Agronomía Costarricense 25(2): 57-64. 2001

EFFECTS OF INCREASING SOIL ACIDITY AND DECREASING NUTRIENT AVAILABILITY ON THE GROWTH OF *Vochysia ferruginea* A SECONDARY RAIN FOREST OF NORTHERN COSTA RICA[1]

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Key words: Acid soils, Costa Rica, Forest soils, *Vochysia ferruginea*, Growth, Succession.

RESUMEN

Efecto del aumento en la acidez del suelo y la disminución en la disponibilidad de nutrimentos sobre el crecimiento de *Vochysia ferruginea* en el bosque húmedo de la región Norte de Costa Rica. En el presente trabajo se compara el crecimiento de la especie *V. ferruginea* en 3 sitios del bosque húmedo secundario de edad avanzada, ubicados en la zona norte de Costa Rica, bajo condiciones crecientes de acidez y de menor disponibilidad de nutrimentos en el suelo. Se instalaron un total de 28 parcelas temporales de muestreo (20x20m), de tal forma que cubrieran toda la variación del sustrato presente en los sitios de estudio. Como parámetros indicadores de la capacidad productiva del sitio se utilizaron la altura esperada de un árbol a los 25 cm de dap (estimada en una investigación previa), el área basal/ha y la altura total. Las comparaciones estadísticas ($P<0.05$) mostraron diferencias significativas en cuanto a la productividad de los sitios. Los sitios con mayor productividad presentaron el menor grado de pendiente, el mayor porcentaje de saturación de Al, los mayores contenidos de Fe y P, así como las menores concentraciones de bases intercambia-

ABSTRACT

We compared the production of 3 tropical secondary forest sites dominated by the species *Vochysia ferruginea* with different soil acidity and nutrient conditions. Twenty-eight sample plots (20x20m) were installed to cover the whole range of substrate variation at the sites. The expected height of a tree of 25 cm dbh (estimated in a previous research), basal area per ha and total height of each plot were used and compared as parameters of site production. The forest showed differences in growth among sites. Sites with gentler slopes, the highest Al saturation, Fe, and P, and the lowest concentration of bases, Cu, Mn, and Zn, and a content of sand between 40 and 50% had the highest yield. *V. ferruginea*, growing under acid soil conditions, was capable to accumulate 18.7 m^2/ha with 475-485 trees/ha >10 cm dbh. The results confirm the adaptation of this species to acid soil conditions and reveal its capacity to be more productive than other species under increasing soil acidity and decreasing nutrient availability.

1/ Recibido para publicación el 28 de marzo del 2001.

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* Cooperative Research Project between the Tropical Agricultural Research and Higher Education Centre (CATIE) and the Agricultural Research Centre (CIA) of the University of Costa Rica (UCR). Post Code 2060, CIA, UCR. San José, Costa Rica.

bles del suelo y de Cu, Mn y Zn. Estos sitios presentaron a su vez los mayores porcentajes de arena en el suelo, oscilando este valor entre 40 y 50. Bajo estas condiciones edáficas, *V. ferruginea* presentó un área basal promedio de 18.7 m^2/ha, correspondiente a 475-485 árboles/ha con un dap >10cm. Los resultados obtenidos no solamente confirman la adaptación de esta especie para crecer bajo condiciones de acidez del suelo, sino que también demuestran la capacidad de la misma en aumentar su rendimiento bajo condiciones crecientes de Al presente en el suelo y decrecientes en términos de la disponibilidad de nutrimientos.

INTRODUCTION

In tropical forests, substrate variation has an important effect on different forest characteristics such as floristic composition, structure, dynamics and production. This effect in old-forest characteristics is well documented (Whitmore 1984, Liebermann et al. 1985, Basnet 1993, Clark et al. 1995, Wesch 1999). However, in wet tropical secondary forests only 2 isolated studies have been carried out. Lacoste (1991, cited by Herrera and Finegan 1997) found that variation in soil drainage conditions, in secondary forests in French Guyana, did not affects the structure and dynamics of 2 canopy species. Herrera and Finegan (1997) found that variation in the composition of a secondary forest in Costa Rica could be related to soil acidity and a slope gradient; sites with high relief and more exchangeable Al were dominated by *Vochysia ferruginea,* while sites in gentler slopes and lower exchangeable Al were dominated by *Cordia alliodora.*

The relation between forest production and substrate variation in tropical secondary forests is scarce. Uhl et al. (1988) showed the effect of the intensity of land use in the production of young secondary forests: sites used for other activities than forest during longer periods of time showed lower production. Morán et al. (1996) found, at a landscape level, a relationship between variation in canopy height of young secondary forests and fertility variation of different soil types. Herrera et al. (1999) found that the variation in the production of *Vochysia ferruginea* in a secondary forest was indirectly linked to soil properties.

Several authors have reported good growth of *Vochysia ferruginea* in acid soils with low nutrient potential (Hartshorn and Poveda 1983, Pérez et al. 1993, Montagnini and Sancho 1994, González and Fisher 1994, Herrera and Finegan 1997, Horn and Montagnini 1999). However, the response of this species to increasing soil acidity and low nutrient conditions, in natural ecosystems, is still unknown. With this paper we sought to contribute to the knowledge of the autoecology of secondary species, specifically the capacity of the species to grow under an increasing soil acidity condition and the importance of substrate variation in the characteristics of tropical secondary forests. At the same time we expected to document the potential of species like *Vochysia ferruginea* for plantation forestry, considering that actually soil requirements of the most native species in Costa Rica are practically unknown (ACEFEN 1992, Chavarría and Valerio 1993).

The main objective of the present work is to compare the production of old secondary forests dominated by 1 tree species under 2 different acidity and low-nutrient soil conditions.

MATERIALS AND METHODS

Study sites and species

The study sites were located 1 at Florencia, San Carlos, Alajuela Province and 2 other at Cureña, La Virgen of Sarapiquí, Heredia Province, Costa Rica. The Florencia site is fully described by Herrera and Finegan (1997) and Herrera et al. (1999). It is located in Holdridge's tropical wet forest life zone (Tosi 1969) at 320 m.a.s.l. Mean annual precipitation is 3300 mm and mean annual temperature 28°C. The 32.5 ha of forest of this site are 28 years old. At this site, predominant soils are Inceptisols (Typic Dystropepts) originated from volcanic mudflows, with slopes between 15 and 60% (Vásquez 1994).

At the Cureña site 2 stands of approximately 4 ha each were selected. They are located in the Holdridge's tropical wet forest life zone (Tosi 1969) at 40 m.a.s.l. Mean annual precipitation is 3600 mm and mean annual temperature 21°C (Instituto Meteorológico Nacional 1998). Forests age varied between 16 and 18 years old since they were abandoned at the time of the study. Both places supported pasture for cattle and horses grazing for a short period of time. Site soils are Ultisols (Humic Hapludults) originated from alluvial deposits (Fernández 1997) in slopes between 4 and 60% (Herold 1994, Vásquez 1991). Table 1 shows a representative soil profile of each study site.

All of the studied stands were dominated by *Vochysia ferruginea* (Mart.) (Vochysiacea) (Table 2), a large, commercial and long lived pioneer species (Finegan 1992, 1996), common in secondary forest of the northern zone of Costa Rica and an occasional canopy tree in old-growth forests (Finegan and Sabogal 1988, Finegan 1992). The species is distributed from Nicaragua to Peru and Brazil (Withmore and Hartshorn 1969). Naturally, it grows between 30 and 900 m.a.s.l., under an annual precipitation range of 2500 and 4000 mm and 20-27°C of mean annual temperature. It is particularly associated with well-drained and less fertile soils of slopes and hilltops (Montagnini and Sancho 1994, Herrera and Finegan 1997, Herrera et al. 1999).

Table 1. Profile of the 2 soil types in the secondary rain forest study sites of northern Costa Rica[1].

	Florencia site Typic Dystropepts				Cureña sites[2] Humic Hapludults			
Horizon	A	Bw	Bt*	Bt**	A	AB	Bw*	Bw**
thickness (cm)	0-12	12-31	31-59	59-169	0-11	11-21	21-48	48-130+
pH	4.7*	4.5	4.5	4.7	3.9**	4.3	4.2	4.4
O.M (%)	6.9	2.16	1.3	0.4	7.9	5.2	3.0	1.8
Bases saturation (%)	17.5	7.2	8.7	7.6	20.6	16.6	10.0	11.2
Al (cmol (+)/L)	0.8	1.5	1.6	1.6	4.1	3.2	3.0	2.1
ECEC (cmol (+)/L)	3.2	3.2	2.7	2.6	5.1	3.8	3.3	2.3
Sand (%)	24.4	19.4	23.4	15.4	2.3	1.9	2.6	2.0
Silt (%)	38.6	62.6	56.6	48.6	15.1	12.8	11.3	11.6
Clay (%)	34.0	18.0	30.0	36.0	82.6	85.3	86.1	86.4

1/ Vázquez 1994 and Herold 1994.
2/ The soil of Cureña site was reclasified using the data reported by Herold (1994) and according to USDA soil taxonomy (Soil Survey Staff 1998).
* H_2O
** $CaCl_2$

Table 2. Abundance of the main tree species in the study sites.

Species	Relative abundance (%)
Florencia site	
Vochysia ferruginea	50.0
Miconia sp.	8.7
Cordia alliodora	8.0
13 additional species	33.3
Cureña site (Stand 1)	
Vochysia ferruginea	60.0
Miconia sp	11.3
Simarouba amara	9.2
20 additional species	19.5
Cureña site (Stand 2)	
Vochysia ferrugina	68.3
Inga sp	11.3
Laetia procera	5.6
10 additional species	14.8

Sampling and laboratory methods

A total of 28 sample plots of 20x20m were established for this study: 12 at the Florencia site and 16 at Cureña sites. The present work was carried out within the framework of Herrera et al. (submitted) work. Therefore, criteria to establish the plots was predetermined as: sampling of the complete gradient of soil conditions present within the site; uniform soil and topography within each 20x20m plot and no evidence of disturbance of the plot. At Florencia, approximately half of the total forest area was subjected to an experimental thinning in 1994, therefore plots were not located within this area. Further limitations to the area to be sampled were imposed by the decision to sample only that part of the forest available for timber production under current Costa Rican forestry law, which exclude all areas of slope >50° or within 20 m of permanent or seasonal water courses (Herrera et al. 1999).

In each 400 m^2 plot, dbh (diameter at breast height) was measured for all individuals ≥10 cm dbh and these were identified by vernacular name. Total height was measured in each plot for individuals ≥10 cm dbh of *V. ferruginea.* Composite soil samples were taken with the help of an auger at 2 depths, 0-12 cm and 12-30 cm in each plot.

Soil analysis was carried out in the laboratory of the Agricultural Research Centre (CIA) at the University of Costa Rica in San José, Costa Rica, using standard laboratory methods (Henríquez et al. 1995), pH was determined in water with a potentiometer. P, K, Fe, Cu, Zn and Mn were extracted with a modified Olsen solution, Ca and Mg by 1 M KCl. P was determined colorimetrically and the rest of elements by atomic absorption spectrophotometry. Exchangeable acidity was determined using 1M KCl as a neutral solution and titrating with 0.01 M NaOH, organic matter by the method of Walkley and Black and soil texture by Bouyoucos' method.

Data analysis

The parameter site form was used to compare the production of the forests. In a previous research, site form was estimated for *V. ferruginea* (see Herrera et al., submitted), showing the advantage that it could be considered as an age-independent indicator of site production (Vanclay and Henry 1988). A complete random design to detect differences in production parameters (i.e. site form, basal area, total height) and soil conditions among the 3 stands was applied.

RESULTS AND DISCUSSION

Production differences between sites

Differences in production between Cureña stands were minimal (Table 3) probably due to the general environmental similarities of the sites. However, important differences between the Cureña sites and the Florencia stand were found. The Cureña stands had higher mean dbh

Table 3. Differences in production of *V. ferruginea* between the study sites.

Stand attribute	Florencia site (n= 12)	Cureña sites	
		Stand 1 (n=11)	Stand 2 (n=5)
N (ha)	158^b	475^a	485^a
Dbh (cm)	26.7^a	21.3^b	21.3^b
Basal area (m²/ha)	9.6^b	18.7^a	18.6^a
Basal area (all species, m²/ha)	13.2^b	25.4^a	24.0^a
Total height (m)	20.3^a	22.9^a	20.9^a
Dominant height (m)	22.3^b	26.3^a	24.0^{ab}
Site form (m)	19.3^b	27.4^a	24.5^a

Different letters horizontally indicate significant differences P<0.05.

and total height; the mean basal area of these stands was 2 times higher than those at Florencia. The differences between sites can be explained in terms of ecological variability and their age (between 16 and 18 years old in the case of Cureña sites, and 28 years old in the case of Florencia stand).

Topographical and soil differences between sites

Significant differences ($P \leq 0.05$) in slope were found between the Cureña and Florencia stands. Average slope at Florencia was 25%, meanwhile Cureña slope was 15%. Slope may have affected the species production to the extent that it is associated with other soil factors; which show a more direct relationship to plant nutrition.

The following soil variables showed differences between Cureña stands: exchangeable Al (12-30 cm), %Al saturation (12-30 cm) and Fe concentration at both depths (Table 4). In spite of the statistical differences in soil Al and Fe in the Cureña stands, differences with respect to Florencia stand were even higher. Because the magnitude of the differences, the Cureña stands will be considered as 1, and will be compared against Florencia stand.

Significant differences ($P \leq 0.05$) in 16 soil variables at 2 depths were found between Florencia and Cureña forests (Table 4). At the Cureña stands the acidity characteristics were higher than those found at the Florencia stand: pH was lower, exchangeable Al was 3 times higher, and % Al saturation was 4 to 6 times higher than Florencia stand (Table 4). Cureña soils showed Ca concentrations 8 to 13 times lower than those at Florencia, K values were 2 times lower, and Mg values were 7 to 15 times lower in the former soils (Table 4).

These results suggest the adaptation of *V. ferruginea* to grow on acid and low-nutrient soil conditions and reveal the capacity of the species to be more productive under increasing soil acidity conditions. The capacity of *V. ferruginea* to grow under these soil conditions has been attributed to its capacity to accumulate Al in their leaves (Pérez et al. 1993). Other studies have shown that Vochysiacea botanical family and some species of *Vochysia* genera have the capacity to accumulate Al in their leaves as an adaptation mechanism to grow in acid soils (Haridasan et al. 1986, Haridasan and Monteiro de Araujo 1988).

It is important to note the low soil bases requirement of *V. ferruginea,* associated to acid soils (Sánchez 1982). This suggests a high use efficiency of nutrients by this species to produce a unit of biomass. None other studies, in natural or planted forests, have reported the capacity of this species to grow under such soil conditions.

The differences in the soil availability of P between sites (Table 4) have little interest, since P values in all cases were below 14 mg/L, for most cultivated crop species growth, those levels

Table 4. Differences in soil conditions between the study sites.

Soil variable	Florencia site (n=12)	Cureña site Stand 1 (n=11)	Cureña site Stand 2 (n=5)
pH	5.1^{a*}	4.5^{b}	4.4^{b}
	5.0^{a**}	4.5^{b}	4.5^{b}
Ca (cmol(+)/L	4.9^{a*}	0.72^{b}	0.28^{b}
	3.5^{a**}	0.27^{b}	0.12^{b}
Mg (cmol(+)/L	2.1^{a}	0.41^{b}	0.30^{b}
	1.5^{a}	0.21^{b}	0.10^{b}
K (cmol(+)/L	0.16^{a}	0.07^{b}	0.06^{b}
	0.10^{a}	0.05^{b}	0.06^{b}
Al (cmol(+)/L	0.78^{c}	2.5^{b}	3.5^{a}
	1.2^{c}	2.7^{b}	3.4^{a}
Al sat. (%)	10.9^{c}	67.5^{a}	84.5^{a}
	21.1^{c}	83.1^{b}	92.3^{a}
ECEC (cmol(+)/L	7.9^{a}	4.1^{b}	3.7^{b}
	6.3^{a}	3.2^{b}	3.6^{b}
P (mg/L)	7.9^{b}	12.7^{a}	13.0^{a}
	9.2^{a}	11.5^{a}	13.8^{a}
Cu (mg/L)	27.8^{a}	7.7^{b}	7.1^{b}
	31.0^{a}	9.6^{b}	9.8^{b}
Fe (mg/L)	288^{c}	2762^{b}	3791^{a}
	272^{c}	3219^{b}	4685^{a}
Mn (mg/L)	66.0^{a}	8.1^{b}	7.3^{b}
	75.0^{a}	6.4^{b}	6.3^{b}
Zn (mg/L)	11.9^{a}	3.1^{b}	2.2^{b}
	10.7^{a}	3.5^{b}	2.7^{b}
O.M. (%)	7.4^{a}	8.2^{a}	9.3^{a}
	5.0^{a}	5.3^{a}	5.7^{a}
Sand (%)	28^{b}	49^{a}	51^{a}
	24^{b}	40^{a}	41^{a}
Silt (%)	17^{a}	14^{a}	12^{a}
	17^{a}	13^{a}	11^{a}
Clay (%)	55^{a}	37^{b}	37^{b}
	59^{a}	48^{b}	49^{b}

Different letters horizontally indicate significant differences $P<0.05$.
* 0-12 cm.
** 12-30 cm.

are considered low(Bertsch 1995). These results are in accordance to those reported by Herrera et al. (1999) who concluded that *V. ferruginea* is a low P demanding species. The fact that P availability correlates with larger amounts of extractable Al might be due to a similar correlation with the organic matter content, and the large dependency of P availability in the organic fraction of the soils.

The microelements Cu, Mn, and Zn were found in higher concentrations at the Florencia soils. The specific roll of these elements on the nutrition of native species (e.g. *V. ferruginea*) has not been studied yet (Pérez 1993). Therefore, more research needs to be conducted to elucidate critical levels of these elements and their effects in forest production.

Soil Fe concentration at Cureña was 11-13 times higher than at Florencia, values probably associated with the acidity conditions found at Cureña. The stands growing in soils with more than 2000 mg/L of Fe were good, suggesting that this species is capable to be more productive under these conditions by also accumulating Fe in their leaves. On this respect, *V. ferruginea* foliar Fe concentrations, in secondary forests, ranged between 52 and 402 ppm (Herrera 1996).

The differences in soil texture between sites also influenced *V. ferruginea* growth. Courser soils at the Cureña were expected to have higher production values. Herrera et al. (submitted), in a research carried out in the Florencia site found a positive correlation between the production of *V. ferruginea* and sand percentage in the soil.

CONCLUSIONS

Secondary forests dominated by *V. ferruginea* had a higher production in sites with gentler slopes, the highest percentage of Al saturation, Fe, and P, the lowest concentration of bases (Ca, K, and Mg), Cu, Mn, Zn, and a content of sand between 40 and 50%. These results strongly suggest the adaptation of this species to soil acidity conditions and reveal the capacity of this species to be more productive under increasing soil acidity and low-nutrient conditions. It is expected that under extremely infertile soil conditions even *V. ferruginea* will reduce its production. Moreover, this is an important fact to consider when environmental degradation to a none recover point is a concern.

The ability of *V. ferruginea* to successfully grow under acid soil conditions allows this species to become dominant in environments such as the northern zone of Costa Rica. For this species the concept of "unproductive" or "infertile" soils needs a further revision, because under such soil conditions, considered as a hostile soil environment for most tropical plants, *V. ferruginea* is capable to produce 18.7 m^2/ha with 475 to 485 trees/ha $\geq$10 cm dbh. To a lesser extent, other tropical tree species follow a similar adaptation pattern (Haridasan and Monteiro de Araujo 1988, Wesch 1999).

Due to the potential of this species for forestry or agroforestry systems, nutrient requirements should be subjected to a specific research, considering that the new knowledge on plant-soil relationships will increase the planning efficiency for forest management. The results of the present study could be consider as a departure point for specific experiments, to determine nutrient requirements of the species in the former production systems, mainly considering the natural adaptation of this species to acid soil conditions, which could be another important alternative to land management in northern Costa Rica.

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