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IMPACT OF MICROCLIMATE AND MINERAL STATUS ON NITROGEN FIXATION IN THE MOIST GULLY FORESTS OF BARBADOS, WEST INDIES

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ABSTRACT. Plant community structure, the related intra-gully climate, soil and fine litter nitrogen fixation, and nutrient dynamics were studied. Applewaite Gully, Barbados, supports a sunken forest with a temperature/precipitation ratio of 0.017 placing it on the moist end of the dry forest spectrum (25°C/1475 mm annual rainfall). The abrupt topographic change characteristic of the gullies results in a reduced vapor pressure deficit which maintains adequate litter and soil moisture to support nitrogen fixation. Mean acetylene reduction activity (ARA) value for fine litter was 25.1 mM $C_2H_4 \cdot m^{-2} \cdot year^{-1}$ at 191% moisture content and the mean soil ARA value was 14.3 mM $C_2H_4 \cdot m^{-2} \cdot year^{-1}$ at 59.5% moisture content. The potential nitrogen contribution by litter and surface soil nitrogen fixation ranged between 0.78 and 0.95 $kgN \cdot ha^{-1} \cdot year^{-1}$. Fine litter and soil nitrogen fixation potentially amends the low nitrogen content of infertile gully soils. The N values for fine litter and soil were low and characteristic of infertile soils, whereas P values were high. ARA exhibited a strong negative correlation with both soil and litter %N. Soil ARA may have been reduced due to high soil clay content limiting the availability of organic material.

INTRODUCTION

The 150 kilometers of fissures or gullies in the coral dome of the West Indian island of Barbados support moist dry forests. From a distance, only the canopy surface is seen extending from cracks and coursing, ribbon-like, across a dry landscape. Change in vegetation types usually occurs across broad environmental gradients. The abrupt topographic changes associated with the surface geology of Barbados result in a sudden shift from non-gully xeric surface to moist gully subsurface vegetation.

The "gullies," typical of Barbados, are unique because the geological history of this island differs significantly from others of the Caribbean Archipelago. Barbados is the only large Caribbean island that is not volcanic in origin. The basal rocks of Barbados are tertiary sandstones and clays deposited by an ancient river flowing northward from the South American land mass. Uplifting brought these deposits near the surface where 85% of the island was capped by coral reefs (Fermor 1973). Subsequent uplifting above sea level fractured the coral cap and formed the extensive gully system. Gullies radiate in a southwesterly direction from a northeastern point off shore from Morgan Lewis. Certain gullies may represent collapsed tunnels in the coral cap. The coral limestone capping Barbados ranges in age between 600,000 at high elevation and 20,000 years old at lower elevations. Since the colonization of Barbados in 1627, the gully network has been exploited by adjacent sugar cane plantations, and today represents, to varying degrees, disturbed habitats. Applewaite represents one of the least disturbed gullies. Gooding (1974) divided the gully toposequences into three distinct habitats: wall, floor and slope. We included the gully rim habitat in this study.

Approximately 40% of the earth's tropical land area is closed or open canopy forest which can be divided into three types: 25% rain forest, 33% moist forest, and 42% dry forest (Holdridge 1967, Brown & Lugo 1982, Murphy & Lugo 1995). Research interests have centered on rain forests and savannas with little attention focused on moist and dry forest ecosystems (Murphy & Lugo 1986, 1995). Community structure of dry and moist tropical forests is controlled predominantly by the quantity and the seasonal distribution of rainfall (Richards 1952, Holdridge 1967, Walter 1971, Dolely, 1981). Long-term variability of rainfall quantity and annual distribution may play a key role determining the community structure (Pook *et al.* 1966, Dolely 1981, Gentry 1995, Murphy & Lugo 1995) and important physiological processes such as litter and soil nitrogen fixation.

The gully moist forests offer an excellent opportunity to study the relationship between climatic conditions provided by the recessed habitat and nutrient dynamics that sustain these forests in an otherwise highly water-stressed sur-

face environment. Soil and fine litter nitrogen content are low in comparison to other forests (Nye 1961, Golley *et al.* 1975, Folster & de las Salas 1976, Franco 1979, Cuevas & Medina 1986, Silver 1994, Silver *et al.* 1994). In this paper we describe the geology and plant community structure of Applewaite gully. We studied the role of nitrogen fixation in fine litter and surface soils, and related the potential nitrogen contribution to soil and litter nutrient content, soil pH, soil organic material (%OM), soil moisture, litter standing crop, air and soil temperature, and percent humidity.

Materials and Methods

Applewaite Gully topography varies from narrow to broad floor toposequences and east versus west slopes. Stations 1 and 2, the two study sites, were selected to include these variations. Station 1 transect was 39 m in length beginning at the vertical east wall, extending across the floor for 12 m and ascending the 53° slope to the western rim (Figure 1,A). Six sampling sites were established along the transect. Station 2 transect was 47 m long extending for 23 meters down the eastern slope of 16° then across the floor to the western, vertical wall (Figure 1,B). Nine sampling sites were located at approximately 6 m intervals along the transect. Sampling of Stations 1 and 2 was synoptic. At Stations 1 and 2, species and vegetation heights were noted along the 3 meter belt transects.

Acetylene assay. Fine litter and soil nitrogen fixation was measured using the acetylene reduction technique calibrated by ^{15}N. This technique substitutes acetylene (H-C≡C-H) for nitrogen (N≡N). Nitrogenase enzyme bonds to acetylene and reduces it to ethylene ($H_2C=CH_2$). The resulting ethylene concentrations were then determined using a Gow-Mac gas chromatograph (Gow-Mac Instrument Company, Bound Brook, New Jersey) model 69–750 fitted with a Porapak R filled 114 cm long stainless steel column (40°C) employing N_2 as carrier gas. Scotty Analyzed Gases (Longmont, Colorado) were used to calibrate the GC every 20th sample. The temperature inside the incubation chambers employed in ARA assays was monitored at 5-minute intervals with a Li-Cor 1000 (Lincoln, Nebraska) datalogger fitted with 64μ diameter, copper-constantan thermocouples. The incubation temperature was compared to a second thermocouple inserted into the soil or into the litter. Only those samples that were within 2°C of the undisturbed soil or leaf litter temperature were used for analyses to ensure that incubation proceeded at ecologically relevant temperatures.

The following controls were included in each sample set: (1) vials without litter or soil samples were injected with C_2H_2 to detect contaminating C_2H_4; (2) vials were incubated with samples but without C_2H_2 to detect endogenously produced C_2H_4; (3) five vials were injected with a standardized gas mixture (Scotty I Analyzed Gases, 8.12 ppm C_2H_4) to detect C_2H_4 losses due to leakage, adsorption, and absorption during incubation or during transportation in the sampling syringe. These showed C_2H_4 concentrations within 1% of specifications.

C_2H_2 : ^{15}N reduction ratio. To mathematically convert the amount of ethylene formed to potential nitrogen fixed, the ratio of ethylene production to nitrogen fixed was determined using ^{15}N (Shearer & Kohl 1986). The ratio is normally 3:1, but this can vary due to numerous interfering processes. The ratio of C_2H_2 reduction to N_2 reduction rates was determined by converting field and laboratory ARA values to equivalents of nitrogen. One half of the air of three vials was withdrawn and it was replaced with air containing 99% ^{15}N. Three additional vials injected with acetylene (from calcium carbide + H_2O) to make an atmosphere 10% acetylene by volume. The test was repeated. Vials containing soil or litter samples were incubated in parallel under field conditions at representative temperatures and light intensities. Gas samples were withdrawn at the study site and the test samples of soil or litter dried (85°C, 48 hours). Samples were returned to the laboratory and digested with sulfuric acid/persulfate and the ammonium was diffused into H_2SO_4, evaporated to dryness and analyzed in an isotope ratio mass spectrometer. Termination efficiency, atom $\%^{15}N$ headspace N_2, C_2H_4 impurities and analysis for endogenously produced C_2H_4 in the C_2H_2 were tested and the appropriate corrections made. The ratio and measurement error of C_2H_4: ^{15}N was 3.4 ± 0.9 and 3.7 ± 1.1 for litter and soil samples respectively; they were close to the theoretical ratio of 3.

Soil ARA measurement. Ten soil samples (1 cm diameter and 1 cm deep) were taken from each sample site along the transect lines for ARA determinations. These samples were combined and placed into 200 ml glass cuvettes along with 20 ml of C_2H_2 (calcium carbide + H_2O). The cuvettes were incubated in situ for 24 hours. The temperature within the cuvette was monitored using a 64μ diameter thermocouple and compared to surface soil temperature. The temperature differential was not greater than

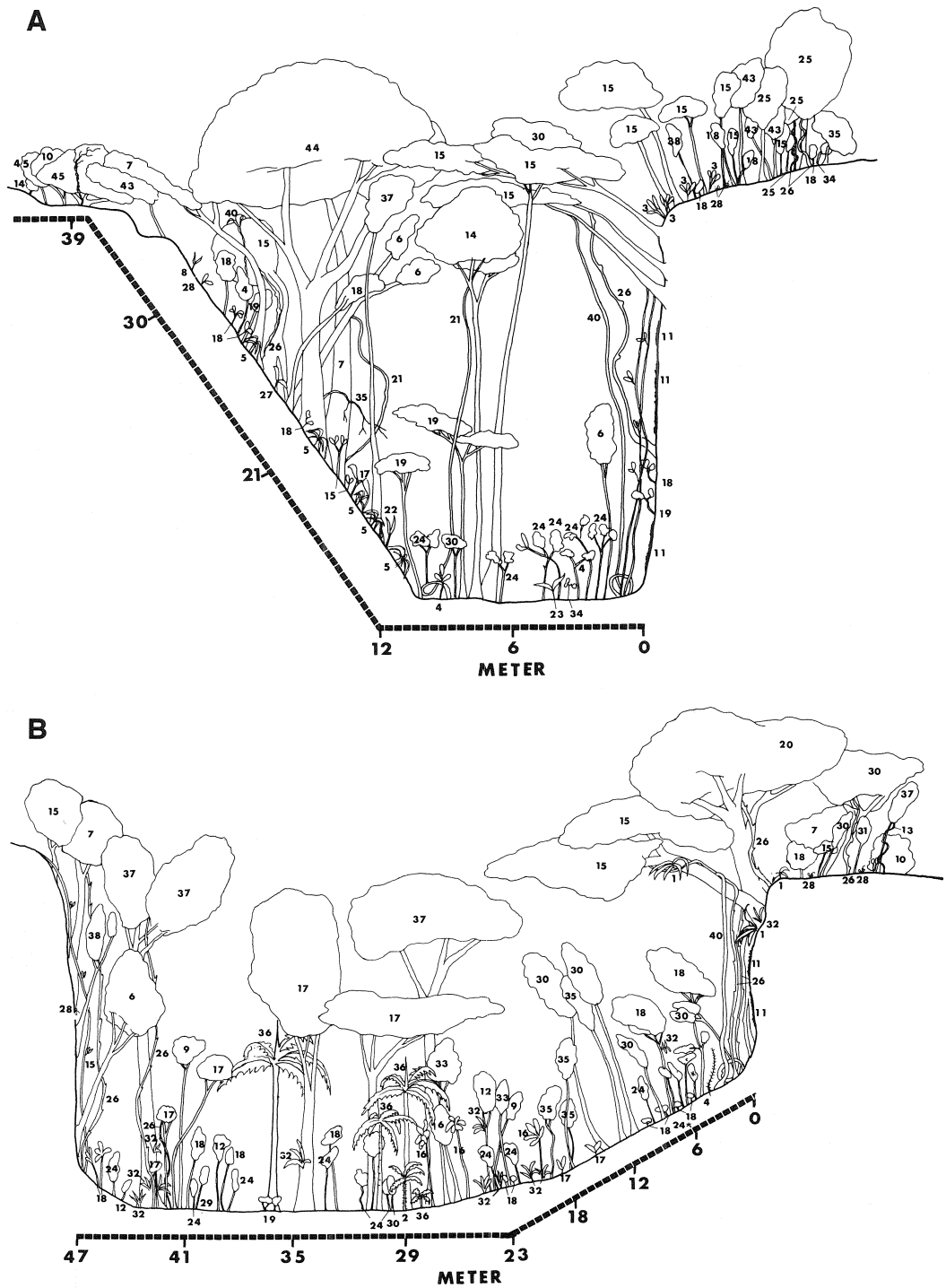

FIGURE 1. Vegetation profiles of Applewaite Gully study sites. A, Station 1. B, Station 2. Key to species and their distribution in gully habitats is summarized in TABLE 1.

2°C. The gaseous contents were mixed by shaking and 1 ml samples were withdrawn for analysis. The entire sample was dried to constant weight (85°C, 48 hrs), weighed, and saved for mineral analysis.

FINE LITTER ARA MEASUREMENT. Fine litter was defined as leaves, twigs, flower parts, and fruits. Surface litter was sampled by combining 5 random 400 cm^2 quadrant at each sample site along the transect. Care was taken to minimize soil contamination of the litter sample. Subsamples were placed into 530 ml flasks and injected with acetylene (C_2H_2, from calcium carbide + water) to 10% by volume. These were incubated in situ for 4 hrs; afterwards the gaseous atmosphere was mixed by shaking and gas samples were withdrawn for analysis. The entire sample was dried to constant weight (85°C, 48 hrs), weighed, and saved dry for mineral analysis.

FINE LITTER AND SOIL NUTRIENT ANALYSES. The pH was determined using distilled water-saturated pastes of soil or ground litter. Percent soil organic matter was determined by weight loss following ignition. Total nitrogen was determined by microKjeldahl analysis (Bremner & Mulvaney 1982). A Jerrel-Ash inductively coupled argon plasma spectrophotometer (ICAPS) was used to measure Ca, P, K, Mg, Na, Al, B, Cd, Co, Cu, Fe, Mn, Mo, Si, Ti and Zn in ammonium acetate extracts of 2 g fine litter and soil sub-samples extracted 4 times with 35 ml of 0.5 N ammonium acetate. U.S. National Bureau of Standards orchard leaves were the standard.

STATISTICAL TESTS. The Mann-Whitney nonparametric test was employed throughout to compare the means of data for slope versus floor and between sites. Multiple regression analysis was applied to evaluate the relationship between data obtained in the slope and floor habitats. Application of multiple regression analysis as an analytical tool was validated by dividing slope and floor habitats into upper and lower halves (east, west floor) and applying the Mann-Whitney Test. No significant difference ($P \leq 0.05$) was detected for any measured factor in these comparisons.

PERCENT MOISTURE. The moisture content of litter and soil samples was calculated from the difference between fresh and the dry weights (85°C, 48 hours).

PHOTON FLUX DENSITY, TEMPERATURE AND PERCENT HUMIDITY. Photon flux density (PFD) along the transect was measured to quantify below canopy light intensity. PFD measurements were taken at one meter intervals along the transect lines using a Li-Cor LI-190SA cosine-corrected light intensity sensor (PAR 400–700 nm) set to integration mode. The temperature of soil (surface and 10 cm deep), litter and air (1 m above soil, measured at noon under clear skies) was measured by inserting the soil temperature probe into each layer and recording the temperature using a Li-Cor 1000 datalogger. Percent humidity was taken at a height of 1 m with an analog percent humidity meter.

RESULTS

PHYSIOGRAPHY OF STUDY SITES. The Applewaite Gully study area is located on the West Indian island of Barbados 13°30′N, 59°00′W, St. Thomas Parish. Dry and moist tropical forest ecosystems have an annual average rainfall between 600 to 1,800 mm distributed over 4 to 9 months with at least one major and one minor dry period (Murphy & Lugo 1986). Applewaite Gully receives 1,360–1,500 mm annual rainfall (Anon. 1987). February–April is the dry period with only 48 mm in March. The ratio of mean annual temperature to mean annual precipitation for the Applewaite Gully study site was 25°C/1475 mm = T/P 0.017. The T/P ratio for Applewaite Gully was compared to those presented by Murphy and Lugo (1986). This placed the Applewaite Gully forest at the moist end of the dry forest spectrum between a deciduous woodland in Zaire and seasonal Ivory Coast forests having T/P ratios of 0.016 and 0.018, respectively. Wet forest types have three or more canopy layers, whereas dry forests are simpler with one or two layers (Murphy & Lugo 1986). Both sample Stations 1 and 2 established in Applewaite Gully exhibit a three-layered profile which is consistent with the classification of this forest as a moist dry forest (FIGURE 1,A, B).

At Station 1, six species occurred within the floor habitat only, 12 on the slope, and 5 species in both floor and slope habitats (TABLE 1). At Station 2, 8 species were limited to the floor habitat, 3 occurred only on the east slope and 7 species were found growing in both slope and floor habitats. The cyanobacterium *Chroococcus indicus* colonized the vertical wall habitat exclusively at both stations, and did not occur in the other habitats. At Station 2, *Ficus citrifolia* and *C. indicus* were established within the wall habitat.

LIGHT INTENSITY, PERCENT HUMIDITY AND TEMPERATURE. Measurement of the understory light environment is essential for understanding the physiological (Pearcy 1983, Mulky 1986), ar-

TABLE 1. The distribution of species between gully floor, slope, rim and vertical wall habitats. Species indicated by numbers from FIGURE 1A and B.

	Station 1					Station 2				
	Wall	Floor	Slope	West Rim	East Rim	East Wall	Slope	Floor	West Wall	East Rim
1. Aechmea lingulata						X				X
2. Aiphanes minima								X		
3. Anthurium willdenowii					X					
4. Argythamnia polygama		X	X		X					
5. Bromelia plumieri			X							
6. Bunchosia polystachia		X	X					X	X	
7. Bursera simaruba			X						X	X
8. Capparis flexuosa			X							
9. Casearia guianensis								X		
10. Cordia curassavica				X						X
11. Chroococcus indicus	X					X				
12. Chrysophyllum cainito								X		
13. Cissus verticillata										X
14. Citharexylum spinosum		X		X						
15. Clusia plunkenetii	X	X	X		X	X			X	X
16. Coccoloba swartzii							X	X	X	
17. Cupania americana	X		X				X	X		
18. Eugenia monticola	X	X	X		X		X	X		X
19. Eugenia procera		X					X			
20. Ficus citrifolia										
21. Gouania lupuloides		X								
22. Hymenocallis caribaea			X							
23. Lasiacis divaricata		X								
24. Odontonema nitidum		X					X	X		
25. Tabebuia heterophylla					X					
26. Paullinia cururu	X		X		X	X	X	X	X	X
27. Peperomia magnoliifolia			X							
28. Peperomia myrtifolia			X		X				X	X
29. Piper dilatatum								X		
30. Pisonia fragrans		X					X	X		X
31. Pithecellobium unguis-cati										X
32. Polypodium latum						X	X	X		
33. Psidium guajava								X		
34. Psychotria nervosa		X								
35. Randia aculeata			X		X		X			
36. Roystonea oleracea								X		
37. Sapium hippomane			X					X	X	X
38. Schoepfia schreberi									X	
39. Scleria lithosperma										
40. Securidaca diversifolia		X	X				X			
41. Smilax oblongata							X			
42. Spondias mombin										
43. Swietenia mahagoni			X							
44. Tabebuia pallida			X							
45. Tecoma stans				X						

chitectural (Hogan 1986), and spatial distribution (Richards & Williamson 1975, Formann & Hahn 1980, Hogan 1986) of plants in a community. Station 1 (FIGURE 1A) had a dense canopy structure which resulted in low light intensities across the transect. Mean transect photon flux density (PFD) was 118 $\mu M \cdot m^{-2} \cdot s^{-1}$ (above canopy 2112—cloudless). Mean PFD values for the floor and slope were significantly different ($P \leq 0.05$) at 31 and 106 $\mu M \cdot m^{-2} \cdot s^{-1}$, respectively. At Station 2 (FIGURE 1B), the mean floor and slope PFD value was 294 $\mu M \cdot m^{-2} \cdot s^{-1}$ (above canopy 2097—cloudless). Station 2 also had very low light intensities along the eastern slope (182 $\mu M \cdot m^{-2} \cdot s^{-1}$) that were significantly different ($P \leq 0.05$) from the higher light intensities measured across the wide floor (663 $\mu M \cdot m^{-2} \cdot s^{-1}$). Below-canopy photosynthetically active radiation (PAR) at Station 2 was 2.5 times greater than PAR radiation at Station 1, but both

TABLE 2. Mean litter acetylene reducing activity (ARA), percent moisture and potential nitrogen measured during wet and dry conditions.

Conditions	ARA mM $C_2H_4 \cdot M^{-2} \cdot y^{-1}$	ARA ± SE (*N*=)	% moisture	% moisture ±SE (*N*=)	$kgN \cdot ha^{-1} \cdot y^{-1}$
Station 1					
Wet Floor & Slope	30.08	4.48 (23)	191	12.21 (23)	0.61
Dry Floor & Slope	34.19	6.35 (12)	139	14.70 (12)	0.70
Wet Slope	37.91	7.36 (12)	195	20.64 (12)	0.77
Wet Floor	22.50	3.49 (12)	197	15.30 (12)	0.46
Dry Floor	35.19	8.65 (6)	141	12.22 (6)	0.72
Station 2					
Wet Floor & Slope	20.67	2.28 (36)	190	14.11 (36)	0.74
Dry Floor & Slope	6.02	1.57 (33)	23.2	1.36 (33)	0.12
Wet East Slope	20.04	2.31 (24)	188	18.14 (24)	0.41
Wet Floor	21.94	5.18 (12)	196	22.8 (12)	0.45
Dry East Slope	9.34	2.81 (12)	21.6	1.44 (15)	0.19
Dry Floor	3.26	1.44 (15)	24.6	2.17 (18)	0.06

Stations had PFD values characteristic of a closed wet forest canopy.

Mean air temperature within the gully (N = 5) at Stations 1 and 2 was 28.9°C and relatively constant across the transect. The gully air temperature averaged 1°C lower than the temperature measured in adjacent open fields.

Both Stations 1 and 2 had high relative humidity values compared to the rim and adjacent open fields. Percent humidity decreased with increasing elevation up the slopes. Station 1 gully habitat was 14% and 7% more humid than the rim during wet and dry seasons, respectively. Station 2 gully habitat was 18% more humid than the rim during the wet season and 9% more humid during the dry season. The percent humidity of the floor and slope habitats was compared for Stations 1 and 2. Only during dry conditions at Station 2 was there a significant difference ($P \leq 0.05$) between these habitats. The percent humidity across the transect for Stations 1 and 2 measured during wet season was not significantly different, however, during the dry season. Station 2 was significantly more humid ($P \leq 0.001$) than Station 1. Station 2 percent humidity across the floor habitat during the wet ($P \leq 0.05$) and dry season ($P \leq 0.001$) was higher than Station 1. Percent humidity values for the slope habitat during the wet season were similar at Stations 1 and 2; but during the dry season, Station 2 slope percent humidity was significantly higher ($P \leq 0.05$).

LITTER NITROGEN FIXATION. The mean slope plus floor ARA values for Station 1 wet versus dry litter were not significantly different ($P \leq 0.05$), but percent moisture values were ($P = 0.001$) (TABLE 2). The similarity between wet and dry ARA values may have been caused by the depressing effect of high percent litter moisture on nitrogen fixation rates. Station 1 slope and floor litter ARA values were analyzed separately and compared. Station 1 mean wet litter ARA values for the slope and floor were significantly different ($P \leq 0.05$). The percent moisture values for the floor sample sites were not significantly different ($P \leq 0.05$) from the mean litter ARA and percent moisture values determined for the west slope sites. Mean floor ARA values measured during somewhat drier conditions with a moisture content of 141% were greater than those obtained during wet conditions.

Station 2 mean floor and slope ARA and percent moisture values were determined during wet and dry conditions. Litter ARA values during dry conditions were higher and significantly different from each other ($P \leq 0.01$). Mean east slope versus floor ARA and percent moisture values measured during wet conditions were not significantly different ($P \leq 0.05$) from each other (TABLE 2). However, during an extended dry period, mean ARA values for litter collected on the east slope were higher and significantly different ($P = 0.02$) from those measured for the floor habitat, but percent moisture values were not ($P \leq 0.05$).

The Stations 1 and 2 litter ARA and litter moisture values were similar.

STRATIFICATION OF LITTER ARA. Litter collected at Station 2 floor sample sites was divided into upper (0–1 cm) and lower samples (1–3 cm). The mean ARA for the upper was 463 (173% moisture) and lower layer 173 nM $C_2H_4 \cdot gdw^{-1} \cdot day^{-1}$ (150% moisture content). ARA and percent moisture values were significantly different ($P \leq 0.001$).

TABLE 3. Mean soil acetylene reducing activity (ARA), percent soil moisture and potential nitrogen measured during wet and dry conditions.

Conditions	mM $C_2H_4 \cdot M^{-2} \cdot y^{-1}$	ARA ± SE (*N*=)	% moisture	% moisutre ±SE (*N*=)	$kgN \cdot ha^{-1} \cdot y^{-1}$
Station 1					
Wet Floor & Slope	25.7	9.02 (11)	54	3.57 (11)	1.84
Wet Floor	15.3	9.09 (5)	59.2	6.24 (5)	0.29
Wet West Slope	34.2	14.4 (6)	50.6	3.76 (6)	0.64
Station 2					
Wet Floor & Slope	3.0	1.54 (10)	65	5.13 (10)	0.21
Dry Floor	0	— (10)	40	1.37 (10)	0
Dry East Slope	5.7	3.31 (5)	47	5.66 (4)	0.39

SOIL NITROGEN FIXATION. The mean Station 1 wet floor and slope soil ARA value was greater by a factor of 8.7 than mean ARA values at Station 2 when measured at similar soil moisture contents (TABLE 3). Mean Station 1 ARA and percent moisture values for floor versus slope were not significantly different ($P \leq 0.05$). Mean Station 2 ARA and percent moisture content values for slope versus floor habitat measured during dry conditions were not significantly different ($P \leq 0.05$).

SOIL AND FINE LITTER NUTRIENT CONTENT. Station 1 soil P values were significantly different between floor and slope habitats ($P \leq 0.05$), but litter depth, litter %N and P, and litter standing crop were not (TABLE 4). Multiple regression analysis yielded a high correlation between N − P litter ($r^2 = 0.74$), N − P soil ($r^2 = 0.93$), and soil P − %OM ($r^2 = 0.60$). The correlation coefficients for litter standing crop, soil %OM, litter depth or soil N and P were less than $r^2 \leq 0.6$.

Station 2 slope versus floor litter N and depth values were significantly different from each other ($P \leq 0.05$). The difference between floor versus slope values for soil N, P and litter P, litter standing crop, and soil %OM were not significant. Regression analysis of Station 2 included N and P soil, litter standing crop, litter depth, and soil %OM. Strong correlations were found between the following: Soil N − soil %OM ($r^2 = 0.92$), soil N − litter depth ($r^2 = 0.64$), litter P − soil %OM ($r^2 = 0.61$) and soil % moisture − %OM ($r^2 = 0.60$). The remaining correlations had r^2 values < 0.6.

RELATIONSHIP BETWEEN LITTER AND SOIL NUTRIENT CONTENT AND ARA. Soil and litter N and P, litter P and %OM were significantly higher ($P \leq 0.05$) at Station 1 than 2. Litter standing crop and depth were similar at both stations.

Stations 1 and 2 mean litter ARA values were compared to litter N, litter P, litter standing crop and litter depth. There were no correlation coefficients greater than $r^2 > 0.6$.

Multiple regression analysis of Station 1 soil ARA, soil N, soil P and soil %OM showed a correlation of $r^2 = 0.64$ between soil P − %OM, but the others were $r^2 \leq 0.6$. A similar analysis of Station 2 soil ARA, soil N, soil P and soil %OM showed a correlation of $r^2 = 0.61$ between soil N − $\%H_2O$, $r^2 = 0.92$ between soil

TABLE 4. Mean litter and soil percent nitrogen, phosphate, soil organic material, litter standing crop and litter depth.

	%N	%P	%OM	Litter standing crop $g \cdot m^{-2}$	Litter depth cm
Station 1					
Litter Floor	1.06	0.1135	—	368	3.33
Litter Slope	1.13	0.1256	—	571	2.57
Soil Floor	1.14	0.0020	35.1	—	—
Soil Slope	1.02	0.0014	29.8	—	—
Station 2					
Litter Floor	1.03	0.1477	—	5.72	4.21
Litter Slope	1.31	0.1073	—	666	2.32
Soil Floor	1.75	0.0038	35.1	—	—
Soil Slope	1.42	0.0036	46.8	—	—

TABLE 5. Nutrient content of floor and slope litter are compared. Five samples pooled from each sample station.

	ppm				
	Ca	Fe	Mg	K	Al
Station 1					
0–12 m floor $N = 3$	34,281	804	2,348	2,777	1,387
18–29 slope $N = 3$	36,588	2,641	2,713	3,048	4,688
floor + slope $N = 6$	35,418	1,723	2,530	2,913	3,037
Station 2					
0–23 slope $N = 5$	40,340	554	3,335	4,282	901
29–47 m floor $N = 4$	36,787	290	3,511	3,308	456
floor + slope $N = 9$	38,761	436	3,413	3,849	703

N − %OM, and $r^2 = 0.60$ between %OM − soil H_2O. The others were $r^2 \leq 0.6$.

SLOPE VERSUS LITTER-SOIL NUTRIENT CONTENT AND ARA. Station 1 has a longer and steeper (53°) slope than Station 2 (16°) which resulted in less down slope accumulation of N and P at Station 2.

At Station 1, litter ARA was greater for the slope, whereas N and P soil, and soil %OM were higher for the floor habitat. Station 2 litter depth and N were higher on the floor than the slope. Station 2 floor habitat exhibited litter N and depth values that were higher than those determined for the slope, whereas soil %OM, soil N and P and litter standing crop values were not significantly different between floor and slope.

NUTRIENT ELEMENT CONTENT OF LITTER. Of the 5 elements tested at Station 1, only Al and Fe soil concentrations for floor versus slope were significantly different from each other at $P \leq 0.05$ (TABLE 5). Station 2 exhibited statistically significant differences in concentrations between the floor and slope for Al, Ca, Fe, and K.

SOIL PH. Soil pH values for Station 1 were nearly constant across the transect with a mean floor pH of 7.6 (range 7.5–7.7) and a west slope mean pH of 7.7 (range 7.7–7.8). Station 2 pH values were also nearly constant with an east slope mean pH of 7.4 (range 7.2–7.6) and a floor mean pH of 7.4 (range 6.9–7.7).

DISCUSSION

The abrupt changes of topography characteristic of the gullies result in a dramatic change from a xeric surface to a moist gully environment. Topography affects the microclimate which, in turn, affects biotic and abiotic processes.

Mean litter %N values measured in Applewaite Gully stations are at the low end of the range of dry forest litter (TABLE 6). Our litter and soil collections for nutrient analyses were taken to yield data that was biologically meaningful relative to the habitat of the nitrogen fixing organisms. Surface litter was sampled to minimize soil contamination, and soil samples limited to the upper 1 cm of soil surface. To compare our litter and soil nutrient contents to the few other moist forest studies, the following assumptions were made: 1.) That our standing crop litter collections are comparable to litter from traps having collection intervals ranging from 1 week (Lambert *et al.* 1980) to a month

TABLE 6. Litterfall nutrient contents of tropical dry forests.

Forest	Location	%N	%P	N/P	%Ca	%K	Source
Moist forest	Venezuela	1.60	0.15	10.6	2.1	0.74	Franco 1979
Moist forest	Venezuela	0.70	0.05	14	0.77	—	Cuevas and Medina 1986
Moist forest	Ghana	2.1	0.09	23	2.0	1.0	Nye 1961
Moist forest	Colombia	1.3	0.03	37	0.80	—	Forster and de las Salas 1976
Moist forest	Panama	—	0.08	—	2.2	—	Golley et al. 1975
Moist forest	Barbados STA 1	1.06	0.11	9	3.54	0.29	Present study
	STA 2	1.31	0.11	12	3.90	0.39	Present study
	Mean STA 1 & 2	1.18	0.11	10	3.72	0.34	Present study
Mixed deciduous	Belize	1.23	0.07	17	2.9	—	Lambert et al. 1980
Drought deciduous	Costa Rica	1.43	—	—	2.4	—	Gessel et al. 1980
Dry tropical	India	1.12	0.07	16	0.71	0.30	Singh 1992
Dry tropical	Puerto Rico	1.34	0.03	44	—	0.14	Lugo and Murphy 1986

(Singh 1992); and that 2.) Our surface soil samples are similar to, but perhaps higher than soil samples designated as surface or cores 10 cm deep.

Applewaite Gully litter phosphorous concentrations fall at the high end of the range shown in TABLE 6 for moist to dry forest litter (0.03–0.15%P) resulting in a low N/P ratio. Our litter P concentrations are similar to those found for leaf litter in forests with moderately fertile soils (Vitousek & Sanford 1986). The litter N/P ratios are very low due to P levels 10 times higher than those reported by Vitousek and Sanford (1986) for tropical montane leaf litter. Surface soil P in the gully was somewhat greater than the average P content (0.08%) of the five moist tropical forest soils listed (TABLE 6). Nitrogen values were low and typical of forests on infertile soils, whereas P was relatively high and characteristic of leaf litter values for forests on moderately fertile soils (Vitousek & Sanford 1986). Litter %Ca was the highest of those values reported for dry forest litter, and these Ca values relate to the coral substrate of the surface of Barbados (TABLE 6). The concentration of litter K was low to intermediate compared to other dry forest litter (Vitousek & Sanford 1986). The averaged annual potential nitrogen contributed by litter and soil nitrogen fixation during wet and dry conditions was 0.78 $kgN \cdot ha^{-1} \cdot y^{-1}$.

Because the gully environment reduces water loss by evaporation, the dry season is moderated. Therefore this averaged annual nitrogen contribution is conservative. A better approximation of the potential annual nitrogen contribution can be calculated by applying litter and soil nitrogen fixation rates measured during wet and dry conditions to the average 7 wet and 5 dry months (Jan.–May) yielding 0.93 $kgN \cdot ha^{-1} \cdot y^{-1}$. Assuming the dry season was ameliorated by the gully environment, rates during 9 wet and 3 dry months (Feb.–Apr.) yielding 0.95 $kgN \cdot ha^{-1} \cdot y^{-1}$ were fixed by litter plus soil nitrogen fixation. For comparison, we calculated the nitrogen input from rainfall using the annual nitrogen input at El Verde, Puerto Rico reported by Edmisten (1970), and McDowell *et al.* (1990). Total nitrogen ($NH_4^+ - NO_3^-$) contributed by the average annual rainfall of 1,475 mm at Applewaite Gully is calculated to be 5.4 based on data of Edmisten or McDowell *et al.* of 0.93 $kgN \cdot ha^{-1} \cdot y^{-1}$. Based on these calculations, the N contribution by atmospheric deposition ranged from similar to five-fold greater than the combined litter and soil potential N contribution by biological nitrogen fixation in Applewaite Gully.

Illustrating the seasonal variation in atmospheric deposition, cation concentrations in rainfall varied three-fold in studies conducted at the same El Verde site in different years (Jordan *et al.* 1972, McDowell *et al.* 1990). Litter nitrogen fixation in an open-canopied Hawaiian forest was 0.2 $kgN \cdot ha^{-1} \cdot y^{-1}$. Nitrogen from all nitrogen fixing organisms (decaying wood, lichens and bryophytes) was 0.5 $kgN \cdot ha^{-1} \cdot y^{-1}$ with a rainfall N input of 5 $kgN \cdot ha^{-1} \cdot y^{-1}$. In this system, N from rainfall was 25-fold greater than that of leaf litter nitrogen fixation and 11-fold greater than that fixed by all organisms (Vitousek *et al.* 1987). Leaf litter nitrogen fixation measured along a soil age gradient in Hawaii Volcanoes National Park was 0.01 (soil aged 27 yrs), 0.33 (200 yrs) and 1.29 (ca. 2,000 yrs) $kgN \cdot ha^{-1} \cdot y^{-1}$, and rainfall N input was 4 $kgN \cdot ha^{-1} \cdot y^{-1}$. Rainfall N was 12 times greater than the highest rate of litter nitrogen fixation.

The higher percent humidity in the gully, a result of the steep, narrow profile, was critical to the maintenance of this forest in the generally xeric surface environment of Barbados. Percent humidity during wet and dry conditions at Stations 1 and 2 were higher within the gully than those values measured at the gully rims. Station 2 was more humid than Station 1 during dry conditions. High percent humidity within the gully environment reduces water evaporation from the soil and litter extending optimal moisture conditions between rain events during the wet season, and ameliorating water stress during the dry season. Severely reduced soil ARA was measured only during an extended dry season. The process of litter nitrogen fixation was moisture dependent. ARA activity was distinctly stratified with the greatest activity located in the upper 1 cm of litter which is most susceptible to desiccation. Station 1 and 2 litter percent moisture values did not correlate with ARA because within the gully habitat, adequate moisture was available to maintain ARA except during prolonged dry periods. Mean floor ARA values measured during somewhat drier conditions were greater than those obtained during wet conditions. The depression of litter ARA noted when percent litter moisture values were high was probably related to reduced gas diffusion to nitrogen-fixing prokaryotes within the waterlogged litter (Sheridan 1991, Kershaw & Smith 1978).

Litter N, standing crop and depth were similar at both stations. Nitrogen fixation is dependent upon the availability of energy-rich compounds; however, the presence of combined N decreases nitrogenase activity (Burris 1977), and may also decrease the numbers of diazotrophic bacteria relative to non-diazotrophs (Kolb & Martin 1988). Our ARA values for both soil and litter exhibited a strong negative correlation with %N. Below canopy PFD values measured at Station

2 were 2.5 times those measured at Station 1 resulting in increased desiccation of surface litter and depression of ARA.

Schimel *et al.* (1985) and Aguilar and Heil (1988) reported that soil %OM, N and P increase systematically from ridgetops to lower slopes and depressions. Since topography directs water flow, runoff results in the deposition and storage of erosion products at lower levels. Phosphorus distribution is controlled by the movement of fine particles (Burk 1989). Schimel *et al.* (1985) showed that fine soil particles are P enriched. The topography and the high clay content of gully soils should favor P accumulation in floor samples. Station 1 floor versus slope habitat soil N, P and soil %OM were significantly different from each other, with the floor values higher than those measured along the slope; but litter depth, litter P and litter N, and litter standing crop were not. Slope versus floor soil ARA values were not significantly different from each other. Slope litter ARA was higher than that measured for the floor habitat, whereas Station 2 ARA values for floor and slope were not significantly different. We expected that the elevated soil %OM values may be correlated with high ARA values. However, clay soils bind organic matter, coat soil microorganisms, adsorb enzymes and retard decomposition rates and associated N mineralization (Uehara & Gillman 1981, Vitousek & Sanford 1986). Soil ARA may not have correlated with soil %OM due to unavailable OM resulting from clay limiting the accessibility to soil diazotrophs.

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