

SHORT COMMUNICATION

## Root mat depths and surface soil chemistry in Southeastern Venezuela

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Tropical forest litter layers impregnated with roots have usually been described as 'root mats'. Most attention has been focused on the very thick root mats found beneath forests on atypical soils, such as giant podzols, but less dramatic root mats can be found beneath forests on more typical oxisols and ultisols, especially in the Neotropics (Klinge 1973, M. Kellman, *pers. obs.*).

A variety of hypotheses have been proposed to account for root mat development. The extreme infertility of many of the soils beneath thick root mats, and the effectiveness of nutrient retention exhibited by these mats (Stark & Jordan 1978), has led some to interpret them as the products of natural selection for nutrient retentiveness (Jordan 1982, Jordan & Herrera 1981). More mechanistically, St. John (1983) has shown that root proliferation is stimulated by dead organic matter. Other experiments by Cuevas & Medina (1988) in Amazonian root mats have shown that root proliferation is stimulated by the presence of Ca and Mg and, on infertile soils, decomposing organic matter may provide access to greater quantities of these nutrients than are available in underlying mineral substrates (Stark & Spratt 1977). Alternative hypotheses view root mats as a response to mineral soil environments that are inhospitable to roots, with seasonal waterlogging and high exchangeable Al concentrations being most often cited as potentially inhibitory (Stark & Spratt 1977, St. John 1983).

Here we use data from one region where forests exhibit varied root mat depths and occur on a variety of soils, to examine whether significant correlations exist between these depths and chemical properties of the surface soil. Because the data come from well-drained sites in a small geographic region, the effects of waterlogging can be excluded, and the effects of climate and

composition of the regional flora on root mat development can be assumed constant.

Data were gathered as part of a survey of site selection by the shifting cultivators of two settlements (locations) in the Gran Sabana area of Southeastern Venezuela: Kavanayen (5°35'N, 61°47'W), located in an area regarded by local cultivators as having soils of 'average' fertility for the region, and Monte Bello (5°2'N, 61°10'W), an area regarded as possessing soils of high fertility. The area is part of the Guiana Shield, and lies at elevations between 850 and 1300 m a.s.l. Bedrock of the region is primarily sandstones and quartzites that weather to sandy soil of extreme infertility (Dezzeo 1994). However, most agriculture is concentrated on more fertile oxisols that have developed from diabase intrusions; this biasing our samples towards the more fertile soils of the region. The region receives between 2000 and 2600 mm of rainfall per year with a distinct dry season between December and February.

Root mat depths were measured to the nearest cm, and the underlying 0–7 cm of mineral soil sampled, at five evenly-spaced points along a 12 m transect in forest adjacent to 80 swiddens. Transects were located at least 5 m farther into the forest than any signs of fire intrusion from the swidden. Soil samples were bulked for each site, and the mean root mat depth for the site was calculated. To exclude potential successional effects, only samples from mature forests, showing no signs of earlier shifting cultivation, and with canopy heights >15 m were used in the analysis. This reduced the sample size to 65.

Soil samples were analysed for pH (1 : 2 soil : water ratio), exchangeable Ca, Mg, K, Al, Mn and Fe, and readily-available P. Because of the probable dominance of the soils' exchange complex by variable-charge clays, BaCl<sub>2</sub> was used as the extracting solution (Hendershot *et al.* 1993), and the ion concentrations were determined by atomic absorption spectrophotometry. Effective CEC (ECEC) was estimated by summing molar concentrations of all cations extracted (Hendershot *et al.* 1993). Readily-available P was determined by the anion-exchange resin method (Saggar *et al.* 1990, Tiessen & Moir 1993), using a 16-h exposure period, with desorbed P analysed by an autoanalyser. Concentrations of cations are expressed as cmol<sup>+</sup> kg<sup>-1</sup> of oven-dry soil and those of P as µg g<sup>-1</sup> of oven-dry soil. Correlations between root mat depth and soil nutrients, Al and pH were analysed by regression analysis using SYSTAT (Wilkinson 1990), after log-transformation to improve normality, and reduction of the variable set to minimize colinearity.

Root mat depths varied from 0.2–10.6 cm (Table 1), with an overall mean depth of 2.8 cm; this is considerably thinner than root mat thicknesses reported on some soils in Amazonia (e.g. 15–40 cm, Jordan & Herrera 1981), and those depths observed elsewhere in the study area on quartzitic sands. The soil chemical analyses showed a wide variation in soil properties and confirmed a large difference in the fertility of soils at the two sites (Table 1). At Kavanayen, soils were uniformly acid, low in readily-available P and nutrients, and of low

Table 1. Root mat depths and surface soil chemical properties at the 65 sites sampled in two locations in Venezuela.

	Kavanayen (n = 41)		Monte Bello (n = 24)	
	mean $\pm$ SD	Range	mean	Range
Root mat depth (cm)	3.65 $\pm$ 2.31	0.36–10.60	1.28 $\pm$ 1.67	0.20–8.20
pH	4.19 $\pm$ 0.33	3.58–5.14	5.06 $\pm$ 0.78	3.82–6.41
ECEC (cmol <sup>+</sup> kg <sup>-1</sup> )	1.69 $\pm$ 0.59	0.89–3.22	11.91 $\pm$ 15.69	1.38–80.28
Extractable cations (cmol <sup>+</sup> kg <sup>-1</sup> )				
Ca	0.70 $\pm$ 0.06	0.01–0.30	8.68 $\pm$ 12.09	0.30–59.50
Mg	0.09 $\pm$ 0.05	0.02–0.21	2.11 $\pm$ 3.46	0.11–17.93
K	0.16 $\pm$ 0.08	0.06–0.53	0.34 $\pm$ 0.25	0.10–1.38
Al	1.36 $\pm$ 0.54	0.57–3.03	0.51 $\pm$ 0.70	Tr–2.21
Resin-extractable P ( $\mu$ g g <sup>-1</sup> )	2.98 $\pm$ 2.23	0.27–10.08	23.23 $\pm$ 26.73	4.23–128.42

ECEC, with this dominated by Al. At Monte Bello, soils were generally much more fertile and of lower Al concentration, but soil properties were much more variable than those at Kavanayen and partially overlapped with these (Table 1).

Soil nutrients, Al and pH in the pooled data set exhibited strong colinearities (Table 2). All nutrients were strongly correlated with each other and with pH, while all, except K, were negatively correlated with Al. To avoid interpretational problems caused by these multiple colinearities, only a single variable from the nutrients and pH data set was used in the regression analysis; K was chosen because of its lack of correlation with Al (Table 2).

Table 2. Correlation matrix for root mat depth (RtMat) and soil chemical properties. Coefficients significant at  $P \leq 0.01$  shown in bold. All variables log-transformed.

Al	—					
Ca	<b>-0.686</b>	—				
Mg	<b>-0.602</b>	<b>0.965</b>	—			
K	-0.126	<b>0.642</b>	<b>0.745</b>	—		
P	<b>-0.450</b>	<b>0.801</b>	<b>0.767</b>	<b>0.635</b>	—	
pH	<b>-0.863</b>	<b>0.774</b>	<b>0.728</b>	<b>0.342</b>	<b>0.471</b>	—
RtMat	<b>0.408</b>	<b>-0.315</b>	-0.254	-0.191	-0.294	<b>-0.376</b>
	Al	Ca	Mg	K	P	pH

Table 3. Results of step-wise, multiple regression analysis of root mat depth on Al and K.

(a) Multiple-r values:				
LogAl, 0.408; LogAl + LogK, 0.431				
(b) Final regression model:				
	Coefficient	SE	t	P
Constant	0.848	0.193	4.392	<0.001
LogAl	0.647	0.191	3.379	0.001
LogK	-0.709	0.580	-1.223	0.226

Analysis of variance of regression:  $F_{2,62} = 7.09$  ( $P = 0.002$ )

The resulting multiple regression analysis using Al and K as independent variables, selected Al as a significant correlate of root mat depth, but excluded K (Table 3). Separate substitution of Ca, Mg, P and pH for K in the equation resulted in a lower multiple-r value than that provided by Al+K in every instance, and the correlation between root mat depth and the ratio  $(Ca+Mg+K)/Al$  was not significant ( $r = -0.21$ ). The results thus identify Al as the only significant correlate of root mat depths in this area, although the small proportion of variance explained (17%), indicates an effect that is relatively weak.

Root mats are heterogeneous phenomena, and it is therefore not surprising that relationships between some aggregate measure of these, such as depth, and environmental conditions, should yield relatively low correlations. Mats are comprised of two distinct components whose response to environmental conditions may be partially independent of each other: (a) a litter layer derived from above-ground plant tissues, and (b) living and dead root tissues.

At least two processes of root mat development seem possible: (i) Mat development is driven by accumulations of organic matter on the soil surface, which in turn stimulate upward root proliferation into the layer. If litter that is less readily decomposed is produced by forests growing on infertile soils (e.g. Edwards 1977), more mat development would be expected there. (ii) Mat formation represents primarily a preferential location of roots in a superficial layer due to toxic conditions in the mineral soil, or to low nutrient concentrations there relative to those present in the decomposing litter above. Whether root development into a litter layer decreases its rate of decomposition and therefore promotes further mat deepening is unknown. Cuevas & Medina (1988) report increased decomposition rates when litter was in contact with fine roots, but impregnation with roots often produces a fibrous and well-drained litter layer that may reduce moisture content and decomposition rates.

Our results indicate that some elements of process (ii) are operating, driven by Al toxicity in the mineral soil. However, they provide no evidence that low soil fertility status is a significant contributor to the process. If these results apply to the larger domain of tropical forests generally, it would seem unwise to interpret root mats as primarily an adaptation for nutrient conservation, although effective conservation may be a beneficial effect of their development.

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