Photosynthesis and water relations of savanna tree species differing in leaf phenology

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Summary
Godmania macrocarpa Hemsley, a deciduous tree characteristic of fire protected areas of the savanna region of central Venezuela, was more drought tolerant, allocated more N to leaves and had consistently higher photosynthetic rates than Curatella americana L., a ubiquitous species growing successfully within the grasslands of tropical American savannas. Godmania macrocarpa maintained higher leaf conductance and photosynthesized at higher xylem water tensions than C. americana. As the dry season progressed, G. macrocarpa was more affected by water stress than C. americana, which may explain why G. macrocarpa shed its leaves before forming new leaves. For both species, leaf sap osmolality was strongly correlated with, but not completely accounted for by, soluble sugars. Integrated water-use efficiency, as measured by δ^{13}C, was similar for both species, but young leaves were more efficient than old leaves. Water-use efficiency of adult leaves was similar in both species as a result of higher photosynthetic rates in G. macrocarpa and lower leaf conductances in C. americana. Compared to G. macrocarpa, instantaneous photosynthetic N-use efficiency was higher in C. americana despite its lower maximum photosynthetic rates. The absence of G. macrocarpa trees from open grasslands, despite their high productive capacity, is possibly the result of unfavorable conditions for germination, poor survival of seedlings, and lack of resistance against fire.

Keywords: Curatella americana, Godmania macrocarpa, leaf sap osmolality, N-use efficiency, water stress, water-use efficiency.

Introduction
The central plains of Venezuela are occupied by a complex of savannas (grassland and isolated woody plants) and semideciduous forest patches. In the savannas, the grass layer is frequently dominated by a species of the genus Trachypogon (Blydenstein 1962, Sarmiento 1984), whereas the tree layer is never continuous and consists of a few evergreen tree species (Monasterio and Sarmiento 1976). The forest patches are dominated by truly semi- or fully deciduous tree species (Medina 1982, Sarmiento 1984). This vegetational complex is found under climatic conditions characterized by strong rainfall seasonality, the rainy season extending from April to September. The present distribution of savannas and forest patches appears to be related to soil structure, water availability, and fire regime (Medina and Silva 1990).

Both climatic and edaphic conditions are important forces operating in the selec-

1 This paper is dedicated to Prof. Dr. H. Ziegler, retiring director of the Institute of Botany and Microbiology, Munich Technical University, Germany, on the occasion of his 70th birthday.
tion of morphological and physiological properties of savanna vegetation. In the neotropical savannas, woody species are generally evergreen, that is, they maintain a permanent leaf canopy that turns over once a year during the dry season (Monasterio and Sarmiento 1976, Montes and Medina 1977, Medina 1982, Sarmiento et al. 1984). Leaves of evergreen trees tend to be scleromorphic (Medina 1984). In areas protected against fire, the tree species are mostly deciduous, remaining leafless for periods of two to five months during the dry season, and developing leaves with relatively high leaf area/weight ratios (Medina 1984).

Coexistence of tree species with contrasting phenological behavior has been taken as an indication of differences in depth of the root systems. Trees capable of exchanging their leaves during the dry season should be able to use water from deeper soil layers, whereas deciduous species have more superficial root systems and therefore, are strongly limited by water during the dry season (Medina 1982, Sarmiento 1984, Goldstein et al. 1989). However, the encroachment of deciduous species into open grasslands seems to be restricted more by fire than by nutritional requirements or competition (Montes and Medina 1977). Long-term protection against fire results in a marked increase in deciduous species in tropical savannas (San José and Fariñas 1991).

In several ecosystems, deciduous species generally have higher N concentrations per unit leaf weight (Medina 1984, Sobrado 1994) and photosynthetic rates than evergreen species (Mooney and Gulmon 1982, Field and Mooney 1986). However, in savanna and dry deciduous forests, photosynthetic differences are frequently small (Goldstein et al. 1989, Sobrado 1994).

Comparative analysis of gas exchange in trees with contrasting phenological behavior growing under the same climatic conditions enabled us to test the hypotheses that water-use efficiency is higher in evergreen trees that expand their leaves and photosynthesize during the dry season, and that N-use efficiency is higher in deciduous trees that are active mostly during the rainy season.

We measured seasonal variations in water relations and photosynthesis in two common tree species differing in distribution and phenological behavior in a savanna in central Venezuela: Curatella americana L. (evergreen) and Godmania macrocarpa Hemsley (deciduous).

**Materials and methods**

**Habitat and plant material**

The study site is located at 125 m above sea level within a *Trachypogon*-savanna area in Cojedas state, Venezuela (9°25’ N and 60°15’ W). It is characterized by a grass cover dominated by *Trachypogon plumosus* and *Thrasya petrosa*, and a tree layer consisting of evergreen species scattered within the grass layer (*C. americana*, *Bowdichia virgilioides*, *Byrsonima crassifolia* and *Casearia sylvestris*) and deciduous species mostly restricted to small tree groves or areas protected against fire (*G. macrocarpa*, *Cochlospermum vitifolium*, *Genipa caruto*) (Blydenstein 1962,
Rainfall is seasonal. Of an average 1100 mm per year, nearly 90% falls during the period from May to October. Rainfall between November and April is not enough to compensate for potential evapotranspiration. Measurements were performed at the end of the rainy season 1988, during the dry season 1988–89 and during the rainy season 1989 (Figure 1). The rainy season 1988 extended until the end of the year.

_Curatella americana_ trees reach up to 5–8 m in height and have sclerophyllous, highly undulated leaves. Leaf duration averages 12 months, and leaf exchange takes place within one month near the middle of the dry season (Monasterio and Sarmiento 1976, Montes and Medina 1977). During the period of leaf exchange, two leaf cohorts are present on the same tree, one about 12 months old, developed during the previous dry season (adult leaves + old leaves), and the new leaves being developed in the current dry season (young leaves). Young and adult leaves could be sampled throughout the measuring period because of slight asynchrony in leaf exchange among trees. In the field, leaves were collected and separated according to their apparent age, as judged by color and texture.

_Godmania macrocarpa_ trees reach up to 5 m tall and are drought deciduous, with compound mesophytic leaves of soft texture and dark green color. Leaves are produced at the beginning of the rainy season in May and last until the middle of the next dry season, with an average leaf life span of eight months. At each collection time, leaves were of similar age, because there was no overlap between previous and current growing seasons.

![Figure 1. Annual distribution of rainfall in the study site, Sembra, Edo. Cojedes. Rainfall collector was located about 2 km south of the study site. The short arrows indicate the measurements periods.](image-url)
Field measurements

Monthly measurements of gas exchange (portable ADC gas analyzer, Model LCA2), xylem water tension (Soil Moisture Equipment pressure chamber, Model 3000), and leaf sampling for measurement of osmolality, soluble cations and carbohydrate contents, leaf area/weight ratios, and total nitrogen (N) and chlorophyll contents, were carried out from the end of the rainy season (November) until the middle of the next rainy season (August).

Xylem water tension and gas exchange measurements were routinely conducted from sunrise at 0630 h to shortly after noon (1300 – 1400 h) to assess daily changes in leaf water status (minimum and maximum water tensions) and the relationship between stomatal conductance and photosynthesis. Leaf disks from the same leaves used for measurements, or from separate sets of leaves, were collected in paper bags for measurement of N content, or in plastic syringes and frozen in dry ice for extraction of leaf sap.

Laboratory measurements

Methods for leaf sap extraction and measurement of soluble compounds have been described elsewhere (Olivares and Medina 1992). Briefly, frozen leaf disks of 3-cm diameter (three replicates) were thawed in the laboratory, and their sap extracted with a hand press. A subsample was taken immediately for measurement of osmolality with a Wescor 5500XR osmometer. Osmolality values (Os in mmol kg$^{-1}$) were transformed to pressure units at 25 °C based on a regression derived from tables in Lang (1967) for NaCl: osmotic pressure (MPa at 25 °C) = 0.029521 + 2.17490 Os + 0.065058 Os$^2$. Concentrations of potassium in the cell sap were measured by atomic absorption spectrometry (Varian AA-6) after appropriate dilution. Soluble carbohydrates were measured by the procedure of Hassid and Neufeld (1964). Nitrogen content was measured in oven-dried leaf samples by a Kjeldahl procedure (Jackson 1964). Leaf chlorophyll content was measured in leaf disks frozen in the field and extracted in the laboratory with 80% acetone (Arnon 1949).

In a subset of the leaf samples used for N determinations, the natural abundance of $^{13}$C ($\delta^{13}$C values) was also measured to obtain an index of integrated water-use efficiency. Samples were analyzed by Susan Wood in the Research School of Biological Sciences, Australian National University, following standard procedures (Farquhar et al. 1989).

Results

Leaf area/weight ratios, and the contents of nitrogen and chlorophyll

Leaf area/weight ratios (LAW m$^2$ kg$^{-1}$) and leaf N per unit area (LNA mmol m$^{-2}$) decreased with leaf age. Young leaves of both species had higher values of LAW and LNA than old leaves. The bulk of samples collected from *C. americana* showed a relatively narrow distribution of LAW and LNA values, whereas the spread was more
pronounced in *G. macrocarpa* (Table 1). The average of all samples indicated that *G. macrocarpa* had significantly lower values of LAW and higher values of LNA than *C. americana*. Chlorophyll content and the molar ratio of chlorophyll/N were twice as high in *G. macrocarpa* as in *C. americana*.

**Leaf xylem water tension and osmolality of leaf sap**

During the end of the rainy season, minimum leaf xylem water tensions remained around 0.4 MPa in *G. macrocarpa* and 0.1–0.4 MPa in *C. americana*, indicating sufficient water supply (Figure 2). Minimum values increased markedly as the dry season progressed, reaching nearly 1.2 MPa in *G. macrocarpa* and 0.6–0.8 MPa in *C. americana*. A similar trend was observed in the maximum xylem water tensions (Figure 2). The daily fluctuations in xylem water tension were always higher in *G. macrocarpa*, varying from 0.50 MPa in young leaves to 1.88 MPa in adult leaves, compared to the variations from 0.19 to 0.53 MPa in young leaves and from 0.43 to 0.87 MPa in adult leaves of *C. americana*. Daily fluctuations of leaf sap osmolality followed the same pattern. *Godmania macrocarpa* showed fluctuations from 86 mmol kg\(^{-1}\) (≈ 0.19 MPa) in young leaves to 297 mmol kg\(^{-1}\) (≈ 0.68 MPa) in old leaves, whereas in *C. americana*, young leaves varied from 23 to 62 mmol kg\(^{-1}\) (≈ 0.05–0.14 MPa) and adult leaves from 37 to 125 mmol kg\(^{-1}\) (≈ 0.08–0.30 MPa). Maximum leaf xylem water tensions were similar to, or slightly larger than, the maximum osmotic pressures calculated from sap osmolalities. Leaf dehydration, as measured by the morning–noon increases in leaf-sap osmotic pressure, was less pronounced in *C. americana*, particularly the young leaves, than in *G. macrocarpa*. After the onset of the dry season, both species experienced water stress, but it was less pronounced in *C. americana* than in *G. macrocarpa* (cf. differences in scale in Figure 2).

The maximum leaf osmotic pressures measured throughout the seasons were positively correlated with the maximum xylem water tensions measured in the same

### Table 1

Average and 95% confidence intervals of leaf area/weight ratios, leaf nitrogen content and chlorophyll content of *Curatella americana* and *Godmania macrocarpa* leaves in the *Trachypogon*-savannas of Cojedes state. Within rows, values followed by the same letter are not statistically different (Fisher’s least significant difference at \(P \geq 0.95\)).

<table>
<thead>
<tr>
<th>Variable</th>
<th>Curatella americana</th>
<th>Godmania macrocarpa</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(n)</td>
<td>Min</td>
</tr>
<tr>
<td>Leaf area/weight (m(^2) kg(^{-1}))</td>
<td>112</td>
<td>9.4</td>
</tr>
<tr>
<td>Nitrogen content (mmol m(^{-2}))</td>
<td>109</td>
<td>42</td>
</tr>
<tr>
<td>Chlorophyll content (µmol m(^{-2}))</td>
<td>18</td>
<td>210</td>
</tr>
<tr>
<td>Chlorophyll/nitrogen (mmol mol(^{-1}))</td>
<td>18</td>
<td>2.2</td>
</tr>
</tbody>
</table>
tree (Figure 3). Average values of both leaf-sap osmotic pressure and maximum xylem water tensions were larger throughout the measuring period in *G. macrocarpa* than in *C. americana*.

**Composition of leaf sap**

Leaf sap osmolality, measured on leaves collected during early morning, was highly correlated with the concentrations of K and soluble sugars. In *G. macrocarpa*, K concentration in leaf sap was generally higher in young than in adult leaves, whereas...
the opposite was true for sugars and osmolality (Table 2). In *C. americana*, no significant differences were detected between young and old leaves. The best predictor of leaf sap osmolality was the concentration of soluble sugars (Figure 4), which explained about 80% of the osmolality variance (osmolality (mmol kg\(^{-1}\)) = 236.82 + 4.91 soluble sugars (mol m\(^{-3}\)), \(r^2 = 0.81\)). However, soluble sugars and K accounted for less than 25% of total osmolality, indicating that other osmolites, possibly organic compounds, were also present.

Leaf conductance and photosynthesis

In *G. macrocarpa*, maximum photosynthetic rates differed greatly between the rainy

![Figure 3. Relationship between maximum leaf-xylem water tension and maximum leaf-sap osmotic pressure (averages ± standard deviations, \(n = 6\)).](image)

<table>
<thead>
<tr>
<th>Variable</th>
<th><em>Godmania macrocarpa</em></th>
<th><em>Curatella americana</em></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Young ((n = 6))</td>
<td>Adult ((n = 8))</td>
</tr>
<tr>
<td>Osmolality</td>
<td>526a</td>
<td>751b</td>
</tr>
<tr>
<td>Potassium</td>
<td>74a</td>
<td>48b</td>
</tr>
<tr>
<td>Soluble sugars</td>
<td>62a</td>
<td>117b</td>
</tr>
</tbody>
</table>

Table 2. Differences in leaf sap osmolality (mmol kg\(^{-1}\)), potassium and soluble sugars concentrations (mol m\(^{-3}\)) in young and adult leaves of *Godmania macrocarpa* and *Curatella americana*. Within rows, values followed by the same letter are not statistically different (Fisher’s least significant difference at \(P \geq 0.95\)).
season and the dry season, decreasing from an average of 14 to 5.5 $\mu$mol m$^{-2}$ s$^{-1}$. In *C. americana*, changes were less pronounced, varying from 5.5 to 9.5 $\mu$mol m$^{-2}$ s$^{-1}$ in young leaves and from 8.5 to 9.5 $\mu$mol m$^{-2}$ s$^{-1}$ in adult leaves. Leaf conductance and photosynthesis per unit area were positively and significantly correlated in both young and adult leaves of *G. macrocarpa* and in young leaves of *C. americana*, but not in adult leaves of *C. americana* (Figure 5). *Godmania macrocarpa* leaves showed consistently higher maximum photosynthetic rates per unit area than young *C. americana* leaves throughout the conductance range. Therefore, the former species maintained a lower ratio of CO$_2$ concentration between the intercellular spaces and the surrounding air ($c_i/c_a$ ratio) during the periods of maximum photosynthesis. Average values of intrinsic water-use efficiency (ratio of photosynthesis/conductance, IWUE) (Osmond et al. 1980), calculated from maximum photosynthetic rates, were higher in *G. macrocarpa* than in *C. americana* (Table 3).

Photosynthesis and leaf nitrogen concentration

Maximum photosynthesis per unit leaf weight was linearly correlated with leaf N concentration, with the exception of a few *G. macrocarpa* leaves with very high N concentrations (Figure 6). The correlation was also detectable on an area basis, but it was much weaker. Instantaneous N-use efficiency (INUE), calculated as the average ratio of maximum photosynthesis and leaf N content, was significantly higher in *C. americana*, particularly the young leaves, than in *G. macrocarpa* (Table 3).
Average water-use efficiency

In both species, δ¹³C values tended to increase (become less negative) as the dry season progressed, but were consistently less negative in young leaves of *C. americana* (Figure 7). Values ranged from a minimum of −29.5‰ in *G. macrocarpa* to −26‰ in *C. americana*. In both species, δ¹³C values above −27.8‰ corresponded to young leaves, differentiated in the field according to their texture, and characterized later by LAW and N concentration. Young leaves of *C. americana* also had a significantly higher LAW than adult and old leaves, although average N concentration did not vary with leaf age (Table 4). In *G. macrocarpa*, young leaves were characterized by significantly higher N concentrations than old leaves, whereas no differences in LAW were detected.

Table 3. Intrinsic water-use efficiency (IWUE), calculated as the average ratio of maximum photosynthesis and leaf conductance, and instantaneous N-use efficiency (INUE), calculated as the average ratio of maximum photosynthesis and leaf nitrogen concentration, both on a dry weight basis. Within columns, values followed by the same letter are not statistically different (Fisher’s protected least significance difference at $P \geq 0.95$).

<table>
<thead>
<tr>
<th>Species</th>
<th>$n$</th>
<th>IWUE (mmol mol⁻¹)</th>
<th>INUE (µmol CO₂ mol⁻¹ N)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Godmania macrocarpa</em></td>
<td>22</td>
<td>46.0a</td>
<td>56.8a</td>
</tr>
<tr>
<td><em>Curatella americana</em></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Young leaves</td>
<td>15</td>
<td>30.4b</td>
<td>71.4b</td>
</tr>
<tr>
<td>Adult leaves</td>
<td>22</td>
<td>36.0b</td>
<td>65.9ab</td>
</tr>
</tbody>
</table>

Average water-use efficiency

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During the measuring period, *G. macrocarpa* differed from *C. americana* in leaf...
phenology and properties associated with water relations and gas exchange: (1) it lost all its leaves toward the end of the dry season, whereas *C. americana* produced new leaves as the older leaves were being shed, (2) it always had higher leaf N and chlorophyll contents than *C. americana*, (3) its values of leaf xylem water tension and osmolality were considerably higher, indicating that under natural conditions, this species tolerated much lower leaf water potentials than *C. americana*, and (4) its leaves had consistently higher photosynthetic rates at similar conductances than *C. americana*.

In both species, leaf sap osmolality was correlated with the maximum leaf xylem water tension, indicating similar mechanisms of response to water stress, i.e., maintenance of leaf conductance at low water potential was accomplished through a reduction in osmotic potential. In both species, soluble sugars were highly correlated with leaf sap osmolality. *Godmania macrocarpa* had consistently higher concentrations of soluble sugars, but not of K, than *C. americana*.

Osmotic pressure measured in sap extracted from frozen leaves tends to underestimate actual values because of dilution with cell wall water (Tyree and Jarvis 1982). Meinzer et al. (1983) measured water relations parameters in *C. americana* leaves using pressure–volume curves and reported osmotic pressure values at full turgor ranging from 0.9 MPa in young leaves to 2.4 MPa in mature leaves to 1.3 MPa in one-year-old leaves. Our values were similar for young and old leaves, but lower for mature leaves. However, the range of variation of osmotic pressures between full and zero turgor in the different leaf types was almost identical to the values of minimum and maximum leaf-sap osmotic pressures reported here. Therefore, we believe that extraction of leaf sap does not result in significant dilution in *C. americana*. In addition, *G. macrocarpa* showed equal or larger diurnal variations of both leaf xylem water tension and osmotic pressure than the evergreen trees reported by Meinzer et al. (1983). Diurnal variations in leaf-sap osmotic pressure result from leaf tissue dehydration and indicate that there is a delay in the transport of xylem water to cover for transpiration losses during the day.

In agreement with the high osmolality and N content, *G. macrocarpa* showed
consistently higher leaf conductances and photosynthetic rates than *C. americana*. Photosynthesis and leaf conductance were linearly correlated in *G. macrocarpa* and young leaves of *C. americana*, the former having higher maximum values of IWUE. No relationship between photosynthesis and leaf conductance was detected in old leaves of *C. americana*, because they lacked stomatal control. The cause for the loss of stomatal control in *C. americana* is probably the large accumulation of silica in the epidermis, leading to guard cell rigidity (Rodríguez 1979). This phenomenon has been observed in several tropical tree species (Reich and Borchert 1988).

Photosynthetic rate was linearly correlated with N content, but maximum, instantaneous N-use efficiency in photosynthesis was lower in *G. macrocarpa* than in *C. americana*. A linear relationship between total leaf N and photosynthetic rates has been reported for numerous species (Field and Mooney 1986). The large variations observed among species may be due to differences in the fraction of leaf N allocated to RuBP carboxylase and the accumulation of nitrogen compounds not associated with the operation of the photosynthetic machinery (Evans 1989). We found a contrasting pattern of intrinsic water-use efficiency and N-use efficiency. High photosynthetic rates were attained by allocating large amounts of N to the leaves and tolerating low water potentials. This combination led to higher maximum IWUE and lower INUE in *G. macrocarpa* than in *C. americana*. A similar pattern of behavior was reported by Field et al. (1983) for woody evergreen species of the Californian chaparral.

The average values of INUE reported here are lower than those reported for herbaceous plants (Seeman et al. 1987, Evans 1989), but generally larger than those reported for trees from Miombo and Mopane woodlands in Zimbabwe (Tuohy et al. 1991). Comparisons of INUE values from deciduous and evergreen trees of a dry deciduous forest with our results reveal differences in the behavior of evergreens with and without water stress during the dry season. In contrast to the species studied here, evergreen species of dry tropical forests frequently have higher N and chlorophyll contents per unit leaf area, and lower photosynthetic rates than deciduous species (Medina 1984, Sobrado 1994). However, the chlorophyll/N ratio is higher in deciduous species than in evergreen species in both dry forest and savanna species (Sobrado 1994 and Table 1). In dry deciduous forests, lack of water during the dry season limits photosynthetic productivity, and maintenance of leaf area through the dry season is associated with large water deficits (Sobrado 1986) and possibly with the accumulation of herbivore deterrents (Mooney and Gulmon 1982). In savanna evergreens, water deficits during the dry season are less pronounced than in dry deciduous forests (Meinzer et al. 1983), and photosynthetic productivity seems to be limited by N allocation to leaves.

Average water-use efficiency, as measured by the abundance of $^{13}C$, indicated that young leaves of both species were more efficient than old leaves. Similarity of average water-use efficiency in both species probably resulted from higher photosynthetic capacity in *G. macrocarpa* and lower leaf conductances in *C. americana*. Goldstein et al. (1989) compared the water-use efficiency of several deciduous and
evergreen species of savannas in Venezuela and found only minor differences for the species taken as a group. However, *C. americana* had higher assimilation/transpiration ratios, but more negative $\delta^{13}$C values, than *G. macrocarpa*. Differences between our results and those of Goldstein et al. (1989) might derive from timing of collection and age of leaves used to measure natural abundance of $^{13}$C, because their values are within the range of variation reported in this paper.

During the sampling period, $\delta^{13}$C values increased markedly toward the dry season, indicating variations in the carbon source used to build the leaves (Figure 7). These seasonal variations in $\delta^{13}$C values of leaves have been related to water stress (Mooney et al. 1989) and the development of leaves from stored carbon with higher $\delta^{13}$C values (Ehleringer et al. 1992) in other vegetation types. In a dry deciduous forest, leaves of trees that remain green during the wet season have significantly more negative $\delta^{13}$C values than those of trees producing leaves early in the dry season (Mooney et al. 1989). Moreover, both deciduous and evergreen trees have more negative $\delta^{13}$C values in sites with high water availability than in drought-prone sites. We hypothesize that, if carbohydrates stored at the end of the rainy season are richer in $^{13}$C because of higher water-use efficiency during this period, the new leaves formed in the middle (*C. americana*) or at the end of the following dry season (*G. macrocarpa*) will show more positive $\delta^{13}$C values. As leaves grow into the next rainy season, $\delta^{13}$C values decrease as a result of the accumulation of carbohydrates progressively impoverished in $^{13}$C.

In summary, our results indicate that, compared with *C. americana*, *G. macrocarpa* is a more productive species, with higher intrinsic water-use efficiency during periods of unrestricted water availability, and is able to withstand water stress well into the dry season without losing turgor. In contrast to the behavior of deciduous species in tropical dry forests, the INUE and long-term water-use efficiency of *G. macrocarpa* are lower than those of *C. americana*. However, these differences are not enough to explain the absence of *G. macrocarpa* in open grasslands. Possible explanations are the differences in germination requirements and higher nutritional demands of deciduous species. *Godmania macrocarpa* produces numerous short-lived seeds with small amounts of reserves, which reduces the probability of the seedlings surviving in open grasslands. *Curatella americana* seeds, in contrast, are long-lived and may remain buried in the soil until humidity conditions are enough to guarantee successful establishment (Blydenstein 1962, Medina and Silva 1990). Montes and Medina (1977) explored the nutritional restriction for establishment of deciduous trees in open grasslands and concluded that fire is the determining factor eliminating deciduous trees from central Venezuelan savannas. Long-term observations on the changes in tree frequency and density in savannas protected against fire in central Venezuela show that the number of isolated trees in open grasslands increased by a factor of 100 after 25 years of protection (San José and Fariñas 1991). Both *C. americana* and *G. macrocarpa* benefit from fire protection; however, *G. macrocarpa* was recorded in the open grassland only after 15 years without fire. We have shown that *C. americana* trees allocate relatively small amounts of N to their
leaves, and this changes little with leaf age. This character might be significant for N conservation in a tree regularly suffering the effects of canopy burning.

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References


