Variation in Foliar Elemental Composition in Mature Wild Trees and Among Families and Provenances of *Vochysia guatemalensis* in Costa Rica

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Abstract

Variation in foliage elemental composition provides insights into the adaptive mechanisms of species to a particular site and provides the bases for selection for greater nutrient use efficiency. Studies of this variation in tropical trees have been limited to a small number of species, mainly pines and eucalypts. This study compared the foliage elemental composition of mature trees of *Vochysia guatemalensis* D. SMITH from 3 sites in Costa Rica. At each site foliar and soil samples were collected individually per tree and analyzed for elemental composition. Differences in foliar P, Mg, Fe, Cu, Zn and Mn were found among sites. No significant nor consistent correlations were found between soil chemical properties and tissue elemental composition. Even though there were large differences in pH and cation exchange capacity among sites, tissue Ca (mean 12.4 g kg^{-1}) and Al (20,100 mg kg^{-1}) content did not vary significantly. In order to assess the variation in foliage composition among provenances and families within provenances, a progeny test planted on an acidic, infertile Inceptisol was studied. For the 6 provenances planted, 3 families and 2 trees per family were randomly selected and individually sampled for foliage and soils. At 4 years of age, significant differences among provenances and families were found for P concentration, varying from 0.42 g kg^{-1} for the Siquirres provenance (Costa Rica) to 0.52 g kg^{-1} for La Ceiba provenance (Honduras). For Ca, Mg, Al, and Zn only differences among families within provenances were detected. Foliar Fe concentration was found to differ significantly only among provenances. Even though no final conclusions about genetic differences in elemental composition among families and provenances of this species can be made due to the small number of provenances and families sampled, these findings indicate that genetic differences in foliage elemental composition occur, suggesting that genetic differences in response to nutrient availability can also be expected.

Key words: Tissue elemental composition, calcium, aluminum, acid soils, progeny test.

FDC: 160.201; 165.5; 232.11; 232.12; 114.441; 176.1 *Vochysia guatemalensis;* (728.6).

Introduction

Variation in nutrient composition of different plant species exits and may be an indication of differences in nutrient absorption mechanisms (EPSTEIN, 1972). At the present time most of the research has been done with agricultural crops (e.g. maize, wheat), and the results indicate that many nutritional characteristics are independently inherited and could be improved through breeding programs (GERLOFF, 1976; LINDGREN *et al.,* 1977; SARIC, 1983; BOWEN, 1987). Several mechanisms have been proposed to explain genotypical differences in nutrient efficiency and uptake, being mainly related to differences in uptake, transport and utilization within the plant (CLARK, 1976; GERLOFF, 1976; LONERAGEN, 1976).

Investigations on genetic variation have been carried out mainly with temperate pines (i.e. Southeastern pines in United States) and several broadleaf species (WOESSNER *et al.,* 1975; GODDARD *et al.,* 1976; GODDARD and HOLLIS, 1984; LI et al., 1991). Differential responses to soil conditions and fertilizer applications have been found in several forest tree species. For example, MERGEN and WORRAL (1965) reported differences in N uptake in seedlings of *Pinus banksiana* L. from different seed sources. Similarly, FORREST and OVINGTON (1971) found genetic variation in dry weight and mineral nutrient content among *Pinus radiata* D. DON. progenies on infertile soils. Tolerance to low P availability has also been reported to be under genetic control in *P. radiata* (BURDON, 1971). GODDARD *et al.* (1976) reported significant differences in response to fertilization for both *Pinus taeda* L. and *Pinus elliotii* ENGELM. grown on low P availability soils. These significant genetic differences among tree species in response to soil conditions and fertilizers suggest that their growth and productivity on nutrient deficient soils could be improved by using better adapted trees or species.

A major way in which forestry practice overcomes soil fertility problems is to change the soil according the species' requirements (e.g. soil pH by liming, nutrient availability by fertilization). However, in tropical zones where nearly 70% of soils are acidic and infertile (SANCHEZ, 1976), such practices cannot easily ameliorate the soil conditions because of the extent of the problems, the cost of improving soils, or both (SANCHEZ and SALINAS, 1981). A more reasonable way, both economically and ecologically, appears to be the use of genotypes showing higher efficiency in taking up and using soil and fertilizer nutrients. This latter approach also allows for the establishment of breeding programs that can develop better genotypes for a given soil condition.

Unfortunately little is known about nutrient uptake or nutrient requirements for tropical hardwoods, and even less is known regarding their genetic differences associated with provenances or families within provenances for a particular species. The objective of this work was to study the variation in foliage elemental composition in naturally occurring, mature trees of *Vochysia guatemalensis* D. SMITH. at 3 sites in Costa Rica and the variation associated with families and provenances of this species planted on an Inceptisol in the Atlantic lowlands of Costa Rica. If differences occur in nutrient accumulation among provenances of this species, they might have important implications for the establishment of forest plantations on degraded or impoverished tropical soils.

Materials and Methods

Mature wild trees

For this study, 3 natural stands were systematically selected in Costa Rica to study the foliage elemental composition of

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mature trees of *V. guatemalensis*. At each site, 6 to 10 trees were randomly selected for foliage sampling. Fully mature leaves (between 30–40 leaves) of the current year growth were gathered from the uppermost part of the crown for each tree in July 1994. Compound soil samples were collected from 0 cm to 15 cm and 15 cm to 30 cm depth at each site for each individual tree.

Leaves were lightly washed with distilled water and dried in an oven at 65 °C for 48 hours. Wet digestion using a mixture of 12 M H_2SO_4 and 30% H_2O_2 was used to analyze all the nutrients but Al (PARKINSON and ALLEN, 1975). Since sulfuric acid has been reported to cause interference for reading Al (HANSEN *et al.,* 1969), and may also cause aluminum precipitation at high Al concentrations (FEAGLEY S., personal communication, 1996), to determine this element the tissue was digested in 16 M HNO3 using a modification of the method of ISAAC and JOHNSON (1975). Phosphorus was determined colorimetrically after reaction with $(NH_4)_2MoO_4$ and $SnCl_2$ using a spectrophotometer (BRICEÑO and PACHECO, 1984) and the cations Ca, Mg, K, Fe, Cu, Zn, and Al were analyzed using an Atomic Absorption Spectrophotometer.

Soils samples were air dried, ground and sieved through a 2 mm mesh sieve. The pH was measured in a 2:5 mixture of soil and solution of either deoinized water or 0.01 M $CaCl_2$ solution. Exchangeable acidity was determined using 1 M KCl (BRICEÑO and PACHECO, 1984). Ca and Mg were extracted with a 1 N KCl solution, while P, K, Fe, Cu, Zn and Mn were extracted with a modified OLSEN solution (ISFEIP 1971, 1972, cited by SANCHEZ, 1976; DÍAZ-ROMEU and HUNTER, 1978). Cations were measured using an Atomic Absorption Spectrophotometer and phosphorus was determined by the colorimetric method after reaction with $(NH_4)_2MoO_4$ and $SnCl_2$, using a spectrophotometer. Cation exchange capacity and percent base saturation were determined by summation. Organic matter was determined by the WALKLEY-BLACK method (ALLISON, 1975).

Statistical comparisons between sites with regard to foliar elemental concentrations were performed using the SAS' General Linear Model Procedure. When necessary, mean comparisons were performed using the Duncan's multiple range test. Correlations between soil and tissue variables were also calculated using data for individual trees for a particular site and soil depth.

Progeny test

To study the variation in elemental composition associated with families and provenances of *V. guatemalensis,* a progeny test established by CAMCORE and CATIE (Centro Agronómico

Table 1. – Soil chemical properties at 0 cm to 15 cm depth under naturally growing trees of *V. guatemalensis* in 3 sites in Costa Rica.

Site	No. Trees	pH H_2O	pH $CaCl_2$	Org. Matter (%)	Ac_{ex}^{1}	Ca	Mg	K	ECEC^2	Ac. sat.^{3}	P	Fe	Cu	Zn	Mn
					(cmol kg^{-1})					(%)	(mg kg^{-1})				
Florencia, San Carlos	6	5.18	4.67	5.89	0.48	5.74	4.60	0.36	11.19	4.63	2.61	720	32.1	7.4	201.9
San Isidro, Pérez Zeledón	10	5.25	4.63	14.50	0.62	6.96	5.58	0.33	13.48	7.68	3.01	821	9.4	1.0	30.6
San Miguel, Sarapiquí	10	4.83	4.16	4.58	1.98	2.17	1.74	0.27	6.16	37.0	3.64	578	16.3	4.5	58.5

Ac_{ex}^{1}) Exchangeable acidity; ECEC^2) Effective Cation Exchange Capacity; Ac. sat.^{3}) acidity saturation.

Table 2. – Foliar elemental composition of naturally occuring, mature trees of *V. guatemalensis* in 3 sites in Costa Rica.

Site	P	Ca	Mg	K	Fe	Cu	Zn	Mn	Al
	g kg^{-1}				mg kg^{-1}				
Florencia, San Carlos									
Mean	0.38 c^1	12.6 ns^2	1.05 b	4.37 b	34.2 b	9.2 b	85.2 a	265 b	19800 ns
Maximum	0.46	14.2	1.56	6.99	45.8	10.9	126.2	397	21000
Minimum	0.31	11.4	0.69	3.26	22.8	5.5	54.7	214	18600
San Isidro, Pérez Zeledón									
Mean	0.54 a	13.0 ns	1.61 a	6.30 a	61.7 a	13.7 a	48.8 b	187 b	20200 ns
Maximum	0.58	16.3	2.26	7.19	129.4	14.4	81.0	291	22100
Minimum	0.46	9.8	1.22	4.44	38.1	10.9	29.5	91	18300
San Miguel, Sarapiquí									
Mean	0.49 b	11.7 ns	1.37 a	5.12 ab	38.8 b	10.7 b	57.1 b	378 a	20300 ns
Maximum	0.52	13.1	1.85	7.34	46.7	13.7	76.8	607	21200
Minimum	0.46	10.3	0.75	3.62	30.5	8.2	21.1	149	18600

^{1}) Means in the same columns followed by different letters are significantly different at 1% level. ^{2}) ns = no significantly different.

Tropical de Investigación y Enseñanza, Costa Rica) at La Selva Biological Station in Sarapiquí, Costa Rica (10° 26'N, 86° 59'W), was used. The site is classified as tropical rain forest, with mean annual precipitation of 3921 mm and mean annual temperature of 24 °C (HARTSHORN, 1983). The experimental plantation is on a flat upper-terrace with an acid (pH 4.8), infertile soil (CATIE, 1990).

The progeny test was set up using a randomized complete block design with nine replications. Each family was represented by 1 to 6 tree row in each block. For the present study, 2 trees per family and 6 replications were randomly selected and sampled. Only 3 families per provenance were randomly included in the sampling, except for the provenance Florencia, Costa Rica, where only 2 families were planted. At the time of sampling the trees were 4 years old. Foliage and soil samples were taken for individual trees and analyzed in the same way as the naturally grown trees. Statistically, each foliar element was analyzed with the following model: Response variable = μ + replications + provenances + replications x provenances + family(provenance) + replications x family(provenance) + ϵ, where μ is the general mean and e is the error term. The provenance effect was analyzed as a fixed effect, while the family within provenance effect was analyzed as a random effect. In cases where there was no valid F test, the SATTERTHWAITE pseudo-F statistic was used according to HICKS (1973).

Results

Mature trees

Large variation in soil chemical properties were found among the 3 sites studied (*Table 1*). In general, the San Isidro site appears to have better soil chemical characteristics than Florencia and San Miguel. The pH_{H2O} was found to be relatively high for this site (pH 5.25), and the same applies for organic matter and cations (Ca, Mg and K), when compared with the Florencia and San Miguel sites. The San Miguel site had a slightly higher soil P content than the other 2 sites. On the other hand, the soil micronutrient reserves (Fe, Cu, Zn and Mn) appear to be better at the Florencia site (*Table 1*).

Statistical differences were found in foliar elemental composition of mature trees growing at the 3 different sites (*Table 2*). Calcium and Al were the only 2 elements found to be not statistically different among sites, and their concentrations were relatively high. The overall mean for Ca was 12.4 g kg^{-1} and for Al 20,100 mg kg^{-1}. With regard to P, Mg, K, Fe and Cu, trees growing at San Isidro site had higher foliar concentrations for these nutrients, being in most of the cases significantly different from those of Florencia and San Miguel trees. For Zn, trees growing at the Florencia site showed significantly higher foliar content, while for Mn, trees at San Miguel site had the highest foliage content (*Table 2*).

In order to see if the differences in soil nutrient reserves are reflected in foliage nutrient concentration, simple correlations were run between soil chemistry characteristics and the foliar elemental concentration. No consistent relationship between soil chemistry characteristics and the foliar elemental concentration was found for any site or soil depth.

Progeny test

The site is relatively infertile, as indicated by the pH, cation exchange capacity and P availability (*Table 3*). However, the top soil has low exchangeable acidity (ca. 15%) and relatively high organic matter content.

Significant differences were found among provenances and families within provenances for foliage P content (*Table 4*). The provenance from La Ceiba had significantly higher P concentration (0.52 g kg^{-1}) than the other provenances (*Table 5*),

Table 3. – Soil chemical properties under a progeny test plantation with *V. guatemalensis* in Costa Rica.

Soil property	Depth 0-15 cm	Depth 15-30 cm
pH (H_2O)	4.64	4.63
pH ($CaCl_2$)	4.17	4.48
Organic matter (%)	5.67	2.82
Exchangeable cations (cmol kg^{-1})		
Al^+ and H^+	0.39	0.35
Ca	1.80	0.98
Mg	0.73	0.37
K	0.51	0.41
ECEC[1] (cmol kg^{-1})	3.44	2.11
Acidity saturation (%)	12.9	17.3
Modified Olsen extractable nutrients (mg kg^{-1})		
P	4.93	3.44
Fe	536	296
Zn	2.96	1.98
Cu	28.3	22.9
Mn	122.3	82.1

[1]) Effective cation exchange capacity

Table 4. – F test and variance component for foliage elemental composition of families and provenances of *V. guatemalensis* planted in the Atlantic lowlands of Costa Rica.

Source of variation	DF	P	Ca	Mg	K	Fe	Cu	Zn	Mn	Al
Provenances										
F test	5	5.74 **	1.39 ns	1.92 ns	2.01 ns	3.38 **	1.18 ns	1.67 ns	1.72 ns	0.94 ns
Variance component (%)		29.9	---	---	---	48.0	---	---	---	---
Families(provenances)										
F test	11	3.07 **	2.91 **	1.99 *	0.81 ns	1.69 ns	1.33 ns	3.03 **	1.33 ns	9.89 **
Variance component (%)		26.0	16.5	10.0	---	---	---	4.9	---	9.5

ns, *), **) = no significantly different, significantly different at 5% and 1%, respectively.

while the provenance from Siquirres had the lowest P content. The family effect was not evident for all the provenances (*Figure 1A*). Significantly higher variation in P contents were detected for families within the provenances Guápiles, La Ceiba, Siquirres and San Miguel (*Figure 1A*).

Significant differences were found among provenances but not among families within provenances for foliage Fe content (*Table 4*). The provenance from La Ceiba, had significantly lower Fe concentration (0.38.3 mg kg^{-1}) than the other provenances which averaged near 80 mg kg^{-1}(*Table 5*). The variation among families within the La Ceiba provenance was considerably less than that for the other provenances (*Figure 1B*).

Significant differences were found only for families within provenances for Al, Ca, Mg, and Zn foliar concentration (*Table 4*). The family effect was much more evident for both Ca and Mg among families of the Siquirres provenance (*Figure 1A*). The variance components for P, Ca and Mg were relatively low for provenances and families within provenances (*Table 4*). The concentrations of Al and Zn were significantly different for families within all the provenances studied (*Figure 1B*). No provenance effect nor family effect within provenances was found for K, Cu and Mn (*Table 4*).

Discussion

Mature trees

The differences in soil chemical properties among the sites studied are difficult to explain since several other factors acting upon soil characteristics (e.g. type and rate of organic matter decomposition) are unknown; nevertheless, several trends in nutrient availability can be analyzed. In general, the organic matter content is relatively high for the 3 sites, especially for San Isidro, where the organic matter was found to be near 15%. For this site, the high organic matter content could partially account for the low Cu, Zn and Mn found, since it has been shown to form stable complexes with these micronutrients (McLaren and Crawford, 1973; Shuman, 1979); however, as suggested by McBride (1982), other factors such as pH and type of humic substances, might also exert an effect on micronutrients availability. According to Bertsch (1986), Florencia and San Isidro sites have an optimum cation content (Ca, Mg and K) and low levels of acidity that would support agricultural crops; on the other hand, the Ca content and acidity for the San Miguel site could impose some restraints on crop growth. All 3 sites have low pH and P availability, which is characteristic for most of the tropical soils (Sanchez, 1976).

Site to site differences in foliage elemental concentration for a given species are due to both genetic differences and environmental factors (Epstein, 1972). For the present study, since mature wild trees were sampled, the genetic component is unknown and indistinguishable. Site factors are only partially covered by the soil characteristics studied; nevertheless, some patterns in elemental composition are noteworthy. Firstly, even though there were remarkable differences in soil Ca among the three sites the foliage Ca content was not different among them. This result suggests that this species may have an efficient mechanism for Ca uptake, especially if it is considered that its Ca content was even higher than that of a forest species described as Ca accumulators such as *Gmelina arborea* L. (Chijioke, 1980). Secondly, regardless of soil type, this species accumulates remarkable amounts of Al in its foliage, which has been reported before for this and other species of the Vochysiaceae family (Foy et al., 1978; Haridasan, 1982; De Madeiros and Haridasan, 1985; Pérez *et al.,* 1993). Besides, there appears to be a relationship between Ca and Al accumu-

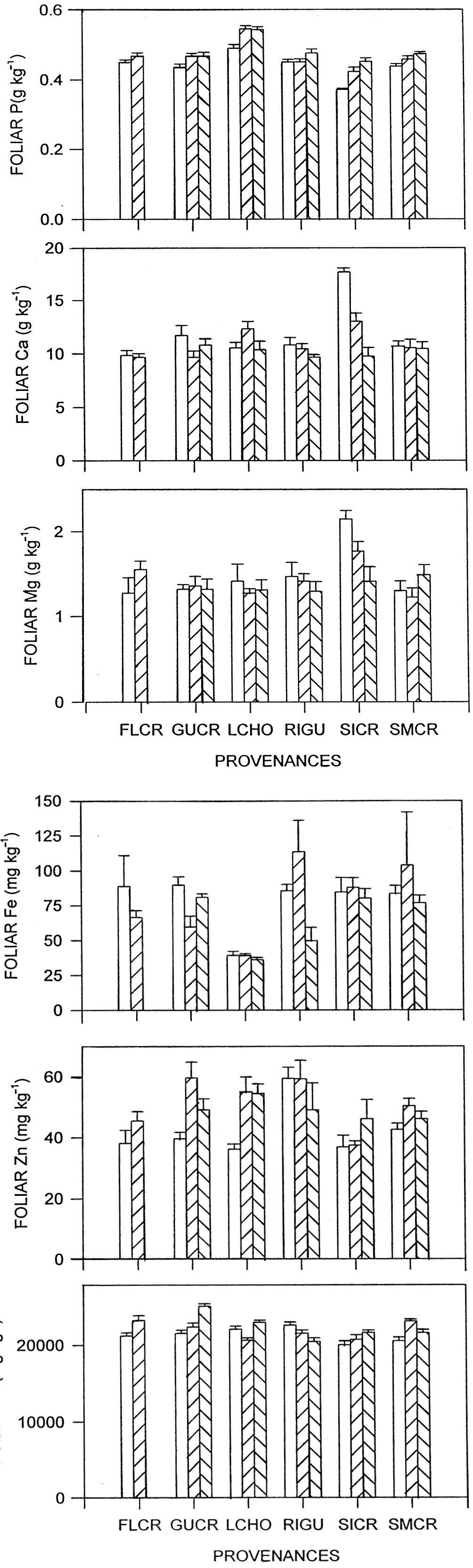

Figure 1. – Phosphorus, Ca, and Mg (A) and Fe, Zn and Al (B) foliage content in families by provenance of *V. guatemalensis*. Provenances and families (numbers in parentheses) are as follows: FLCR = Florencia, Costa Rica (10 to 21); GUCR = Guápiles, Costa Rica (2 to 19 to 20); LCHO = La Ceiba, Honduras (50 to 54 to 55); RIGU = Río Izabel, Guatemala (30 to 33 to 39); SICR = Siquirres, Costa Rica (4 to 5 to 6); SMCR = San Miguel, Costa Rica (9 to 11 to 15).

Table 5. – Mean elemental concentration in provenances of *V. guatemalensis* planted in the Atlantic lowlands of Costa Rica.

Provenance	P	Ca	Mg	K	Fe	Cu	Zn	Mn	Al
	----------g kg^{-1}	----------	----------	----------	----------mg kg^{-1}	----------	----------	----------	----------
Florencia, Costa Rica	0.46 b[1]	9.7 ns	1.41 ns	5.98 ns	77.6 a	9.4 ns	41.7 ns	236 ns	2229
Guapiles, Costa Rica	0.46 b	10.7 ns	1.38 ns	6.19 ns	76.9 a	9.6 ns	49.4 ns	346 ns	23050 ns
San Miguel, Costa Rica	0.45 b	10.6 ns	1.39 ns	5.40 ns	87.8 a	10.1 ns	46.3 ns	342 ns	21790 ns
Siquirres, Costa Rica	0.42 c	13.5 ns	1.80 ns	6.11 ns	84.0 a	11.3 ns	40.0 ns	288 ns	20800 ns
La Ceiba, Honduras	0.52 a	11.1 ns	1.35 ns	6.78 ns	38.3 b	11.8 ns	48.6 ns	440 ns	21900 ns
Rio Izabal, Guatemala	0.46 b	10.3 ns	1.40 ns	6.52 ns	82.9 a	10.8 ns	55.9 ns	330 ns	21600 ns
Overall mean	0.46	11.0	1.41	6.21	74.6	10.5	47.0	330	21900

[1]) Means in the same column followed by different letter are significantly different at 5% level.

lation, which is often reported for Al accumulating species (Foy et al., 1978). This Al accumulation does not necessarily reflect high Al tolerance of leaf tissue but is most likely the result of root induced chelation of Al^{n+} in the rhizosphere and translocation of chelated (non-toxic) Al into the leaf tissue where it is deposited in the epidermal layer (Matsumoto *et al.,* 1976).

The results showed that mean foliar K, Mg, Ca, and P concentration were very similar whether the trees were grown at San Miguel at low pH and high acidity saturation, or at San Isidro in less acid soil with low acidity saturation (*Tables 1* and *2*). This may indicate that *V. guatemalensis,* like other Al accumulator species, has a lower internal demand for nutrients, or has a root system capable of securing nutrients, particularly P, which exist at very low levels in solutions or as precipitates (Foy *et al.,* 1978).

Although no significant correlations were found between soil P availability and foliar P content, the higher P foliage contents were found at San Isidro and San Miguel sites, both having slightly higher soil P than the Florencia site. For Zn, the opposite was found. Trees at Florencia had much more foliar Zn than those at other sites. The contrasting differences among sites could be due to imbalances in these 2 nutrients as suggested by Robson and Pitman (1983), since the soil P/Zn ratio for the Florencia site was relatively low (less than 0.4) compared with that of the other sites (ca. 1.0).

The lack of a relationship between soil chemical analyses and foliar analyses in this study may well be due to soil analysis method. The extracting procedures we used for soil nutrients have been developed for agriculture. They have been chosen to give a good relationship between crop yield and extractable nutrients. Trees may behave quite differently than agronomic crops (Khanna, 1981). It could be that a different extracting procedure would discover a relationships between soil and foliar nutrient levels.

Progeny test

This study supports the view that foliar nutrient concentrations are under genetic control. It also suggests that genetic differences in response to nutrient availability may also exist since all the families and provenances of *V. guatemalensis* were planted at the same site. It could be argued that microsite variation can induce differences in nutrient uptake; however, this is unlikely since soil samples were collected for each individual tree, an analysis of variance was run to test for replications or blocks and no significant effects due to these factors were found with regard to soil characteristics, nor was the effect significant for the foliage elements studied.

An important issue to address here is the fact that though significant differences were found for certain elements, the variation due to provenances and families did not contribute much to the total variance (except for P and Fe concentration) (*Table 4*). The variation due to provenances and families was relatively low compared with those reported for other forest species (i.e. Knight, 1978; Kleinschmit, 1982). This is probably due to the small number of provenances and families used in this study, which indicates that much of the genetic variation was underestimated. This also implies that if significant variation was found even when a reduced number of families were analyzed, the contribution to the total variation could be expected to be much higher.

If differences in tissue nutrient concentration found in this study reflect genetic differences in nutrient uptake among provenances and families as found for other tree species and agricultural crops (Goddard *et al.,* 1976; Goddard and Hollis, 1984; Sheppard and Cannell, 1985), these findings have 2 major implications. First, the best adapted families or provenances are expected to use soil nutrient reserves more efficiently, which might represent an alternative for reforestation on marginal sites using relatively low input technologies (i.e. less nutrient demanding genotypes). Second, through genetic programs breeding procedures can be developed for the identification, selection, and improvement of the best adapted genotypes.

Although in this study the relationship between tree growth and mineral nutrient uptake was not investigated; a correlation would be expected since nutrient uptake in a plant is regulated by nutrient requirement for a given growth rate (Clarkson and Hanson, 1980). Some, but by no means all, foliar nutrient concentration differences can be explained by growth rate demands. It is important to determine if higher tissue nutrient concentration in some genotypes is necessary for growth processes, or whether part of the nutrient pool represents a storage component for use at other times or by other tissues when demands increase (Goddard and Hollis, 1984).

The results reported here should be interpreted with caution. First, the study was based on only 1 site, so the genetic x site interactions were not evaluated. This should be borne in mind, especially when interactions have been reported to be significant for some forest tree species (Jahromi *et al.,* 1976). Second, the study was only for young trees and extrapolation should not be made for older trees even growing on the same site. Thirdly, although significant differences were found for certain nutrients among families and provenances, it may or may not be correlated with growth or form parameters used in forest tree breeding programs to select the most promising genotypes.

Conclusions

Differences in foliage elemental composition were found among natural stands of *V. guatemalensis;* however, these differences do not appear to be related to the soil chemical characteristics studied since no consistent correlations were observed between these 2 factors. Regardless of site conditions, this species appears to accumulate relatively high amounts of Ca and Al. The role of these 2 elements in the physiology of this forest tree species deserves more research.

Significant variation in P foliar concentration among provenances and families within provenances was found for this species planted in a progeny test. Aluminum, Ca, Mg and Zn tissue content varied significantly only for families within provenances. Foliage Fe concentration was found to vary solely among provenances. Potassium, Cu, and Mn did not vary significantly between provenances or among families within provenances. The variance components for provenances and families were found to be relatively low, probably because a small low number of provenances and families studied; nevertheless, the results are encouraging and suggest that genetic differences in foliage composition are likely to exist for this species. These findings also suggest that genetic differences in response to nutrient availability might also exist.

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