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# Spatial variation in basic chemistry of streams draining a volcanic landscape on Costa Rica's Caribbean slope*

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## Abstract

Spatial variability in selected chemical, physical and biological parameters was examined in waters draining relatively pristine tropical forests spanning elevations from 35 to 2600 meters above sea level in a volcanic landscape on Costa Rica's Caribbean slope. Waters were sampled within three different vegetative life zones and two transition zones. Water temperatures ranged from 24–25 °C in streams draining lower elevations (35–250 m) in tropical wet forest, to 10 °C in a crater lake at 2600 m in montane forest. Ambient phosphorus levels (60–300 $\mu g$ SRP $L^{-1}$; 66–405 $\mu g$ TP $L^{-1}$) were high at sites within six pristine drainages at elevations between 35–350 m, while other undisturbed streams within and above this range in elevation were low (typically $< 30.0$ $\mu g$ SRP $L^{-1}$). High ambient phosphorus levels within a given stream were not diagnostic of riparian swamp forest. Phosphorus levels (but not nitrate) were highly correlated with conductivity, Cl, Na, Ca, Mg and $SO_4$. Results indicate two major stream types: 1) phosphorus-poor streams characterized by low levels of dissolved solids reflecting local weathering processes; and 2) phosphorus-rich streams characterized by relatively high Cl, $SO_4$, Na, Mg, Ca and other dissolved solids, reflecting dissolution of basaltic rock at distant sources and/or input of volcanic brines. Phosphorus-poor streams were located within the entire elevation range, while phosphorus-rich streams were predominately located at the terminus of Pleistocene lava flows at low elevations. Results indicate that deep groundwater inputs, rich in phosphorus and other dissolved solids, surface from basaltic aquifers at breaks in landform along faults and/or where the foothills of the central mountain range merge with the coastal plain.

## Introduction

The timing and nature of geologic processes determine the nature of parent material, soil age, soil type and also the biogeochemistry of waters that drain the landscape (Freeze & Cheery, 1979). Geologic deposits unique to volcanic landscapes are lava flows, ashfall, and lahars (volcanic mudflows). There is a lack of fundamental knowledge of how regional geochemistry is reflected by water chemistry and aquatic biota in volcanic landscapes of Central America. Because of the recent

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*This paper is dedicated to the memory of Peter Kilham.

volcanic activity in Central America, many watersheds are underlain by basalt and are characterized by relatively young soils that contain more phosphorus than older, more weathered soils of the Amazon (Vitousek, 1984).

La Selva Biological Station, located at the base of a dormant volcano in the Caribbean lowlands of Costa Rica, has soils developed on volcanic rocks and has been the location for a number of studies on element cycling in the terrestrial environment (e.g. Bourgeois *et al.*, 1972; Gessel *et al.*, 1980; Jordan, 1985; Johnson *et al.*, 1975, 1979; Parker, 1985; Robertson, 1984; Sollins *et al.*, 1984; Werner, 1984; Vitousek & Denslow, 1986). However, little information exists on the chemical properties of waters draining the reserve (McColl, 1970; Pringle *et al.*, 1986; Paaby-Hansen, 1988). No investigations have examined the water chemistry of major and minor drainages at La Selva with respect to soil type, geologic parent material and/or geomorphic processes. Furthermore, virtually nothing is known of stream nutrient chemistry in the context of the overall volcanic landscape and elevational continuum.

Past and ongoing studies on nutrient cycling in a swamp forest drainage at La Selva (Pringle *et al.*, 1986), indicate high ambient phosphorus levels at some locations (250–300 $\mu$g SRP $L^{-1}$) and relatively low levels at others ($<5\ \mu$g SRP $L^{-1}$). Extreme variation in nutrient chemistry between adjacent streams indicates the need for understanding such variations prior to systematic examination of biogeochemical processes related to nutrient cycling and production.

To enhance understanding of stream function and nutrient cycling in the context of the regional volcanic landscape and elevational continuum, this paper examines patterns of spatial variability of phosphorus levels and other variables in streams draining La Selva and adjacent lands (Pringle & Triska, 1986), addressing the following questions: 1) What is the spatial variability in ambient phosphorus and nitrogen levels within and between watersheds along an elevational gradient?; 2) Can extreme variability in ambient stream phosphorus levels at La Selva be explained by the nature of geologic parent material in a given drainage?; 3) Are streams draining riparian swamp forests characteristically high in phosphorus?; 4) Are phosphorus or nitrogen concentrations in stream waters related to life zones based on the Holdridge classification (Holdridge *et al.*, 1971)?; 5) What are phosphorus levels in streams draining other landscape units in the region, such as alluvium and older Pliocene basalts?; and 6) Can regional generalizations be made regarding chemical properties of stream waters?

## Study site

La Selva Biological Station (10° 26′ N, 83° 58′ W) is owned and operated by the Organization for Tropical Studies and is located on Costa Rica's Caribbean slope in the transition zone between the coastal plain and the steep foothills of the central mountain range (Cordillera Central). The 3300 hectare reserve is the lowermost portion of a tract of rainforest that extends from 35 m above sea level to 2900 m in Braulio Carrillo Park to the south. This land corridor constitutes the last intact gradient of primary rainforest spanning such extremes in altitude remaining on the entire Atlantic slope of Central America (Pringle *et al.*, 1984; Pringle, 1988). La Selva represents the terminus of two lava flows deposited in the Pleistocene, whose boundaries are marked by the Puerto Viejo and Sarapaqui Rivers (Figs. 1, 2). Alluvium, also derived from volcanic rock, overlies lava flows in terraces bordering both rivers. To the northwest, older Pliocene lavas are overlain by red soils (iron bauxites; Alvarado, 1985) and to the northeast, alluvium prevails (Nuhn, 1978; See Fig. 1). Ashfalls have been negligible in the study area because it is upwind of the craters of the Cordillera Central (Sollins, pers. comm.).

The oldest of the two lava flows of La Selva (Salto) is andesitic/basaltic and was deposited in the middle of the early Pleistocene. The younger flow (Sabalo) apparently overlies the older flow and is andesitic, dating from the transition between the early and late Pleistocene (Alvarado,

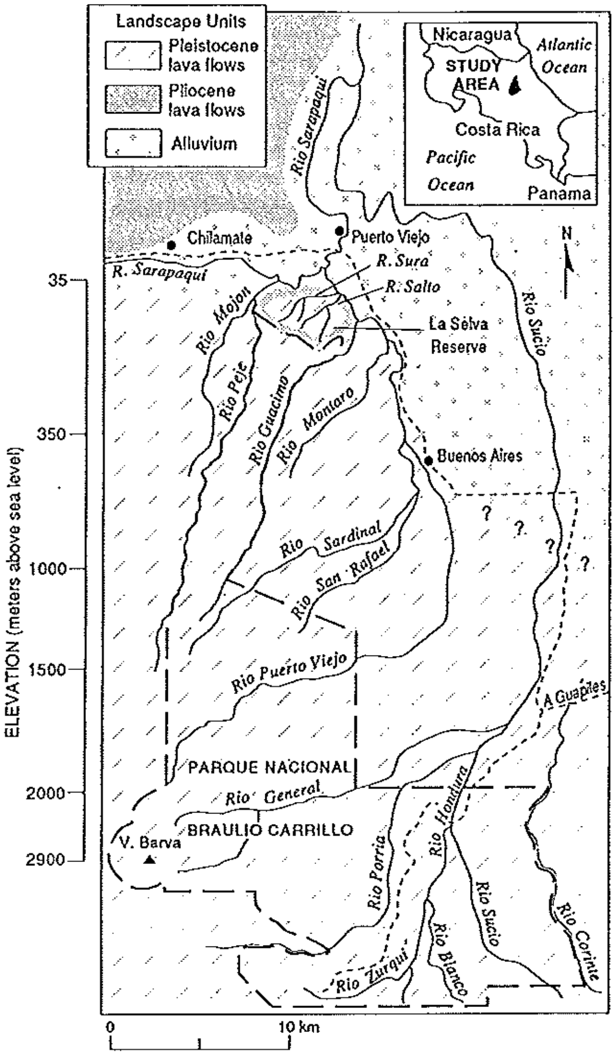

*Fig. 1.* Major drainages sampled in the study area, illustrating regional location of lava flows and alluvium (based on Nuhn 1978). The location of the La Selva – Braulio Carrillo Park land transect on Costa Rica's Caribbean slope is indicated in the inset. Elevation (m.a.s.l.) is approximate due to the deeply incised topography.

1985). The Salto flow appears similar to lavas from Volcan Barva, containing higher levels of Al, Fe, Mn, Mg, Ca, Sr and Cr relative to the Sabalo flow (Alvarado, 1985). In contrast, the Sabalo flow displays higher levels of Ba, Zr, Cu and P than the Salto flow and its elemental composition is more similar to lavas of Volcan Turrialba (Alvarado, 1985), located in the Cordillera Central southeast of Barva.

One unique result of La Selva's geologic structure is rich organic soil in lowland riparian areas where basaltic bedrock can impede drainage, causing swamp-like conditions. Such areas contain different subdominant tree species than more well-drained regions (Lieberman *et al.*, 1985) and have been classified as swamp forest (Hartshorn, 1983).

Soil types of La Selva span an unusually large proportion of the range in soil properties found anywhere in the humid tropics (Sancho & Mata, 1987; Sollins *et al.*, in press; Bourgeois *et al.*, 1972). The two major residual soil consociations of La Selva are derived from the weathering of the Salto and Sabalo lava flows (Fig. 2). While Sancho & Mata (1987) found few chemical differences between residual soils derived from these two flows, Vitousek & Denslow (1987) measured higher levels of extractable phosphorus in soils derived from the Sabalo, the most recent of the two flows (flow 1; Fig. 2). Highest levels of extractable phosphorus were found in recent alluvium and progressively lower levels found in old alluvium. Sollins *et al.* (in press) also report higher levels of extractable phosphorus for alluvial soils and soils of swamps and valley bottoms, relative to residual soils derived from lava flows. In particular, Taconazo soils (classified as a valley bottom soil consociation), which are derived from the oldest lava parent materials observed at La Selva (Alvarado, 1985), yielded very high levels of extractable phosphorus (Sollins *et al.*, in press). This soil is restricted to the margins of the Taconazo stream.

## Methods

Patterns of spatial variability of phosphorus levels and other chemical/physical variables were examined by sampling waters of selected streams spanning vegetative life zones from 35 m to 2000 m elevation within the La Selva-Braulio Carrillo transect. Water samples were analyzed for: 1) major nutrients ($NO_3$-N, $NH_4$-N, SRP, TP); 2) major solutes (Cl, $SO_4$, Mg, Na, Ca); and 3) other chemical and physical parameters (e.g. pH, temperature).

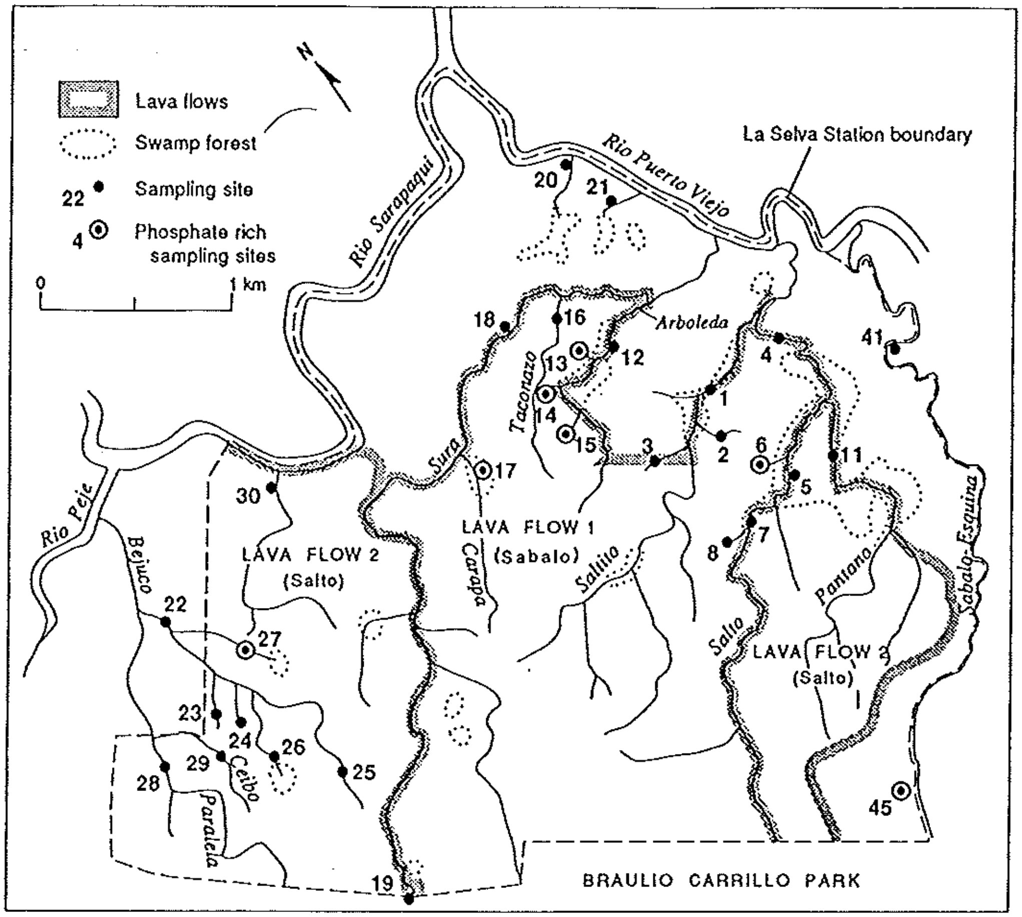

*Fig. 2.* La Selva Biological Station, showing the boundaries of two major lava flows (Salto and Sabalo) within the reserve and the location of swamp forests. Numbers in stream drainages correspond to site numbers designated in Table 2. Sites exhibiting high phosphorus levels ($> 100\ \mu g\ L^{-1}$ SRP) are indicated by an open circle.

A National Geographic Society-sponsored expedition in April 1986 provided the infrastructure to sample streams in Braulio Carrillo Park to the south of La Selva (Fig. 1). At elevations above 800 m, the terrain is steep and deeply incised. Consequently, sample collection was restricted to stream sites along a newly-cut expedition route. Two replicate filtered (0.45 $\mu$m Millipore®) and two replicate unfiltered samples were collected in clean polyethylene bottles at each site. One filtered sample was preserved with nitric acid (Ultrex brand) for later trace metal analysis and the remaining filtered sample was placed in a cooler on dry ice, transported to the roadhead (by oxcart and/or horseback) and then taken by car to a freezer in San Jose. Frozen samples were subsequently transported to either the US Geological Survey Laboratory at Menlo Park, CA or the Survey's Central Laboratory in Denver, CO.

Within La Selva Biological Reserve, improved access allowed a more comprehensive and systematic sampling regime including all major and minor drainages (Fig. 2). Several undisturbed first- and second-order streams were sampled that drained older Pliocene lava flows located in two distinct clusters of hills [Cerros Los Arrepentidos (Puerto Viejo) and Cerros Sardinal (Chilamate); Fig. 1]. These hills rise from the coastal plain (30–35 m) to heights of up to 189 m, and are located just north of the terminal edge of the Pleistocene lava flows that cover La Selva (Fig. 1). Alluvial areas to the northeast of La Selva and the Rio Sucio have been almost completely deforested. Sampling in these alluvial areas was limited to three highly disturbed streams with drainages in pasture and minimal amounts of secondary forest.

Soluble reactive phosphorus (SRP) was measured in filtered samples using the molybdenum blue technique (Strickland & Parsons, 1972; APHA, 1985) and total phosphorus (TP) was measured in unfiltered samples using this technique, preceded by acid hydrolysis. Filtered samples were also analyzed for ammonia ($NH_4$-N) and nitrate ($NO_3$-N) using the indophenol method modified from Solarzano (1969) and Liddicoat *et al.* (1975), and the hydrazine reduction method (Kamphake *et al.*, 1967), respectively. pH was measured with an Orion probe. Cl and $SO_4$ were measured with an ion chromatograph, and Mg, Na and Ca were measured with atomic absorption spectrophotometry. Pearson correlation analysis was performed to determine the relationship between SRP, major solutes and conductivity.

Descriptive observations of stream order, elevation, life zones (bioclimatic classification of forest types developed by Holdridge *et al.*, 1971), land-use patterns (primary forest, secondary forest, pasture), presence or absence of riparian swamp forest, and general substratum type within the streambed were also recorded to provide an overall picture of stream ecosystems and potential impacts of vegetation on stream chemistry within the land corridor. At La Selva, major lava flow(s) within stream drainages above sampling sites were recorded, along with minor residual soil consociations, swamp and valley soil consociations, and alluvial soil consociations using detailed maps recently constructed by Sancho & Mata (1987).

## Results and discussion

Streams spanning the La Selva – Volcan Barva transect show distinct physical/chemical changes along the altitudinal gradient (Table 1) that reflect geological, biological and climatic changes.

### *Life zones, vegetation cover, water temperature and light penetration*

Streams at the lower end of the continuum draining La Selva exhibit water temperatures of 24–25 °C (Table 1). The tall multistratal canopy characteristic of this tropical wet forest life zone provides dense shade cover, resulting in low light penetration to the stream, except in areas where natural light gaps have occurred or where streams are very wide. Streams draining tropical lower montane rainforest at higher elevations (e.g. Rio Santo Domingo, 2020 m; Table 2) had lower water temperatures (13–14 °C). The dense understory of 10–20 m tall trees, combined with frequent cloud cover, also result in low light penetration in premontane and montane life zones.

A feature of riparian stream vegetation that severely restricts light penetration within many streams between 650–1 600 m is the woody shrub, *Cuphea epilobifolia* (Lythraceae), that is established directly over the stream bed on emergent, moss-covered rocks and boulders. Densities of this plant are often so great that stream channels are distinguishable as canyons of the pink-flowering shrub. Seeds of *C. epilobifolia* germinate on moss covered boulders (M. Grayum, Missouri Botanical Garden, pers. comm.). Roots extend under the moss and around individual boulders to reach stream water. *C. epilobifolia* is usually absent in sunny areas where moss does not become established. *Dicranopygium wedelii* (Cyclanthaceae) was also observed in great abundance on streambed boulders in some areas. Presumably it thrives in more densely shaded environments than *C. epilobifolia*. The density of macrophyte cover on emergent boulders presumably reduces light penetration, contributes leaf litter and potentially depresses ambient nutrient levels.

*Potamogeton pusillus* (Potamogetonaceae) is the only true aquatic angiosperm we observed along the entire La Selva-Braulio Carrillo land corridor. Dense growths of *P. pusillus* were observed in the Salto River (50 m), rooted in silty sediments within a light gap. *P. pusillus* has also been

*Table 1.* Life zones and their approximate elevational range and annual rainfall along the La Selva-Braulio Carrillo transect (from Hartshorn and Peralta 1988). General substratum type within stream channels is also indicated along with the range of water temperatures (°C) measured in each life zone.

| Elevation (m.a.s.l.) | Life zone | Rainfall (mm $yr^{-1}$) | Substratum type | Temperature (°C) |
|---|---|---|---|---|
| 35–250 | Tropical Wet | 4000 | Fine, silt/clay and organic material, to small cobbles, large rocks and boulders | 24.0–25.0 |
| 250–600 | Tropical Wet-Cool Transition | 4400 | Small cobbles to large rocks and boulders | 20.5–23.5 |
| 600–800 | Premontane Perhumid Transition | 4600 | Small cobbles to large rocks and boulders | 20.0–20.5 |
| 800–1450 | Premontane Rain | 5100 | Large cobbles to large rocks and boulders | 15.0–20.0 |
| 1450–2500 | Lower Montane Rain | 3400 | *Lower:* large rocks and boulders<br>*Upper:* porous, red pumice-like material and friable agglomerate | 13.0–15.0 |
| 2500–2900 | Montane | 3200 | Pumice-like material and friable agglomerate | 10.0 |

*Table 2.* Nutrient concentrations ($\mu g\ L^{-1}$ $NO_3$-N, $NH_4$-N, SRP, TP) at stream sampling sites. (Site numbers of streams draining La Selva Biological Station correspond to site numbers in Fig. 2). Stream drainage, name, order, elevation (elev. = m.a.s.l.), and landscape unit (U, where L = Pleistocene lava flow; P = Pliocene lava flow; A = alluvium) are also indicated.

| Site | Drainage | River | Order | Elev. | U | $NO_3$-N | $NH_4$-N | SRP | TP |
|---|---|---|---|---|---|---|---|---|---|
| 1 | Salto | Saltito | 3 | 60 | L | 69 | 10 | 21 | 21 |
| 2 | | Saltito tributary 1 | 1 | 60 | L | 75 | 9 | 15 | 25 |
| 3 | | Saltito tributary 2 | 1 | 60 | L | 175 | 38 | 14 | 23 |
| 4 | | Salto | 3 | 35 | L | 89 | 31 | 59 | 76 |
| 5 | | Salto | 3 | 60 | L | 59 | 3 | 61 | 71 |
| 6 | | Salto spring 1 | 1 | 60 | L | 44 | 5 | 236 | 248 |
| 7 | | Salto | 3 | 75 | L | 110 | 18 | 62 | 66 |
| 8 | | Salto spring 2 | 1 | 75 | L | 161 | 13 | 14 | 15 |
| 9 | | Salto | 3 | 140 | L | 191 | 10 | 34 | 36 |
| 10 | | Salto | 3 | 240 | L | 234 | 12 | 46 | 48 |
| 11 | | Pantano | 2 | 60 | L | 61 | 17 | 15 | 20 |
| 12 | Sura | Arboleda | 3 | 50 | L | 32 | 5 | 169 | 220 |
| 13 | | Arboleda spring 1 | 1 | 50 | L | 168 | 23 | 256 | 405 |
| 14 | | Arboleda spring 2 | 1 | 50 | L | 154 | 16 | 198 | 199 |
| 15 | | Arboleda spring 3 | 1 | 50 | L | 173 | 25 | 101 | 42 |
| 16 | | Taconazo | 2 | 50 | L | 10 | 102 | 8 | 15 |
| 17 | | Carapa | 2 | 60 | L | 99 | 23 | 249 | 249 |
| 18 | | Sura | 3 | 50 | L | 233 | 12 | 108 | 133 |
| 19 | | Sura | 2 | 160 | L | 195 | 18 | 18 | 20 |
| 20 | Puerto Viejo | Leonel | 1 | 35 | A | 69 | 59 | 11 | 19 |
| 21 | | Experimental | 1 | 35 | A | 133 | 43 | 9 | 15 |

*Table 2.* (continued).

| Site | Drainage | River | Order | Elev. | U | NO$_3$-N | NH$_4$-N | SRP | TP |
|---|---|---|---|---|---|---|---|---|---|
| 22 | Peje | Bejuco | 3 | 80 | L | 78 | 0 | 5 | 10 |
| 23 | | Bejuco tributary 1 | 1 | 80 | L | 266 | 17 | 0 | 0 |
| 24 | | Bejuco tributary 2 | 1 | 80 | L | 207 | 65 | 9 | 13 |
| 25 | | Bejuco tributary 3 | 1 | 80 | L | 74 | 5 | 3 | 5 |
| 26 | | Bejuco tributary 4 | 1 | 80 | L | 103 | 1 | 3 | 4 |
| 27 | | Bejuco tributary 5 | 1 | 80 | L | 112 | 0 | 94 | 116 |
| 28 | | Paralela tributary 1 | 2 | 80 | L | 186 | 42 | 5 | 10 |
| 29 | | Ciba | 1 | 80 | L | 78 | 11 | 5 | 7 |
| 30 | | Piper | 3 | 45 | L | 162 | 16 | 3 | 16 |
| 31 | | Peje | 5 | 120 | L | – | – | – | – |
| 32 | | Zoncho | 2 | 380 | L | 85 | 10 | 2 | – |
| 33 | | Cathy | 2 | 400 | L | 109 | 9 | 2 | – |
| 34 | | Cascante | 3 | 690 | L | 82 | 28 | 4 | – |
| 35 | | Cascante | 2 | 950 | L | 70 | 8 | 3 | – |
| 36 | | Cascante | 1 | 1000 | L | 391 | 64 | 21 | – |
| 37 | | Peje | 4 | 500 | L | 107 | 12 | 14 | – |
| 38 | | Peje tributary 1 | 1 | 850 | L | 163 | 10 | 7 | – |
| 39 | | Peje tributary 2 | 2 | 1100 | L | 234 | 52 | 23 | – |
| 40 | | Peje tributary 3 | 1 | 1080 | L | 138 | 16 | 8 | – |
| 41 | Guacimo | Sabalo-Esquina | 5 | 40 | L | 75 | 18 | 21 | – |
| 42 | | Guacimo | 4 | 80 | L | 186 | 11 | 33 | – |
| 43 | | Guacimo artesian well | 1 | 90 | L | 30 | 1 | 301 | 290 |
| 44 | | Gata | 2 | 420 | L | – | – | – | – |
| 45 | | Cantarrana | 3 | 290 | L | 238 | 17 | 85 | – |
| 46 | | Cantarrana | 2 | 330 | L | 252 | 27 | 76 | – |
| 47 | | Cantarrana | 2 | 330 | L | 177 | 11 | 94 | – |
| 48 | | Cantarrana | 1 | 330 | L | 16 | 23 | 24 | – |
| 49 | | Sardinalito | 3 | 420 | L | 109 | 13 | 39 | – |
| 50 | | Cavalonga | 2 | 900 | L | 70 | 10 | 3 | – |
| 51 | | Guacimo | 3 | 420 | L | 29 | 12 | 10 | – |
| 52 | | Guacimo | 3 | 500 | L | 35 | 12 | 8 | – |
| 53 | Sardinal | Tigre | 2 | 560 | L | 185 | 11 | 0 | – |
| 54 | | Sardinal tributary 1 | 2 | 640 | L | 108 | 9 | 3 | – |
| 55 | | Sardinal tributary 2 | 2 | 600 | L | 110 | 16 | 0 | – |
| 56 | | Sardinal tributary 3 | 2 | 610 | L | 92 | 5 | 0 | – |
| 57 | San Rafael | San Rafael tributary 1 | 3 | 1520 | L | 29 | 9 | 2 | – |
| 58 | | San Rafael tributary 2 | 1 | 2000 | L | 118 | 9 | 1 | – |
| 59 | Sarapaqui | West Santo Domingo | 2 | 2020 | L | – | – | – | – |
| 60 | | East Santo Domingo | 2 | 2020 | L | 170 | 15 | 1 | – |
| 61 | | Sarapaqui | 4 | 1800 | L | 14 | 15 | 22 | – |
| 62 | | Finca Bejuco tributary 1 | 1 | 50 | P | 34 | 19 | 2 | 12 |
| 63 | | Finca Bejuco tributary 2 | 1 | 80 | P | 34 | 8 | 0 | 2 |
| 64 | | Finca Bejuco tributary 3 | 1 | 80 | P | 164 | 13 | 0 | 0 |
| 65 | | Finca Bejuco tributary 4 | 1 | 80 | P | 154 | 42 | 0 | 3 |
| 66 | | Sarapaqui tributary 5 | 2 | 35 | P | 68 | 12 | 3 | 16 |
| 67 | | Caño Empujon | 1 | 50 | P | 145 | 21 | 1 | 2 |
| 68 | | Caño Negro Sur tributary | 2 | 100 | P | 60 | 5 | 0 | 2 |
| 69 | | Caño Estero Grande | 1 | 30 | P | 107 | 40 | 0 | 6 |
| 70 | | Sardinal | 3 | 50 | P | 103 | 10 | 5 | 4 |
| 71 | Marias | Marias tributary 1 | 2 | 30 | A | – | 71 | 141 | 248 |
| 72 | | Marias tributary 2 | 1 | 30 | A | – | 264 | 149 | 309 |
| 73 | | Caño Negro | 2 | 30 | A | – | 15 | 6 | 80 |
| 74 | Sucio | Rio Sucio | 6 | 30 | A | 37 | 15 | 5 | 79 |
| 75 | | Barva Crater Lake | 0 | 2900 | L | 12 | 11 | 4 | – |

collected in light gaps of a third-order stream to the northwest of La Selva.

*Chemical properties*

In undisturbed streams above 350 m, phosphorus levels were generally low (range: 0–22 μg SRP $L^{-1}$; Table 2) while between 35–350 m, streams exhibited high variability in phosphorus levels (0–301 μg SRP $L^{-1}$). At La Selva in particular, variability in phosphorus levels is very high, both within and between stream drainages (Table 2). Undisturbed first- and second-order streams draining older lava flows to the northeast of La Selva exhibited low phosphorus levels (< 1.0 μg SRP $L^{-1}$; Table 3). High phosphorus levels (e.g. Table 2, sites 71 and 72) exhibited by streams draining the extensive, deforested alluvial plains to the northwest (Fig. 1) may reflect agricultural land-use. However, the small sample size precludes any generalizations.

With one exception, all first- and second-order, phosphorus-rich streams sampled at La Selva drain swamp forest soils underlain by the Sabalo lava flow. This is consistent with the higher phosphorus levels measured in the Sabalo flow relative to the Salto flow (Alvarado, 1985). The exception, Quebrada Bejuco (Fig. 2; site 27), drains non-swamp forest soils on the older Salto flow and, in contrast to other high phosphorus streams, displays low chloride levels.

Ambient stream phosphorus levels are not consistent with existing knowledge of phosphorus levels in soils of stream valleys and swamps and alluvial terraces. Ambient phosphorus levels in the Taconazo were low, as were ambient phosphorus levels of streams whose entire drainages were within phosphorus-rich soils of alluvial terraces bordering the Puerto Viejo River (Table 2; Fig. 2).

Phosphorus-rich streams draining lava flows cannot be explained by land-use patterns or Holdridge (1971) life zones. Of the thirty-one first- and second-order streams sampled that drain primary forest, eight exhibited high phosphorus levels (76–300 μg SRP $L^{-1}$), while remaining streams displayed relatively low levels (0–24 μg SRP $L^{-1}$). Low phosphorus levels were recorded in the two streams sampled that drain pasture (< 3.0 μg SRP $L^{-1}$) and of the seven streams sampled that drained secondary forest, all displayed low phosphorus levels (< 20 μg SRP $L^{-1}$), with the exception of the Carapa (250 μg SRP $L^{-1}$). McColl (1970) attributed the relatively high conductivity (80 μS $cm^{-1}$) that he measured in the Sura stream (Fig. 2, Site 18) to the presence of actively-grazed pasture upstream

*Table 3.* Means ($\bar{x}$), standard deviations (SD), ranges (min-max) and sample size (n) for chemical variables measured in first- and second-order streams draining primary forest on Pleistocene (Pleist) and Pliocene lava flows (Plio). Conductivity (cond.) is measured in μS $cm^{-1}$, nutrients ($NO_3$-N, $NH_4$-N, $PO_4$-P, TP) in μg $L^{-1}$ and other major ions (Cl, $SO_4$, Na, Mg, Ca) in mg $L^{-1}$.

| Landscape | | Variable | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Unit | pH | Alk. | Cond. | $NO_3$-N | $NH_4$-N | SRP | TP | Cl | $SO_4$ | Na | Mg | Ca |
| *Pleist* | $\bar{x}$ | 6.1 | 42.7 | 94.0 | 122.6 | 20.0 | 75.3 | 89.1 | 5.8 | 1.8 | 7.7 | 3.3 | 2.4 |
| *lava* | SD | 0.5 | 55.9 | 117.8 | 64.9 | 21.8 | 94.5 | 110.1 | 6.6 | 2.7 | 10.2 | 6.3 | 4.3 |
| | min | 5.6 | 0.0 | 11.0 | 0.0 | 0.0 | 0.0 | 0.0 | 1.8 | 0.3 | 0.6 | 0.0 | 0.0 |
| | max | 7.1 | 220.0 | 425.5 | 391.2 | 102.0 | 301.2 | 405.0 | 28.5 | 12.8 | 44.0 | 25.3 | 19.0 |
| | n | 27 | 27 | 27 | 27 | 27 | 27 | 28 | 28 | 28 | 28 | 28 | 28 |
| *Plio* | $\bar{x}$ | 5.7 | 8.0 | 31.0 | 95.5 | 18.8 | 0.8 | 5.2 | 2.8 | 2.0 | 2.9 | 0.8 | 1.1 |
| *lava* | SD | 0.8 | 7.3 | 9.2 | 53.7 | 13.6 | 1.2 | 5.2 | 1.3 | 1.6 | 1.9 | 0.7 | 0.8 |
| | min | 4.0 | 0.0 | 20.1 | 59.7 | 4.7 | 0.0 | 0.0 | 2.2 | 0.9 | 1.6 | 0.3 | 0.0 |
| | max | 6.4 | 20.1 | 43.2 | 163.6 | 42.4 | 3.0 | 5.9 | 6.1 | 4.6 | 7.0 | 2.4 | 2.4 |
| | n | 9 | 9 | 9 | 9 | 9 | 9 | 9 | 9 | 9 | 9 | 9 | 9 |

of his sampling site, in what is now secondary growth. It is clear from the present study that high conductivities are due to solute-rich inputs of the Carapa ($150\,\mu S\,cm^{-1}$) and Arboleda ($325\,\mu S\,cm^{-1}$) tributaries (Fig. 2). While the Carapa drains secondary forest, the Arboleda drains primary forest upstream of all sampling points. Springs feeding into the Arboleda displayed high conductivities (175–325) and the highest total phosphorus level ($405\,\mu g$ TP $L^{-1}$) recorded for all sampling sites.

High ambient phosphorus levels in a given stream was not a diagnostic characteristic of riparian swamp forest. Of the eleven first- and second-order streams sampled that drain swamp forest, five exhibited high phosphorus levels ($100–244\,\mu g$ SRP $L^{-1}$) while the remaining displayed relatively low levels ($5–13\,\mu g$ SRP $L^{-1}$). Swamp forests such as those found in the Salto, Arboleda and Carapa drainages are seepage areas located at the gradient break between the foothills of the central mountain range and the flat coastal plain (Fig. 5). Springs commonly surface at such breaks in landform (e.g. Drever, 1982), and basaltic lava flows, in particular, are associated with some of the largest springs in North America (Todd, 1980).

Phosphorus concentration was highly positively correlated ($P < 0.00001$) with conductivity ($r = 0.93$), Cl ($r = 0.89$), Na ($r = 0.90$), $SO_4$ ($r = 0.73$), Ca ($r = 0.84$) and Mg ($r = 0.85$) in undisturbed streams (Fig. 3). Those streams exhibiting highest levels of these solutes were generally first-order streams and/or spring seeps. Trace element analyses of selected streams also indicate high levels of Fe ($160–200\,\mu g\,L^{-1}$), Si ($50–54\,mg\,L^{-1}$), Mn ($16–24\,\mu g\,L^{-1}$) and Sr ($130–140\,\mu g\,L^{-1}$) in phosphorus-rich versus phosphorus-poor streams. Since the most common weathering process of phosphatized rock yields clay and free ions such as phosphate, silicate, iron and aluminum hydroxides, data provide strong evidence that the source of high phosphorus is dissolution of phosphorus-rich minerals and not mineralization of organic matter adjacent to the drainage.

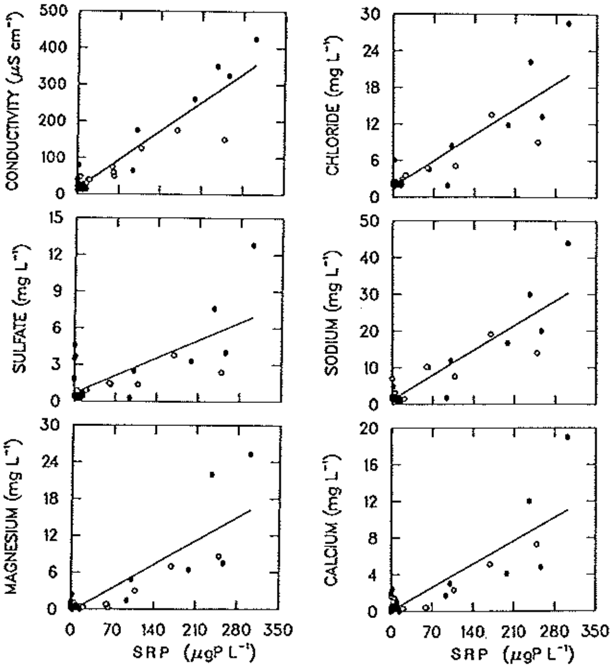

*Fig. 3.* Relationship between phosphorus ($\mu g\,L^{-1}$ SRP): (a) conductivity ($\mu S\,cm^{-1}$); (b) chloride; (c) sulfate; (d) sodium; (e) magnesium; and (f) calcium ($mg\,L^{-1}$ Cl, $SO_4$, Na, Mg and Ca, respectively) for 37 Costa Rican streams. First-order streams and spring seeps (●) are differentiated from larger order (○) streams (≥ second order).

It is apparent that processes which determine stream phosphorus levels are different than those which control nitrogen concentrations. In contrast to other measured solutes, nitrogen was poorly correlated with phosphorus ($r = -0.09$; Fig. 4) and appears to be controlled by local processes. The nature of this control is not obvious and will require further research at the process level. Since nitrogen cycling is intensely biologically mediated, it is possible that processes such as nitrification and denitrification in forest soils (e.g. Robertson, 1984) or stream sediments may regulate stream nitrate concentrations in conjunction with precipitation pattern and light input (open versus closed canopy). While soil nitrogen mineralization and nitrification were found to decrease with increasing altitude (Marrs *et al.*, 1988), this trend was not reflected by water chemistry.

Previous studies (Pringle *et al.*, 1986) speculated that high phosphorus concentrations

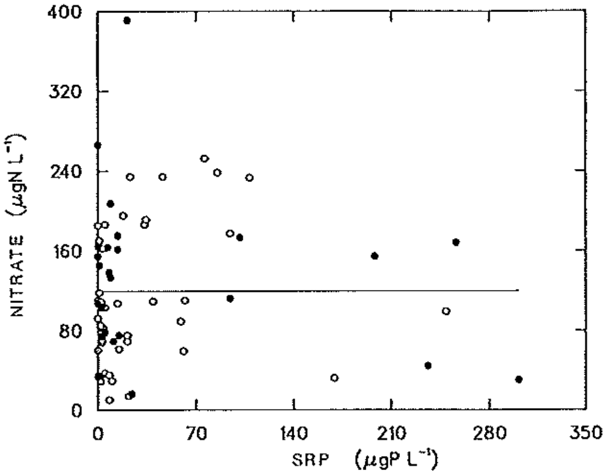

*Fig. 4.* Plot of nitrate ($\mu$g L$^{-1}$ $NO_3$-N) versus phosphorus ($\mu$g L$^{-1}$ SRP) for 70 Costa Rican streams. First-order streams and spring seeps (●) are differentiated from all larger order streams (○).

measured in some La Selva streams arise by soil input and desorption processes since: 1) soils are tropical andisols which have a high phosphorus binding capacity (Parfitt, 1980); and 2) suspended sediment loads increase visibly during periods of heavy rainfall. Results indicate, however, that high variability in phosphate levels within and between stream drainages at La Selva is due to solute-rich groundwater inputs that commonly arise in topographically low areas (Fig. 5). Phosphorus-rich waters are almost always first-order streams and/or spring seeps that become progressively diluted by larger streams, accounting for the range in phosphorus levels exhibited within stream drainages (Fig. 3). Other studies (Pringle and Triska, ms. subm.) on nutrient dynamics within the Salto River support this hypothesis, indicating that conductivity and ambient phosphorus levels (both SRP and TP) decrease with increasing discharge and sediment load. Solute-rich spring inputs are diluted during high discharge events. Despite dilution effects, large order streams receiving solute-rich spring inputs maintain relatively high levels of dissolved solids (Fig. 3).

Several studies (Talling & Talling, 1965; Golterman, 1973; Lesack *et al.*, 1984) have also shown that high phosphorus concentrations occur naturally in many rivers and lakes in volcanic landscapes of Africa. The water chemistry of headwater streams in volcanic regions of Africa is strongly affected by rock weathering (Kilham & Hecky, 1973). Phosphorus and other ions weather from rocks and are concentrated by evaporation at depth to form the waters of springs (Garrels & Mackenzie, 1967). A strong correlation was observed between high levels of silica and phosphate

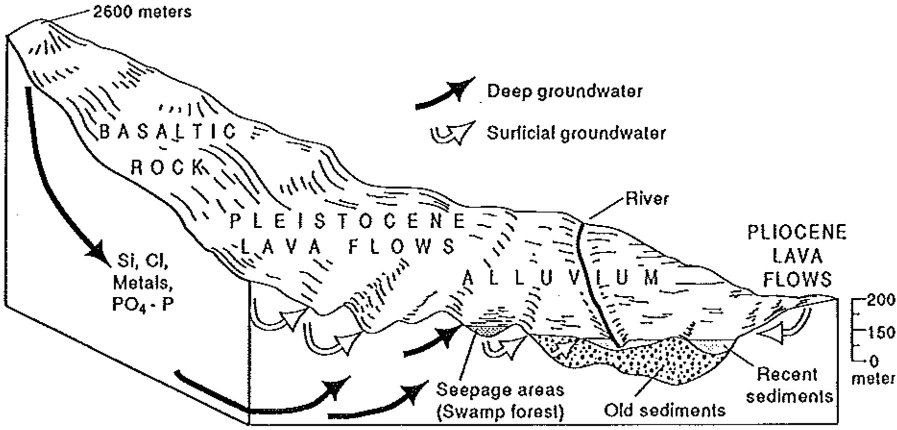

*Fig. 5.* Simple conceptual model of groundwater transport in the La Selva-Braulio Carrillo land corridor. (Cross-sectional diagram of geology of La Selva modified from Bourgeois *et al.*, 1972). Heavy precipitation results in soil saturation and downward percolation of deep groundwater (dark arrows) that weathers basaltic rock. Ion-rich groundwater arises where lava flows merge with the coastal plain, sometimes coinciding with the location of swamp forests. Shallow, solute-poor groundwater (light arrows) arises at various locations along the elevational continuum.

in African waters (Talling & Talling, 1965; Golterman, 1975). Silica levels recorded for phosphorus-rich streams at La Selva, such as the Salto, were correspondingly high (50–54 mg Si $L^{-1}$); with Si : P ratios (230) over two times higher than the mean ratio for African rivers.

Results of a study of nearby Poas volcano, also located in the central mountain range of Costa Rica (Brantley *et al.*, 1987), indicate that acid and metalliferous waters of geothermal origin can percolate downward, remaining stored as groundwater or reissuing from the flanks of the volcano as low-pH, high salinity springs. The downward percolation can provide a significant input of metals (e.g. tens of grams of Fe $sec^{-1}$) into the local groundwater system. We hypothesize that similar processes are responsible for the solute-rich groundwater surfacing at the terminus of lava flows at or near La Selva Biological Station (Fig. 5). Streams draining the moderately active Poas volcano display high chloride (670 mg Cl $L^{-1}$), with silica levels (47 mg Si $L^{-1}$; Brantley *et al.*, 1987) similar to those measured in phosphorus-rich springs that feed into the Salto River at La Selva (50–54 mg Si $L^{-1}$), along with high levels of iron and magnesium.

Groundwater movement is complex and difficult to quantify, particularly so in the volcanic landscape of La Selva. Reasons include: 1) the patchiness of volcanic parent materials; 2) hydrogeochemical properties of parent materials (e.g. permeability, mineralogy and dissolution rates); and 3) the large amounts of water that move through the system [La Selva receives 4 m precipitation $yr^{-1}$, while higher elevation areas receive over 5 m $yr^{-1}$ (Table 1)]. As a result, hydrogeological models developed in temperate areas can be used only as a rough guideline in such a dynamic and highly weathered landscape.

A geologic perspective is a prerequisite to constructing a conceptual model of groundwater transport (Fig. 5) that can explain variability in chemical properties observed in La Selva streams. Volcanic rocks form as a result of magma solidification at or near the ground surface. While lava is in motion, a crust forms on the upper surface as cooling takes place and flow of the lava beneath the crust causes it to become fractured, producing a blocky mass of rock that is commonly pulled under the leading edge of the lava flow (Davis, 1969). The blocky rock masses and associated gravel interbeds that are deposited by streams on lava landscapes, produce high permeability in the tops of lava flows, with highest permeability generally parallel to lava flow (e.g. interstitial spaces in clinkery lava at the tops of flows, cavities between adjacent lava beds). Flow centers are generally dense and impervious, often acting as aquitards (Freeze & Cherry, 1979). While volcanic rock, deposited in multiple lava flows (as occurs at La Selva), generally exhibits highly variable permeability, regional groundwater flow is temporally very consistent since flow is controlled by the shape of the lava flows and possible subsequent faulting. The net result is a regime of highly localized groundwater flow with a few localized discharge points which occur within or near La Selva Reserve (Figs. 2, 5).

Streams draining La Selva generally illustrate a rectangular channel network (lineations and right angles; Fig. 2) instead of. a dendritic pattern, suggesting that faults are common in the area (F. Scatena, pers. comm.). Data suggest that faults may be important in both the location of seepage areas or sag ponds (e.g. swamp forest) and the discharge points of the regional groundwater pattern.

All solute-rich springs within La Selva (Fig. 2) arise at or near Alvarado's (1985) tentative boundaries for the Sabalo lava flow with the exception of the Quebrada Bejuco (Fig. 2; site 27). While little is known of the geographical boundaries of lava flows in Braulio Carrillo Park, the rock wall behind a 30 m waterfall along the Cantarrana (the highest elevation phosphorus-rich stream sampled) exposes two distinct geological strata that appear to be a lahar overlain by a lava flow (W. Melson, pers. comm.).

Regional generalizations have often been made regarding chemical properties of water based on regional geology. For instance, in North America, water draining glacial deposits has been classified into three main composition categories that correspond to basic types of glacial materials drained (Freeze & Cherry, 1979). Regional generalizations have likewise been made regarding ratios of biologically important nutrients in stream waters (e.g. Omernik, 1977). It is difficult to make regional generalizations regarding the chemical properties of water in the volcanic landscape of La Selva due to the complexity of hydrogeochemical factors. Geomorphic processes that create volcanic landscapes (e.g. lava flows, lahars, ashfall) plus colluvial and alluvial processes that operate as well, have resulted in variability within and between patches in a relatively small geographic area. This variability of patch types and respective hydrogeochemical properties is reflected by high variability in chemical properties of stream waters. As a result, features of lotic water chemistry such as nutrient limitation and its role in autochthonous stream production and biogeochemical cycling are apt to vary significantly, not only from watershed to watershed, but even between streams in close proximity in the same watershed.

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