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Water and the Ecosystems of the Luquillo Experimental Forest

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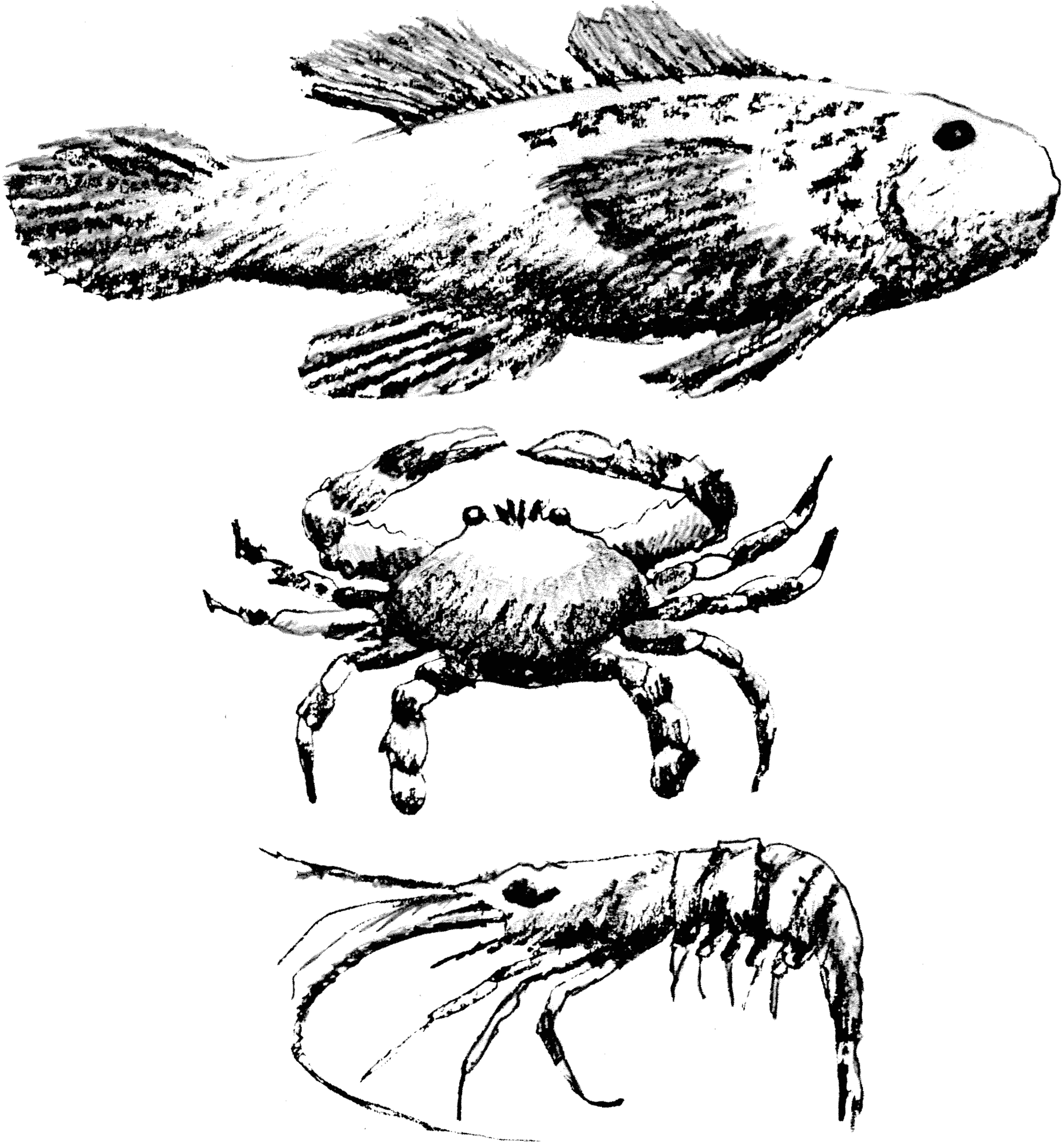

Water and the Ecosystems of the Luquillo Experimental Forest

Ariel E. Lugo

INTRODUCTION

Water is an essential requirement of all living systems. At the cellular level water is needed to maintain cell turgidity and to serve both as a medium and reactant in metabolic processes. On a larger scale, water is critical for transporting materials through plants, animals, and watersheds, and for regulating the temperature of these systems. As water flows to the ocean, it performs many functions for organisms and the landscape, and its value (or its ability to do work) changes in relation to its elevation and its quality (Odum 1970a). The rate of organic matter production and accumulation in tropical forest ecosystems is a function of net water availability, e.g., rainfall minus potential evapotranspiration (Brown and Lugo 1982). Furthermore, Holdridge (1962, 1967) showed water availability to be a regulating factor in the complexity of forest structure. Estuarine productivity and biotic composition are also influenced by freshwater runoff from upland ecosystems (Carter et al. 1973).

Because the amount of water available to any sector of the biosphere is essentially controlled by rainfall and condensation, and because human demands for water are increasing in disproportion to local water supplies, resource managers are required to allocate water-use priorities among competing consumers. Typically, natural ecosystems are not considered legitimate users of water unless a particularly valuable ecosystem is involved. For example, laws in the state of Florida assure a minimum water supply to the wetlands of Everglades National Park, regardless of water shortages in the city of Miami. The water rights of the ecosystems of the Everglades are recognized as legitimate in that state. In other places, however, water flow to the ocean is viewed as a waste of freshwater. Such a view ignores the importance of freshwater to estuaries, coastal swamps, alluvial valleys, and floodplains. The water rights of natural ecosystems are often unrecognized.

This paper review facts about water dynamics, water balance, and water requirements of the ecosystems and aquatic organisms of the Luquillo Experimental Forest (LEF), also known as the Caribbean National Forest. These ecosystems need water to leach plant and soil surfaces, to sustain organic productivity and evapotranspiration, and to maintain stream functions involving flora, fauna, and fluvial processes. The objective of this paper is to draw attention to research needs on this subject and to highlight the importance of freshwater allocations to natural ecosystems. The need for such water allocations has become relevant in Puerto Rico where the Department of Natural Resources (DNR) is currently granting water-use rights as part of regulations that implement the 1976 Water Resources Act.

WATER DYNAMICS AND WATER BALANCE

Rainfall and Condensation

Annual rainfall in the Luquillo Mountains increases with elevation (fig. 1) from 2460 mm in Rio Blanco to 4700 mm at La Mina. Values as high as 6450 mm have been measured at La Mina at 716 m elevation and as low as 1000 mm at Rio Grande, El

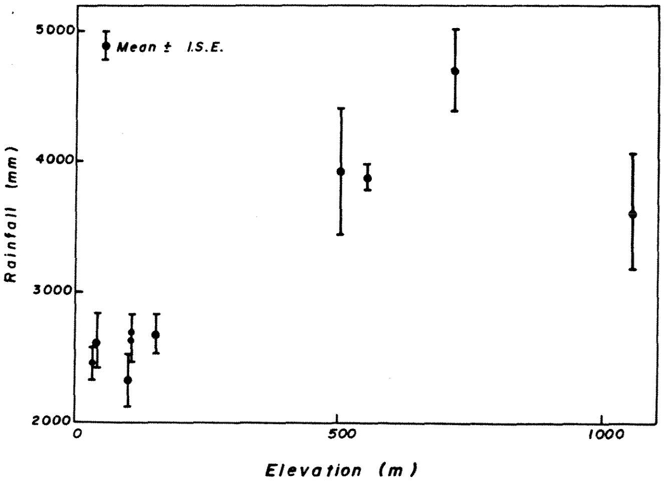

Figure 1.—*Variation of mean annual rainfall with elevation in the Luquillo Experimental Forest. Data are from table 1 (Brown et al. 1983).*

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Table 1.—*Mean annual rainfall and station descriptions for stations within and adjacent to the Luquillo Experimental Forest (Brown et al. 1983)*

Station	Elevation (m)	Location lat/long °N/°W	Years of record	Mean rainfall (cm)	C.V.[§] (%)	S.E.[ξ]
Río Blanco 1	30.5	18°15′/65°47′	12	246	15	11
Río Blanco 2a	40	18°15′/65°47′	16	263	31	20
Paraiso	101	18°16′/65°43′	43	233	19	7
Río Grande El Verde	107	18°21′/65°49′	20	264	30	18
Río Grande El Verde	107	18°21′/65°49′	21	267	28	16
Río Blanco 3	152	18°15′/65°47′	18	268	23	15
El Verde	500		7	392	33	49
Río Blanco 4	549	18°18′/65°47′	27	387	13	10
La Mina	716		8	470	19	32
Pico del Este	1,051	18°16′/65°45′	9	360	38	46

[§] Coefficient of variation (C.V.) = $\frac{\text{(Standard deviation)}}{\text{mean}} \times 100$

[ξ] Standard error of the mean.

Table 2.—*Total rainfall and evapotranspiration by elevation in the Luquillo Experimental Forest and vicinity*

Elevation	Area[§]	Rainfall[ξ]	Evapotranspiration	Total Rainfall	Total Evapotranspiration
M	*Ha*	*M/yr*	*M/yr*	*Cubic hectometers/yr*	*Cubic hectometers/yr*
122–305	5,091	2.9	2.66	147.64	135.42
305–610	9,106	3.8	1.82	346.03	165.73
610–915	4,897	4.6	0.90	225.26	44.07
>915	554	4.1	0.40	22.71	2.22
Total	19,648	3.775*	1.77*	741.64	347.44

[§] Wadsworth 1949.

[ξ] Brown et al. 1983 and fig. 1.

*Weighted average.

Table 3.—*Total rainfall and evapotranspiration by forest type in the Luquillo Experimental Forest*

Forest type	Area[§]	Rainfall[§]	Evapotranspiration	Total Rainfall	Total Evapotranspiration
	Ha	*M/yr*	*M/yr*	*Cubic hectometers/yr*	*Cubic hectometers/yr*
Tabonuco	5,657	3.0	1.76[ξ]	169.71	99.56
Colorado	3,285	4.0	0.83[†]	131.40	27.27
Palm	1,914	3.7	0.83[†]	70.82	15.89
Dwarf	412	4.5	0.16[α]	18.54	0.66
Total	11,269	3.465[√]	1.272[√]	390.47	143.37

[§] U.S.D.A. Forest Service 1984.

[ξ] Odum 1970c.

[†] Frangi and Lugo 1985.

[α] Brown et al. 1983.

[√] Weighted average.

Table 4.—*Total rainfall and evapotranspiration by life zone in the Luquillo Experimental Forest*

Life zone[§]	Area[ξ]	Rainfall[α]	Evapotranspiration[α]	Total Rainfall	Total Evapotranspiration
	Ha	*M/yr*	*M/yr*	*Cubic hectometers/yr*	*Cubic hectometers/yr*
Moist	216	1.6	1.279	3.46	2.76
Wet	4,043	3.0	1.76	121.29	71.16
Rain	1,398	4.66	1.259	65.15	17.60
Lower montane wet	4,331	2.863	1.14	124.00	49.37
Lower montane rain	1,280	4.533	1.096	58.02	14.03
Total	11,269	3.3*	1.375*	371.91	154.92

[§] All subtropical forest.
[ξ] U.S.D.A. Forest Service 1984.
[α] Ewel and Whitmore 1973.
*Weighted mean.

Verde at 152 m elevation (fig. 2). The coefficient of variation for annual rainfall ranges from 13 to 38 percent without relation to elevation (table 1). While rainfall is fairly evenly distributed year-'round, particularly at lower elevations, rainfall is lower in the months of February, March, and April and higher in May or October, depending on elevation (Brown et al. 1983). Holben et al. (1979) found that a network with 2.3–3.1 rain gauges/km^2 was needed to construct 254 mm rainfall isopletes in the Espiritu Santo watershed of the LEF.

I calculated the total annual rainfall in the LEF using three methods: 1) from a relation between elevation and rainfall (fig. 1) multiplied by the area at each elevation interval (table 2); 2) multiplying the area of major forest types by the average rainfall reported for each type (table 3); and 3) multiplying the area of life zones (*sensu* Ewel and Whitmore 1973) by the mean annual rainfall for stations in that life zone (table 4). In all cases total rainfall was divided by the area of the LEF to obtain a weighted rainfall expressed in depth units (mm). Results show a range of 3300 mm to 3775 mm in the estimated mean annual rainfall (tables 2–4). A mean of the three estimates (3513 mm) yields 395.88 cubic hectometers of water over the LEF. Research has shown that amounts of up to 10 percent of rainfall are condensed from clouds in the cloud forest (Baynton 1968, 1969; Weaver 1972). At lower elevations (500 m), condensation accounts for 4 percent of rainfall (Odum et al. 1970). Because at lower elevations this water quickly evaporates, I ignored this input in the analysis. Using an average rainfall of 4400 mm/yr for the cloud forest (tables 2–4) and the area of cloud forest (table 3), I calculated that an additional 1.85 cubic hectometers of water are available to the LEF through condensation. Adding this amount to the mean rainfall results in a total annual water input to the LEF of 397.73 cubic hectometers (3529 mm).

Evapotranspiration

Evapotranspiration includes two processes: water evaporation from free surfaces (soil, plant, and water) and transpiration. Odum (1970b) demonstrated that evapotranspiration in the LEF decreased with increasing elevation because of the decrease in atmospheric saturation deficit. Odum hypothesized that the rate of evapotranspiration possible at any given elevation influenced such forest properties as vegetation height, physiognomy, nutrient uptake, foliar morphology and orientation, and the number, biomass, and distribution of roots.

I calculated the total annual evapotranspiration in the LEF using three methods: 1) from a relation ($y = -0.32\ x + 332$; $r^2 = 0.99$, $n = 3$) between elevation (x in m) and evapotranspiration (y in cm) multiplied by the area at each elevation interval (table 2); multiplying the area of major forest types by the average evapotranspiration for the type (table 3); and 3) multiplying the area of life zones (table 4) by the evapotranspiration of the life zone calculated by the method in Ewel and Whitmore (1973).

The estimated annual evapotranspiration of the LEF was 143.37 cubic hectometers or 1272 mm. This is equivalent to 35 percent of the estimated annual water input. The life zone method resulted in higher values (154.92 cubic hectometers, 1375 mm, and 42 percent, respectively; table 4). Higher values were also obtained using the relation of evapotranspiration with elevation (table 2). The mean annual evapotranspiration estimate based on the three methods is 1472 mm or 42 percent of the total water input to the LEF.

Runoff

Nine rivers have their headwaters in the LEF (fig. 3). Mean annual discharge is directly related to elevation of a gauging station (table 5). Variation in

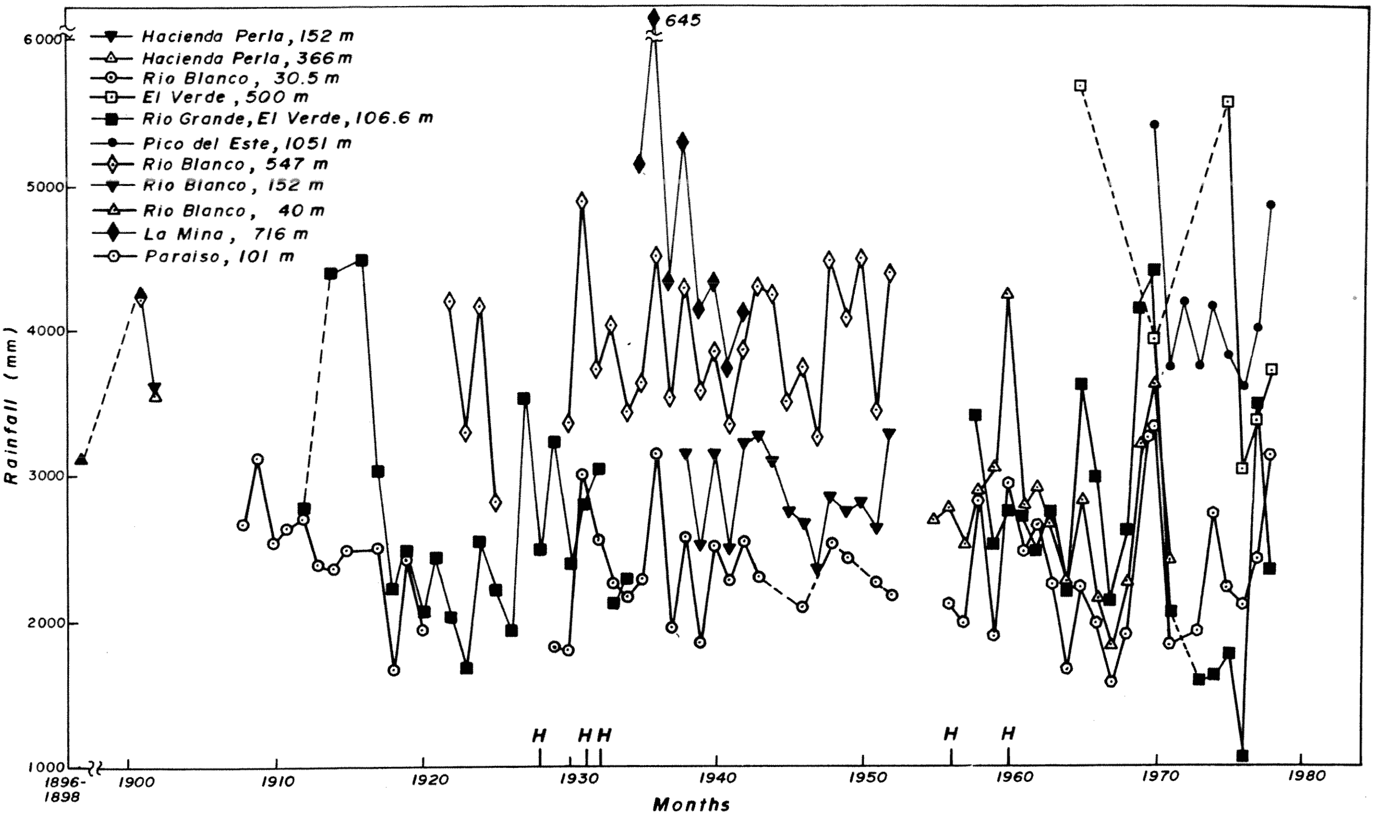


Figure 2.—*Patterns of annual rainfall for stations in and adjacent to the Luquillo Experimental Forest (U.S. Department of Agriculture 1909–1913, 1915–1921, 1921–1939; U.S. Department of Commerce 1940–1952, 1955–1979; Wilson 1899). From Brown et al. 1983.*

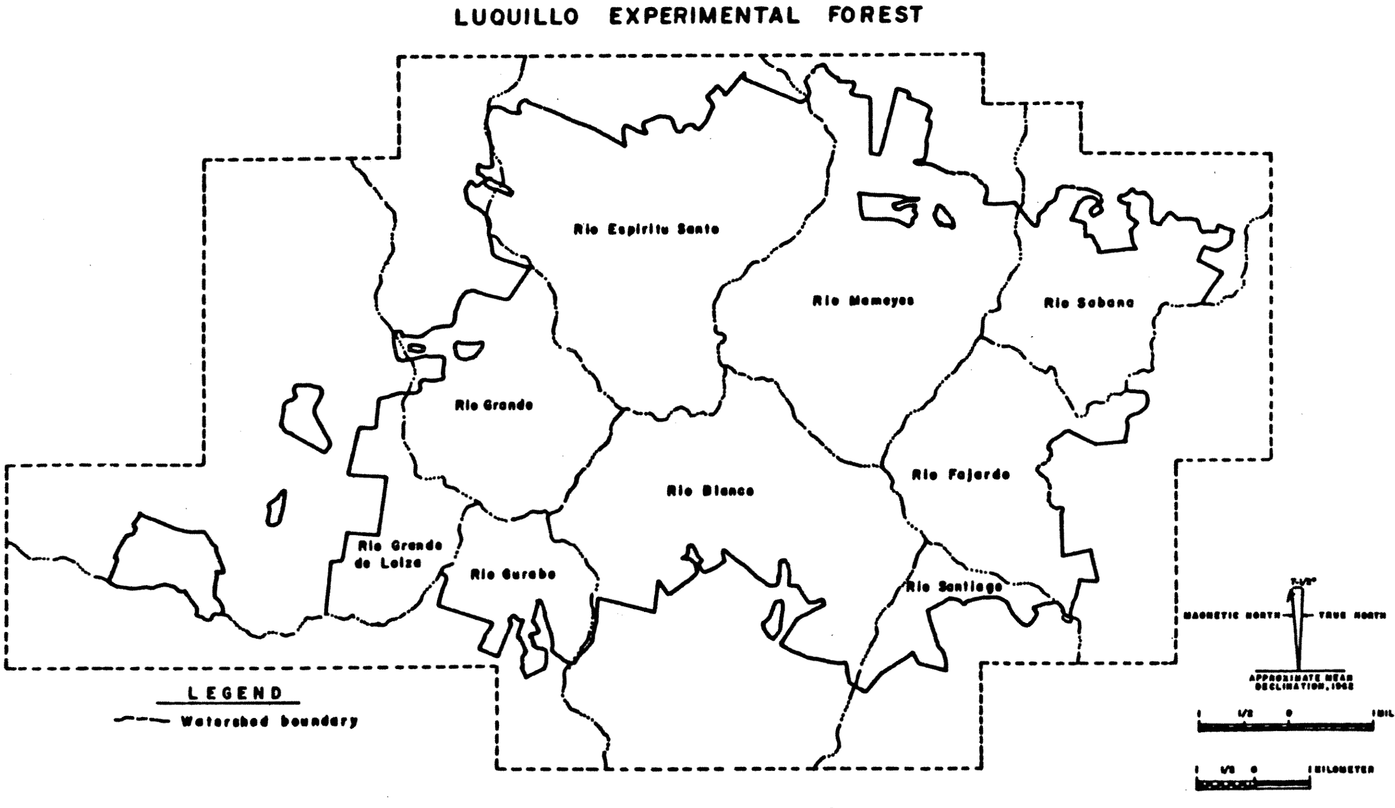


Figure 3.—*Location of watersheds in the Luquillo Experimental Forest (Brown et al. 1983).*

Table 5.—*Station description and mean annual discharge for stream gaging stations within and adjacent to the Luquillo Experimental Forest. Values in parenthesis based on Quiñones et al. 1984*

Station	I.D. No.[§]	Elevation	Latitud °N	Longitud °W	Period of record	Mean annual discharge	S.E.[ξ]	C.V.[α]
		M			*Yr*	*Cm*		*%*
Río Espíritu Santo Basin								
Río Espíritu Santo near El Verde	633	515	18°19′	65°49′	6	469 (426)	45	23
Río Grande near El Verde	642	38	18°21′	65°50′	8	268 (196)*	42	45
Río Espíritu Santo near Río Grande	638	12	18°22′	65°49′	10	214 (220)[†]	20	29
Río Mameyes Basin								
Río Mameyes near Sabana	655	84	18°20′	65°45′	6	300 (282)	44	36
Río Mamayes at highway 191	657	7	18°22′	65°46′	17	197[†]		
Río Sabana Basin								
Río Sabana at Sabana	670	80	18°19′	65°43′	4	145[†]		
Río Fajardo Basin								
Río Fajardo near Fajardo	710	42	18°17′	65°41′	22	141[†]		
Río Blanco Basin								
Río Blanco	770	15	18°13′	65°46′	9	189*		

[§] U.S. Geological Survey identification, numbers shown are preceeded by 500 and followed by 00.

[ξ] Standard error of the mean.

[α] Coefficient of variation (C.V.) = (standard deviation/mean) × 100.

*Based on 1973 discharge.

[†] Based on flow duration data, Quiñones et al. 1984.

annual discharge, measured by the coefficient of variation, was lowest for the highest and lowest elevation stations. The pattern of annual water discharge is similar for all stations, but the magnitudes are different (fig. 4). Most streams for the 2 consecutive years of 1969 and 1970 had unusually high flows. This was due to high rainfall induced by stationary northern fronts and tropical depressions (Brown et al. 1983).

Mean monthly discharge decreases from high to low elevations. Peaks of flow coincide with rainfall peaks (fig. 5a). Frangi and Lugo (1985) reported a logarithmic relation between rainfall and stream discharge and linear ones between rainfall and stemflow and throughfall at 750 m elevation (table 6). Apparently most of the rainfall at high elevations, particularly during intense storms, finds its way to stream channels and causes typical fluctuations in stream stage (fig. 6a).

Most variability in river discharge was recorded during the months of peak discharge (fig. 5). Flow duration curves (fig. 7) illustrate monthly variations in river discharge as a function of aspect and elevation. Large month-to-month variations typify the Rio Blanco on the drier south side of the forest (fig. 7a). This river exhibits both the lowest and highest monthly base flows in the LEF. In contrast, the Rio Fajardo (fig. 7b), located on the humid eastern boundary of the forest, exhibits little month-to-month variation in discharge. Changes with elevation are illustrated with the three flow duration curves for Rio Espiritu Santo (fig. 7c–e). There is less variation at higher elevations that at the low elevation stations. Rio Grande (fig. 7f) and Rio Mameyes (fig. 7g) have high rates of discharge with little monthly variation, while the Rio Sabana (fig. 7h) has low rates of discharge and high month-to-month variability of flow.

Table 6.—*Relations between rainfall (x) and stream runoff, stemflow, and throughfall at 750 m elevation in the Luquillo Experimental Forest (Frangi and Lugo 1985). All values are in mm except runoff (mm/week)*

Y Parameter	Equation	r^2
Runoff	$\ln y = 3.07 + 0.01x$	0.89
Stemflow	$y = 0.10x - 0.09$	0.95
Throughfall	$y = 0.86x - 1.29$	0.98

Runoff is the difference between water input (rainfall and condensation) and evapotranspiration. From tables 2, 3, and 4, annual runoff is estimated to be between 1941 and 2209 mm (mean of 2052 mm). These estimates can be verified by independent measurements of stream discharge by the U.S. Geological Survey (USGS). However, the USGS gauges are usually located at lower elevations outside or just at the boundary of the LEF.

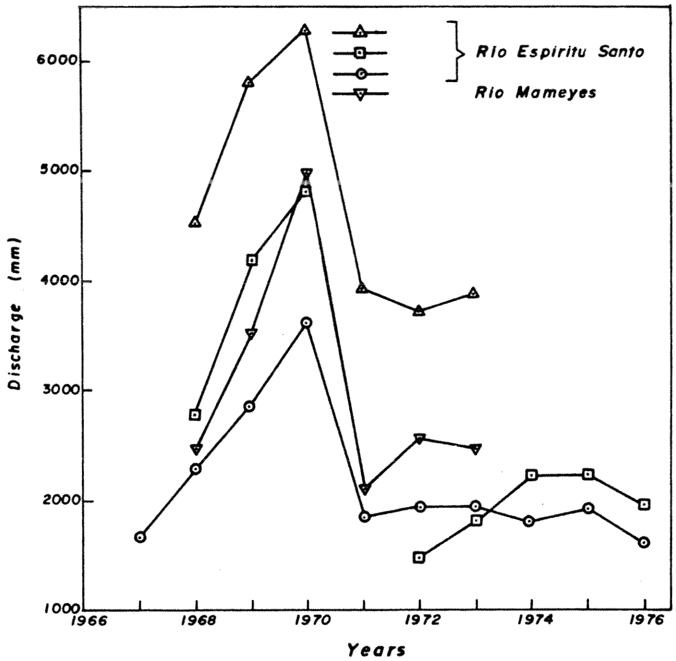


Figure 4.—*Annual stream discharge for rivers draining the Luquillo Experimental Forest (U.S. Department of Interior 1967, 1968–1977). From Brown et al. 1983.*

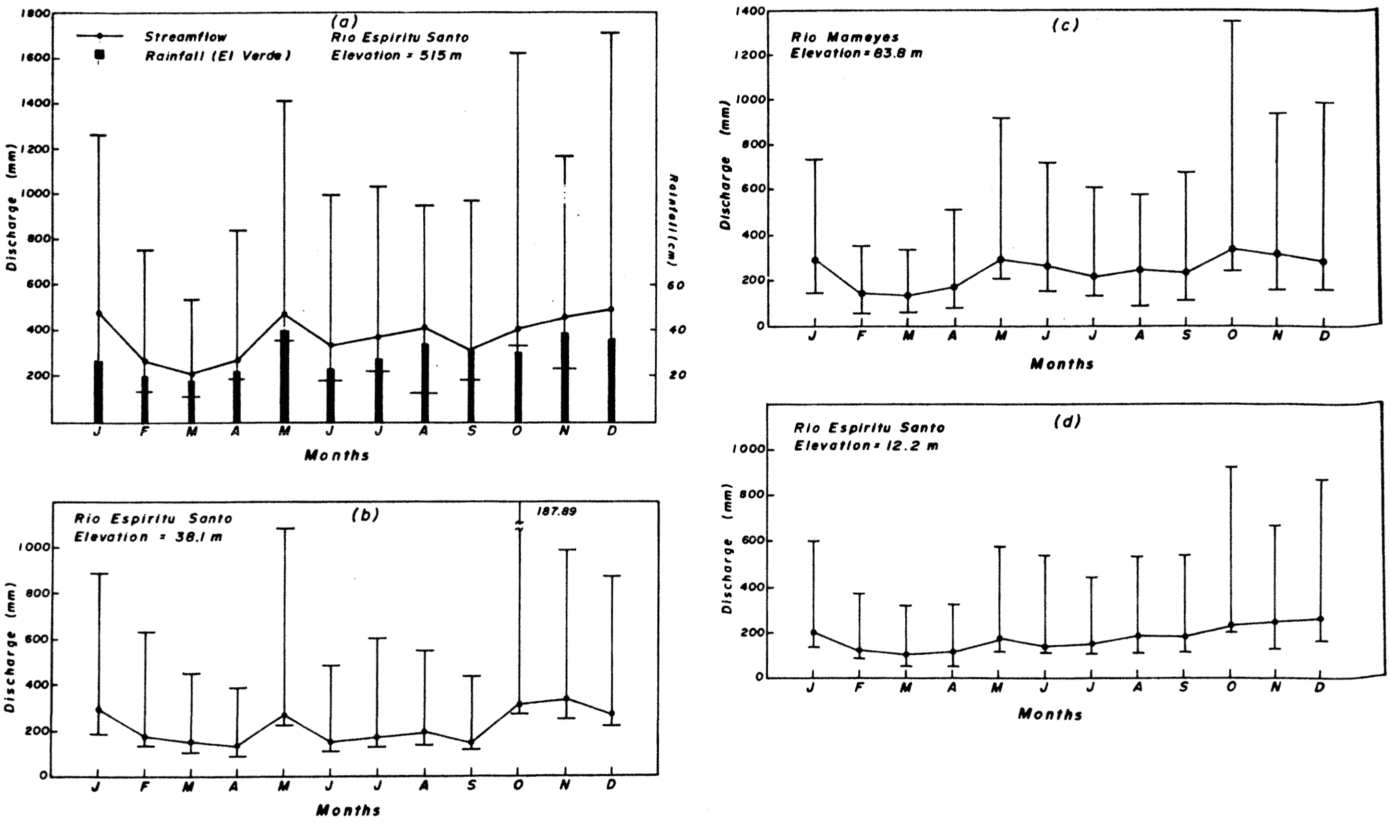


Figure 5.—*Mean range of monthly discharge from rivers draining the Luquillo Experimental Forest (U.S. Department of Interior 1967, 1968–1977). From Brown et al. 1983.*

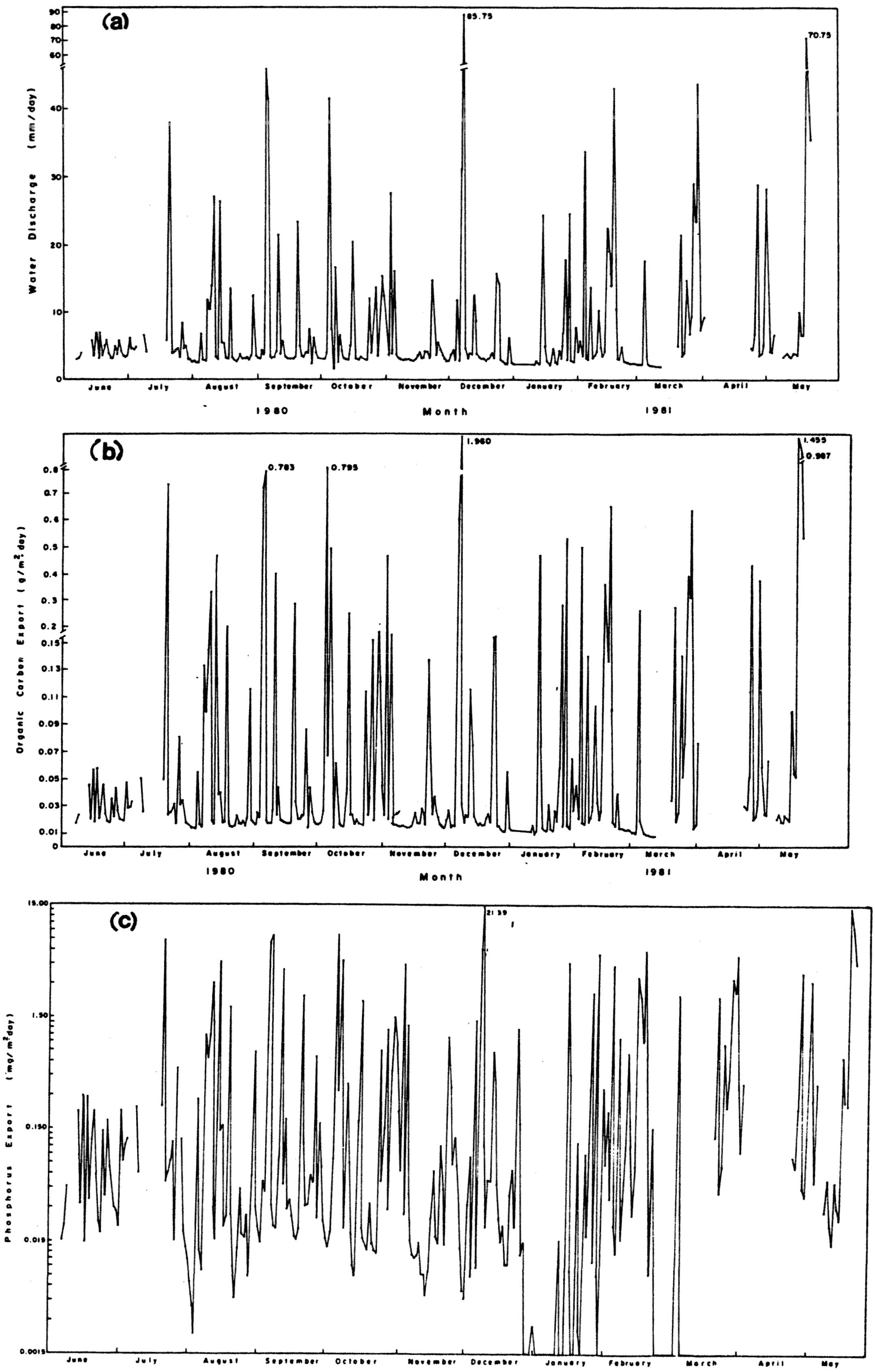


Figure 6.—*Daily water (a), carbon (b), and phosphorus (c) discharge of the Rio Espiritu Santo at 750 m elevation (Frangi and Lugo 1985).*

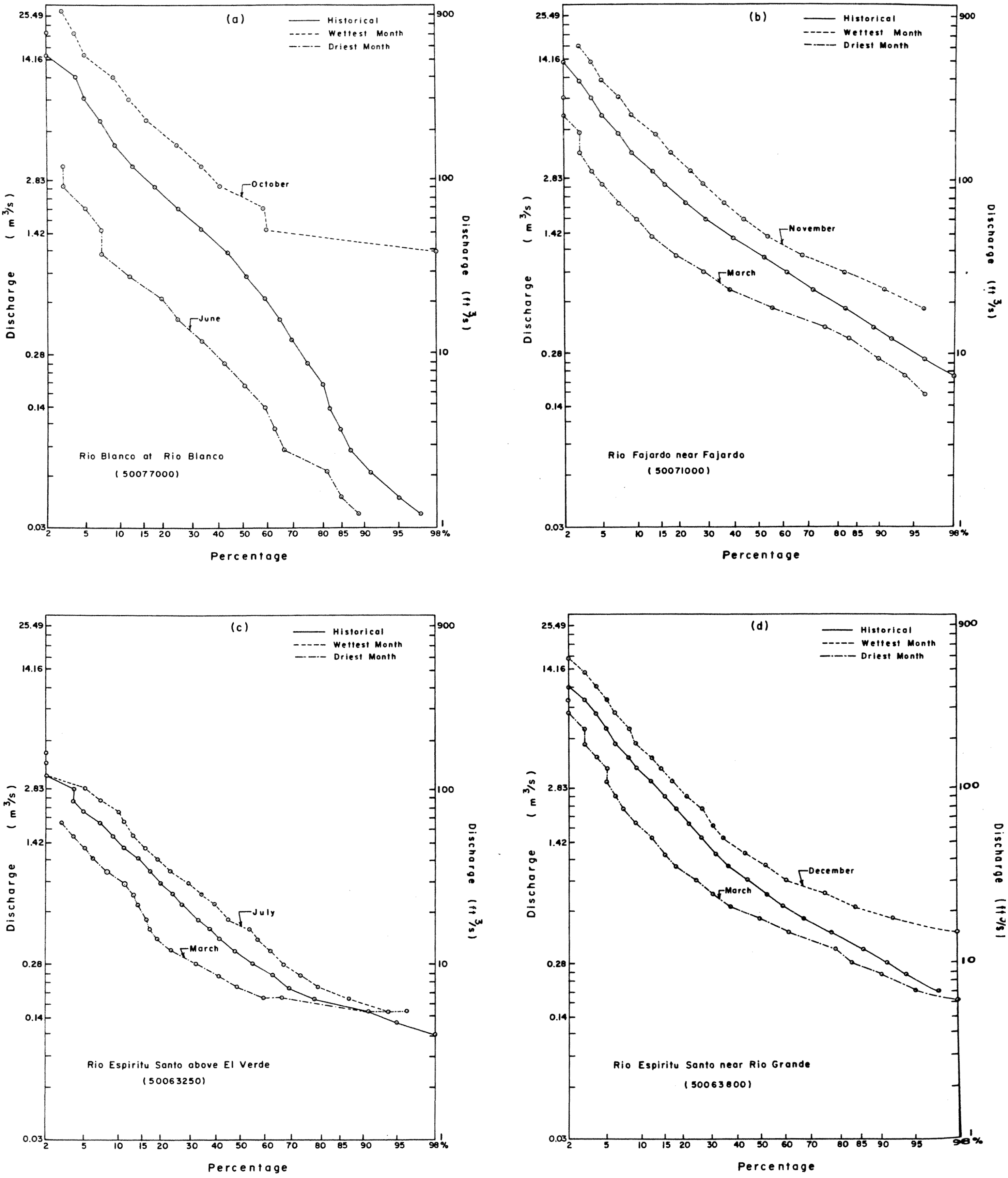
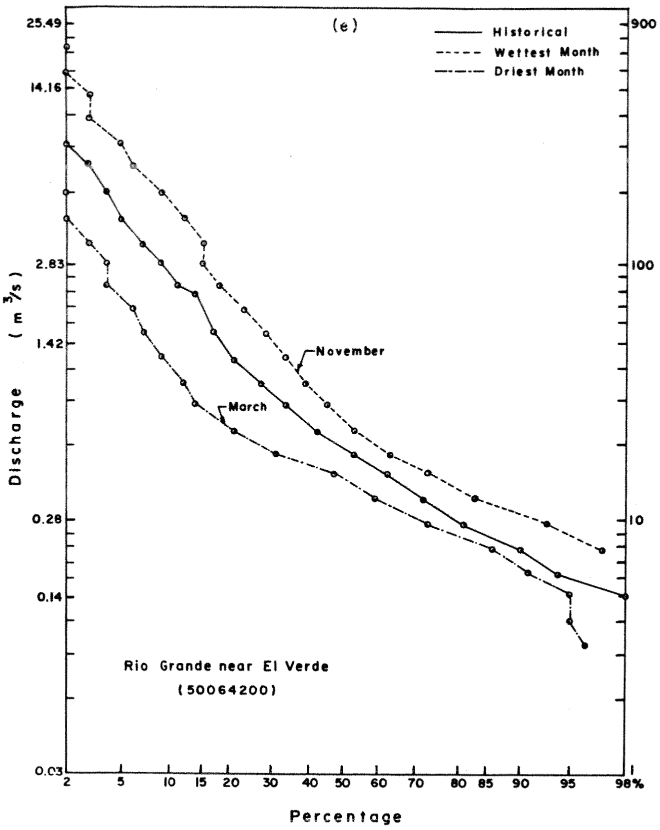


Figure 7.—*Flow-duration curves for rivers draining the Luquillo Experimental Forest. Historical average and the months with maximum and minimum flows are shown. Data are from Quiñones et al. 1984.*


(e)
Historical
Wettest Month
Driest Month
November
March
Rio Grande near El Verde
(50064200)
Discharge (m³/s)
25.49
14.16
2.83
1.42
0.28
0.14
0.03
Discharge (ft³/s)
900
100
10
1
Percentage
2
5
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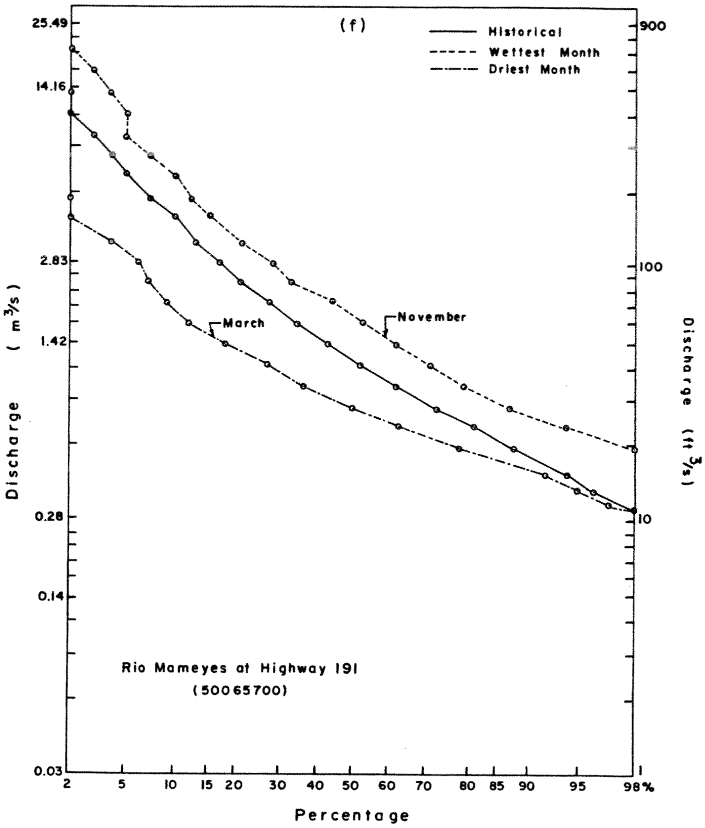
15
20
30
40
50
60
70
80
85
90
95
98%


(f)
Historical
Wettest Month
Driest Month
November
March
Rio Mameyes at Highway 191
(50065700)
Discharge (m³/s)
25.49
14.16
2.83
1.42
0.28
0.14
0.03
Discharge (ft³/s)
900
100
10
1
Percentage
2
5
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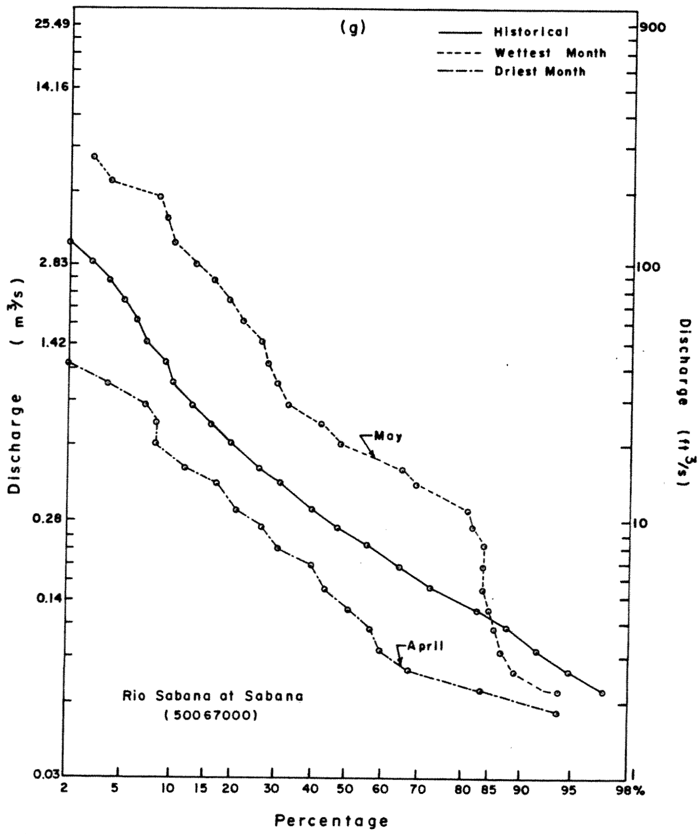
(g)
Historical
Wettest Month
Driest Month
May
April
Rio Sabana at Sabana
(50067000)
Discharge (m³/s)
25.49
14.16
2.83
1.42
0.28
0.14
0.03
Discharge (ft³/s)
900
100
10
1
Percentage
2
5
10
15
20
30
40
50
60
70
80
85
90
95
98%

Table 7.—*Runoff and total water discharge from the Luquillo Experimental Forest and vicinity*

Watershed	Area[§]	Runoff[α]	Total discharge
	Ha	*Cm/yr*	*Cubic hectometer/yr*
Espíritu Santo	4,977	220	109.49
Grande de Loíza	4,753	196*	93.16
Mameyes	2,465	197	48.56
Sabana	1,609	145	23.33
Fajardo	2,053	141	28.95
Blanco	3,791	189*	71.65
Total	19,648	190.9[†]	375.14

[§] Wadsworth 1949.
[α] Quiñones et al. 1984.
*Based on 1973.
[†] Weighted average.

The USGS-derived estimate of runoff was calculated by multiplying the area of watersheds (table 7) be the mean annual discharge of each watershed. Mean annual discharge was obtained from flow duration curves (fig. 7) according to the method of Miller (1951). For two watersheds without flow duration curves, I used mean flow for 1973, a year of "typical" flow (fig. 4). The measured annual water runoff out of the LEF is 375.14 cubic hectometers or 1909 mm (table 7). This value is within 7 percent of the mean estimate based on the three methods discussed above (tables 2–4). The life zone estimate (table 4) was even closer (within 2 percent of the measured amount).

Previous studies show that the fraction of rainfall that appears as runoff ranges widely in different sectors of the LEF (table 8). As elevation increases, more rainfall appears as runoff (from 52 percent at 500 m to 95 percent at 1,000 m elevation). The runoff estimate using elevation, forest types, and life zone result in >58 percent of rainfall as runoff reflecting the strong influence of high elevation forests. The estimate based on the USGS network shows 54 percent of the rainfall as runoff, a value closer to the results obtained at 500 m elevation (52 percent). This reflects the low elevation location of gauging stations.

WATER QUALITY

Rainfall in the LEF is slightly acid (average pH = 5.51; n = 27; Trinidad Pizarro 1985) and relatively rich in salts of marine origin (Odum 1970c). The pH of clouds (5.19; Trinidad Pizarro, personal communication, December 1985) that pass over the forest at 1,000 m elevation is lower than that of rainfall; their chemical composition is variable but nutrient and element concentrations are higher than those of rainfall. For example, preliminary data collected by Trinidad Pizarro in a cooperative study with the Institute of Ecosystem Studies in New York (K.C. Weathers, Personal communication, February, 1986) showed that the mean concentrations (mg/l in parenthesis) of Ca (4.3), Mg (2.1), K (1.0), Na (14.7), NH4 (0.5), SO4 (10.5), NO3 (4.9), and Cl (25.3) were (respectively) 4.3, 3.5, 1.3, 2.8, 1.7, 3.8, 8.2, and 2.8 times higher in cloud (n = 7) than in rain (n = 14) water samples collected simultaneously. The chemistry of cloud water was more variable than that of rain water.

The factors that influence the chemical composition of clouds and rain in the LEF include wind direction, time of year, and land use in the lowlands. The mechanisms and details of the interaction of these factors are largely unknown. However, it is known that northern winter winds are associated with storms rich in marine salts (Odum 1970c), which affect forest stands on northern exposures. During the dry season, southern winds cause similar events over forests on south-facing slopes. These winds transport dust from the African continent. Burning of lowland agricultural fields on the eastern and southern boundaries of the forest also influences the quality of clouds passing over the LEF.

Riverine waters are usually oligotrophic (table 9) with little diurnal (McDowell 1984) and monthly (Cuevas and Clements 1975; McDowell 1984) variation in nutrient concentrations. Because of the high inputs of salt spray, rivers in the LEF have high sodium and chlorine concentrations. At higher elevations (>700 m) stream waters transport high quantities of organic carbon and phosphorus (Frangi and Lugo 1985; fig. 6b and c). Natural populations of the fecal indicators *Escherichia coli* and *Bifidobacterium adolescentis* have been found in these waters where no human influence can be found (Carrillo et al. 1985). Continuously saturated soils at high elevations play important roles in maintaining high organic matter in streams and possibly in the support of the fecal bacteria.

The amount of dissolved solids transported by rivers in the LEF is directly related to river discharge (fig. 8). However, the waters at higher elevation transport less solids than those at lower elevations in spite of the differences in water discharge (table 10). High elevation forests appear to be efficient in maintaining high water quality.

SPECIALIZED AQUATIC HABITATS

In addition to rivers, streams, bogs, and floodplain and slope wetlands, the LEF harbors many small, highly specialized aquatic habitats that support a variety of freshwater organisms. These habitats include tank bromeliads, supersaturated and highly decomposed woody tissue, tree cavities, rock crevices, and saturated soils. With the exception of some preliminary work on the aquatic ecosystems that develop in

Table 8.—*Summary of water budgets for the Luquillo Experimental Forest. Percent of rainfall in parenthesis*

Calculation based on:	Rainfall and condensation	Evapotranspiration	Runoff
	Mm/yr		
Elevation	3,791	1,770 (42)	2,021 (58)
Forest types	3,481	1,272 (37)	2,209 (63)
Life zone	3,316	1,375 (41)	1,941 (59)
River gages	3,529	1,620 (46)	1,909 (54)
Odum et al. (1970) at 500 m elevation		(48)	(52)
Bogart et al. (1964) at 600 m elevation		(15)	(85)
Frangi and Lugo (1985) at 750 m elevation		(22.3)	(77.7)
Baynton (1968, 1969) at 1000 m elevation		(5)	(95)

Table 9.—*Mean water quality parameters of rivers and streams draining the Luquillo Experimental Forest. Data are for the period 1969–1974 (U.S. Department of Interior, Geological Survey, 1968–1977 and for 1983–1984). One standard error is given in parenthesis*

Parameter	Río Espíritu Santo (515 m)* (n = 31)	Río Mameyes, Sabana (84 m)* (n = 34)	Río Grande El Verde (38 m)* (n = 12)	Río Espíritu Santo (12 m)* (n = 15)	Quebrada° Sonadora°	Río° Icacos°	Quebrada° Toronja°
Temperature (C)	21.4 (0.5)	22.9 (0.2)	24.8 (0.7)	24.7 (0.7)			
Specific conductance (micro mhos)	56.6 (2.9)	85.3 (17.1)	107.9 (6.5)	184.9 (95.2)	40	49	91
pH	6.9 (0.09)	7.2 (0.10)	7.5 (0.10)	7.1 (0.11)			
Alkalinity (mg/l)	14.1 (1.7)	32.8 (2.7)	39.5 (3.2)	23.7 (6.5)			
Ca (mg/l)	3.9 (0.3)	10.5 (0.4)	8.6 (0.7)	6.6 (0.8)	2.2	3.0	5.6
Mg (mg/l)	1.7 (0.1)	2.5 (0.03)	4.2 (0.3)	3.0 (0.5)	1.5	1.2	4.6
Na (mg/l)	5.6 (0.1)	6.7 (0.2)	8.5 (0.4)	6.8 (0.4)	4.2	4.6	6.6
K (mg/l)	0.42 (0.05)	0.60 (0.04)	0.43 (0.02)	0.40 (0.02)	0.25	0.52	0.28
Cl (mg/l)	7.7 (0.1)	8.4 (0.2)	10.3 (0.4)	9.1 (0.6)	6.6	5.7	7.9
SO_4 (mg/l)	2.2 (0.2)	4.0 (0.4)	2.5 (0.3)	2.6 (0.3)			
NO_3 (mg/l)	0.23 (0.07)	0.20 (0.05)	0.10 (0.03)	0.01 (0.01)	0.05	0.07	0.07
Dissolved PO_4 (mg/l)	0.05 (0.03)	0.30 (0.3)	0.04 (0.04)	0.03 (0.02)	0.002	0.003	0.006
SiO_2 (mg/l)					8.5	14.2	20.5
Sediments (mg/l)					7.5	36.7	8.5

*Elevation.
°Flow-weighted means from McDowell 1984.

Table 10.—*Water and dissolved solid discharge by two rivers in the Luquillo Experimental Forest (Brown et al. 1983)*

River and station	Discharge		Elevation
	Water	Solids	
	Cm	*T/yr*	*M*
Río Espíritu Santo			
633	469	953	515
638	214	2,320	12
Río Mameyes	300	3,324	84

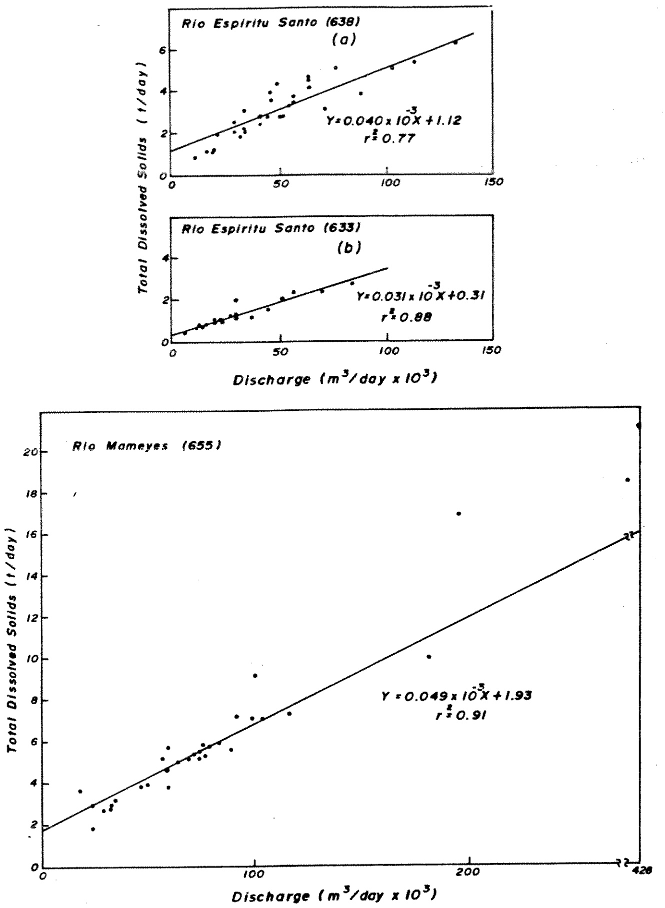

Figure 8.—*Relationship between stream discharge and the export of total dissolved solids (U.S. Department of Interior 1968–1976) From Brown et al. 1983.*

tank bromeliads (Maguire 1970), very little research has been conducted in these habitats. However, these habitats may prove to be critical links to the larger aquatic environments and perhaps even to estuarine systems in the lowlands.

LINKS BETWEEN AQUATIC HABITATS INSIDE AND OUTSIDE THE FOREST

Brown et al. (1983) described the ways the forests of the LEF are finely tuned to variations in moisture availability. They also listed those characteristics of forests that minimize the negative (stressful) effects of too much water while taking advantage of the availability of moisture (table 11). This "push-pull" effect of water on forests, the altitudinal arrangement of forest types with increasing rainfall, and the complex flow of water through a forest stand (fig. 9) leave no doubt as to the overriding importance of water to the ecosystems of the LEF. However, about 58 percent of the rainfall leaves the forest boundary as runoff (tables 7 and 8). To what extent does the water that flows to the ocean from the LEF contribute to the maintenance of biotic activity in the LEF? To address this question, it is necessary to know how the ecosystems of the LEF are related to downstream ecosystems and to what degree that dependency is itself dependent on freshwater runoff.

Many animal species in the LEF are known to depend on runoff for survival (table 12). A survey of the Espiritu Santo River reported 10 decapod crustaceans, 9 species of shrimp, one species of crab, 5 orders of drifting insect larvae, and 2 species of fish from forested areas of the watershed (Bhajan et al. 1980). Two additional species of freshwater fish may inhabit rivers in the lower elevations of the forest (Corujo Flores 1980). Altitudinal ranges of these species are given in fig. 10. Bhajan et al. (1980) verified the estuarine dependence of larval phases of several species of freshwater shrimp. Seven of these species are seasonally commercial and are considered vulnerable by the DNR. Canals (1979a) documented the estuarine dependence of another freshwater shrimp species (*Macrobrachium crenulatum*) in the Rio Espiritu Santo. Other species in this genus exhibited the fastest development at a salinity of 16 percent (Villamil and Clements 1976). Fairly detailed studies of the habitat relationships of four freshwater shrimp species in the same watershed were conducted by Villamil and Clements (1976). Intraspecific habitat selection in *Atya lanipes* (fig. 11) result in male predominance in high flow areas and females in lower flow areas with rubble and gravel substrate.

The only freshwater crab in Puerto Rico (*Epilobocera situatifrons*) utilizes both land, where it burrows in stream banks, and aquatic habitats, to which the young are restricted. The species feeds on decaying material. Stream invertebrates are important year-round consumers of forest leaf litter (Covich 1985a). For example, caddisfly larvae (*Phylloicus pulchrus*) use leaves from 20 species of trees, decapod shredders include juvenile potamonid crabs (*E. situatifrons*), atyid shrimp (*Xiphocaris elongata* and *A. lanipes*) and palaemonid shrimp (*M. carcinus, M. crenulatum, M. heterochirus*). Numerically dominant consumers such as *Atya* and *Xiphocaris* feed on a wide variety of leaves, fruits, flowers, and periphyton. *Atya lanipes* filter out suspended microflora and leaf fragments during high flow and scrapes the microflora from decomposing leaves at lower water flows.

Sicydium plumieri, the gobiid fish, also has a marine phase. Eggs are laid under rocks in freshwater from May to October and are washed to sea during heavy rains. Larvae return one month later to migrate upstream. The post larvae or seti are a food delicacy, caught as they enter the river mouth in a massive red-silver ball (Erdman 1961).

Three frog species also depend on runoff for survival. The introduced *Bufo marinus* requires still water pools for reproduction, *Eleutherodactylus*

Table 11.—*Examples of forest responses to water in the Luquillo Experimental Forest (Brown et al. 1983)*

- Tree growth, seed germination, explosive seedling growth, leaf fall, flowering and fruiting are all synchronized to slight changes in rainfall, which was documented in El Verde.
- Bromeliads and other epiphytic organisms store water within their leaves and large and diverse populations of animals utilize these as habitats and for reproduction.
- Tap roots, abundance of deciduous species, and tree growth rings, which are normal responses to moisture seasonality, are not usual features in the forests of the Luquillo Mountains.

Adaptations That Minimize the Impacts of Too Much Water Are:

- Epiphytic coverage of surfaces increases with increasing moisture which in turn, contributes to an even distribution of through-fall by temporarily storing water and reducing its impact on other surfaces.
- Epiphytes also absorb nutrients from incoming waters and this contributes to a reduction in the loss of minerals to downstream ecosystems.
- Anatomical and morphological characteristics of plants growing at high elevations and low saturation deficits contribute to the increase in transpiration rates. For example, number and size of stomata increase with altitude.
- Where saturation deficits are high, anatomical and morphological characteristics of plants reduce water loss.
- Palms develop massive adventitious roots, laden with lenticels, that may contribute to root gas exchange in anaerobic soils.
- Surface and adventitious roots increase dramatically with increasing water logging of soils.
- Trees maintain epiphyte-laden old leaves for long time periods in spite of the low P/R ratio of these leaves. It appears that their role in mineral cycling and nutrient conservation has more selective advantages than their role as net organic matter producers.
- Forests have extensive root mats that are essentially mineral-tight.
- Plants flower for longer periods in the wetter sites and depend on insects and birds for pollination.

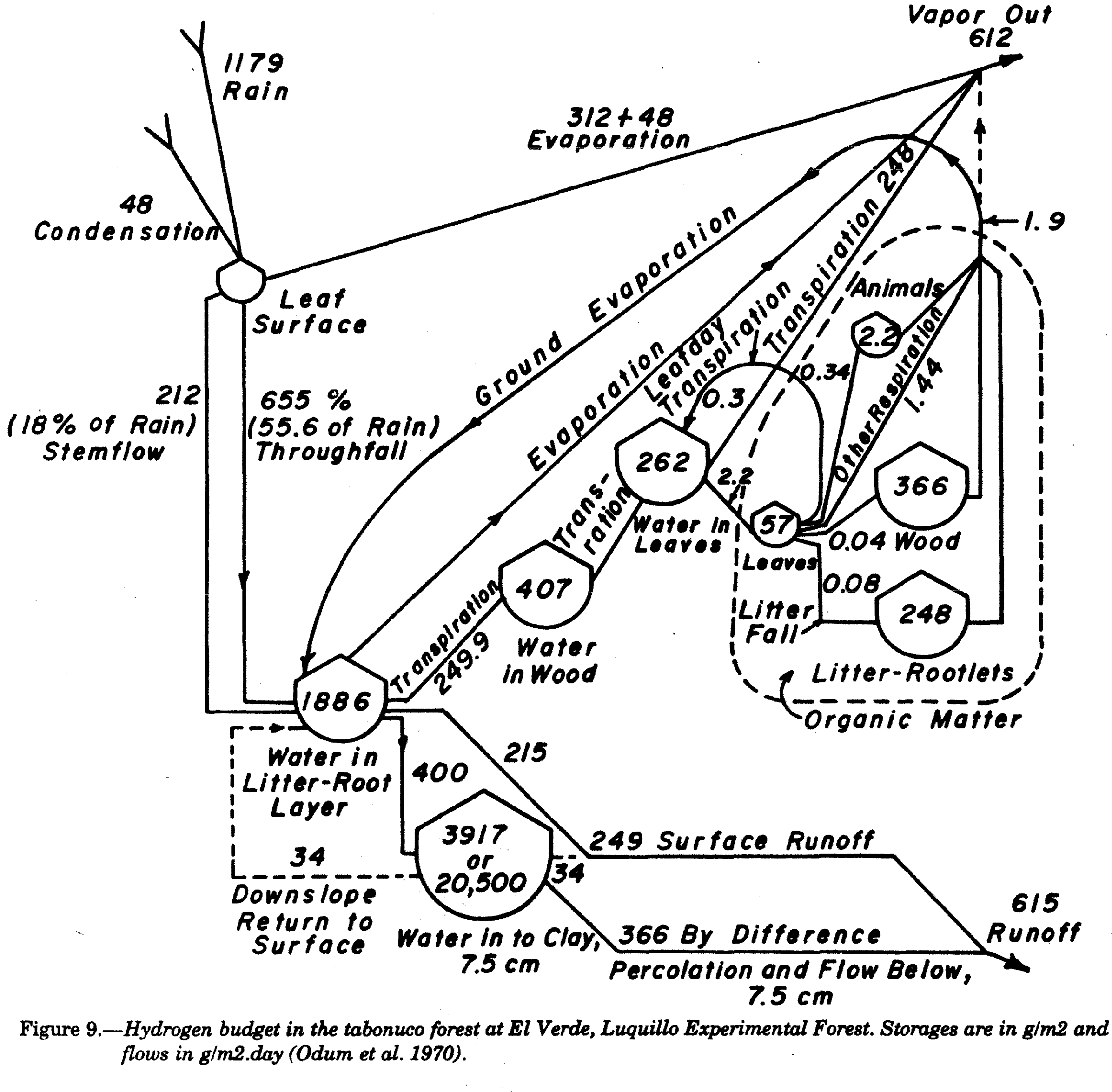

Figure 9.—*Hydrogen budget in the tabonuco forest at El Verde, Luquillo Experimental Forest. Storages are in g/m2 and flows in g/m2.day (Odum et al. 1970).*

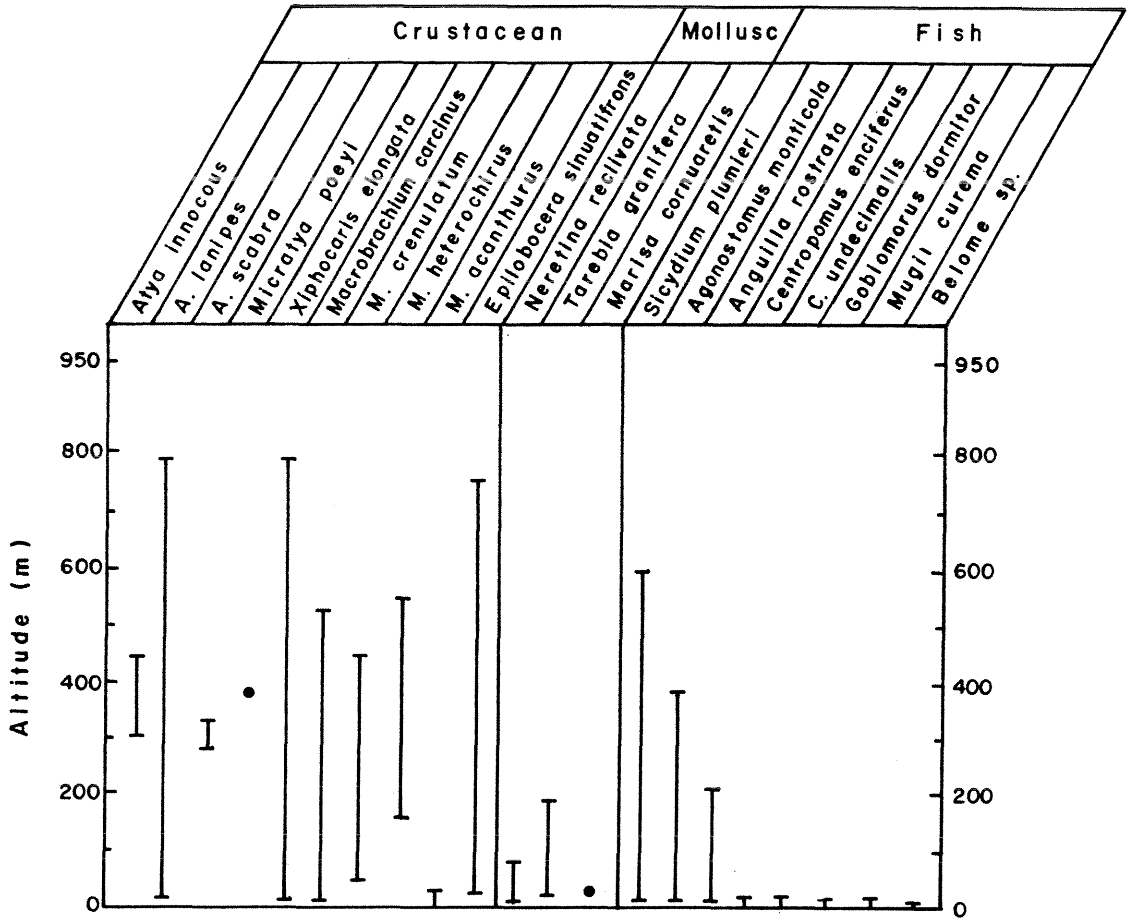

Figure 10.—*Altitudinal distribution of the fauna of the Espiritu Santo River (Bhajan et al. 1980).*

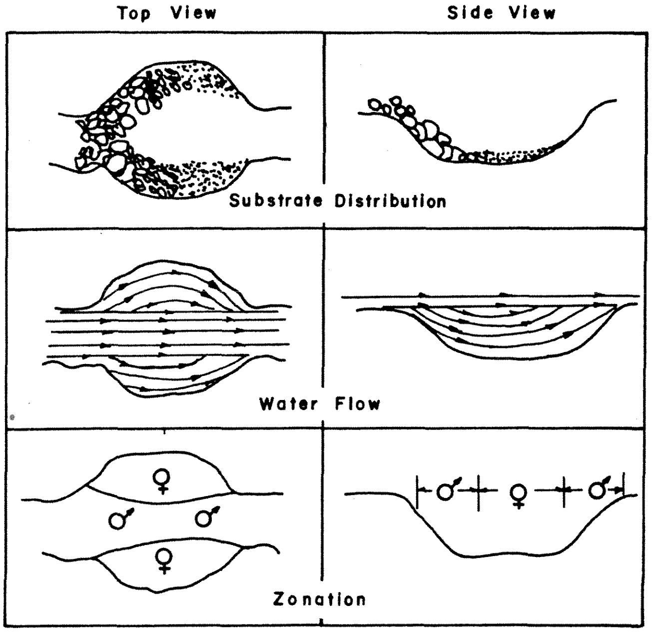

Figure 11.—*Patterns of water flow and substrate distribution in a typical pool in the Espiritu Santo River and their relationship to habitat selection by Atya lanipes (Villamil and Clements 1976).*

karlschmidti uses fast moving streams for its habitat and its food supply (32.4 percent aquatic based), and *E. unicolor* lives in saturated soils at high elevations.

Many species downstream from LEF, including marine, estuarine, and wetland species (table 12), depend on the forest for their survival. Forest evapotranspiration regulates runoff which in turn regulates the salinity of mangrove soils and estuarine waters. The primary production of the coastal complex is a function of salinity, increasing as the salinity decreases with greater runoff (Carter et al. 1973). Corujo Flores (1980) found 60 fish species belonging to 30 families in the Espiritu Santo River estuary alone, their spatial distribution regulated by water salinity. A significant portion of these organisms have commercial value (Erdman 1972; Canals 1979b). Four aspects of water flow are important to downstream ecosystems: water quantity, seasonality of flow, flow variability, and water quality.

Water Quantity

Fast water flows are required to maintain populations of certain aquatic organisms preferring those habitats (Villamil and Clements 1976). Some exam-

Table 12.—*Aquatic fauna of the Luquillo Experimental Forest (Brown et al. 1983)*

Classification	Spanish name
Phylum Chordata	
Class Osteichthyes	
Family Gobiidae	
Scicydium plumieri	chupa piedra
Phylum Arthropoda	
Class Crustacea	
Order Decapoda	
Family Atyidae	
Atya scabra	
A. lanipes	chájara
A. innocous	
Xiphocaris elongata	salpiche
Family Potamonidae	
Epilobocera sinuatifrons	buraquena
Family Palaemonidae	
Macrobrachium carcinus	
M. heterochirus	
M. crenulatum	
M. acanthurus	
Phyllum Insecta	
Order Diptera	
Order Trichoptera	
Order Ephemeroptera	
Order Hydracarina	
Order Odonata	
Phylum Mollusca	
Family Neritidae	
Neritina reclivata	
Family Thiaridae	
Tarebia granifera	
Family Philidae	
Marisa cornuarietis	

ples are the shrimp *A. lanipes, A. innocous, and A. scabra* which predominate in fast flow sectors of montane streams. Substrate, along with water flow, are the critical factors that regulate the abundance and production of aquatic fauna. However, the substrate of a stream bed is itself a function of the water flow available to scour, transport, or deposit materials. Therefore, the seasonal distribution and quantity of water flow are the dominant factors to the maintenance of a diverse riverine aquatic fauna. Water flow also transports larvae to the estuary and food to filter-feeding organisms. Many aquatic organisms time their reproduction to periods of torrential flows which regulate estuarine salinity. Migrations of estuarine organisms in turn are triggered by changes in salinity (Corujo Flores 1980).

Seasonality of Flow

Seasonality of flow provides a measure of predictability in the signals that trigger reproduction and migration of organisms in the aquatic environment. The periodicity of these events ranges from seasonal change in base flow (Fig. 7) to occasional phenomena, such as higher than average annual flows due to offshore storms (Fig. 4). In the south coast of Puerto Rico, rains with frequencies of less than 1 in 50 yr triggered a massive reproduction of *Peltophyrne lemur*, a species thought extinct in that area (Canals and Moreno 1985).

Flow Variability

Although the importance of flow variability to aquatic organisms has not been researched in the LEF, knowledge from other regions suggests this to be a critical factor in their survival (Covich, personal communication, December, 1985). Variability in the stream and accessibility of alternative foods, rather than variability in leaf input or temperature regulate the rate and degree of leaf processing by stream invertebrates (Covich 1985a and b). During very low stream flow the leaching of secondary compounds from leaves causes mortality in stream shrimp and affects their role as detritivores (Covich 1985a and b). For example, leaf leachates caused differences in mortality of *X. elongata* and *A. lanipes* in laboratory and field tests (Covich 1985b). Seven of 12 tree species caused 40–100 percent mortality in *Xiphocaris* while 2 caused high mortality in *Atya*. Low water flows reduce available dissolved oxygen and increase concentrations of toxic elements in stream pools causing reduction, and in some cases elimination of some species of crustaceans and other arthropods in first and second order streams that drain closed canopy forests. High water flows become critical for the reestablishment of optimal habitat conditions and aid the recolonization by invertebrates. Variability in flows presumably prevents the development of prolonged extreme conditions that could be deleterious to organisms. The data on flow rates of LEF streams amply demonstrate the high rate of variability that typifies the streams and rivers of the forest (table 5; figs. 4, 5, 6, and 7).

Water Quality

Salinity is known to trigger larval development of shrimp species in the LEF (Villamil and Clements 1976). Filter-feeders depend on water quality to obtain food and to minimize stress associated with high sediment concentrations. Low chemical oxygen demands contribute to higher dissolved oxygen conditions, which in turn are required to maintain the metabolism of aquatic organisms. Deterioration of water quality is usually associated with drastic reductions in the diversity and productivity of aquatic fauna in Caribbean islands (Harrison and Rankin 1976). In fact, the condition of macroinvertebrate populations can be indicative of the effects of forest management activities on the water quality of rivers (Munther 1985).

CONCLUSION

Water is clearly the driving force of the forests of the LEF. The influence of water over the ecosystems of the LEF is transcendental. Forests consume about half of the annual rainfall, transform water quality, and influence ecosystems in the lowland and coastal areas. A large suite of aquatic organisms take advantage of the variable runoff from the LEF and move up and downstream using estuaries as reproductive nurseries and the oceans or upper watersheds for the adult stages of the life cycles. In the process, these organisms transport materials in both directions, influence processes in the forest and the ocean, and contribute to an intricate food web that yields considerable economic, social, cultural, ecological, and aesthetic value to humans. It behooves water and ecosystem managers to protect the hydrologic flows that make all this traffic and biotic activity possible. Researchers have the complex job of understanding these phenomena so that they can be managed wisely.

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Water dynamics, water balance, and water requirements of the ecosystems and aquatic organisms of the Luquillo Experimental Forest (aka Caribbean National Forest) are reviewed. Objective is to draw attention to research needs and to highlight importance of freshwater allocations to natural ecosystems.

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