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# SEASONAL CHANGES IN NUTRIENT CONTENT OF LEAVES OF SAVANNA TREES WITH DIFFERENT ECOLOGICAL BEHAVIOR

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## RESUME

Le contenu en substances nutritives (N, P, K, Ca et Mg) des feuilles de cinq espèces d'arbres de la savane du Vénézuela Central a été étudié au cours de ses variations saisonnières. Les espèces retenues sont soit à feuilles caduques (*Luenea candida, Godmania macrocarpa* et *Genipa caruto*) soit à feuilles persistantes (*Curatella americana* et *Byrsonima crassifolia*). Elles représentent les deux types de comportement adoptés par les arbres dans cette région à saison des pluies très tranchées. Le mode de croissance et de chute des feuilles montre que le renouvellement du feuillage se produit chaque année pour toutes les espèces. La période productive dure six à sept mois chez les espèces à feuilles caduques, onze mois chez les autres. La floraison se produit selon des modalités en relation avec la chute des feuilles. *G. macrocarpa* et *G. caruto* fleurissent après la chute des feuilles vers la fin de la saison sèche; *C. americana* et *B. crassifolia* fleurissent dès que les vieilles feuilles sont tombées, c'est-à-dire au milieu de la saison sèche; enfin *L. candida* fleurit après le début de la saison des pluies, lorsque la plupart des nouvelles feuilles sont apparues. Le contenu en azote et en phosphore des feuilles scléromorphes est significativement plus bas que celui des feuilles caduques. Il semble que l'utilisation du phosphore soit sous la dépendance de facteurs génétiques et que la compétition entre les arbres à feuilles persistantes ou caduques soit contrôlée, dans ce milieu, par des facteurs différant de la richesse des sols en éléments nutritifs.

## ABSTRACT

Seasonal changes of nutrient content (N, P, K, Ca, and Mg) of leaves of 5 tree species in the savanna region of Central Venezuela are reported. Selected species were deciduous ( *Luenea candida; Godmania macrocarpa* and *Genipa caruto*) and sclerophyllous perennials (*Curatella americana* and *Byrsonima crassifolia*), representing the two coexisting ecological behaviors of trees in this region of marked seasonal rainfall regime. Patterns of leaf growth and leaf fall show that all species change canopy yearly, productive period of deciduous being 6–7 months while by perennials it is 11 months in average. Flowering activity shows different patterns in relation to leaf shedding. *G. macrocarpa* and *G. caruto*

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flower after leaf shedding, toward the end of the dry season. *C americana* and *B. crassifolia* flower while old leaves are shed, at the middle of the dry season. *L. candida* flowers after the beginning of the rainy season, when most new leaves have been developed. N and P content of scleromorphic leaves are significantly lower than that of the leaves of the deciduous species. It seems that P utilization is regulated by genetic factors, and that competition between deciduous and perennial trees in this habitat is controlled by factors different to soil nutrient status.

## INTRODUCTION

Plants growing in savannas, natural or derived, present several adaptations to the following factors : a) marked rainfall seasonality ; b) low soil nutrient content and c) recurrent fire.

Among the main adaptations to dry season have been reported leaf loss by deciduous trees or death of aboveground plant tissue in grasses ; development of scleromorphic leaves by perennial trees and development of deep root systems which allow to use, at least during part of the year the freatic water reservoir.

Low soil nutrient content is correlated with an assemblage of species characterized by scleromorphic leaves, whose metabolism works at low Nitrogen and Phosphorus availability, particularly in acid soils ; higher root capacity for nutrient extraction from soil and higher retention capacity of nutrients before leaf shedding (BEADLE 1954, 1966 ; LOVELESS 1961 ; MONK 1966 ; SMALL 1972). Scleromorphic characters of leaves can be induced by cultivating plants under low nutrient supply (mainly N and P) and in this case the concept of peinomorphy instead of xeromorphy was introduced some time ago (WALTER 1960). It has been established that the strong morphological changes induced in leaves through nitrogen deficiency, are also accompanied by significant changes in the physiological and biochemical behavior of the leaves (MEDINA 1971).

The difference between adaptations to water and nutrient deficiencies has been shown by plants growing in peat bogs, where sclerophylly clearly correlated with the low nutrient availability of those habitats (SMALL 1972, WALTER 1960). BEADLE (1954, 1966) has shown that Phosphorus deficiency in Australian soils is the main factor determining differentiation of sclerophyllous plant communities.

Leaf scleromorphism seems to be only indirectly coorelated with fire, since it might affect nutrient availability in soil.

In this paper results on seasonal changes of macro nutrient content in leaves of savanna trees are reported. The study was conducted within the framework of a project intending to establish quantitatively the relationship between the nutrient retention capacity, mainly Nitrogen and Phosphorus of dominating plant species and the soil nutrient status. It is hypothesized that there is an increased retention capacity as soil nutrient availability diminishes, and that in humid habitats under limited nutrient supply, perennial, sclerophyllous plant species are mainly selected.

## MATERIALS AND METHODS

Measurements were conducted in the Trachypogon savannas near Calabozo in Central Venzuela, in places protected against fire at least during the last five years (BLYDENSTEIN 1963). During 1972 and 1973 five tree species were selected to measure leaf growth, leaf duration and changes of leaf nutrient content (N, P, K, Ca and Mg) through the year. Species selected were the evergreens *Curatella americana* L. and *Byrsonima crassifolia* ((L.) H.B.K., which are two of the main woody species growing isolated in the Trachypogon savannas; and the deciduous *Luenea candida* (D.C.) Mart., *Godmania macrocarpa* Hemsley and *Genipa caruto* H.B.K. The last 3 species are components of forest islands interspersed in the Trachypogon grassland and they do not grow in open savanna, with the exception of *G. caruto*, when there is protection against fire.

Three individuals from each species were selected and in each of them, branches were marked for growth measurements, and 1 $m^2$ woody frames were located down below to collect flower and leaf litter.

Leaf growth was evaluated by measuring length and width and calculating, after convenient sampling, the regressions between length x width and leaf area and weight. Separate sampling was made for measurement of area/weight relationships.

Leaf sampling for nutrient determinations was performed monthly, in three replicates from leaves in similar position and exposition as those used for measuring growth. Leaf and litter samples were dried at 80°C, homogenized and digested with a ternary acid mixture (JACKSON 1964). K, Ca and Mg were measured by atomic absorption, N by microkjeldahl and P with the molybdo-vanado-phosphoric acid method (JACKSON 1964).

## RESULTS AND DISCUSSION

### Habitat conditions.

Climate, soil and vegetation in the Central Venezuelan Llanos have been extensively described (BLYDENSTEIN 1962 ; MONASTERIO 1971 ; MONASTERIO & SARMIENTO, 1968) and here it is enough to summarize as follows. Climate is seasonal, dry season between October and April, 1300 mm rainfall in average, mainly concentrated in 6-7 months. The vegetation is a tree savanna, with four woody species growing mainly isolated within the grassland (*Curatella americana ; Bowdichia virgilioides ; Byrsonima crassifolia* and *Casearia sylvestris)* and two dominant grass genera, Trachypogon and Axonopus. This savanna includes little forest islands, whose main components are members of the deciduous forest which surrounds the whole savanna region in Guarico state (SARMIENTO and MONASTERIO 1969; ARISTEGUIETA 1966). Soil has a strong lateritic character, with 25 % clay, 55 % sand and 20 % silt in average, pH around 5, and low nutrient content with around 0.03-0.128 % N, 4-25 ppm extractable P and 10-60 ppm extractable K. A lateritic cuirasse is present in this savanna type, apparently conditioning distribution of trees within the grassland (BONAZZI 1967 ; WALTER 1969).

**Leaf shedding, flowering and climate.**

Figure 1 shows the pattern of litter production by the species studied. Rainfall during 1972 was well below average, causing a reduced leaf production and an accelerated leaf fall, which was almost completed to the end of the year. Both perennial and deciduous species shed all their leaves during the dry season. By perennials new leaves are simultaneously produced and leaves are photosynthetically active during the whole dry season (MEDINA 1967).

Flowering shows slight different peaks as shown by the flower + fruit litter production curves. *C. americana* and *B. crassifolia* flower while old leaves are shed (December–February). *G. macrocarpa* and *G. caruto* produce flowers well after leaf shedding, toward the end of the dry season. Finally, *L. candida* flowers after the beginning of the rainy season, when all new leaves have been formed. This behavior agrees with observations on the phenology of the same species (except *G. caruto*) reported by MONASTERIO (1968), and indicates the coexistence under the same climate of different ecological strategies, not only regarding leaf duration but also reproductive activity.

**Patterns of leaf growth.**

Figure 2 shows the patterns of leaf growth in the five species studied. All deciduous trees produce their leaves between April and July, and one leaf is completely developed within 30 days of less. Normally leaves last until November–December, but at this time they are not completely active in photosynthesis, above 75 % of the leaves present severe chlorosis and necrosis. The productive period is nearly seven months.

Evergreen trees produce most new leaves between December and April, and present similar growth rates as the deciduous leaves. Photosynthetic active period last 11 months in average.

During the growth period leaf size varies depending on the time when leaves are produced, maximal leaf size in attained apparently when soil water is not limiting. Figure 3 shows the curves of maximal leaf size of leaves formed during the growing period of 1972 and 73. The water could be limiting leaf growth is indicated by the differences in maximal leaf size between the first leaf formed and the largest leaf produced by each species. In fact, first leaf to largest leaf size ratio is 37 % in *C. americana* and 51 % in *B. crassifolia,* while by deciduous it is 60

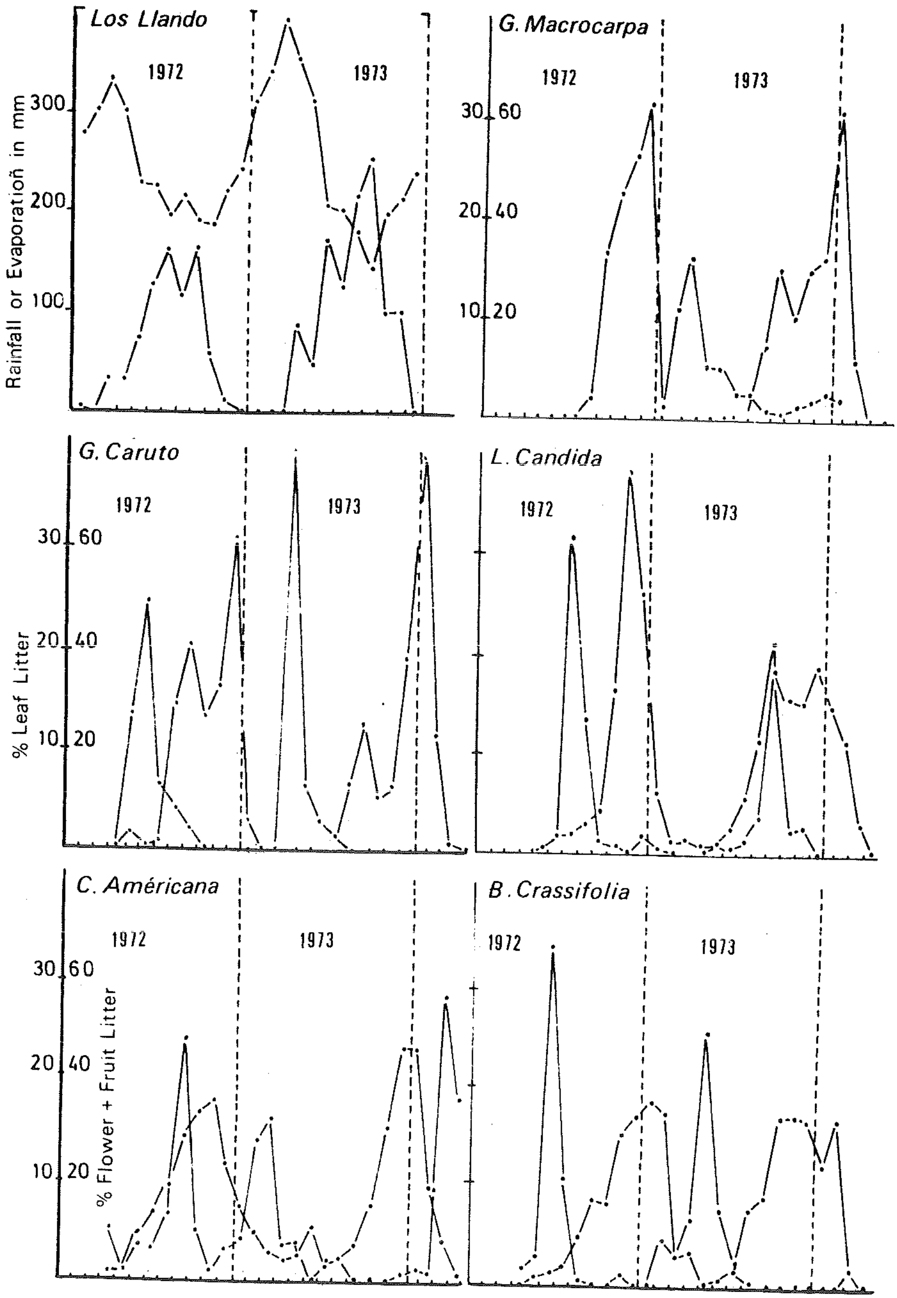


*Figure 1* : Rainfall and evaporation during 1972-73 and patterns of leaf and flower + fruit shedding in 5 tree species in the Calabozo savanna.

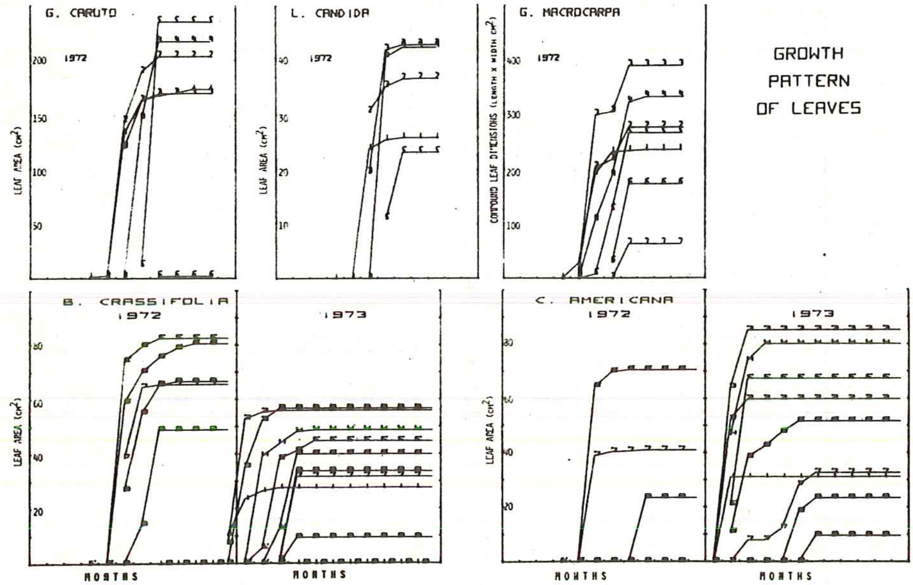


*Figure 2* : Patterns of leaf production and growth in the tree species studied in the Calabozo savanna.

or larger (60.3 °/o in *L. candida* ; 73.9 °/o in *G. caruto* and 60.6 °/o in *G. macrocarpa*). That is, leaves which begin to grow during the rainy season attain a more uniform size.

## Annual changes of leaf nutrient content.

Curves of the five elements examined (K, Ca, Mg, N and P) are presented in figure 4, each element is compared for all species.

If nutrient content is expressed per unit dry weight all species behave similary. There is a reduction in N, P and K with age, and an increase in Ca and Mg. This behavior is also observed in leaves developed during different times of the year. For N, P and K there is a stable situation after leaf matures, between July and September. During this period, until leaf shedding, there is no significant increase in area/weight ratio of leaves. Table 1 presents average values of area/weight ratios in adult leaves of the species studied.

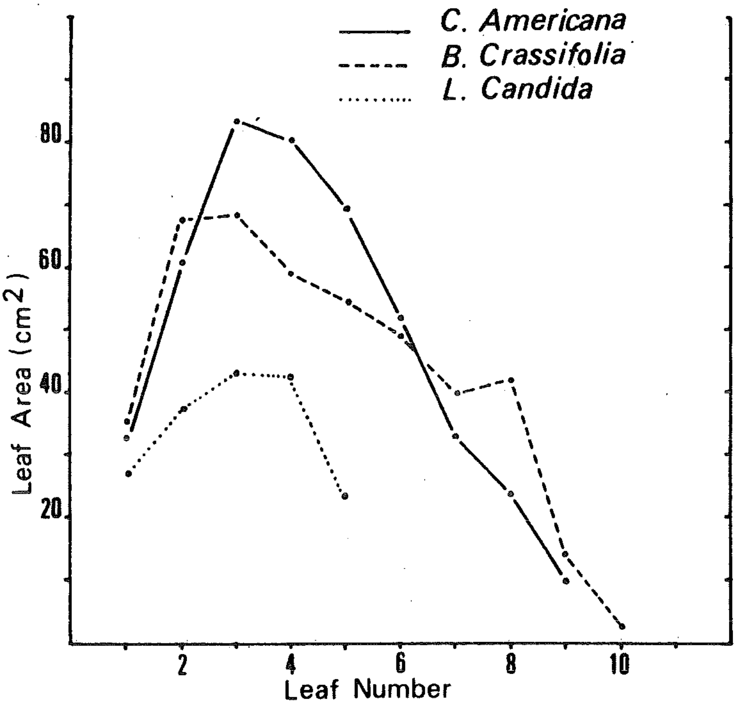


*Figure 3* : Variation of leaf area at the end of the growing season. Leaf number indicates leaves produced at different times during the year.

**TABLE 1**

AREA/WEIGHT RATIOS OF MATURE LEAVES

| Species | $cm^2/g$ dry weight |
|---|---|
| Luenea candida | 317 ± 39 |
| Godmania macrocarpa | 113 ± 15 |
| Genipa caruto | 107 ± 18 |
| Curatella americana | 69 ± 6 |
| Byrsonima crassifolia | 57 ± 7 |

Average content of nutrients in adult leaves was calculated for the period August–September (Table 2) and this amount compared with nutrient content of fresh fallen leaves, at the end of the rainy season. This figures allowed the calculation of the retention factor included in Table 2 for each species.

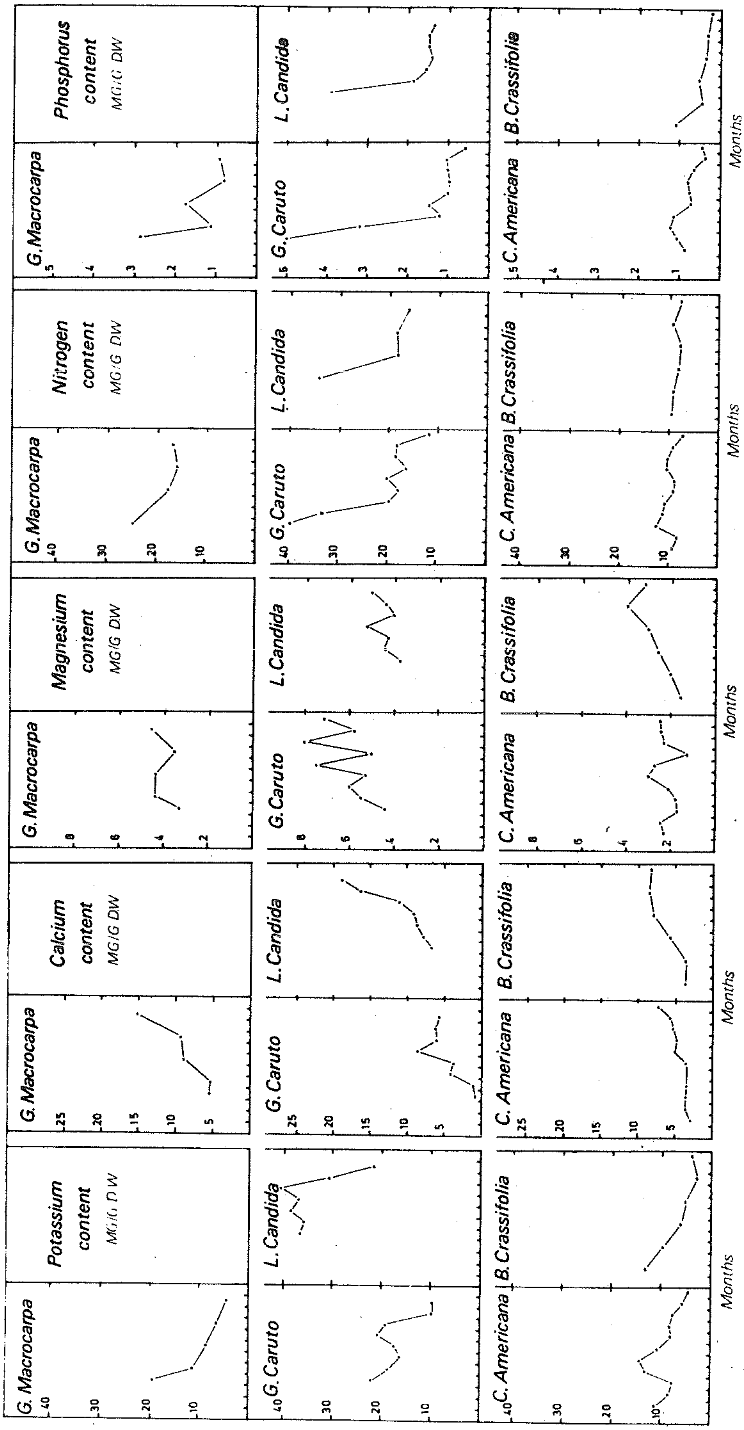


*Figure 4 :* Seasonal changes in macronutrient content of the tree species studied. Year period from January to December.

**TABLE 2**

MATURE LEAF NUTRIENT CONTENT (mg/g dry weight) AND APPARENT RETENTION FACTOR

| | AVERAGE ADULT LEAF | | | | | FRESH FALLEN LEAF | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | N | P | K | Ca | Mg | N | P | K | Ca | Mg |
| Genipa caruto | 18.0 ± 2.6 | 0.99 ± 0.2 | 19.8 ± 1.9 | 7.3 ± 2.2 | 6.3 ± 1.8 | 9.7 | 0.53 | 6.8 | 13.0 | 8.6 |
| Retention Factor °/o | 46 | 46.5 | 65.7 | | | | | | | |
| Luenea candida | 18.3 ± 0.8 | 1.45 ± 0.1 | 38.6 ± 3.0 | 10.2 ± 1.6 | 4.6 ± 0.7 | 9.9 | 0.81 | 7.8 | 18.9 | 3.5 |
| Retention factor °/o | 46 | 44.2 | 80 | | | | | | | |
| Godmania Macrocarpa | 16.0 ± 0.7 | 0.79 ± 0.1 | 6.5 ± 1.9 | 9.3 ± 2.1 | 3.9 ± 0.7 | 7.6 | 0.30 | 2.5 | 13.6 | 2.7 |
| Retention factor °/o | 52 | 62 | 61 | | | | | | | |
| Curatella americana | 9.3 ± 1.1 | 0.75 ± 0.1 | 8.3 ± 0.8 | 4.9 ± 0.3 | 2.7 ± 0.1 | 4.6 | 0.14 | 4.1 | 8.6 | 3.1 |
| Retention factor °/o | 51 | 81.4 | 51 | | | | | | | |
| Byrsonima crassifolia | 8.0 ± 0.9 | 0.35 ± 0.05 | 5.4 ± 0.8 | 8.0 ± 0.7 | 3.0 ± 0.2 | 5.7 | 0.20 | 1.4 | 11.3 | 2.2 |
| Retention factor °/o | 29 | 43 | 74 | | | | | | | |

It appears that deciduous trees present a higher N and P content per gram dry leaf weight than evergreens. This is clear from the fact that leaves of *C. americana* and *B. crassifolia* contain a high proportion of leaf material as cutine and sclerenchym (MERIDA * MEDINA 1967). Proportion of K and Ca present a noteworthy relation. Evergreens and *G. macrocarpa* have a higher relative fraction of Ca as compared to *L. candida* and *G. caruto.* The same relation holds when contents are expressed per unit area, or when the sum of Ca and Mg against K is considered.

For competition between evergreens and deciduous types it is considered that cost of new leaf building is critical. While perennials have the advantage of using the whole year for photosynthesis, deciduous have normally the advantage of producing larger leaf area at lower nutrient cost. This can be seen from leaf area/weight ratios (Table 1). If the amount of N and P invested per unit leaf area is considered, relations are not so coherent. With the exception of *L. candida*, which shows the lowest N concentration per unit leaf area, the rest present similar values of N/area which might suggest a similar photosynthetic capacity per unit leaf area. Increased leaf cost in N and P might be compensated by a higher photosynthetic rate per unit leaf area. It would be worthwhile to investigate which relation exists between N and P content and photosynthesis in scleromorphic leaves to appreciate the consequences of sclerophylly on dry matter production.

Retention factors calculated for N, P and K indicate that in the species considered retention of N and P is higher than in plants growing in richer soils (compare data given by SMALL 1972). Due to presumable K leachability from leaves, retention factors calculated for K might not be considered reliable.

Degree of scleromorphism is related to P content, when it is expressed on a dry weight basis and not on an area basis (LOVELESS 1961, 1962). N and P contents seem to be strongly correlated and it has been suggested that sclerophylly means low N probably causally related to low P. Figure 5 shows the distribution of all values of P and N content ($n = 154$) for the plants studied. It appears clearly that deciduous species have throughout, irrespective of leaf age, higher N content than pernnial leaves. P contents overlap considerable around the 1 mg/g dry weight region. Correlation coefficients are significant for both groups at the 0.1 °/o level (deciduous 0.886 ; perennials 0.516), although correlation by perennials is weaker. Leaf N content of deciduous species seems to be more sensitive to P changes than it is in perennials. In fact, regression coefficients are significantly different at the 0.1 °/o level (see fig. 5).

**Final remarks.**

Differences in N and P content in leaves of these species indicate clearly that mainly genetic factors regulate uptake and utilization of soil nutrients. Sclerophyllous leaves use less P, irrespective of availability in soil than deciduous do, therefore, they have also lower total N in the leaves.

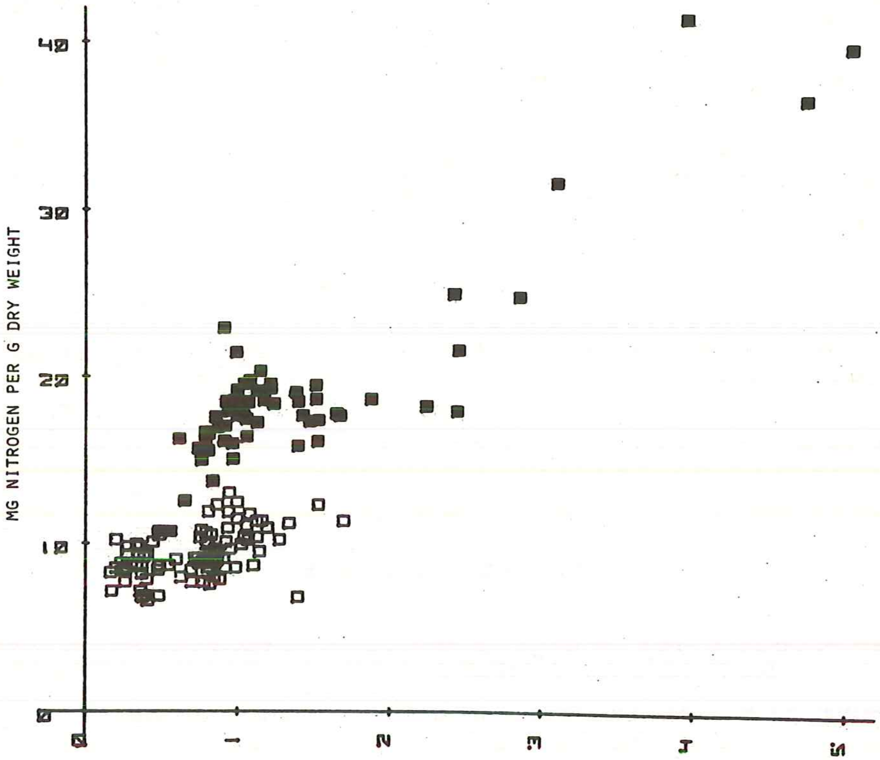


*Figure 5* : Relationship between N and P content of all leaves measured in the tree species studied.

■ Deciduous trees : *G. caruto, L. candida* and *G. macrocarpa*
$N = 11.48 + 5.43\ P$

□ Perennial trees : *B. crassifolia* and *C. americana*
$N = 7.77 + 2.22\ P$

In this environment two different nutritional and physiological strategies coexist, although soil nutritional conditions apparently would favor development of deciduous tree types. It appears that other factors, like fire and soil shallowness, control competition between deciduous and perennials, determining a separation of sclerophyllous dominating in open savannas, while deciduous are confined to the forest islands described earlier, where either fire has no effects or soil physical conditions are better suited for root development. Sclerophyllous tree species also grow in the forest islands, but examination of life form spectrum in this forest shows a significant higher proportion of deciduous over perennial and sclerophyllous tree species (ARISTEGUIETA 1966).

Following LOVELESS (1961) and BEADLE (1966) it could be speculated that soils with lower P availability would displace deciduous types favoring sclerophyllous tree types, while the contrary would be true where no fire effect is present and where soil structural conditions do not avoid competition between perennials and deciduous species.

Comparison of nutrient composition of species of different ecosystems might shed some light on the selection mechanisms of the metabolic types best adapted to each particular environment.

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