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Mineral nutrition, soil factors and growth rates of *Gmelina arborea* plantations in the humid lowlands of northern Costa Rica

M. Stuhmann^{a,*}, C. Bergmann^b, W. Zech^a

^aInstitute of Soil Science and Soil Geography, University of Bayreuth, 95440 Bayreuth, Germany

^bCentre for Agricultural Landscape and Landuse Research (ZALF), e.V.-Institute of Forestecology, 16225 Eberswalde, Germany

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Abstract

The purpose of this study was to determine the factors which are responsible for clearly visible growth irregularities in *Gmelina arborea* stands by relating growth rates to soil and site properties. All *Gmelina* plantations under study, established on degraded pasture soils in the Atlantic lowlands of Costa Rica, showed the same growth pattern: very poor growth and chlorotic foliage of trees in mid-slope positions, and fast growth and healthy leaves of trees on hilltops and hillbases. The variation in site and soil properties and tree growth rates was analysed, investigating 24 plots in eight different plantations. Leaf samples were taken from 120 trees (five trees per site). Foliar analysis revealed that the tree growth is highly dependent on the supply of N, P, K and S, indicating that poorly growing trees suffer from a multiple nutrient disorder. To identify the most restricting soil factor, simple correlations between growth rates and soil chemical and physical properties were applied to the entire data set. The best correlation was obtained with exchangeable soil K ($r=0.78$, $P<0.001$). Subdivision of the data set into plots on brown soils (eight) and plots on red soils (16) and subsequent correlation analysis resulted in much stronger relationships. Growth depressions in mid-slope positions had other causes on brown soils than on red soils. On the acid brown soils the combination of the variables Al saturation and bulk density could explain 82% of the variation of tree growth. Al saturation of up to 80% in brown soils inhibits nutrient uptake, particularly of N and P. The red soils dominate on Ca–Mg-enriched, alluvial terraces and were among the first soils to be cultivated in the region. During the agricultural use and at the establishment of the tree plantations, they received dolomitic lime to reduce Al toxicity. Here, very low K/Mg ratios (less than 0.03) may induce K deficiency. Therefore, the best multiple regression model for tree growth rates on red soils is obtained with K/Mg ratio and thickness of the humic A-layer ($r^2=0.75$, $P<0.001$). Inclusion of the variable bulk density resulted in a clear improvement of the model, explaining 91% of the growth variability.

Keywords: *Gmelina arborea*; Foliar analysis; Tropical soil; Reforestation; K–Mg antagonism

1. Introduction

In Costa Rica, the urgent demand for timber

production leads to an increasing effort to reforest pasture land in the northern tropical lowlands. More exotic than native species (e.g. *Cordia alliodora*; see Bergmann et al., 1994) can be observed in the already established plantations. Apart from *Eucalyptus deglupta*, *Tectona grandis* and *Acacia mangium*, *Gmelina arborea* is a

* Corresponding author at: Bayreuth Institute of Terrestrial Ecosystem Research (BITÖK), Dr.-Hans-Frisch-Str. 1–3, 95440 Bayreuth, Germany. Tel.: (0921) 55-5762. Fax: (0921) 55-5799.

commonly used species because of its rapid growth and easy establishment (Lamb, 1968). Although it is generally assumed that *Gmelina* needs a distinct dry season for best development (Lamb, 1968; Boulet-Gercourt, 1977), this species reaches very high growth rates (up to 65 cm height growth per month) in the perhumid study area. In the plantations under study, patterns of growth irregularities can be observed: in slope positions *Gmelina* always shows stunted growth and often chlorotic foliage, whereas on hilltops and hillbases its development is much better. This work aims at characterizing the nutritional status of *Gmelina* and at relating growth of this species to soil and other site factors of the plantations, to determine the main factors which influence the productivity of a site and which are responsible for the observed growth irregularities.

2. Materials and methods

2.1. Study area

All plantations included in this study are located in the Atlantic lowlands of Costa Rica at elevations below 300 m above sea-level, generally at about 100 m above sea-level. The landscape is undulating to terraced, partly with steep slopes (maximum 36°). Before reafforestation the land was used for cattle grazing, sometimes for over 20 years.

Soil parent materials are fine to coarse lahars of basaltic-andesitic composition and basaltic and andesitic lava flows of Plio-Pleistocene age. In some parts, Tertiary volcano trunks occur. The climatic conditions are perhumid with an annual rainfall of 2200–4500 mm, a relative dry season (more than 200 mm per month) between January and May, and mean annual temperatures above 25°C.

Soils show influences of volcanic ashes and strong tropical weathering. Texture is clayey but structure generally is well aggregated and, hence, physical conditions are favourable. Exceptions are eroded soils in slope positions, poor in organic matter, that are heavily compacted. Soil colour is strong red or brown, and soil reaction is acidic to strong acidic. Red soils are generally classified as Nitisols, brown soils as Cambisols (Food and Agriculture Organization (FAO), 1988; see Stuhmann, 1992).

2.2. Site selection and sampling

Within the study area, eight plantations of *Gmelina arborea*, all about 3 years old, were chosen. In all of these plantations, fast-growing trees are restricted to hilltops, lower slope positions, and well-aerated depressions, whereas poorly growing trees are typical for mid-slope positions. Twenty-four homogeneous plots (about 20 m×20 m) with excellent, medium, or poor growth were identified and characterized by evaluating soil, relief, and stand parameters. Site descriptions comprise records of altitude above sea-level, exposure, slope inclination, ground vegetation, damage caused by cattle grazing and erosion, kind and duration of former land use. For soil descriptions and sampling, soil pits (2 m×1 m, 1.5 m depth) were dug. Samples were taken from each horizon for chemical analyses. Undisturbed 100 ml cores (five per horizon) were sampled at soil depths of 0–5 cm, 50–55 cm, and 100–105 cm for soil physical characterization. The site of the pit was chosen carefully allowing the harvest of at least five (co-)dominant trees in the direct vicinity of the pit for foliar analyses. Foliar sampling took place in April and May 1991, at the end of the relative dry season. Only the first mature and sun-exposed leaves of the uppermost part of the tree crown were taken and analysed per tree. Of these trees, which did not reveal any symptoms of pests or damage by animals, top height and diameter in breast height (dbh) were measured.

2.3. Laboratory methods

Leaf samples were oven-dried at 65°C and ground to pass a 0.2 mm sieve. Total N was determined gas chromatographically after combustion (Carlo Erba ANA 1500 (Milan, Italy)). For total concentrations of the elements P, K, S, Ca, Mg, Al, Fe, Mn, Zn, Cu, and B, milled samples were digested with concentrated HNO₃ and measured by inductively coupled plasma atomic emission spectrometry (ICP-AES).

Soil samples were air-dried and passed through a 2 mm sieve. For total N and C, an aliquot was ground to dust and analysed gas chromatographically after combustion (Carlo Erba ANA 1500); pH was determined in distilled water and 1 N KCl (soil–solution 1:2.5; FAO, 1988). Phosphorus was determined as ‘available phosphorus’ with the Bray 1 method and as ‘total phosphorus’ (without the occluded fraction) with the method of Saunders and Williams (described by Olsen and Sommers (1982)). Both fractions were measured photometrically with a Molybdenum Blue type reaction. The effective cation exchange capacity (CEC) was calculated as the sum of exchangeable bases (Ca, Mg, K, Na) plus Mn, Al and protons exchangeable with 0.5 N NH₄Cl (Trüby and Aldinger, 1986).

Hydraulic conductivity was measured with a constant water table above the surface of undisturbed, water-saturated soil cores. For the water retention curves, water content of undisturbed soil cores was determined at 0.4, 6, 10, 30, 60, 200, 600 and 1500 kPa tension. Bulk density (dB) was calculated by weighing undisturbed core samples after drying at 105°C. Soil texture was determined in the field. For statistical analyses the SAS statistical package (Statistical Analysis Systems Institute, Inc., 1990) was used.

3. Results and discussion

3.1. Leaf analysis: nutritional status

Little is known about the mineral contents of *Gmelina arborea* leaves. The few studies which exist (Evans, 1979; Chijioke, 1980; Zech and

Weinstabel, 1983; Zech, 1984; Drechsel and Zech, 1991; Zech and Drechsel, 1992; Zech et al., 1991) were compared with the data of this study to classify our values. A brief summary of the data obtained from our leaf analyses is given in Table 1.

Ranges of foliar nutrient levels (Table 1) of our study are similar to ranges of previous studies carried out in Africa (Drechsel and Zech, 1991). In comparison with *E. deglupta* and *P. caribaea* (see Stuhmann, 1992) foliar N, P, and K levels of *Gmelina* are higher, but still much lower than of the native plantation tree *Cordia alliodora* (Bergmann et al., 1994). As mentioned above, trees varied by appearance, from well-growing ones with dark green foliage on hill-tops and hillbases, to stunted, chlorotic trees on mid-slopes. Foliar analyses revealed clear differences between dark green and chlorotic leaf samples. According to Table 2, hilltop trees have significantly higher N, P, S, and K concentrations ($P < 0.001$) and significantly lower Ca, Mg, and Mn concentrations ($P < 0.01$) than slope trees. Furthermore, chlorotic slope trees have much lower K/Mg ratios in their leaves ($P < 0.001$).

3.2. Relations between foliar nutrient levels and tree height increments

Plotting height growth rates vs. foliar element concentrations allowed us to identify critical levels for some elements (Table 2). In this study, critical levels are defined as those foliar nutrient levels which seem to be necessary to guarantee good tree growth (growth rates of more than 30 cm per month). In Table 2, foliar N, P, K, and S concentrations of slope trees are all below the critical level, and Mn contents are above the ‘toxic’ level (Table 2, Figs. 1(a) and 1(b)).

To quantify the dependence of tree growth on nutrient supply as reflected by foliar nutrient concentrations, simple correlation analysis was conducted (Table 3). For all macronutrients, high Pearson correlation coefficients were found, indicating that tree growth depressions are not caused by a mono-elemental deficiency but by the insufficient supply of several macronutrients. As the highest positive correlation coefficient is

Table 1

Ranges and mean values of foliar nutrient levels of 3-year-old *Gmelina* (n=24) in Costa Rica at the end of the relative dry season (perhumid climate)

	N	P	S	K	Ca	Mg	Mn	Fe	Al	Cu	K/Mg
	(%)						(mg kg ⁻¹)				
Minimum	1.1	0.07	0.08	0.2	0.4	0.3	72	40	50	4	0.2
Maximum	3.7	0.22	0.22	1.5	4.0	1.2	768	300	270	14	4.5
Mean	2.5	0.15	0.15	0.8	1.7	0.6	185	115	95	7	2.0

Table 2

Differences in foliar nutrient contents between healthy trees on hilltops and stunted trees on slopes; for some elements critical levels could be deduced

	N	P	S	K	Ca	Mg	Mn	Fe	Al	Cu	K/Mg
	(%)						(mg kg ⁻¹)				
Hilltops	3.2a ¹	0.19a	0.19a	1.0a	1.3c	0.3a	145a	152	107	9.1c	3.2a
Slopes	1.8b ¹	0.13b	0.12b	0.4b	2.3d	0.9b	312b	122	132	5.8d	0.7b
Critical level	<2.5	<0.15	<0.13	<0.8			>200				<2

¹ Different letters indicate significant differences — a, b: *P* < 0.001; c, d: *P* < 0.01; e, f: *P* < 0.1.

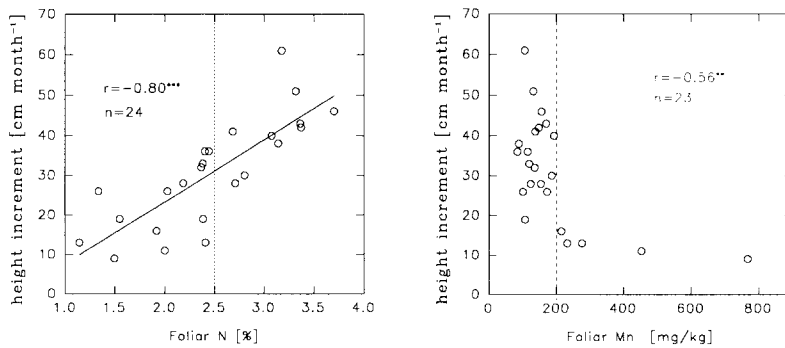


Fig. 1. Correlation between foliar nutrient levels and monthly tree height increments (cm per month): (a) foliar N (%); (b) Mn (mg kg⁻¹).

Table 3

Pearson correlation coefficients between tree height increments and foliar nutrient concentrations (n=24)

	K/Mg	N	S	K	P	Mn	Mg
Correlation coefficient	0.81***	0.80***	0.72***	0.70***	0.64***	-0.56*	-0.77***

* *P* < 0.05. *** *P* < 0.001.

found for foliar K/Mg ratio, this may indicate not only short K supply (K poverty of the soils) but also an inhibition of K uptake caused by an

antagonism of K and Mg in the soil. Young *Gmelina* trees seem to have an extremely high K demand, as Chijioke (1980) showed for 5–6-year-

old stands in Nigeria. As all macronutrients are intercorrelated, even N and K ($r=0.87$, $P<0.001$), it is probably one common factor, e.g. the amount and quality of the soil organic matter, which determines the supply of several nutrients. In kaolinitic soils with very low CEC values, the K supply for plants may essentially depend on the amounts of K adsorbed on the organic substance. Possibly, the main factor is not the organic matter but a general inhibition of nutrient uptake caused by 'toxic' elements such as Al or Mn, or it is an inhibition caused by unfavourable physical soil properties such as, for instance, soil compaction by cattle trampling (see Fig. 2).

3.3. Soil analysis: general characterization

According to our field observations, 16 of the 24 studied plots revealed deeply weathered red soils (Nitisols) on old dissected terraces of fluvi-basaltic origin, and eight plots had brown soils (Cambisols) derived from Pleistocene lava flows or Tertiary volcanic remnants. Table 4 summarizes some important soil properties as well as mean total soil reserves of C, N, P, and exchangeable cations calculated to 1 m soil depth; results are given separately for red and brown soils.

The comparison of the two soil units illustrates that the brown soils have significantly lower bulk densities, are more strongly acidic, and contain less exchangeable Ca and Mg, and more exchangeable Al. These differences, apart from variations in parent material, may be due to the management practice, which farmers told us to be commonly applied, of putting dolomitic limestone on the red old soils to improve their low fertility for tree plantation establishment. Furthermore, the red soils on dissected terraces are topographically better suited for cultivation, and had been used for agriculture before the pasture use and the reforestation, whereas the steep areas of the brown soils had been used only for cattle grazing for a few years, and had never received any lime.

All soils have generally high reserves of total C and N but very low amounts of P and particularly of exchangeable K. Similar data have been documented for the Atlantic soils of Costa Rica by Martini and Macias (1974). The relatively high amounts of organic matter and total N seem to be due to the high annual precipitation of 2200–4500 mm in the Atlantic lowlands, and very low K and P contents are characteristic for these soils. Also, low bulk densities are typical for soils of the study area, developed in volcanic material (Wielemaker and Lansu, 1991).

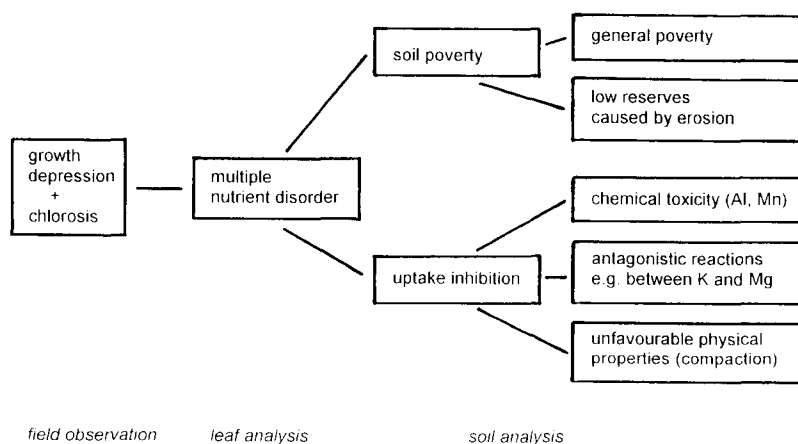


Fig. 2. Possible relationships between growth depressions, nutrient deficiencies or disorders and soil properties.

Table 4

Mean total reserves of C, N, P, exchangeable cations, effective CEC, bulk density (0–5 cm) and pH (30–60 cm) of the red ($n=16$) and brown soils ($n=8$)

	C	N	P _{Bray}	K	Ca	Mg	Al	CEC _{eff}	dB_0	pH _{H₂O}	K/Mg
	(t ha ⁻¹ m ⁻¹)		(kg ha ⁻¹ Ah ⁻¹)	(kmolc ha ⁻¹ m ⁻¹)					(g cm ⁻³)		
Red soils	126	12	0.32	9	349a ¹	149a	81a	609c	0.99a	5.9a	0.07a
Brown soils	119	11	0.25	9	55b ¹	29b	214b	326d	0.83b	4.8b	0.4b

¹ Different letters indicate significant differences; a, b: $P < 0.001$; c, d: $P < 0.005$; kmolc, kilo mole ionic equivalent (change).

3.4. Relations between soil factors and tree height increments

In a first step to quantify the degree of relationship between soil variables and tree growth rates, a correlation matrix was created using data from all 24 soil pits. All of the independent soil variables selected were individually plotted and correlated with monthly tree height increments, but this did not result in strong relationships. The best correlation was obtained with the soil parameter 'exchangeable K' with a correlation coefficient of 0.78 ($P < 0.001$).

Subdivision of the data set according to the two soil units and subsequent calculation of regression analysis for each soil unit separately resulted in much stronger relationships between soil parameters and monthly tree height increments. These results will be presented in the following sections and will be discussed according to Fig. 2.

3.5. Low nutrient reserves caused by erosion

In tropical soils, most of the nutrients are stored in the organic substance, which is easily lost by erosional activity. Among the studied red soils, a highly significant, negative correlation between inclination and the thickness of the humic A-layer ($r = -0.73$, $P < 0.001$) indicates that severe erosion has already taken place. In Table 5, it can be seen that in the red soils almost all soil nutrient reserves depend significantly upon the thickness of the humic A-layer. For the brown soils this relationship is only obvious for exchangeable K reserves; no other nutrients are

significantly related to the Ah-thickness, indicating more nutrient reserves in deeper horizons of these soils. As plant uptake of nutrients depends on the availability of soil nutrient reserves, the thickness of the humic A-layer should also play an important role in plant nutrition. For the red soils this is shown in Table 6.

Only on the red soils, foliar element levels are, additionally, correlated well with soil element reserves, as foliar P with P_{Bray} ($r = 0.78$, $P < 0.01$) or even foliar K/Mg ratios with soil K/Mg ratios ($r = 0.68$, $P < 0.05$). However, foliar N is not correlated with total N reserves in the soil. This may be due to the presence of heterocyclic N compounds in which N is bound tightly and unavailable to the plants. The very low K/Mg ratios in the red soils, of sometimes less than 0.03, prove the supposition of a K–Mg imbalance in the soil, probably made worse by the above-mentioned liming practice. Carvajal (1978) also described the problem of a K/Mg antagonism for crop plants in Costa Rica, and defined K/Mg ratios below 0.26 as critical for plant K supply. The foliar nutrient levels of *Gmelina* growing on brown soils are not correlated with the soil nutrient reserves, indicating that on these sites not poverty in soil nutrients but other processes such as uptake inhibition may be a possible factor in the observed nutrient disorder.

3.6. Chemical toxicities

As mentioned above (Table 4), the two soil units differ in pH and Al amounts, or rather in the Al saturation of the cation exchange complex. By plotting tree height increments vs. Al

Table 5

Correlation coefficients indicating the dependence of the soil nutrient reserves upon the thickness of the humic A-layer (K and Ca in exchangeable amounts)

	$K_{(0-30\text{ cm})}$	P_{Bray}	$N_{(0-30\text{ cm})}$	$Ca_{(0-30\text{ cm})}$	CEC_{eff}	% Al-saturation
Red soils ($n=16$)	0.87***	0.71**	0.65**	0.60*	0.57*	-0.61*
Brown soils ($n=8$)	0.78*	n.s.	n.s.	n.s.	n.s.	n.s.

* $P < 0.05$. ** $P < 0.01$. *** $P < 0.001$. n.s., not significant.

Table 6

Correlation coefficients indicating the dependence of the foliar nutrient contents upon the thickness of the humic A-layer

	N	S	K/Mg	K	Cu
Red soils ($n=16$)	0.71**	0.71**	0.67**	0.62*	0.59*
Brown soils ($n=8$)	n.s.	n.s.	n.s.	n.s.	n.s.

* $P < 0.05$. ** $P < 0.01$. n.s., not significant.

saturation the two soil units can be clearly separated (Fig. 3). Fig. 3 shows that the two soil units can be distinguished not only by their Al saturation but also by different growth responses of *Gmelina* in respect to concentrations of exchangeable Al in each soil unit. Al specification was not carried out, but brown soils may have more non-toxic complexed Al. Even Al saturations up to 50% do not influence tree growth on

brown soils negatively. According to Table 7, the negative correlation coefficients for the brown soils demonstrate the negative influence of high Al saturation on plant nutrient uptake, mainly on P and N uptake ($r = -0.79$, $P < 0.05$, and $r = -0.78$, $P < 0.05$, respectively). High amounts of exchangeable Al in the soil restrict root development and especially P uptake (Von Uexkull, 1986). In the less acid red soils with lower amounts of Al, a negative influence of this element on foliar nutrient levels is not detectable (Table 7).

3.7. Soil physical properties

To evaluate the impact of cattle trampling on soil physical properties, we determined bulk density, hydraulic conductivity rates, and water retention curves. These variables were correlated with the duration of land use as pasture before the establishment of the plantations. The results indicate that after about 10 years of grazing (Fig. 4) bulk densities of the surface soil layer increase to values of higher than 0.9 g cm^{-3} . As the maximum values do not exceed 1.2 g cm^{-3} , it is not easy to understand that soils are really compacted but the parent material of these soils is of volcanic origin and its bulk density values are originally much lower (less than 0.8 g cm^{-3}).

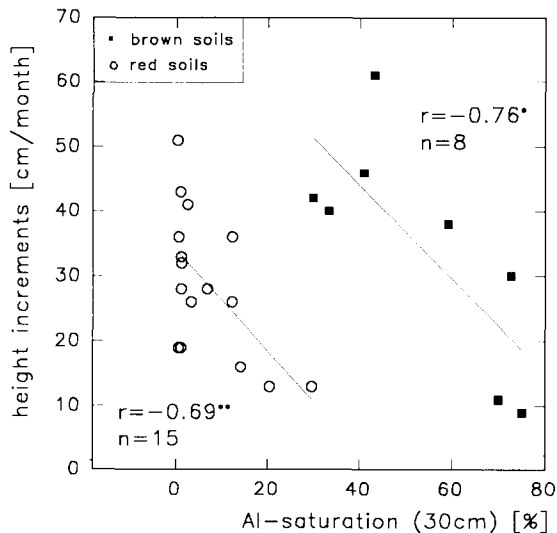
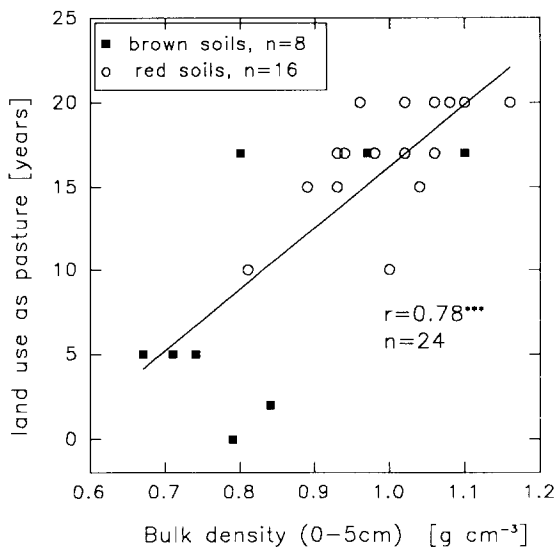


Fig. 3. Correlation between Al saturation in 0–30 cm depth (%) and monthly tree height increments (cm per month).

Table 7

Correlation coefficients between the foliar nutrient contents and the Al saturation of the topsoil

	P	N	S	Cu	K	Mn
Red soils ($n=16$)	n.s.	n.s.	n.s.	n.s.	n.s.	0.75***
Brown soils ($n=8$)	-0.79*	-0.78*	-0.70*	-0.64	-0.59	0.62

* $P < 0.05$. *** $P < 0.001$. n.s., not significant.Fig. 4. Correlation between the duration of land use as pasture (number of years) and bulk density in 0–5 cm depth (g cm^{-3}).

Similar data were obtained, e.g. by Wielemaker and Lansu (1991).

Pore volume and pore distribution of the brown soils are influenced negatively by the duration of cattle trampling (Table 8). This is a further demonstration of the relative compaction. Many years of cattle grazing lead to less

plant-available water, more fine pores, and higher bulk densities in the soil, which may have a negative influence on root development and root oxygen supply.

Because only the duration, but not the intensity, of grazing could be determined from information given by farmers, we attempted to take bulk density as a measure of cattle trampling (see Bergmann et al., 1994). Correlation of bulk density with soil pore data gave significant relationships for the brown soils (Table 9). This dependence indicates that the soil structure of the brown soils is much more sensitive and vulnerable to compaction by cattle trampling than the (already degraded) insensitive structure of the red soils.

3.8. Multiple regression analyses

Growth depressions appearing on both soil units in mid-slopes position do not have the same causes. Linear correlation between monthly tree height increments and soil properties clearly illustrates these differences (Table 10).

To determine the joint influence of more than one factor on growth irregularities of *Gmelina*, multiple regression analyses were applied for each soil unit. The use of more than one variable in one model could greatly improve the ex-

Table 8

Correlation coefficients indicating the dependence of soil physical properties upon the grazing period

	pv	fp (%)	mp (%)	paw	dB_0
Red soils ($n=16$)	n.s.	0.51*	n.s.	n.s.	0.62*
Brown soils ($n=8$)	-0.54	0.71*	-0.65	-0.68	0.67

pv, pore volume; fp, fine pores; mp, medium pores; paw, plant available water; dB_0 , bulk density 0–5 cm.

* $P < 0.05$. n.s., not significant.

Table 9
Correlation coefficients indicating the dependence of the soil physical properties upon soil bulk density

	pv	fp (%)	mp (%)	paw
Red soils (n=16)	n.s.	n.s.	n.s.	n.s.
Brown soils (n=8)	-0.85**	0.69*	-0.88**	-0.90**

** P<0.01. n.s., not significant.

Table 10
Correlation coefficients showing the dependence of monthly tree height increments upon soil chemical and physical properties (K and Mg exchangeable in the 0–30 cm layer)

	Ah	K	N	% Al saturation	K/Mg	P _{Bray}	P _{tot}	pH _{H₂O}	dB ₀
Red soils	0.86***	0.79***	0.77***	-0.61*	0.51*	0.61*	n.s.	n.s.	-0.63
Brown soils	n.s.	n.s.	n.s.	-0.76*	(0.5)	n.s.	0.56	0.61	(-0.5)

* P<0.05. ***P<0.001. n.s., not significant.

plained variance. For the red soils, the following two-variables model was found:

$$\text{INCR} = 14 + 0.6 \times \text{A layer thickness} + 25 \times \text{K/Mg ratio (30 cm)};$$

$$r^2 = 0.75 \quad (P < 0.001); \quad n = 16$$

where INCR is monthly tree height increment of *Gmelina*. When bulk density (dB₀) is included in this model to try a three-variables model, 91% of the growth variation can be explained (Fig. 5(a)):

$$\text{INCR} = 80 + 0.6 \times \text{Ah} + 40 \times \text{K/Mg ratio} - 60 \times \text{dB}_0; \quad r^2 = 0.91 \quad (P < 0.001); \quad n = 16$$

Tree growth on red soils depends mainly on the thickness of the humic A layer, which is partly eroded on sloping sites. Multiple regression demonstrates that the imbalanced K/Mg ratio in the soil has an important influence on tree growth by inducing K deficiency. This ratio, which is lowest in slope profiles, is not intercorrelated with the humic A horizon because it is mainly affected by the liming with dolomitic limestone. Bulk density as an indicator for the negative influence of cattle trampling completes the regression model.

For the brown soils, a completely different regression model was calculated (Fig. 5(b)):

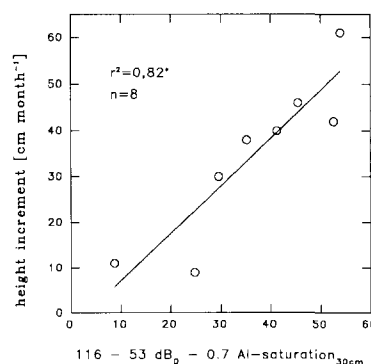
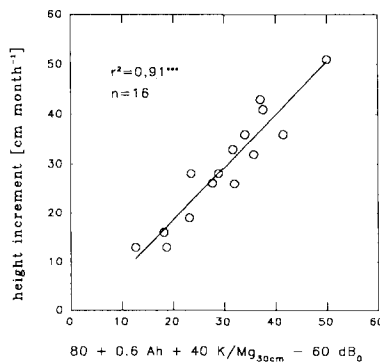


Fig. 5. Multiple regression analysis after subdivision of the entire data set into two soil units: (a) red soils; (b) brown soils.

$$\text{INCR} = 116 - 53 \times \text{bulk density} - 0.7 \\ \times \text{Al saturation (30 cm);}$$

$$r^2 = 0.82 \quad (P < 0.05); \quad n = 8$$

On the brown soils, other factors than macronutrient reserves are responsible for stunted growth of *Gmelina*. Aluminium saturation in the soil, reaching at mid-slope almost 80%, restricts nutrient uptake (as shown in Table 7 and Fig. 3) and limits growth. Another important factor is bulk density, which is highly correlated with the soil structure and soil pore system (Table 9).

4. Conclusion

Within the studied plots, *Gmelina* trees, growing on red or brown soils, showed similar growth irregularities. However, leaf and soil data revealed that growth depressions in mid-slope positions had other causes on red soils than on brown soils. The red soils received more dolomitic lime, which reduced Al toxicity but increased or induced K deficiency. In slope positions, much of the soil organic material, the reservoir for most of the plant nutrients, is lost by erosion. The soil variables thickness of the humic A layer and K/Mg ratio could explain 75% of the growth variability of *Gmelina* on red soils. The inclusion of bulk density resulted in a model in which 91% of tree growth variability could be accounted for. On brown soils the variables Al saturation and the compaction parameter bulk density together explained 82% of tree growth irregularities.

For further reafforestations on degraded soils in Costa Rica the following advice can be given. To avoid K/Mg and K/Ca imbalances in these K-poor soils, each lime application should be coupled with a K fertilization. K/Mg and K/Ca ratios should be checked regularly by soil analyses. On steep slopes, *Gmelina* is not the right tree species. Its rooting system is shallow and its N and K demand is too high for these sites. *Pinus caribaea* var. *hondurensis* has deeper roots, a lower N demand, and a higher Al tolerance (W. Zech, unpublished data, 1991), but there is no

need to plant this exotic tree species on slopes. In Costa Rica, there is a vast diversity of native tree species, and many of them probably cope better with steep slope conditions than exotic plantation trees. In the 'La Selva' biological station in Puerto Viejo, Sarapiquí, just next to the study area, species screening trails have shown that native trees such as *Vochysia hondurensis* and *Stryphnodendron excelsum* can surpass growth rates of exotic top species such as *Eucalyptus deglupta* and *Pinus caribaea* (Espinoza and Butterfield, 1989). *Vochysia ferruginea*, which is also in Panama one of the fastest-growing native trees (Condit et al., 1993), shows good growth on slopes in spite of very high foliar Al concentrations of 1–2% (W. Zech, unpublished data, 1991). This tree species seems to be very Al tolerant and suited for slopes of the brown soil unit. On extremely N-poor sites (slopes and some plateaux of the red soil unit) N-fixing species such as the fast-growing native species *Dalbergia tucurensis*, *Stryphnodendron excelsum*, or *Pentaclethra macroloba* (Butterfield, 1990) should be planted, or at least interplanted. In future, reafforestation management on degraded pasture soils should select tree species with more care, considering the variability of soil properties. Not monocultures of exotic trees, but mixed stands of different tree species according to microsites, will help to achieve sustainable forestry in the neotropics.

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