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Edaphic influences on plant community adaptation in the Chiquibul forest of Belize

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Abstract

Edaphic variables figure significantly in plant community adaptations in tropical ecosystems but are often difficult to resolve because of the confounding influence of climate. Within the Chiquibul forest of Belize, large areas of Ultisols and Inceptisols occur juxtaposed within a larger zone of similar climate, permitting unambiguous assessment of edaphic contributions to forest composition. Wet chemical analyses, X-ray diffraction and X-ray fluorescence spectroscopy were employed to derive chemical (pH, exchangeable cations, CEC, total and organic C, total trace elements) and physical (texture, mineralogy) properties of four granite-derived Ultisols from the Mountain Pine Ridge plateau and four limestone-derived Ustepts from the San Pastor region. The soils of these two regions support two distinct forests, each possessing a species composition reflecting the many contrasting physicochemical properties of the underlying soil. Within the Mountain Pine Ridge forest, species abundance and diversity is constrained by nutrient deficiencies and water-holding limitations imposed by the coarse textured, highly weathered Ultisols. As a consequence, the forest is highly adapted to seasonal drought, frequent fires and the significant input of atmospherically derived nutrients. The nutrient-rich Inceptisols of the San Pastor region, conversely, support an abundant and diverse evergreen forest, dominated by *Sabal mauritiformis*, *Cryosophila stauracantha* and *Manilkara* spp. Moreover, the deep, fine textured soils in the depressions of the karstic San Pastor landscape collect and retain during the wet season much available water, thereby serving as refugia during particularly long periods of severe drought. To the extent that the soils of the Chiquibul region promote and maintain forest diversity, they also confer redundancy and resilience to these same forests and, to the broader ecosystem, of which they are a central part.

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1. Introduction

The extent and origins of tropical forest diversity remain the focus of much current research, not least

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because of concern surrounding the potential effects of global warming on species richness and ecosystem function (Parmesan and Yohe, 2003; Williams et al., 2003). Many factors, including climatic variation, altitude, soil heterogeneity, seed dispersal, randomness of seedling availability, as well as the role of predators and parasites on successful colonisation, have been identified as key determinants of forest diversity in the tropics and elsewhere (Givnish, 1999; Hubbell et al., 1999; Swaine and Becker, 1999; Torti et al., 2001; Okland et al., 2003; Skov and Svenning, 2003). Among the many factors influencing forest diversity and adaptation within a similar climate, soils are perhaps both the most important and least understood. Fundamental to this lack of understanding is the difficulty distinguishing soil contributions from, for example, climatic determinants such as temperature and precipitation regimes, which frequently confound attempts to identify unambiguously those soil properties governing forest heterogeneity and diversity (Amundson et al., 1994).

Resolving and quantifying edaphic influences on plant community adaptation in tropical forests is of considerable relevance to those within several disciplines, most notably forest ecologists, who have long sought to identify and measure the biotic and abiotic factors governing forest diversity (Smith and Smith, 2001). Such quantitative descriptions of plant–soil interactions are also fundamental to the development of carbon cycle models, in particular those models describing the movement of carbon into and through soils (Trumbore, 2000; Baisden et al., 2002). Pedologists, too, have an interest in these studies, as the derived plant–soil dynamics will shed light on the processes governing the co-evolution of forest and soil across landscapes (Amundson and Jenny, 1997). Perhaps most importantly, establishing causative links between soil properties and forest adaptation will assist those attempting to predict the effect of climate change on tropical forest ecosystem function (Scholes and van Breemen, 1997).

The Chiquibul forest within the Maya Mountains of Belize presents a rare opportunity to identify, with considerable clarity, edaphic influences on plant community adaptation in a sub-tropical ecosystem. Within the forest, large areas of two markedly contrasting soil types occur juxtaposed within a larger region of similar climate, permitting direct and

unambiguous assessment of edaphic contributions to forest composition. The Chiquibul forest is additionally suitable for such a comparative study because the region has for many decades been the subject of numerous, detailed vegetation surveys (Lundell, 1937; Wright et al., 1959; Iremonger and Brokaw, 1995; Penn et al., 2004). The objective of this study was therefore to identify those soil properties most important to plant community adaptation, as well as forest composition and structure, in a tropical ecosystem.

2. Materials and methods

2.1. Physiographic setting and sample locations

The central region of Belize is dominated by the Maya Mountains, a group of igneous, metamorphic and sedimentary rocks dating from the Pennsylvanian to early Cretaceous. During the late Cretaceous, abundant and widespread limestone sediments were deposited over all but the highest outcrops (Bateson and Hall, 1977). Subsequent uplift during the Pliocene has resulted in a relatively flat land surface with scattered limestone hills. Exposures of igneous rocks are common in the Maya Mountains, with large areas occurring in the Mountain Pine Ridge (MPR) region (Fig. 1). Soils derived from these bedrocks have been described previously for the Belize River Valley (Jenkins et al., 1976a,b) and also for the whole of Belize (Baillie, 1993).

Belize experiences a sub-tropical climate with distinct wet and dry seasons and an average daily temperature of 26 °C. The wet season extends from June to December, with the dry season extending from January to May, giving rise to an ustic soil moisture regime (Soil Survey Staff, 1998). Rainfall within Belize is highly variable, increasing from \approx 1500 mm in the north to \approx 4000 mm in the south, but within the Chiquibul forest averages 2000 mm/year. The relatively wet present climate contrasts sharply with an exceptionally arid period between 1785 and 930 years BP, as revealed by $\delta^{18}\text{O}$ measurements (Curtis et al., 1996). As with many regions of the Caribbean, Belize is subject to frequent and severe tropical storms and hurricanes, the recent effects of which are well documented (Friesner, 1993).

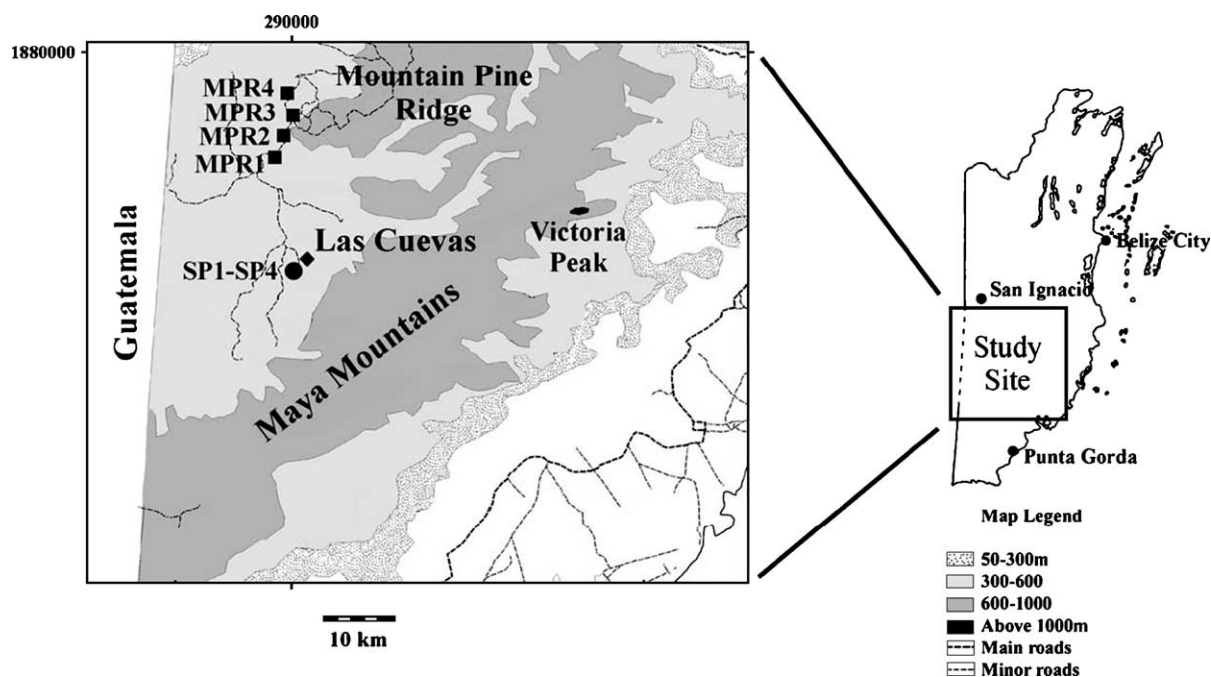


Fig. 1. Location of the San Pastor plot (●) and the four Mountain Pine Ridge sample sites (■), within the Chiquibul forest, Belize.

Eight sampling sites were chosen: four within the MPR region, which is underlain by granitic rocks, and four from the limestone-derived landscape near San Pastor (SP) (Fig. 1). All MPR sites are located on mid-slope positions within 10 m of Guacamala road, with the exception of MPR1, which is located near a minor track to the east of Guacamala road. The four San Pastor sites are located along a catenary sequence (SP1 at the crest, SP4 at the footslope) within the San Pastor research plots, near the Las Cuevas Research

Station. Table 1 gives the Universal Transverse Mercator (UTM) locations for each site.

2.2. Forest composition

The four MPR sites occur within two slightly different vegetation zones, both of which belong to the broad ‘Savannah’ class of Penn et al. (2004). Specifically, MPR1 is located in ‘Savannah: class 18, oak and pine’, whereas MPR2, 3 and 4 occur within

Table 1

Location, taxonomy and associated vegetation class for each of the eight soils from the Mountain Pine Ridge and San Pastor regions of the Chiquibul forest, Belize

Soil	Location (UTM) ^a	Taxonomy ^b	Vegetation class ^c
MPR1	283400 E, 1865650 N	Typic Haplustult	Savannah: class 18, oak and pine
MPR2	285600 E, 1867700 N	Typic Haplustult	Savannah: class 17, pine forest
MPR3	290500 E, 1880300 N	Typic Kandiuult	Savannah: class 17, pine forest
MPR4	289621 E, 1878755 N	Typic Haplustult	Savannah: class 17, pine forest
SP1	287504 E, 1849677 N	Lithic Haplustept	Broadleaf: class 2, seasonal forest
SP2	287508 E, 1849685 N	Lithic Haplustept	Broadleaf: class 2, seasonal forest
SP3	287509 E, 1849693 N	Typic Haplustept	Broadleaf: class 1, deciduous forest
SP4	287510 E, 1849707 N	Typic Haplustept	Broadleaf: class 1, deciduous forest

^a Universal Transverse Mercator.

^b Soil Survey Staff (1998).

^c Penn et al. (2004).

‘Savannah: class 17, pine forest’. Detailed descriptions of each vegetation class can be found in Penn et al. (2004); a brief description follows. Vegetation class 18 is dominated by species of oak, primarily *Quercus oleoides* Schltld. and Cham., and includes *Vitex kuylenii* Standl. The savannah, which has a canopy height of approximately 7–10 m, has an open structure with abundant light reaching a shrubby graminoid understory, which is dominated by *Melastomataceae* spp. Other prominent species include *Cochlospermum vitifolium* (Willd.) Spreng and *Inga pinetorum* Pittier. MPR sites 2, 3 and 4 are located in vegetation class 17, which includes the main forestry production zone within Mountain Pine Ridge. The dominant tree species are *Pinus caribaea* var. *hondurensis* (honduras pine), *Pinus oocarpa* Schiede ex Schltld. (ocote pine) and *Clusia* spp.

The San Pastor sites, in contrast, are located in an area of tropical broadleaf forest. The forest structure here is closed and dense, with a canopy height of 20–30 m and a locally associated abundant palm understory. The site borders two slightly different vegetation zones, described by Penn et al. (2004) as tropical ‘Broadleaf: class 2, seasonal forest’ and ‘Broadleaf: class 1, deciduous forest’. The species composition of San Pastor is markedly different from that of the MPR sites. The dominant species in San Pastor include: *Manilkara zapota* (L.) P. Royen, *Manilkara chicle* (Pittier) Gilly, *Vitex gaumeri* Greenm., *Schizolobium parayhya* (Vell.) S.F. Blake, *Sebastiania tuerckheimiana* (Pax and K. Hoffm.) Lundell, *Swietenia macrophylla* King, *Spondias mombin* L., *Protium copal* (Schltld. and Cham.) Engl., *Brosimum alicastrum* Sw., *Cedrela odorata* L., *Dialium guianense* (Aubl.) Steud., and pockets of *Sabal mauritiformis* (H. Karst.) Griseb. and H. Wendl. ex Griseb.

2.3. Soil collection and analysis

Soil pits were dug at each of the eight sampling locations to expose at least one face of the soil profile, thus facilitating profile description and sample collection. An auger was used to sample depths >1 m. Three soils within the MPR region are classified as Typic Haplustults; the fourth is a Typic Kandiuistult (Soil Survey Staff, 1998) (Table 1). Two of the limestone-derived soils of San Pastor are Lithic Haplusteps; the remaining two are Typic Haplusteps.

Bulk samples from each horizon of the eight soil profiles were air dried, then crushed to pass through a 2 mm sieve. A particle size analysis of the <2 mm fraction was carried out for each sample according to the procedure of Gee and Bauder (1986). Briefly, following pretreatment with HCl and H₂O₂ to remove carbonates and organic matter, the samples were dispersed with sodium hexametaphosphate in a reciprocating shaker. The proportion of sand (2.0–0.05 mm) was determined by sieving; silt (0.05–0.002 mm) and clay (<0.002 mm) proportions were determined by sedimentation using the pipette method. A portion of the <2 mm fraction from sites MPR3 and MPR4 was sieved further to obtain four size fractions (2–0.5, 0.5–0.25, 0.25–0.05 and <0.05 mm) for trace element analysis by X-ray fluorescence (XRF) spectroscopy.

Soil pH was determined on a suspension of 10 g air dry soil and 10 mL 0.01 M CaCl₂. Total N, organic C and inorganic C were measured by dry combustion (ThermoFinnigan® CHN analyser). Organic C was calculated as that C remaining following pretreatment with 0.1 M HCl to remove carbonate carbon. Inorganic C was expressed as CaCO₃ equivalent. Exchangeable cations were measured by first combining 1.0 g air-dried soil with 30.0 mL unbuffered 0.1 M BaCl₂, then agitating the suspensions slowly on an end-over-end shaker (15 rpm) for 2 h. The supernatant solution was obtained by filtering the suspension twice through Whatman® No. 41 filter paper. Cations (Ca²⁺, Mg²⁺, K⁺, Na⁺, Al³⁺, Si⁴⁺, Fe³⁺) in solution were measured by ICP-AES. The effective cation exchange capacity (ECEC) was calculated as the sum of exchangeable cations. Each of the above analyses was performed in duplicate; the mean of the two trials was reported. Total trace element concentrations in the MPR3 and MPR4 soils were determined by XRF spectroscopy on pressed powder pellets using a Philips PW1480 instrument. Data were processed using Philips X40 software.

Mineral phases in the clay fractions of the MPR3 and SP3 soils were identified by powder X-ray diffraction (XRD) using an Enraf-Nonius PDS 120 diffractometer with a curved position-sensitive detector configured in vertical geometry with a 2 θ detection range of 120°. A Ge-111 monochromator was used to select CuK α ₁ radiation. Tube operating conditions were 45 kV and 45 mA. Measurements

were made in reflection geometry with the sample surface at a fixed angle of 12° to the incident beam. Magnesium-exchanged clay samples were powdered, then loaded into a circular well mount (15 mm diameter \times 1 mm deep), ensuring a smooth and flat surface. Data acquisition time was 10 min for both the external silicon standard and the multi-phase clay samples. The 2θ linearisation was performed with ENRAF-GUFI software (Cressey and Schofield, 1996). Mineral identification was aided by comparing diffraction patterns with those in the JCPDS database.

3. Results

3.1. Soil chemical properties

All Mountain Pine Ridge soils are strongly acidic, with pH values ranging from 4.7 to 5.7 (Table 2). Surface horizons are generally more acidic than the subsoil, although pH is remarkably uniform throughout each soil profile, with little more than 0.5 pH unit variation within the top metre. The limestone-derived soils near San Pastor are, unsurprisingly, less acidic than those of the Mountain Pine Ridge, and also encompass a greater pH range, varying from 6.7 near the surface of SP1 to 8.7 for the C horizon of SP2.

Inorganic carbon, expressed as % CaCO_3 , is largely absent from the MPR soils but occurs abundantly with increasing depth in the San Pastor soils, exceeding 77% in the C horizon of SP2. The marked contrast in inorganic C abundance in soils from these two regions reflects differences in parent material and pedogenic age. The limestone-derived San Pastor soils have been subject to continual erosion as a consequence of surface water runoff on the associated hilly, karstic landscape, whereas the granite-derived MPR soils have formed largely uninterrupted for millennia, subject to little erosion, from the stable and relatively flat granite substrate. Intensive use of the San Pastor soils by ancient Mayan civilisations, including the construction of vast terraces (Kunen, 2001; Beach et al., 2002), no doubt also contributed to the erosion of these Inceptisols, thus continually exposing fresh limestone parent material.

The Ultisols of Mountain Pine Ridge contain only 0.1% to 1.2% organic C, which is most abundant in

the surface horizons and decreases with depth. The San Pastor soils, by comparison, are rich in mull humus, with the A horizons containing 2.8% to 10.6% organic C. The greater organic matter content of the San Pastor soils contributes substantially to their cation exchange capacity, as well as to the abundant and well-defined granular aggregates readily apparent in their surface horizons. Organic C correlates positively with total nitrogen abundance, which is highest in the SP soils and decreases with increasing depth.

Aluminum dominates the exchange sites of the MPR soils, comprising a majority of the exchangeable cations in nearly all soil horizons (Table 3). MPR1 is particularly rich in labile Al^{3+} , with nearly 90% of its exchange capacity occupied by Al^{3+} monomers and oligomers. Only the upper horizons of MPR3 contain Ca^{2+} and Mg^{2+} in greater abundance than Al^{3+} . Exchangeable cations in the San Pastor soils are, by contrast, dominated by Ca^{2+} and Mg^{2+} , with Ca^{2+} contributing ≈ 40 to $80 \text{ cmol}(+) \text{ kg}^{-1}$. Exchangeable Mg^{2+} , though second in abundance, occupies only about 10% of the exchange capacity. Potassium is present in exchangeable form as a minor constituent in the San Pastor soils and in only trace amounts within the MPR soils.

Effective cation exchange capacity ranges from 1.5 to nearly $4 \text{ cmol}(+) \text{ kg}^{-1}$ for the MPR soils and from 31 to $89 \text{ cmol}(+) \text{ kg}^{-1}$ for the San Pastor soils (Table 3). The somewhat lower than anticipated ECECs for the MPR soils may arise from hydrolysis and precipitation of OH-Al oligomers during the BaCl_2 extraction, with a consequent underestimation of exchangeable Al^{3+} . The unbuffered BaCl_2 extraction is the preferred method of ECEC determination in calcareous soils because it minimises CaCO_3 dissolution (Sumner and Miller, 1996). Therefore, the ECECs for the SP soils, high as they are, reliably represent the exchange capacity of the SP soils at field pH. The marked differences in ECEC for the MPR and SP soils are due primarily to contrasting mineral assemblages and variable soil organic matter contents.

Within the $<2 \text{ mm}$ fraction of the MPR3 and MPR4 soils, Zr concentrations decrease with increasing depth, indicating that the profiles are undisturbed (Hodson, 2002) (Table 4). These two soils show clear differences in trace element concentrations, with the surface horizons of MPR3 enriched in V and Cr, while

Table 2
Profile descriptions and selected properties of the eight soils

Soil	Horizon	Depth (cm)	Munsell colour (dry)	pH ^a	N _{tot}	C _{org}	CaCO ₃	Texture	Sand ^b	Silt ^b	Clay ^b
					(%)	(%)	(%)		(%)	(%)	(%)
MPR1	A	0–19	7.5 YR 6/6	4.7	0.1	1.0	0.0	L	51	41	8
	Bt1	19–58	2.5 YR 5/8	5.1	0.1	0.8	0.0	SL	60	27	13
	Bt2	58–89	2.5 YR 4/8	5.3	0.0	0.3	0.0	L	47	42	11
	BC	89–120	5 YR 5/8	5.2	0.0	0.1	0.0	L	39	43	18
MPR2	A	0–26	7.5 YR 6/6	5.1	0.1	0.9	0.0	L	48	45	7
	Bt	26–51	5 YR 5/8	5.1	0.1	0.3	0.1	SiL	34	51	15
	BC1	51–87	5 YR 6/8	5.3	0.0	0.1	0.0	L	49	39	12
	BC2	87–120	5 YR 6/8	5.4	0.0	0.1	0.0	SL	52	34	14
MPR3	E	0–33	10 YR 7/4	5.3	0.1	0.2	0.0	SL	58	33	9
	Bt	33–52	10 YR 7/6	5.4	0.2	0.2	0.0	SL	51	30	19
	BC1	52–91	7.5 YR 6/6	5.3	0.1	0.2	0.1	SL	55	31	14
	BC2	91–120	2.5 YR 5/8	4.9	0.1	0.1	0.0	L	33	47	20
MPR4	A	0–6	10 YR 6/3	5.1	0.1	1.2	0.0	SL	57	34	9
	E	6–24	10 YR 7/4	5.3	0.2	0.5	0.0	SL	47	46	7
	Bt1	24–60	10 YR 7/4	5.5	0.1	0.1	0.0	L	38	43	19
	Bt2	60–123	10 YR 7/6	5.7	0.1	0.1	0.0	SL	53	31	16
SP1	BC	123–158	10 YR 7/6	5.6	0.1	0.1	0.0	SL	67	25	8
	O	0–9	7.5 YR 2.5/1	6.7	nd	nd	nd	nd	nd	nd	nd
	A	9–18	7.5 YR 2.5/1	7.9	0.6	4.3	17.5	SiCL	0	61	39
	B	18–32	5 YR 2.5/1	7.7	0.8	3.8	17.5	SiC	0	43	57
	BC	32–42	7.5 YR 3/1	8.0	0.7	5.1	15.4	SiC	0	44	56
SP2	R	42+	nd	nd	nd	nd	nd	nd	nd	nd	nd
	O	0–5	2.5 YR 2.5/1	6.8	nd	nd	nd	nd	nd	nd	nd
	A	5–16	7.5 YR 2.5/2	7.0	0.6	2.8	1.1	SiC	0	55	45
	B	16–27	7.5 YR 2.5/3	6.8	0.5	1.5	14.3	SiC	0	46	54
	C	27–38	7.5 YR 3/4	8.7	0.1	1.2	77.6	SiC	0	49	51
SP3	R	38+	nd	nd	nd	nd	nd	nd	nd	nd	nd
	O	0–10	2.5 YR 2.5/1	6.9	nd	nd	nd	nd	nd	nd	nd
	A	10–31	2.5 YR 2.5/1	7.3	1.2	7.8	13.2	SiC	0	47	53
	AB	31–46	10 R 2.5/1	7.7	0.7	3.8	6.1	C	0	29	71
	2Ab	46–80	7.5 YR 3/1	7.6	0.2	1.9	0.7	C	0	19	81
	2B	80–125	5 YR 4/3	8.1	0.2	0.7	11.8	C	0	6	94
SP4	2BC	125–150	7.5 YR 3/4	8.3	0.0	0.4	16.3	C	0	14	86
	2C	150–180	7.5 YR 4/6	8.4	0.1	0.6	21.8	C	0	8	92
	O	0–8	10 YR 3/1	7.3	nd	nd	nd	nd	nd	nd	nd
	A	8–21	10 YR 2/1	7.8	0.8	10.6	2.7	SiC	0	50	50
	E	21–26	10 YR 3/1	7.8	0.6	6.3	6.4	SiC	0	59	41
	Bt	26–50	7.5 YR 3/1	7.7	0.2	1.7	0.2	C	0	24	76
	B	50–95	7.5 YR 2.5/1	6.8	0.4	1.2	16.8	C	0	37	63
	BC	95–135	10 YR 4/6	6.8	0.2	0.6	30.6	C	0	22	78
	C	135–150	10 YR 5/4	7.9	0.2	0.3	62.2	C	0	14	86

nd=not determined.

^a pH in 0.01 M CaCl₂; 1:1.

^b Sand: 2–0.05 mm; silt: 0.05–0.002 mm; clay: <0.002 mm.

in the MPR4 soil, Ni, Zn, Pb, Rb and Y predominate throughout the profile, indicating inheritance of these elements from the MPR4 parent material. Copper, Zn and Pb are concentrated in the finer fractions (<0.05 mm) of both soils, reflecting sorption to clay minerals

and poorly ordered Fe- and Mn-oxyhydroxides. The other trace elements are distributed largely uniformly among the various size fractions.

The majority of trace elements occur at concentrations normally found in soils (Kabata-Pendias and

Pendias, 2001). However, Y and Rb concentrations in MPR4 exceed those typically in soil (i.e. 10–150 ppm Y, 20–210 ppm Rb), while the V concentrations in the E and Bt horizons of MPR3 are sufficiently high (i.e.

Table 3

Exchangeable cations and effective cation exchange capacity for each of the eight soils

Soil	Horizon	Ca ²⁺	Mg ²⁺	K ⁺	Na ⁺	Al ³⁺	Si ⁴⁺	Fe ³⁺	ECEC ^a
		cmol(+) kg ⁻¹							
MPR1	A	0.06	0.05	0.03	0.01	2.29	0.06	0.00	2.50
	Bt1	0.04	0.13	0.01	0.00	2.48	0.07	0.00	2.74
	Bt2	0.02	0.19	0.02	0.02	2.92	0.15	0.00	3.32
	BC	0.04	0.21	0.01	0.02	3.42	0.17	0.00	3.88
MPR2	A	0.25	0.18	0.09	0.08	1.56	0.22	0.02	2.40
	Bt	0.19	0.28	0.06	0.06	1.86	0.16	0.01	2.61
	BC1	0.21	0.35	0.02	0.06	1.93	0.17	0.00	2.75
	BC2	0.26	0.39	0.03	0.04	1.64	0.14	0.01	2.50
MPR3	E	0.25	0.42	0.01	0.02	0.24	0.16	0.00	1.10
	Bt	0.40	0.59	0.03	0.02	0.70	0.23	0.00	1.97
	BC1	0.17	0.01	0.01	0.00	1.10	0.18	0.00	1.47
	BC2	0.11	0.20	0.01	0.00	1.50	0.12	0.01	1.96
MPR4	A	0.23	0.16	0.10	0.00	1.79	0.05	0.02	2.34
	E	0.12	0.11	0.08	0.00	1.41	0.07	0.01	1.80
	Bt1	0.34	0.27	0.13	0.00	1.27	0.18	0.00	2.19
	Bt2	0.53	0.28	0.22	0.00	1.98	0.11	0.00	3.13
SP1	BC	0.44	0.45	0.14	0.00	0.97	0.22	0.00	2.23
	O	nd	nd	nd	nd	nd	nd	nd	nd
	A	36.1	0.50	0.11	0.00	0.16	0.14	0.00	37.0
	B	29.9	0.22	0.11	0.10	0.83	0.09	0.01	31.3
SP2	BC	38.4	3.61	0.14	0.01	0.01	0.90	0.00	43.1
	R	nd	nd	nd	nd	nd	nd	nd	nd
	O	nd	nd	nd	nd	nd	nd	nd	nd
	A	81.5	6.25	0.57	0.02	0.01	0.33	0.00	88.7
SP3	B	71.8	13.1	1.90	0.10	0.01	0.64	0.01	87.6
	C	62.2	4.22	0.68	0.11	0.00	0.37	0.00	67.6
	R	nd	nd	nd	nd	nd	nd	nd	nd
	O	nd	nd	nd	nd	nd	nd	nd	nd
SP4	A	63.5	8.70	0.83	0.06	0.02	0.54	0.00	73.7
	AB	71.7	6.44	0.54	0.00	0.02	0.31	0.00	79.0
	2Ab	73.5	8.23	0.68	0.01	0.01	0.51	0.00	82.9
	2B	59.3	5.96	1.59	0.00	0.01	0.51	0.00	67.4
SP4	2BC	75.4	5.06	0.53	0.16	0.01	0.31	0.02	81.5
	2C	73.9	5.24	0.86	0.12	0.01	0.39	0.01	80.5
	O	nd	nd	nd	nd	nd	nd	nd	nd
	A	67.4	1.56	0.11	0.10	0.00	0.25	0.01	69.4
SP4	E	53.2	3.37	0.35	0.09	0.02	0.58	0.01	57.6
	Bt	68.4	6.27	0.32	0.13	0.01	0.18	0.01	75.3
	B	55.9	4.63	0.22	0.14	0.01	0.22	0.01	61.1
	BC	52.8	3.81	0.16	0.11	0.01	0.14	0.01	57.0
SP4	C	45.1	3.78	0.15	0.00	0.00	0.00	0.00	49.0

nd=not determined.

^a ECEC—effective cation exchange capacity (includes exchangeable Al³⁺).

Table 4

Total trace element concentrations in various size fractions of the MPR3 and MPR4 soils

Size (mm)	Horizon	V	Cr	Co	Ni	Cu	Zn	Pb	Rb	Sr	Y	Zr
		(ppm)										
<i>Mountain Pine Ridge 3</i>												
<2	E	71	21	5	5	7	13	15	18	4	25	552
	Bt	79	20	5	6	15	20	17	20	2	12	280
	BC1	34	3	2	1	1	13	16	35	0	12	243
2–0.5	BC2	23	0	3	1	1	17	16	47	0	11	231
	E	42	19	4	3	5	10	10	14	1	15	394
	Bt	64	12	6	8	10	19	16	16	1	12	263
0.5–0.25	BC1	36	7	4	4	4	18	13	35	0	11	201
	BC2	19	0	4	1	2	10	14	35	0	10	178
	E	83	22	5	9	15	18	21	19	5	27	675
0.25–0.05	Bt	86	17	8	5	15	18	21	18	0	9	273
	BC1	39	5	3	4	8	18	23	40	0	8	231
	BC2	33	2	6	3	5	14	21	47	0	9	204
<0.05	E	92	23	8	11	15	22	23	24	4	35	843
	Bt	87	25	5	9	19	18	22	17	3	12	272
	BC1	43	10	6	4	15	16	25	31	0	4	258
2–0.05	BC2	31	2	3	4	7	17	21	40	0	5	261
	E	100	30	7	11	32	20	28	21	5	27	1018
	Bt	87	12	8	9	35	29	26	39	5	17	822
0.5–0.25	BC1	53	10	6	5	23	31	23	54	0	12	527
	BC2	30	2	3	3	20	36	23	77	0	15	511
	<i>Mountain Pine Ridge 4</i>											
<2	A	17	0	5	12	1	26	46	295	2	100	383
	E	16	0	6	17	1	20	32	262	1	98	324
	Bt1	31	5	9	32	0	48	74	410	4	252	283
	Bt2	26	0	9	32	0	38	59	384	5	277	213
2–0.5	BC	18	0	6	28	0	60	59	501	4	215	243
	A	13	8	3	16	1	20	33	247	1	82	273
	E	14	2	7	14	1	23	31	250	1	97	315
	Bt1	26	6	7	29	2	40	59	374	3	216	234
0.5–0.25	Bt2	19	0	8	30	0	33	54	362	5	253	189
	BC	12	0	5	25	0	49	61	458	4	193	175
	A	27	0	7	18	6	34	52	335	5	118	400
	E	29	1	5	24	1	39	45	355	4	152	495
0.25–0.05	Bt1	35	0	6	31	1	46	70	395	5	248	274
	Bt2	30	0	9	34	1	42	67	398	5	299	209
	BC	22	0	7	35	0	78	70	573	6	261	281
	A	23	0	5	19	2	38	55	339	4	143	532
<0.05	E	29	0	8	23	1	43	53	376	4	171	589
	Bt1	36	2	12	32	1	50	76	393	4	253	303
	Bt2	27	0	9	32	2	40	64	381	5	277	246
	BC	20	0	7	27	0	81	58	482	3	213	324
2–0.05	A	28	0	11	24	9	55	67	398	6	187	1105
	E	37	0	10	24	20	49	59	385	7	176	781
	Bt1	38	0	9	35	12	58	78	431	6	255	472
	Bt2	31	0	12	32	6	36	73	412	7	289	364
2–0.05	BC	26	0	7	28	2	82	79	489	5	246	458

>50 ppm V) to present risk of toxicity (Kabata-Pendias and Pendias, 2001). However, trace element bioavailability was not directly measured and, therefore, it is not possible to determine unequivocally whether V will restrict plant growth at MPR3.

3.2. Soil texture and mineralogy

Loam and sandy loam textures predominate in the MPR soils (Table 2). Clay abundance is $\leq 20\%$ in all four soils, with only slight subsurface clay accumulations giving evidence of weakly expressed Bt horizons in each of the four profiles. The San Pastor soils, by contrast, are dominated by clay and silty clay textures, with clay contents exceeding 90% in SP3. Extreme textural differences among the MPR and SP soils induce equally strong differences in a variety of soil properties directly influencing plant growth, most notably water holding capacity, cation exchange capacity and susceptibility to water erosion.

X-ray diffraction patterns of Mg-exchanged clay fractions from the SP3 and MPR3 soils are shown in Fig. 2. As the clay fractions from all San Pastor soils give nearly identical diffraction patterns, the pattern for a single representative sample, SP3 (horizon A), is shown. Likewise, the XRD patterns for the MPR3 clay fraction (horizons E and BC2) are representative of the MPR soils generally. Quartz presence is indicated by a single, sharp peak at 0.334 nm in all diffraction patterns. The MPR3 clay fractions are

dominated by well-crystallised kaolinite, as indicated by sharp, intense peaks at 0.714 and 0.357 nm, representing the 001 and 002 reflections, respectively. The broader and weaker set of prismatic peaks between 0.40 and 0.44 nm are also assigned to kaolinite (White and Dixon, 2002). Gibbsite presence in the MPR clay is confirmed by small 0.485 nm peaks in both the E and BC2 horizons. The somewhat larger 0.485 nm reflection from the E horizon clay, indicating greater gibbsite abundance, is consistent with a more intense weathering environment in this leached horizon. The strong red and yellow colours of the MPR soils derive from small amounts of various Fe(III) oxides, principally goethite, whose presence is confirmed by the 0.418 nm peak (110 reflection) in the diffraction pattern for horizon BC2. Clay fractions from the San Pastor soils are dominated by interstratified illite-smectite, as indicated by a broad, low angle 001 reflection at 1.097 nm.

4. Discussion

4.1. Water holding capacity and forest adaptation

The coarse textures of the MPR soils severely restrict water holding capacity. A sandy loam textured soil with an average bulk density of 1.4 g cm^{-3} will hold $\approx 9.8 \text{ cm}$ of plant-available water within the top 100 cm. This soil could therefore hold about a 20-day supply of water, assuming an average consumption rate of 0.5 cm of water per day. Given that the dry season lasts nearly 5 months, from January to May, during which less than 100 mm precipitation falls, the soils of the Mountain Pine Ridge very quickly become deficient in plant-available water.

Within the Mountain Pine Ridge, soil water regimes are generally dry but may fluctuate dramatically, from near saturated conditions during the wet season to wilting point in localised areas during the dry season. As a consequence of seasonal, restricted water availability, a savannah ecosystem has developed. The common tree species within the Mountain Pine Ridge savannah (e.g. *P. oocarpa*, *P. caribaea* var. *hondurensis*, *Q. oleoides* and *Clusia massoniana*) are all highly adapted to these extremes of water availability. For instance, *P. oocarpa* and *P. caribaea* both possess needle leaves, which minimise evapo-

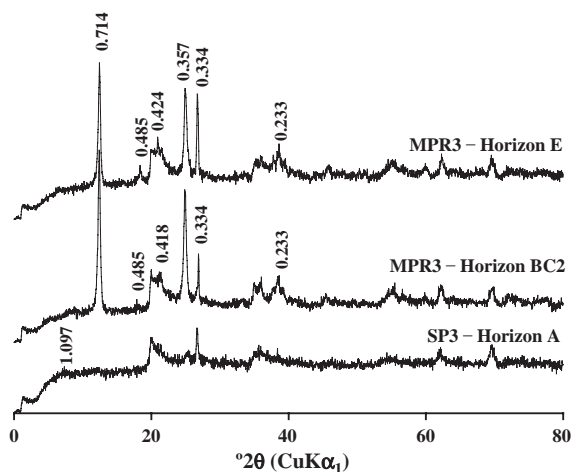


Fig. 2. XRD patterns ($\text{CuK}\alpha_1$) of the Mg-exchanged $<2 \mu\text{m}$ fractions from the MPR3 and SP3 soils (values of reflection in nm).

transpiration, and their rooting systems have a high degree of horizontal growth which is concentrated within 30 cm of the soil surface to capture, for example, water entering the soil as mist or dew. These species also exhibit a high root to shoot biomass ratio, which is typically much higher than that of other trees within tropical forests (Smith and Smith, 2001). Another tree species highly adapted to this extreme environment is *Q. oleoides*, which, over the driest months of the year, will shed its leaves completely to minimise water loss.

Perhaps the most important plant adaptation within savannah ecosystems is the ability of native species to survive the many and widespread fires. For example, all pine species on Mountain Pine Ridge have thick, fire-resistant bark and cones, which open when exposed to heat to disperse their seeds widely. Moreover, the grasses which comprise a significant part of the savannah recover quickly from fire and are thus able to derive early sustenance from the nutrient-rich ash. Although forest composition on MPR is strongly influenced by frequent fire, it is the soil, through its inability to provide sufficient plant-available water during the dry season, which ultimately sanctions the frequency and intensity of the fires.

The silty clay textured San Pastor soils hold considerably more plant-available water than the coarse textured MPR soils. The deep, fine textured soils occupying low positions of the San Pastor landscape serve as important reserves of plant-available water, providing refugia during particularly long and severe periods of drought. Indeed, although fieldwork was conducted in May, at the end of the dry season, subsoil at the base of several catenas still contained plant-available water in amounts sufficient to support lush, dense foliage. These observations corroborate previous work on plant community variation over limestone-derived soils in Belize (Furley and Newey, 1979).

Across the San Pastor landscape there is a gradual change from a semi-deciduous vegetation on the crests, to a dominantly evergreen vegetation in the depressions and at the base of the hillsides. The crests are dominated by *Bursera simaruba* (L.) Sarg., *Sebastiania tuerkheimiana* and *Pimenta dioica* (L.) Merr, all capable of tolerating severe water stresses (Penn et al., 2004), whereas the depressions and base

of the hillsides are dominated mainly by palm species with considerably less drought tolerance, such as *Sabal mauritiiformis*, *Cryosophila staurocantha* (Heynht.) and significant clusters of *Swietenia macrophylla*. This strong causal relationship between water availability and forest composition has been observed previously (Furley et al., 2001; Penn et al., 2005).

4.2. Nutrient availability

Intense weathering over millennia has largely depleted the Mountain Pine Ridge Ultisols of nutrients and eliminated much of the permanent negative charge that once dominated minerals within their clay fraction. Only soils in footslope positions of the landscape possess appreciable amounts of organic matter and available nutrient, as reported previously (Furley, 1974). The resulting nutrient deficient, acidic and poorly buffered soils of upper and mid-slope positions are no longer able to provide nutrients in amounts once possible during the early stages of pedogenesis. Despite considerable nutrient deficiencies, the MPR soils support a forest, which, although sparse when compared to the SP forest, nevertheless encompasses a species diversity seemingly inconsistent with their low nutrient status. Indeed, large tracts of the MPR forest have until recently been subject to routine and frequent tree harvests (Billings and Schmidtke, 2002).

There is growing evidence that highly weathered soils, such as those on Mountain Pine Ridge, receive significant amounts of nutrient in the form of dust and other atmospheric sources (Griffin et al., 2002). Consequently, these highly weathered landscapes subsist either wholly or partially on the slow but steady addition of atmospherically derived nutrient elements (Kennedy et al., 1998; Chadwick et al., 1999). The global importance of dust transport and deposition has been a topic of interest for considerable time, as Darwin himself reported on the composition of Saharan dusts encountered whilst on HMS *Beagle* (Darwin, 1846).

Evidence for atmospheric deposition of elements to the Mountain Pine Ridge soils is shown most clearly in the trace element distribution profiles for MPR3 (Table 4). Chromium, Ni, Cu and Sr concentrations are highest in the surface horizons, and decrease with

increasing depth. The distribution of Cu is of particular interest, as the Bt horizon is more Cu-rich than the overlying E horizon, indicating downward translocation of the atmospherically derived Cu. The profile distributions of exchangeable Ca and Mg (Table 3) mimic that for Cu, hinting at atmospheric sources for these two nutrients as well. It is clear that, in the absence of geological rejuvenation, the productivity of highly weathered tropical landscapes, such as Mountain Pine Ridge, is strongly dependent upon atmospheric inputs of nutrient elements. Recent work on highly weathered Hawaiian Island landscapes, for example, has shown that >80% of plant Ca is derived from atmospheric sources (Chadwick et al., 1999).

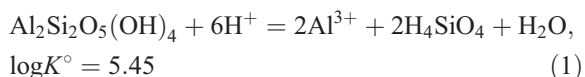
The genetically younger limestone-derived soils of the San Pastor region contain most of the elements essential for plant growth. For example, the substantial cation exchange capacity of each SP soil is dominated by labile Ca^{2+} and Mg^{2+} . Although exchangeable K^+ is present in much smaller amounts, the predominance of illite-smectite in the clay fraction suggests an abundance of plant-available K^+ (Reid-Soukup and Ulery, 2002). Erosion has redistributed much of the A horizon, rich in organic C and N, from the crest to lower positions in the San Pastor landscape. For example, the shallow soils at SP1 and SP2, both Lithic Haplustepts, have been subject to considerable erosion as evidenced by their degraded A horizons and consequently lie within 50 cm of the bedrock surface. Pedogenically immature soils, such as the eroded SP1 and SP2, are generally rich in most of the essential elements, with the possible exception of nitrogen. Both soil N and organic C reach maximum steady-state concentrations following thousands of years of soil development and, consequently, net primary production of the forest will reach a maximum only after a similar time period (Vitousek et al., 1997).

Insufficient soil N in the shallow SP1 and SP2 soils, coupled with limited rooting depth and insufficient plant-available water, have combined to restrict species diversity and alter forest composition on the crest positions of the San Pastor landscape. The largely deciduous forest on the crest positions contributes substantial leaf litter and organic C to the forest floor. However, much of this organic C and associated nutrient is redistributed to lower positions

in the landscape during the many severe water erosion events that occur during the wet season.

4.3. Aluminum toxicity

The dominance of exchangeable Al in the MPR soils reflects their high degree of weathering and, coupled with low pH, hints at the prospect of Al toxicity. One must therefore consider the possibility that species diversity and adaptation on Mountain Pine Ridge is constrained not only by nutrient and water limitations, but also by toxic levels of Al. A detailed assessment of Al toxicity risk in the MPR soils is beyond the scope of this paper, as such analysis requires determination of solubilities of the Al-containing solid phases, as well as quantification and speciation of aqueous Al^{3+} and Al^{3+} -L complexes [where L=fulvic acid, low MW organic acids, F^- , OH^- , SO_4^{2-} , PO_4^{3-} and SiO_4^{4-}]. Moreover, Al toxicity is species-dependent, with some plant species, and even cultivars of the same species, showing considerable variation in their sensitivity to Al (Cronan and Grigal, 1995; Heim et al., 2003). However, one may calculate an approximate Al activity for these soils by considering a model system in which soluble Al^{3+} is controlled by a single Al-bearing solid phase. In the MPR soils, gibbsite and kaolinite are the dominant Al-bearing solid phases and, at H_4SiO_4 activities greater than $10^{-5.31}$ M, kaolinite is less soluble than gibbsite and therefore the former will control Al activity. The dissolution of kaolinite is described by:



which reduces to:

$$2\log(\text{Al}^{3+}) + 2\log(\text{H}_4\text{SiO}_4) - 6\log(\text{H}^+) = 5.45 \quad (2)$$

Assuming an absence of complexing ligands and an H_4SiO_4 activity of 10^{-5} M, Al^{3+} activity for the most acidic soil [i.e. pH 4.7 for horizon A, MPR1] is calculated to be $10^{-6.38}$ M. Although low molecular weight organic ligands will further increase Al^{3+} solubility, the submicromolar concentrations of Al calculated above for Al in equilibrium with kaolinite are sufficiently low (Schaedle et al., 1989) that Al

toxicity can be discounted as a significant factor governing plant community adaptation on Mountain Pine Ridge.

4.4. Ecosystem resilience

The contrasting soils of Mountain Pine Ridge and San Pastor have induced striking compositional differences among the forests of these two regions. These compositional differences, in turn, directly influence the ability of each forest to adapt to both chronic and short-term disturbances, such as fires, windthrows and insect outbreaks. Although such disturbances are considered essential for the creation and maintenance of diversity (Connell, 1978; Bengtsson, 2002), the beneficial effects of disturbance can be realised only if the forest possesses sufficient resilience to adapt successfully to each new environment. Such resilience depends fundamentally on the presence of species, currently redundant, which are able to adopt new roles in response to changing environmental conditions.

To what extent do edaphic factors contribute to ecosystem resilience in the Chiquibul forest? Edaphic controls on forest diversity, with the associated implications for resilience, have been described previously with respect to the Mountain Pine Ridge and San Pastor regions. Evidence of the fragility of ecosystems possessing minimal diversity is illustrated clearly with the recent infestation of the Mountain Pine Ridge forest by the southern pine beetle (*Dendroctonus frontalis*), which led to the destruction of 25,000 ha of old growth pine forest and the cessation of commercial logging activities (Billings and Schmidtke, 2002). Although above-ground vegetation provides the most salient expression of diversity and resilience in these and other ecosystems, the below-ground biomass, the soil biota, possess greater diversity and are perhaps more important determinants of ecosystem resilience (Giller, 1996). For this reason, the functional and genetic diversity of soil biological communities have been the recent subjects of numerous and detailed studies (Ronn et al., 2002; Grayston et al., 2004; Griffiths et al., 2004). Although the origins of soil biodiversity are complex and have only begun to be fully resolved, it is clear that many of the same soil properties governing above-ground diversity (e.g. available water, organic

C and other nutrients, suitable aeration) also control the abundance and diversity of soil biota (Giller, 1996).

To the extent that soils promote and maintain biological diversity in the Chiquibul forest, they also confer resilience to the broader ecosystem, of which they are a central part. Ecological resilience is an adaptation that has guided the development of forests for millennia, and this resilience is of particular importance today, as many forests and other biomes adapt to a rapidly changing global climate. The forests of Belize in particular, located as they are in the subhumid tropics, are especially sensitive to rapid changes in temperature or precipitation regimes (Scholes and van Breemen, 1997).

The complex and intimate soil–forest relationships described within this paper have evolved over millennia, during which the soil has continually established the limits and conditions within which forest evolution and adaption may occur. For example, the Mountain Pine Ridge Ultisols were, at a much younger pedogenic age, able to support a forest far more abundant and diverse than that which currently exists; a forest perhaps as lush and complex as that now found in the San Pastor region. The derivation of these long-term, millennial-scale changes in soil–forest interactions has to date received little attention, possibly due to a perceived difficulty reconciling the differing rates and timescales of development: forests evolve over decades and centuries, whereas soils develop more slowly, over millennia. However, only such detailed studies can provide the insight needed to establish the true and complete dependence of forest composition on a dynamic and evolving soil.

5. Conclusions

In the seasonally dry Chiquibul forest, water holding capacity, along with nutrient availability, are the principal determinants of forest composition. Forest diversity and structure were shown to vary not only between regions of highly contrasting Ultisols and Inceptisols but also, as shown clearly in the San Pastor forest, across landscapes, reflecting variation in water and nutrient availability along catenary sequences. The San Pastor forest changes from drought tolerant semi-deciduous vegetation on

the crests, to a dominantly evergreen vegetation in the footslope positions. The Mountain Pine Ridge is characterised by a savannah ecosystem whose dominant tree species possess adaptive structures (e.g. needle leaves, well-developed horizontal root networks) that minimise evaporative losses of water and maximise the capture of water entering the soil as mist or dew. The abundant, near-surface rooting systems also maximise the utilisation of atmospherically derived nutrients, which, in these highly weathered landscapes, comprise a significant portion of the plant-available nutrient pool.

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