes. The pipette tips were then submerged and the change in gas volume in each pipette was recorded over time. Respiration rates were expressed as µl oxygen consumed per gram dry weight of soil per hour (µl O_2 $*g^{-1} * hr^{-1}$). Respiration measurements were conducted at temperatures near the measured natural soil temperature at each site except Monteverde, where the measurement temperature was ≈10° above soil temperature. Consequently Monteverde measurements were corrected by dividing the measured rate by 2, which is a typical Q_{10} for soil respiration. Soil samples were also used to determine soil moisture content: (wet weight - dry weight) / wet weight) * 100. Correlation analyses examined the relationships of soil moisture and air temperature with respiration rate

RESULTS

There were differences between sites in air and soil temperatures, soil moisture, pH and litterfall (Table 2). Palo Verde soils were distinctly different between hilly limestone slope and the clay flat. The slope had thin soil (12 cm) above bedrock. A coarse, dry organic layer was about 4 cm deep. Below that was an indistinct layer of decomposed organic matter and about 8 cm of dry. light brown, loose granular soil. The clay flat soil was thicker (>25 cm). The litter layer was also dry and about 4 cm deep. The organic layer below that was about 1 cm thick. The subsequent strata consisted of dry, dark brown, blocky soil (4 cm) overlying more or less distinct layers of progressively lighter soil. There was some evidence of occasional anoxic conditions with gray streaks running through the lower horizons (this site was adjacent to a marsh). Monteverde litter was very moist, 8 - 12 cm deep, and overlying moist, uniformly very dark brown and deep (>25 cm) soil. Corcovado litter was sparse (1 -2 cm deep) and dry. Soils there had a thin (1 cm) layer of decomposing organic matter above 6 cm of orange clayey soil and darker red, hard crusty subsoil. La Selva soils were similar to Corcovado except they were moist when sampled, and were more red in color in the upper horizons.

TABLE 2. Summary of soil characteristics for control plots at each site.

Site	Temperature (°C)			Soil moisture (%)	pH	Litter fall g/d,(±SE)
	Air	2 cm	6 cm			
Palo Verde slope	32.7	29.3	27.8	5.6	7.0	8.24 (±2.32)
Palo Verde clay flats	30.6	30.3	27.5	8.7	7.0	4.11 (±0.43)
Monteverde	13.3	13.6	13.8	80.0	6.3	1.76 (±0.46)
Corcovado	26.2	26.0	26.0	19.7	3.5	nd
La Selva	25.4	23.5	23.9	41.4	5.9	7.93 (±5.25)

Soil respiration rates decreased with increasing temperature (r = -0.61, P = 0.016, Fig. 1). Soil respiration increased with soil moisture availability when all treatments except those with sugar were included (r = 0.52, P = 0.055, Fig. 2). Microbial respiration at Monteverde and Palo Verde were most limited by water (Fig. 3), while Corcovado , Palo Verde and La Selva were most limited by carbon (Fig. 4). Water limitation in respiration did not seem to be directly related to soil moisture, but was related to average annual precipitation. Carbon limitation in respiration did not seem to be related to litterfall but was related to accumulation of organic matter.

DISCUSSION

We found vast differences in the physical and biological properties of the tropical soils we studied. Our prediction about the relationship between annual precipitation and soil moisture at each site was complicated by measurements in the dry season at seasonal sites and the effects of an uncharacteristically dry year. Even though average annual rainfall did not predict soil moisture conditions at these sites, it appears that soil respiration was most limited by water in sites with the lowest annual rainfall. Soils at Corcovado and La Selva had no respiratory response to water addition. La Selva soils were quite moist so this is no surprise. Corcovado soils, though moist through most of the year, were quite dry when these measurements were taken. It is likely that Corcovado soils did not respond to water supplementation because they were severely limited by carbon, while La Selva soils did not respond because they were not limited by water. Monteverde exhibited the highest soil moisture readings of all sites, and yet the greatest respiratory response to additional water. Perhaps microbes at these sites are tracking long term trends (e.g. average annual precipitation) and do not respond uniformly to pulses of water. Similarly, litterfall over the course of 1 - 3 days did not predict carbon limitation, but accumulation of organic matter did (e.g. Monteverde was the only site not limited by carbon and had the greatest accumulation of litter). Litterfall in Palo Verde and La Selva appear to contain much recalcitrant organic matter. Sclerophyllous leaves were captured in the traps at Palo Verde, and a large portion of the litter collected at La Selva was coarse woody debris. The respiratory response to added sucrose at these sites suggests that microbes may be limited by the availability of carbon and not by total carbon at these sites. Our short term measurements of litterfall had high variance because coarse woody debris fell in chunks in some traps and not others. Consequently, although these estimates should be unbiased, they have very large confidence intervals.

The cliché of highly weathered acidic soils in the tropics is obviously fallacious. The soil pH at Palo Verde was high even by temperate forest standards. This is apparently due to subsurface limestone bedrock at this site and lower annual rainfall that leaches fewer base cations from this soil. Corcovado soils on the other hand were extremely acidic. This was likely due to well weathered, well drained alluvial soils that accumulate Fe and Al oxides (the red coloration of subsurface soils) and are leached of cations exposing more cation exchange sites to saturation by H^+ ions.

Our respiration measurements seemed reliable within sites, but may be difficult to compare among sites. Volumetric gas measurement is very sensitive to ambient temperature, and we were unable to keep ambient temperatures entirely stable in our experiments. Other factors limiting the scope of our inference in this study was the lack of replication of some measures and missing treatments in other measures. Together these limitations largely precluded rigorous statistical analyses. Finally, dry weight measurements of soils and litter were obtained by air drying samples for up to 2 days, so differences in humidity between sites may have produced unequal drying and biased some comparisons among sites. Future studies should consider ways to maintain controls between sites in temperature and drying conditions.

This study is the first to our knowledge to compare the physical and biological characteristics of soils in these Costa Rican tropical forests. It is our hope that these results can be used in the formulation of new hypotheses addressing belowground ecological processes and the strong potential for interactions between the soil environment and the aboveground community. Questions regarding the decomposition rates of organic matter incorporating rigorous measures of inputs and outputs to the system, and those regarding potential soil environment controls over primary production seem especially apropos.

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