6 Global and local variations in tropical montane cloud forest soils

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ABSTRACT

Although soil resources are widely considered as a major factor that reduces the productivity, stature, and diversity of tropical montane cloud forests (TMCF), systematic comparisons of soil resources within and between TMCF are lacking. This study combines published reports on TMCF soils with new data on the soils and forest structure of the Luquillo Mountains in Puerto Rico to assess the current state of knowledge regarding global and local-scale variation in TMCF soils. At the global scale, soils from 33 TMCF sites and over 150 pedons are reviewed. Compared to soils in humid lowland tropical forests, TMCF soils are relatively acidic, have higher organic matter content, and are relatively high in total nitrogen and extractable phosphorus. Across all sites, significant correlations also exist between mean annual precipitation and soil pH and base saturation, but not between any soil chemical factor and canopy height, site elevation, or air temperature. Although comparisons between TMCF are limited by inconsistent sampling protocols, analysis of available data does indicates that lower montane cloud forests (LMCF) have taller canopies, higher soil pH, lower soil nitrogen, and higher C/N ratios than upper montane cloud forests (UMCF). Within an UMCF in NE Puerto Rico, the abundance of soil nitrogen, carbon, and potassium accounted for 25% to 54% of the variation in canopy height. However, as much as 68% of the variation in stand height could be accounted for when site exposure, slope gradient, and the percent coverage of surface roots were also included in the analysis. The importance of these local site factors is apparently related to interactions between exposure, slope steepness, and stand age on the accumulation of soil organic matter. This review indicates that soils investigations in TMCF need to explicitly include the influence of local site conditions and use consistent sampling and analytical methodologies. Nevertheless, the soils of upper and lower montane cloud forests apparently have distinct characteristics.

INTRODUCTION

Whilst there have been considerable advances in our understanding of the hydrology and ecology of tropical montane cloud forests (TMCF), less emphasis has been placed on understanding their soil resources. This study addresses TMCF soils at the global and local scale through a comparative analysis of published reports on TMCF soils, and new information on local-scale relationships between soils and forest structure in the Luquillo Mountains of Puerto Rico.

The unique features of TMCF are widely recognized and have puzzled natural scientists for decades. Compared to lowland and montane forests not frequently enveloped in fog or clouds, TMCF are typically shorter in stature, have smaller, thicker, and more leathery leaves, and gnarled stems and branches that tend to be covered with bryophytes and epiphytes (Stadtmüller, 1987; Whitmore, 1990). More recent assessments have divided TMCF into lower montane cloud forests (LMCF), upper montane cloud forests (UMCF), and sub-alpine cloud forests (SACF) (Bruijnzeel, 2005). This convention is followed here and considers that LMCF have 25–50% epiphytic cover on their stems vs. 70–80% in UMCF (cf. Frahm and Gradstein, 1991; see Bruijnzeel (2005) for detailed discussion).

Most researchers agree that multiple climatic and site factors influence the structural and functional characteristics of TMCF.

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It is pertinent to note that – with very few exceptions (e.g. Hafkenscheid, 2000) – most earlier reviews seeking an explanation for the distinct characteristics of TMCF (Grubb, 1977; Flenley, 1993; Bruijnzeel and Proctor, 1995; Bruijnzeel and Veneklaas, 1998) made no explicit distinction between conditions prevailing in LMCF and UMCF. As a result, a host of sometimes contradictory mechanisms have been proposed, including the following:

- Periodic water shortage, especially in the case of shallow and stony soils.
- Saturated soils and impeded root transpiration.
- Reduced photosynthesis associated with low radiation inputs and air temperatures.
- Limited nutrient uptake due to (a) climatically controlled reduction in transpiration rates, (b) extreme soil acidity and/or "free" aluminum levels, (c) low soil fertility, and/or (d) reduced decomposition and mineralization of litter.
- Exposure to strong winds or high UV-B radiation levels.
- Presence of phenolic compounds in leaves and soil moisture that interfere with metabolic processes.

Although six out of these ten possible mechanisms are directly related to surface soil resources, these early reviews could not identify an overriding soil chemical factor that uniquely characterizes *all* TMCF (Whitmore, 1990; Bruijnzeel and Proctor 1995). As such, there is a need to examine and quantify key differences (if any) in the soil characteristics of LMCF and UMCF.

DEFINING TMCF SOILS

Defining the spatial dimensions of TMCF ecosystems has proved to be a great challenge (Hamilton *et al.*, 1995; Mulligan, this volume; Scatena *et al.*, this volume). Defining TMCF soils may be an even greater challenge due to the abundance of detritus, roots, and soil micro-organisms that occur above the surface of the forest floor (Edwards, 1982; Cavelier and Peñuela, 1990; Nadkarni and Longino, 1990; Paoletti *et al.*, 1991). This review focuses on surface soils in all TMCF and recognizes differences between UMCF and LMCF where possible (see methods section below). It also recognizes, but does not address, the importance of aerial soils and micro-organisms in these ecosystems (cf. Benner *et al.*, this volume; Hietz, this volume).

Regardless of their precise definition, a review of the literature indicates that several generalizations are commonly made regarding TMCF soils. Namely, that these soils are: (i) waterlogged and anaerobic, (ii) high in soil organic matter (SOM), and (iii) highly acidic. Many also consider these soils to be limiting to above-ground forest productivity because they are either (iv) nutrient poor, or (v) inherently toxic (cf. Benner *et al.*, this volume). These generalizations are discussed briefly below.

Waterlogging and anaerobic conditions

Waterlogging and associated anaerobic conditions have often been cited as principal characteristics of TMCF soils (Herrmann, 1971; Hetsch and Hoheisel, 1976; Kapos and Tanner, 1985; Bruijnzeel *et al.*, 1993; Schawe *et al.*, this volume). In general, soil oxygen decreases with increasing SOM and precipitation, and TMCF soils can be anoxic for extended periods of time (Silver *et al.*, 1999; Silver *et al.*, this volume). Many studies have also found that increasing precipitation and waterlogging are related to changes in soil respiration, redox potential, nutrient content, and productivity in many tropical forests (Cavelier and Peñuela, 1990; Bohlman *et al.*, 1995; Austin and Vitousek, 1998; Raich, 1998; Silver *et al.*, 1999; Santiago *et al.*, 2000; Schuur and Matson, 2001; Austin, 2002; cf. Schawe *et al.*, this volume). Nevertheless, waterlogged and anaerobic soils can support tall and highly productive wetland forests (Lugo *et al.*, 1990). In addition, both observations and soil profile characteristics indicate that the soils from some TMCF sites rarely or never experience extensive waterlogging, even under high-rainfall conditions (Hafkenscheid *et al.*, 2002; Tobón *et al.*, this volume #52). These observations also suggest that waterlogged and anaerobic soils are not the sole cause of the lower above-ground productivity and stature of TMCF. However, the presence of these features may be useful in distinguishing between UMCF and LMCF.

Acidity and SOM

The presence of high SOM, humus, or peat has traditionally been used as a key defining characteristic of TMCF soils (Hamilton *et al.*, 1995). This abundance of SOM is generally explained by slow rates of litter decomposition (Vitousek and Sanford, 1986; Tanner *et al.*, 1998; Hafkenscheid, 2000). In turn, soil acidity and the reduced rates of nutrient cycling that are associated with slow decomposition rates have been suggested as direct or indirect mechanisms causing the perceived low productivity of TMCF (Grubb, 1977; Edwards, 1982; Vitousek, 1984; Hafkenscheid, 2000). Nevertheless, a wide variety of tall lowland forests with high above-ground productivity occurs on organically rich and highly acidic soils (Lugo *et al.*, 1990), suggesting that reduced SOM turnover and high soil acidity are not the sole cause of the relatively low stature and above-ground productivity of TMCF ecosystems (Bruijnzeel and Veneklaas, 1998). In addition, Röderstein *et al.* (2005) and Hertel and Leuschner (this volume) show that – whilst above-ground productivity can indeed decrease strongly with increasing elevation and decreasing temperatures – below-ground productivity becomes increasingly important, thereby dampening the effect of altitude on overall ecosystem productivity (Moser *et al.*, 2007, 2008). Again, most early comparisons of TMCF and their soils did not distinguish between UMCF and LMCF.

Nutrient limitation and toxicity

Both nitrogen and phosphorus limitation have been invoked as restrictors on above-ground productivity in TMCF (Vitousek,

1984; Vitousek and Sanford, 1986; Tanner *et al.*, 1990, 1992; Bruijnzeel *et al.*, 1993; Hafkenscheid, 2000; cf. Benner *et al.*, this volume) as well as in some lowland forests (Sollins, 1998; Tanner *et al.*, 1998). Some TMCF soils have also been considered toxic due to high levels of free aluminum and polyphenols (reviewed in Bruijnzeel and Proctor, 1995; Bruijnzeel and Veneklaas, 1998). Unfortunately, few studies have reported the abundance of free aluminum or polyphenols in TMCF soils (e.g. Grimm and Fassbender, 1981; Coxson *et al.*, 1992; Bruijnzeel *et al.*, 1993; Hafkenscheid, 2000). Comparative work in Jamaica indicated that the concentration of polyphenols is strongly correlated with dissolved oxygen concentration (DOC) levels in soil water; absolute concentrations of polyphenols were much larger in stunted UMCF compared to adjacent taller LMCF, and their influence on forest productivity may therefore be limited to UMCF (Hafkenscheid, 2000). This may partly explain why at least some LMCF soils are used in agriculture (Hamilton *et al.*, 1995). However, polyphenols have varied effects on ecosystem processes, not all of which are detrimental (Hättenschwiler and Vitousek, 2000). For example, Northup *et al.* (1995) demonstrated how phenolic compounds produced by the roots in stunted pine forests helped prevent leaching of scarce nitrogen. Others have argued that the ecological cost of producing these secondary compounds in a nutrient-poor environment may result in reduced above-ground stature (Hafkenscheid, 2000; cf. Hertel and Leuschner, this volume).

Explanations based solely on nutrient limitations or toxicity are also contradicted by the observation that *total* soil nitrogen levels can be higher in UMCF than in adjacent LMCF or lowland forests (Hafkenscheid, 2000; Cox *et al.*, 2002). Nevertheless, plant uptake of *available* nitrogen in UMCF may be influenced by phenols and the temporal variability of NO_3-N in some UMCF soils may be related to antecedent rainfall and stagnant water held in micro-pores (Hafkenscheid, 2000). Studies of nutrient turnover in fine litter in a Costa Rican LMCF also suggested that neither nitrogen nor phosphorus were limiting (Nadkarni and Matelson, 1992). Finally, recent studies in LMCF in southern Ecuador have demonstrated that soil nutrients are very heterogeneously distributed at the local scale, whereas observed concentrations showed no indications for possible limitation of growth due to nitrogen or phosphorus deficiencies (Wilcke *et al.*, 2001, 2002; cf. Soethe *et al.*, 2006). However, forests in the same area showed a marked shift in below-ground carbon allocation with increasing elevation (Röderstein *et al.*, 2005; Leuschner *et al.*, 2007; Moser *et al.*, 2008; Hertel and Leuschner, this volume). In addition, foliar concentrations of nitrogen, phosphorus and potassium in UMCF and ECF at 2400 and 3000 m.a.s.l. were much lower than in the LMCF, suggesting that at these higher elevations the uptake of nutrients was reduced more strongly than above-ground biomass. Furthermore, tree basal area increment rates were significantly correlated with nutrient concentrations in the organic layer whereas rooting patterns at higher elevations suggested a reduced capacity for spatial exploitation of soil nutrients (Soethe *et al.*, 2008a, b).

METHODS

Review of global data

Soil data for a given site were included in this global analysis of TMCF soils if the site met at least two of the following conditions: (i) presence of tropical or sub-tropical forest, with elevation and precipitation being within the characteristic range for TMCF (Jarvis and Mulligan, this volume); (ii) the publication in question mentioned frequent fog occurrence; and (iii) the location was either included in the list of known TMCF sites in Hamilton *et al.* (1995) or known by the authors. In all, soil data from 33 sites and over 150 pedons were compared, thereby updating the previous review of TMCF soils by Bruijnzeel and Proctor (1995) (Table 6.1).

Because the global data-set included a variety of forest types and sampling strategies, individual sites were further grouped and compared by forest type and sampling depth. Three forest types were distinguished initially – LMCF, UMCF, and SACF – following the definitions provided by Bruijnzeel (2005). Classifications were based on published site descriptions and our personal knowledge of the sites. However, because the number of sub-alpine sites was limited, the analysis was restricted to comparisons between all TMCF, and between UMCF and LMCF. Soil chemical data were also divided into two groups, viz. one in which the surface organic horizon was included, and the other in which only the soil below was sampled.

Luquillo field study

Comparisons of TMCF soil data are limited by a lack of standard sampling and analytical methods (Bruijnzeel and Proctor, 1995). To evaluate directly the extent to which soil and site characteristics could account for local variation in forest structure, a complementary study was conducted in which regional climate, bedrock geology, and forest type were all held constant. All sampling was done within the UMCF or elfin cloud forest zone of the Luquillo Experimental Forest of NE Puerto Rico. The study area is underlain by erosion-resistant hornfels formed by contact metamorphism of granodiorites and volcanoclastic sediments and typically receives between 4500 and 5000 mm of rainfall annually. The elfin cloud forests are restricted to the upper elevation ridge tops and steep side slopes between 750 and 1050 m.a.s.l. and have gnarled stems that vary in height between 2.3 and 11.5 m. On ridge tops these soils can have organic surface horizons up to 1 m thick. However, these organic surface layers typically thin away from the ridge tops such that soils on steep side slopes can have rocky

Table 6.1 *Locations and environmental characteristics of tropical montane cloud forest soil studies*

Location	Elevation (m)	Forest type[a]	Average annual temperature (°C)	Average annual precipitation (mm year^{-1})	Canopy height (m)	Soil type	Reference
Bolivia, Cordillera Oriental, Yungas	1850–3050	LMCF UMCF, SACF	10–17	5300–2300	10–20	Humic Dystrudept, Typic Placorthod	Schawe *et al.* (2001)
Colombia, Cordillera Central	2550	LMCF UMCF	12.2	2115	25	Andic Humitropept	Veneklaas (1990)
Colombia, Cordillera Central	1453–2115	LMCF UMCF	7.7–12.2	1453–2115	25	Andic Humitropept, Andaquept	Thouret & Faivre (1989)
Colombia, Cauca, Tambito	1400–2250	LMCF	12–18	5300	8–15	Andept	Letts *et al.* (this volume)
Colombia, Serrania de Macuira	650			855	7–9	Inceptisol, granite	Cavelier (1988)
Costa Rica, Volcan Barva	1500	LMCF	17	4015	25–30	Humitropept	Grieve *et al.* (1990)
Costa Rica, Volcan Barva	2000	LMCF	14	4015	20–25	Tropofibrist	Heaney & Proctor (1990)
Costa Rica, Volcan Barva	2000	LMCF	14	4015	20–25	Tropofibrist, Vitrandept	Lieberman *et al.* (1996)
Costa Rica, Volcan Barva	2600	LMCF	11	4015	20–23	Vitrandept	Marrs *et al.* (1988)
Costa Rica, Monteverde	1550	LMCF	17	2000	12–25	Typic Dystrandept	Vance & Nadkarni (1990)
Ecuador, Loja and Zamora	1900–2450	LMRF LMCF UMCF	15–16.2	2100–3840	7.19–20	Humic Eutrudepts, Typic Dystropepts, Oxyaquic Eutrudepts, Humic Dystrudepts	Wilcke *et al.* (2001) Wilcke *et al.* (2003) Wilcke *et al.* (this volume)
Hawai'i, Mauna Loa	1130–1660	UMCF	13.1–15.5	2620–4320	5.3–11.6	Lithic Tropofolist, Histosol	Raich *et al.* (1997)
Hawai'i, Mauna Loa	1220–1675	UMCF	12–15.5	2700–4450			Vitousek *et al.* (1988)
Indonesia, Rakata Island	680–730	UMCF	~23	3000	5–15	Andeptic Troporthent	Newsome (1986) Shinagawa *et al.* (1986) Schlesinger *et al.* (1998)
Indonesia, Seram, Gunung Kobipoto	1000	LMRF	~22	2100		Typic Humitropept	Payton (1993)
Indonesia, Seram, Gunung Kobipoto Gunung Binaiya	1470–2820	UMCF LMRF	~9–19	2100	10–27	Lithic Tropofolist, Humic Kanhapludult, Typic Hapludalf, Histic Humaquept	Edwards *et al.* (1993)
Indonesia, Kalimantan Bukit Raya	1700–2100	LMCF UMCF	~14–16	4000		Aquept	Van Reuler (1987)
Jamaica, Blue Mountains	1550	UMCF LMCF		2900	5–18	Dystric Cambisol, Folic Histosol	Tanner (1977) Hafkenscheid (2000)

Malaysia, Sarawak, Gunung Mulu	1310	LMCF	~22	4750		Histosol	Tie *et al.* (1979)
Malaysia, Sarawak Gunung Mulu	1310–1860	LMCF UMCF	19–22	4750		Gleysol, Histosol	Martin (1977)
Malaysia, Sabah, Kinabalu	1800	LMCF	16–17	2300	25	Humic, podzol	Kitayama (1992)
Malaysia, Sabah, Kinabalu	2000–3400	LMCF UMCF SACF	9–17	2300	6–30	Histosol, Humaquic Dystropept, Humic podzol	Frahm (1990)
Malaysia, Sabah, Kinabalu	2170–3080	UMCF SACF	10.4–15.9	2376–2887	10–20	Histosol, Humus podzol, Dystropept	Kitayama *et al.* (1998) Kitayama & Aiba (2002)
Malaysia, Sabah Gunung Silam	790	LMCF	~24	2500	10–15	Dystropept, Humitropept	Proctor *et al.* (1988) Bruijnzeel *et al.* (1993)
Mexico, Oaxaca, Sierra Juarez	1500–2380	LMCF UMCF	11–15	2550		Folic Cambisol, Folic Stagnic Podzol, Folic Stagnosol	Alvarez *et al.* (2008)
Mexico, Oaxaca, El Rincon	1850	LMCF	20–22	1720	18	Typic Dystrudept	Bautista-Cruz & Castillo (2005)
Mexico, Veracruz, Xalapa	1250–1840	LMCF	14–18	1517–2200		Cambisol	Williams-Linera (2002)
Puerto Rico, Luquillo	750–1050	UMCF	18–20	4500–5000	3–5		Silver *et al.* (1999) Olander *et al.* (1998) Cox *et al.* (2002)
Tanzania, Mt. Kilamanjaro	2265	LMCF UMCF	7–14	900–2700	10>30	Lithic Endoaquand, Pachic Haplustand, Acrudoxic Fulvudand, Acrudoxic Melanud, and Histic Placaquand	Schrumpf (2004) Hemp (this volume #12)
Venezuela, Parque Nacional Henri Pittier	1140–1580	LMCF UMCF	16–19	1650–1975	13–35	Tropohumult, Typic Dystropept, Typic Tropohumult	Zinck (1986)
Venezuela, Santa Ana, Copey, Zumbaor	730–3100		9–23	1630–4460	7–9	Inceptisol	Cavelier (1988)
Venezuela, Isla Margarita Cerro Copey	500–700	LMCF	>22	1000	15–22		Sugden (1986)
Venezuelan Andes La Mucuy, Monte Zerpa La Carbonera San Eusebio	2420–2670	UMCF	11–14	1500	24–30	Aquic Humitropept	Grimm *et al.* (1981) Schwarzkopf (2003) Steinhardt (1979)

[a] LMCF, UMCF, SACF are lower montane, upper montane, and sub-alpine cloud forests, respectively.

Table 6.2 *Summary of site, tree stem, and soil characteristics for transects in the Luquillo elfin cloud forest, Puerto Rico*

Measurement		Average	Min	Max
Site characteristics	Elevation (m)	873	657	963
(per transect, except slope per sub-plot)	Slope (degrees)	24	9	40
	Aspect (degrees)	135	75	190
	Exposure (1–5 scale)	3	1	5
Tree stem characteristics	Height (m)	6.4	2.3	11.5
(per sub-plot)	DBH (cm)	13.4	2.6	40.8
	Epiphytes (1–5 scale)[a]	3.3	1.7	4.7
	Bromeliad count (# per tree)	2.5	0	16.7
	Aerial roots (1–5 scale)[a]	1.1	1	2
Soil characteristics	Depth (cm)	24.9	1.5	30.0
(per sub-plot)	% Rocks	11	0	60
	% Soil/litter	44	10	80
	% Roots	46	10	80
	pH (log scale)	4.59[b]	3.80	5.34
	Bulk density (g cc^{-1})	1.07	0.60	1.52
	SOM (%)	28.84	17.25	38.85
	% C	13.30	3.87	26.80
	% N	0.59	0.18	0.98
	Ca (meq 100 g^{-1})	0.99	0.25	6.79
	K (meq 100 g^{-1})	1.89	1.07	3.42
	Mg (meq 100 g^{-1})	0.78	<0.01	1.64

[a] Epiphyte and aerial root scale explained in text.
[b] For pH, median is given in place of average.

surfaces without any visible surface organic layer. Weaver *et al.* (1986), Scatena (1995), and Silver *et al.* (1999) provide further details of the study area and forest.

The sampling design involved measuring and comparing soils and tree structure in sub-plots within transects that spanned the range of elfin forest heights, exposures, and slopes. Ten transects were measured on two peaks (El Yunque and Pico del Este) that are covered by elfin cloud forests, underlain by similar hornfels, and 5 km apart (Table 6.2). Transects were located in undisturbed, mature forest, and were chosen to represent a range of canopy heights within the same overall forest type. At each transect, 3–5 sub-plots of 1 m^2 area were established at 5-m intervals along the contour. The underlying assumption of this design was that disturbance history, tree species effects, and bedrock geology remained relatively constant across sites. Published climatic, ecological, and geological information for the Luquillo Mountains support these assumptions (Sieders 1971; Wang *et al.*, 2002). A statistical comparison of the soil cation contents on the two mountain peaks indicated that extractable magnesium was the only variable to show a significant difference, thereby confirming the similarity in soil forming processes operating at the two peaks.

For each sub-plot, the height and diameter at 1.3 m (diameter at breast height, DBH) were measured on the three largest stems within 1 m from the center. Abundance of epiphytes and surface (e.g. aerial) roots growing from the stem were estimated on each of the three stems using a 1–5 percentage scale (1 = 0–20%, 2 = 20–40%, etc.). Bromeliads larger than fist size on each stem were also counted and recorded.

Three 30-cm deep, 2.54-cm diameter soil cores were collected in each 1-m^2 sub-plot to estimate bulk density, after which they were combined for chemical analysis. Thus, the analyses reported here reflect the combined organic and mineral soil layers down to 30 cm. The percentage of rocks, soil/litter, and roots at the ground surface were quantified by randomly sampling 10 times in each sub-plot. Soils were dried at 65 °C and ground. Soil pH was measured in a mixture of 8 g of dry, ground unsieved soil and 15 ml of distilled water. Soils were then passed through a 2-mm sieve, and analyzed at the University of Pennsylvania using previously reported methods (Johnson *et al.*, 1991). Briefly, SOM was determined as percent dry soil mass lost upon ashing in a 500 °C furnace. Soil carbon and nitrogen were measured in a Carlo-Erba elemental analyzer, and exchangeable cations were extracted in NH_4Cl and measured in a Perkin Elmer ICP-AES.

Statistical analysis of the Luquillo data was carried out on a sub-plot basis using a type of multivariate, multi-step, analysis described by Myers (1990). Analysis of variance (ANOVA) and

Tukey tests were used to determine differences between slope gradient (≤20°, 20–30°, and ≥30°) and stem height. Principal component analysis was used to reduce the tree structural measurements of average stem height, maximum stem height, and average DBH into one overall dimension called "tree size." Principal component analysis was also used to reduce these same characteristics, plus epiphyte coverage, bromeliad count, and aerial root coverage into one overall dimension called "tree characteristics." Forward stepwise regression (0.250 probability to enter, 0.100 probability to leave) was then used to assess the degree to which soil and site characteristics contributed towards tree size and tree characteristics. A similar forward stepwise regression was also carried out for average stem height, and for maximum stem height. These four responses (tree size, tree characteristics, average stem height, and maximum stem height) were first analyzed using all possible soil and site characteristics, and subsequently using soil characteristics only.

RESULTS

Trends in global TMCF soils data

Soil orders reported for the collated TMCF data included Inceptisols, Histosols, Ultisols, and Mollisols (Table 6.1). However, only seven of the 33 studies explicitly reported a standard classification for their soil and most studies did not distinguish between organic surface and mineral soil horizons and merely indicated the depth of sampling (typically ranging between 10 and 35 cm; Table 6.1). Although subsequent analysis allowed many of the soils to be accurately classified (Bruijnzeel and Proctor, 1995), the lack of standardized methods does limit quantitative comparisons between sites.

Published levels of TMCF soil pH varied in the range 2.2–7.5, with an overall mean of 4.16 (Figure 6.1a). Soil carbon ranged from 1.1% to 49.6%, with a mean value of 16.2% (Figure 6.1b). This suggests that most studies combined organic and mineral horizons in their analysis. Soil nitrogen (total N) ranged from 0.2% to 3.6% (Figure 6.1b). In contrast, the range of soil nitrogen levels reported for nine different lowland sites in Costa Rica, Malaysia, and Puerto Rico was only 0.2–0.4% (see Silver (1994) for references). TMCF sites also had a higher mean soil nitrogen concentration than the lowland sites: 0.99% vs. 0.3%. Extractable soil phosphorus ranged from 0.2 to over 100 $\mu g\ g^{-1}$ in TMCF (Figure 6.1c), compared to 4.0–26.0 $\mu g\ g^{-1}$ in lowland forests (Silver, 1994). The mean extractable phosphorus concentration in TMCF soils was twice that of lowland forest soils (27.4 vs. 10.3 $\mu g\ g^{-1}$), suggesting that phosphorus is not limiting ecosystem productivity in TMCF. Extractable calcium in TMCF soils ranged from <0.1 to 22.1 meq $100\,g^{-1}$ (Figure 6.1d), compared to 0–12.4 meq $100\ g^{-1}$ in lowland forest soils (Silver, 1994). However, the TMCF data-set had a lower mean calcium concentration: 2.6 vs. 4.9 meq $100\,g^{-1}$.

Separating and comparing the TMCF soils into geologically "young" and "old" groups or "volcanic" and "non-volcanic" groups did not reveal statistical differences in total carbon, nutrient content, or pH. However, the comparisons were severely limited by small sample sizes and differing methodologies and cannot be considered definitive. Nevertheless, several pedons suggested that limestone bedrock can influence soil calcium while ultramafic bedrock may influence soil magnesium. Some altitudinal studies also demonstrated the influence bedrock can have on the genesis of TMCF soils (e.g. Alvarez Arteaga *et al.*, 2008).

When comparing all TMCF sites, higher-elevation sites were cooler and there was an expected negative relationship between elevation and temperature. Nevertheless, statistically strong relationships between mean annual rainfall, canopy height, and most soil properties were elusive. Canopy height did have weak but significant negative correlations ($p < 0.01$) with elevation and temperature for both UMCF and LMCF when the sub-sets of mineral soils were compared. Systematic differences were also apparent between the mineral soils of LMCF and UMCF (Figure 6.2). In general, canopy height and pH were higher for LMCF, whereas total nitrogen, SOM, and C/N ratios were higher in UMCF. Furthermore, UMCF tend to have more subsurface carbon, possibly lower nitrogen, and higher N/P and C/P ratios. As is typical of most soils, the global data-set of TMCF soils and the sub-sets of mineral soils from UMCF and LMCF showed strong and significant ($p < 0.0001$) positive correlations between carbon and total nitrogen concentrations, and between extractable phosphorus and total nitrogen. Significant ($p < 0.01$) but only moderate to weak correlations were found between other soil characteristics, regardless whether they were combined or grouped into LMCF or UMCF types. It should also be noted that these correlations are presented for comparative purposes as no causal or mechanistic relationships can be inferred from the correlations alone.

Luquillo field study

The 45 sub-plots in the Luquillo Experimental Forest, Puerto Rico contained a range of site, tree, and soil characteristics (Table 6.2). As expected, surface soils were acidic (median pH 4.59) and rich in SOM (average 28.8%) and carbon (average 13.3%). Compared to the global data-set (Figure 6.1), the standard deviations of the Luquillo elfin cloud forest soils were lower for pH (by 0.33 log units), carbon (by 3.95%), total nitrogen (by 0.16%), exchangeable Ca (by 1.15 meq $100\ g^{-1}$), and exchangeable Mg (by 0.35 meq $100\ g^{-1}$). The mean values for all these parameters at Luquillo were within one standard deviation of the respective global means, with the exception of exchangeable potassium which was higher in the Luquillo Mountains.

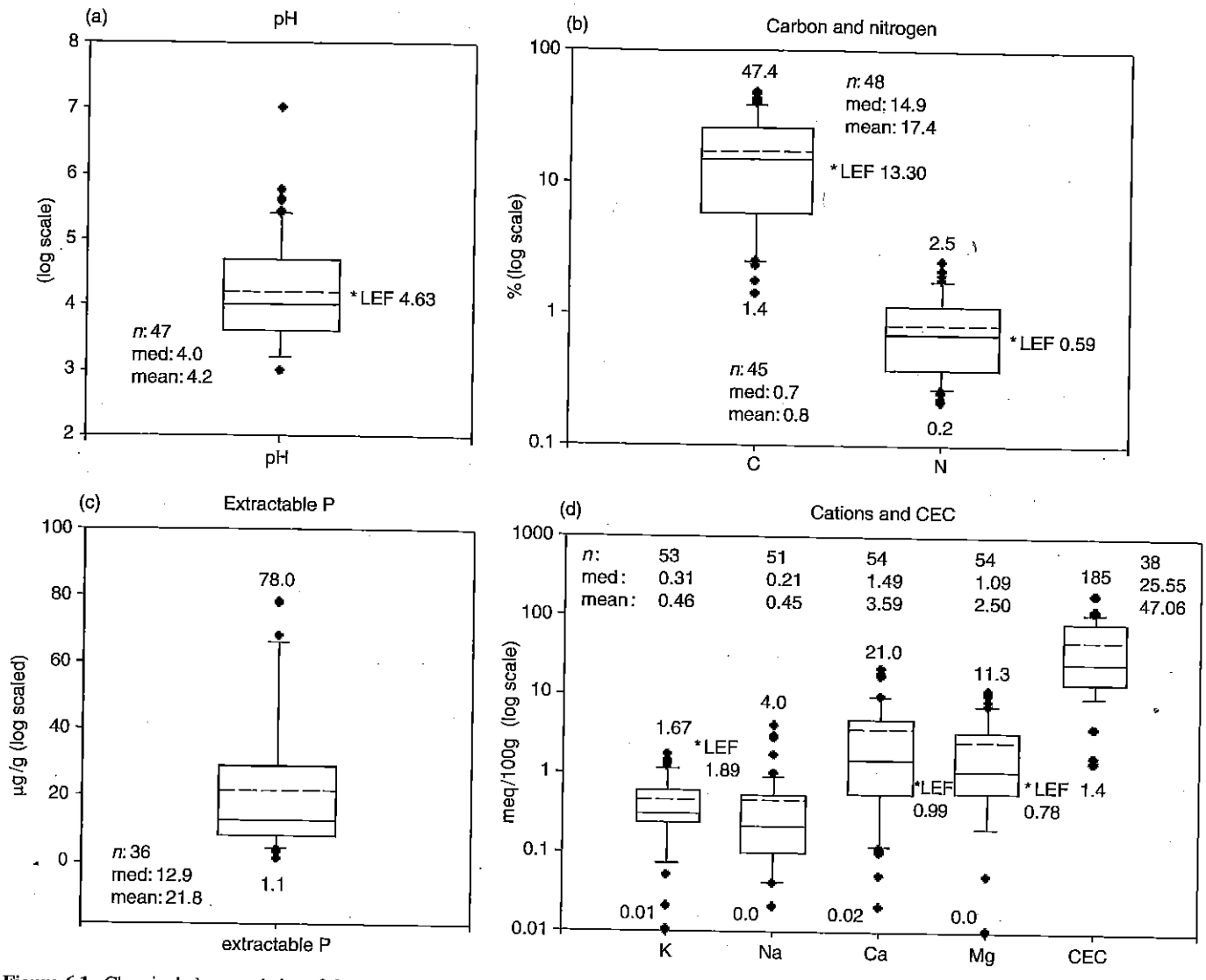

Figure 6.1. Chemical characteristics of the TMCF soils listed in Table 6.1 plus average values for the upper montane cloud forest soils of the Luquillo Experimental Forest (LEF) in Puerto Rico: (a) $pH_{(H_2O)}$, (b) carbon and total nitrogen (%), (c) extractable phosphorus (µg g^{-1}), and (d) exchangeable cations and cation exchange capacity (meq 100 g^{-1}). Box plots show median, 25th and 75th percentiles, outliers, and means (dashed lines). Values for the Luquillo soils are marked with an asterisk.

SOIL CORRELATIONS WITHIN LUQUILLO

As was observed for the global data-set, Luquillo cloud forest soils had significant ($p < 0.0001$) and strong correlations between concentrations of total carbon and nitrogen ($r^2 = 0.89$), and between SOM and carbon ($r^2 = 0.73$) or nitrogen ($r^2 = 0.88$). Again, significant ($p < 0.02$) but weak correlations were also found between exchangeable magnesium and potassium ($r^2 = 0.25$), between potassium and calcium ($r^2 = 0.15$), and between magnesium and calcium ($r^2 = 0.13$). In contrast to the global data-set, significant ($p < 0.01$) but moderate to weak correlations were found at Luquillo between exchangeable potassium and soil carbon ($r^2 = 0.15$), total nitrogen ($r^2 = 0.30$), and SOM ($r^2 = 0.44$). Soil pH correlated with carbon ($r^2 = 0.16$) and exchangeable calcium ($r^2 = 0.21$). The weaker correlations found using the global data-set may well reflect the wider range in soil types covered, as well as inconsistencies in sampling and laboratory analysis between studies.

RELATIONSHIPS BETWEEN TREE HEIGHT, SLOPE GRADIENT, AND SOM

In general, the shortest trees occurred on the steepest slopes (Figure 6.3a), and in areas with lower SOM ($r^2 = 0.15, p = 0.0090$) and soil carbon ($r^2 = 0.14$, $p = 0.0111$). The relationship between slope gradient and tree height became more pronounced when slope steepness was divided into three classes: ≤20°, 20–30°, and ≥30° (Figure 6.3b). Using these classes in an ANOVA, slope class was

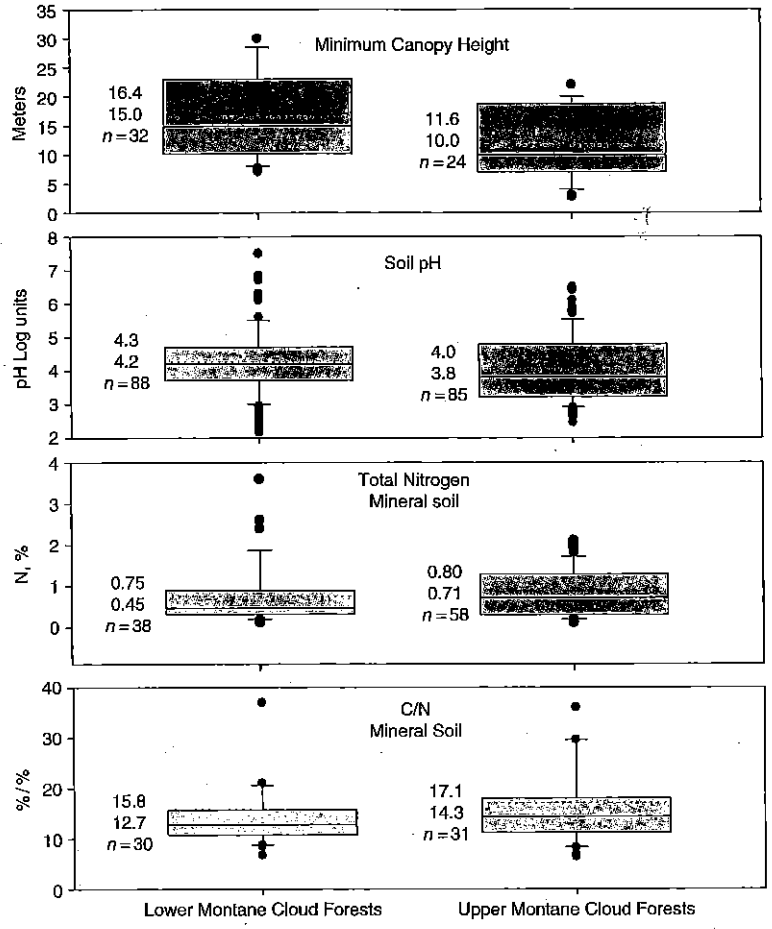

Figure 6.2. Forest canopy height (minimum reported) and soil characteristics by forest type for sites listed in Table 6.1 Comparisons for total nitrogen and C/N are only between mineral soils of comparable depths that are below the organic surface horizons.

significant in explaining average stem height ($p = 0.0284$). Tukey's test also indicated that trees on slopes $\leq 20°$ were significantly taller than those on slopes $\geq 30°$. Similar relationships existed between slope class and maximum tree height. Slope steepness did not appear as a major influencing factor in the multivariate analysis (Figure 6.4). This is apparently because of its cross correlation with other factors like soil depth, SOM content, and aspect.

STEPWISE REGRESSION ANALYSIS

Stepwise regression analysis (Table 6.3) indicated that between 56% and 68% of the variation in stem height within the Luquillo elfin forests could be accounted for by combinations of site exposure, surface root cover, soil carbon, exchangeable potassium and magnesium, and to a lesser extent, slope and total soil nitrogen. Average stem height, maximum stem height, and average DBH contributed approximately equally in the composite principal component variable called tree size (Figure 6.4). The abundance of epiphytes, bromeliads, and aerial roots contributed less to the variable tree characteristics and presumably rather reflect the age and disturbance history of the stand. Considering soil factors alone, only carbon, total nitrogen, and exchangeable potassium contributed and together explained 25% of the variation in tree size. These same variables explained 27% of the variation in tree characteristics, 38% of average stem height, and 54% of maximum stem height.

Stepwise regression analysis was also carried out using soil nutrient contents (e.g. kg ha^{-1}) as opposed to concentrations (e.g. mg g^{-1}). Because of the consistency in bulk density between sites, the resulting regressions and comparisons were similar regardless whether concentrations or contents were used. However, the resulting r^2-values tended to be slightly higher when the analysis was based on contents. Stepwise regressions were also conducted with and without the inclusion of ground cover as a variable, because ground-covering roots may be considered part of tree structure. In these cases, the r^2-values of the regressions were slightly greater when ground-covering roots were included but the general relationships and conclusions remained the same.

Table 6.3 *Results of forward stepwise regressions for all soil and site characteristics determined in 10 transects in the elfin cloud forest zone of the Luquillo Mountains, Puerto Rico, carried out with four different responses: (a) a composite variable for tree size, (b) a composite variable for tree characteristics, (c) average stem height, and (d) maximum stem height. Cell values are coefficients (top) and* p *values (between parentheses)*

Response	Slope (degrees)	Exposure (1–5 scale)	Ground cover of roots (%)	C (%)	N (%)	K (meq $100\,g^{-1}$)	Mg (meq $100\,g^{-1}$)	r^2
(a) Tree size	.	−0.7085	2.8824	0.1531	.	1.1702	1.3542	0.56
		(0.0051)	(0.0168)	(0.0059)		(0.0081)	(0.0559)	
(b) Tree characteristics	.	−0.7342	2.5964	0.1557	.	1.2074	1.4135	0.56
		(0.0040)	(0.0313)	(0.0055)		(0.0068)	(0.0480)	
(c) Avg. stem height (m)	−0.0297	−0.6586	3.1852	0.1681	.	1.0453	1.7055	0.63
	(0.3842)	(0.0310)	(0.0114)	(0.0034)		(0.0265)	(0.0182)	
(d) Max. stem height (m)	.	−0.5941	2.7053	0.3594	−7.1510	2.5093	.	0.68
		(0.0113)	(0.0164)	(0.0337)	(0.1271)	(0.0000)		

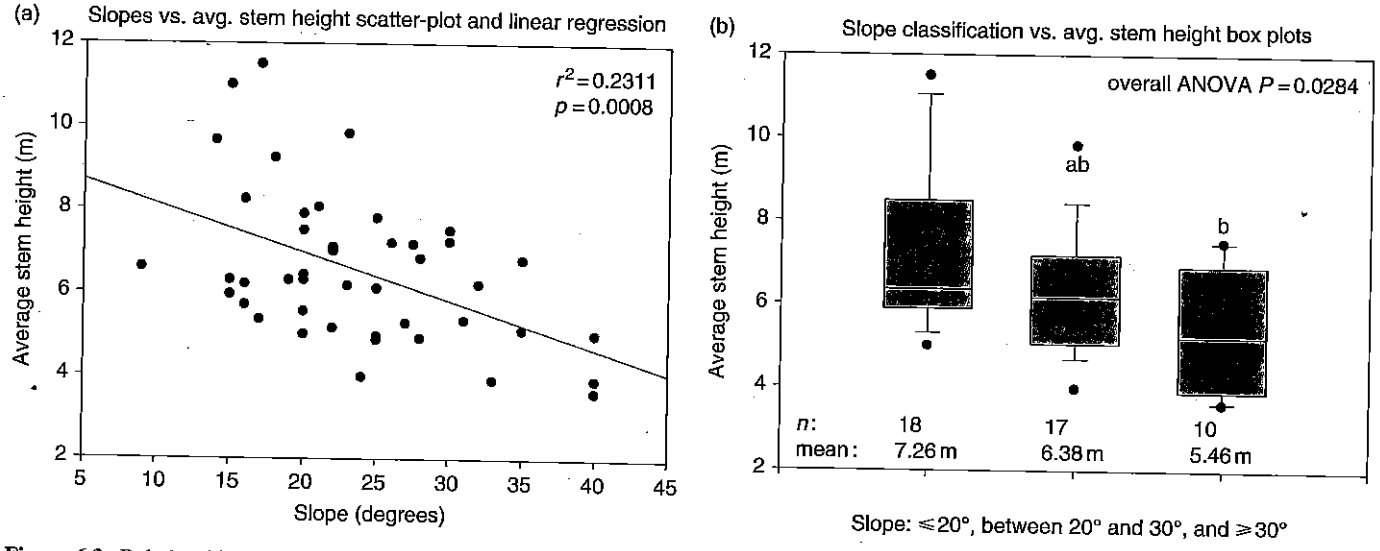

Figure 6.3. Relationships between slope gradient and average stem height in the Luquillo elfin cloud forests, Puerto Rico. (a) Box plots showing stem height distributions for each of three slope gradient classes; Tukey test levels not sharing the same letter are significantly different; (b) scatter-plot and linear regression between slope gradient and average stem height.

DISCUSSION AND CONCLUSIONS

How valid are the common generalizations about TMCF soils made earlier? The available data summarized above confirm that TMCF soils are generally more acidic and have more organic matter than the soils of lowland tropical forests. They may also show more inter-site variation. On average, they also have more total nitrogen and higher levels of extractable phosphorus and they are relatively rich in exchangeable cations. The available data also indicate that not all TMCF grow on peaty soils or soils that are inherently toxic or limiting to forest productivity. Comparisons across all sites also confirmed the results of site-specific studies on UMCF in Luquillo (this study) and LMCF in Ecuador (Wilcke *et al.*, 2002) that the organic layer in TMCF sites is highly variable but better developed in UMCF. Furthermore, the global data also suggest that if there are nutrient limitations to these forests, they are related to the plants' abilities to access the soil resource, rather than to the absolute size of the nutrient pools. However, the paucity of sound comparable soil data severely limits global-scale conclusions and supports the conclusions of earlier reviews that greater consistency in sampling, analysis and reporting is needed (Bruijnzeel and Proctor, 1995; Sollins, 1998). Including standardized soil classifications, making implicit distinctions between organic and mineral horizons, and adding information on geological substrate and local site conditions should be a standard element of future studies.

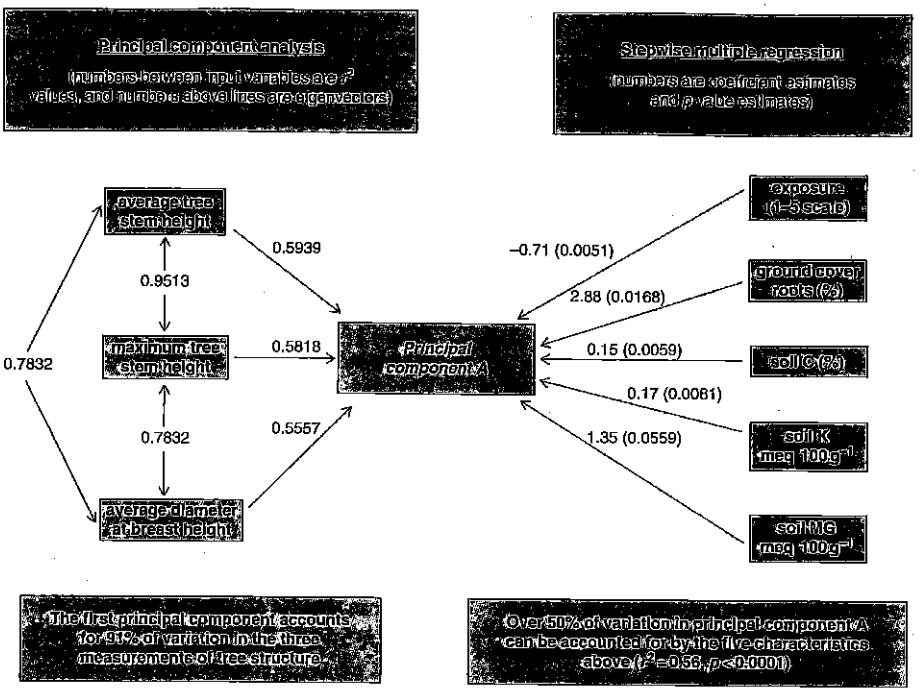

Figure 6.4. Principal component analysis and stepwise regression illustrating the links between tree size in elfin cloud forest in the Luquillo Mountains of Puerto Rico to environmental conditions. See also Table 6.3.

Nevertheless, the available data do indicate that there are distinct differences between UMCF and LMCF, both within and between sites. In general, UMCF have a higher frequency of waterlogging, better developed organic horizons, lower pH, and higher SOM, total nitrogen, total phosporus, and base cations than LMCF soils.

Within the UMCF of the Luquillo Mountains, amounts of soil nitrogen, carbon, and exchangeable potassium were able to account for 25–54% of the variation in stand height. As much as 68% of the variation in tree height could be accounted for when exposure, slope, and ground-cover roots were also included. The importance of these local site factors in explaining forest structure appears to be related to interactions between exposure, slope steepness, and the gradual accumulation of SOM and soil nutrients as stands age. Chronosequence studies of areas cleared during construction also indicate that UMCF in the Luquillo Mountains will not re-establish until the soils have regained sufficient SOM and exchangeable nutrients (Olander *et al.*, 1998). The latter study and the present correlation analysis of the Luquillo soil data-set both indicate that once TMCF are established, their soils accumulate SOM and become increasingly acidic and nutrient-rich over time. Both the correlation analysis, and the observations that steeper areas had more fallen and gnarled trees, suggest that the accumulation of SOM and the development of tree height is limited on steeper and more exposed slopes. Wind- and exposure-centered explanations of elfin cloud forest structure (Lawton, 1982) have received less attention in recent years. However, the importance of local exposure and site conditions demonstrated for the Luquillo Mountains suggests that these deserve greater consideration, at least in non-equatorial settings where wind speeds are often greater (cf. Jarvis and Mulligan, this volume).

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