

INSECT HERBIVORY IN TREE CROWNS OF
TABEBUIA AUREA AND *T. OCHRACEA* (BIGNONIACEAE) IN BRAZIL:
CONTRASTING THE CERRADO WITH THE “PANTANAL
MATOGROSSENSE”

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ABSTRACT. Herbivory rates were contrasted between *Tabebuia aurea* and *T. ochracea* in the cerrado, and on *T. aurea* in cerrado and the wetland Pantanal Matogrossense, where the species occurs in monodominant stands. Variability of leaf size and leaf specific area (LSA) are described. Herbivory rates are correlated with individual mean genetic distance within the population (based on an UPGMA analysis), from previous data, to test the hypothesis that resistance to herbivory increases with increasing differentiation between individuals. In the three populations, levels of herbivory are compared among branches within individuals, and individual trees within populations, and finally among populations. *Tabebuia aurea* in the cerrado showed the highest phenotypic variability of leaf area, and *T. ochracea* showed the highest variance in LSA. Insect chewing (caused by Chrysomelidae, Coleoptera and leaf-mining, Lepidoptera) was studied on two leaf cohorts in 1996. Herbivory rates varied significantly within trees in all populations, while patterns of herbivory among trees were also variable. For both leaf cohorts, herbivory was greater in the cerrado than in the Pantanal, and greater on *T. aurea* than on *T. ochracea*. Stem growth between the two leaf flushes was not affected by species, populations, or sites. It was negatively correlated, however, with individual leaf area lost ($r^2 = 0.15$). In the cerrado, insect damage to leaves was negatively correlated with genetic distance, which means that individuals of *T. ochracea*, which had higher genetic variability in a population, were attacked less than individuals of *T. aurea*. Polymorphism protection and evolution of resistance are discussed, as well as the consistently low herbivory rates in the monodominant population of *T. aurea*.

Key words: cerrado, genetic polymorphism, herbivory, monodominance, Pantanal, *Tabebuia*

INTRODUCTION

The increasing interest in the ecology of insect interactions in tree crowns has brought puzzling results about insect community structure in the canopy, particularly in the tropics. This debate has been revived by the ongoing discussion on the contribution of specialist versus generalist insects to the fauna of canopies, and how much these functional groups differ in their impact on the host plant (Hodkinson & Casson 1987, Stork 1991, Basset 1992, Gaston 1993, Basset et al. 1994, Basset 1996, Coley & Barone 1996, Lowman & Wittman 1996). Although insect herbivory on leaves can seldom be related to diversity of insect species or feeding guilds (Basset & Hoefft 1994, Price et al. 1995), most of the damage on the foliage may be caused by specialists (Lowman & Wittman 1996), and their distribu-

tion within a tree may well be related to herbivory damage on the leaves.

The impact of herbivory on adult tree fitness and performance is better studied in temperate forests (e.g., Kulman 1971), but has not been satisfactorily explored in the tropics (Basset & Hoefft 1994, Filip et al. 1995, Lowman 1995). Moreover, only recently have studies on insect community and ecological processes on tree crowns in tropical savanna ecosystems, e.g., in Africa (Kruger & McGavin 1997, 1998), and South America (Fernandes & Price 1988, 1992, Gontijo & Domingos 1991, Ribeiro et al. 1994, Price et al. 1995, Lara & Fernandes 1997, Fernandes et al. 1997, Ribeiro et al. 1998) been published. Many of the current questions in tropical canopy ecology may be clarified by comparing rain forests with savannas.

The present work compares leaf area damaged among hierarchical levels for two species of *Tabebuia* (Bignoniaceae): a pioneer, *T. aurea*, and a persistent, *T. ochracea*. Both species are na-

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tives and sympatric in the central South American savanna, the Brazilian cerrado, while *T. aurea* is also found as monospecific populations in wetlands. An impressive monodominant population of this species is found over an area of 1200 km², in the Brazilian Pantanal Matogrossense, a large wetland system. Cerrado is rich in herbivorous insect species, while Pantanal is comparatively poorer in insect species (Ribeiro 1999). Despite the co-occurrence of the two species in the cerrado, the impact of herbivory on them seems to differ.

These species have previously been described in terms of their population genetic structure (Ribeiro 1999). The higher genetic polymorphism observed in *T. ochracea* suggested that it evolved under intense frequency and density-dependent selection, which resulted in strong differentiation of one individual from the other (Hamilton et al. 1990). Conversely, *T. aurea* would be adapted to colonize disturbed sites, and so selected towards higher growth rates, resulting in genetically homogeneous populations (Ribeiro & Brown unpubl. data). Genetic differentiation is assumed to be correlated with phenotypic variability of chemical and defensive traits (Strauss & Karban 1994, Lebreton 1995, Floate et al. 1996), and with the evolution of new forms of resistance, or an increase in non-recognition of the host (Holt 1977, Fritz & Price 1988).

The aim of this paper is to examine herbivory on trees of *Tabebuia* from within-individuals to between species, thus comparing damage between both habitats and life strategies. Chewing was predominantly caused by several species of Chrysomelidae. The second most important cause of leaf area loss was an unidentified leaf-mining species (Lepidoptera), common on both host species. Variability in leaf size and leaf toughness were described in an attempt to associate herbivory to host phenotypic variability. The hypothesis that herbivory is more prevalent in the cerrado than in the Pantanal was tested. In addition, herbivory rates are expected to be higher on *T. aurea* than on *T. ochracea* within the cerrado, according to the hypothesis that the latter species is better adapted to insect herbivore pressure in this habitat. Finally, the hypothesis that individual resistance to herbivory increases with increasing differentiation among individuals was tested.

MATERIALS AND METHODS

Study Sites

Cerrado is a mosaic ecosystem in Brazil, varying from grassland to dense arboreal savan-

nas. It occurs in a geologically old region of approximately 1,800,000 km² (Sarmiento 1983). There is evidence that this vegetation has covered the Central Brazilian Plateau since the Tertiary period (Freitas 1951, Rizzini 1979). The so-called "cerrado sensu strictu" (Rizzini 1979) was chosen for this work. It is an arboreal savanna with continuous herbaceous strata and trees of 5–7 m tall, found on poor, acidic soils between 800–900 m above sea level. Plants were marked in four nature reserves in the same region, in the Minas Gerais State, Brazil: National Park of "Serra do Cipó" (Jaboticatubas), reserve of EFLEX/IBAMA (Paraopeba), nature reserve of EMBRAPA/CNPMS (Sete Lagoas), and the ecological station of UFMG (Belo Horizonte). These Reserves are separated by farm and urban land, in which fragments of cerrado vegetation can be found.

The Pantanal is the biggest continuous floodplain of central South America (138,183 km²), composed of several different swamp habitats (Adámoli 1986, Ab'Saber 1988). Like the cerrado, the Pantanal is a mosaic ecosystem, but composed predominantly of pioneer species, with patches of persistent species in more mature habitats. The monodominant woodland of *T. aurea* occurs in the south Pantanal, on very compact clay soil, with the so-called mounds or "murunduns." These are hummock-type elevated patches above the flood level, on which germination and establishment of trees occur. This kind of habitat occurs predominantly at the interface of the "Pantanal do rio Paraguay" and "Pantanal do rio Miranda", a specific region which is highly susceptible to abrupt seasonal climatic changes and unpredictable intensive flooding (Adámoli 1986, Vila da Silva & Kux 1992).

Sampling Strategy

Phenotypic variability

Fifteen leaves per tree were randomly sampled from main branches proportional to the branch's leaf mass (based on estimated number of leaves per branch), to estimate leaf area, and specific leaf area (SLA = dry weight/area). SLA is considered a good estimate of sclerophylly (Turner 1994). The leaves were dried at 60°C for 48 hours, weighed, and area was electronically measured (LI-COR 3100 Area Meter). Bud growth, at the terminal ends of the branches, was measured for each tree ($N = 30$ buds per tree, subdivided between the main branches), one month after fruiting season has finished, in 1996. The distinct color and softness of a recently ex-

panded stem was used to identify the season's growth.

Canopy herbivory

Tabebuia species have a well defined phenology: a period of vegetative growth in the rainy season, with two leaf flushes (over 8 months); a period of leaf senescence and shading of one month or more at the beginning of the dry season; a flowering period of 2–3 weeks (varying among species), in the dry season; fruiting over 3 weeks to one month (Ribeiro & Pimenta 1991, Gentry 1992). This discrete phenology allows a simple analysis of herbivore damage at any stage in the life-history.

During 1996, the percentage leaf area lost was measured before and after flowering from an average of 37.7 and 30.6 leaves per tree, from trees of *T. ochracea* ($N = 44$) and *T. aurea* ($N = 42$) respectively. Ten leaves were sampled randomly from each main branch, totalling 1650 and 1328 sampled leaves for the first and second leaf cohort, respectively. Leaf area lost was visually estimated as percentage scores of damage (0, 5, 25, 50, 75, 99, 100%), then arcsine square-root transformed to estimate geometric means (Basset 1992). Samples were taken at least one month after leaf expansion and maturation, when most of the damage had already occurred (Ribeiro et al. 1994). Therefore, percentage area lost by herbivory, and chewing and mining separately were quantified for two consecutive leaf cohorts. Total herbivory also included smaller damage, like galling, which was of little importance in terms of leaf area loss. A more thorough study on the impact and association of these trees with several gall-forming species will be published elsewhere.

Leaf herbivory was quantified in situ, by climbing the tree to access top branches, and using a ladder for the lower branches. The scheme of subdivision of the tree by main branches provided samples throughout the height and width of the crown, which is normally irregular and laterally expanded. Basic climbing equipment was used for security.

Experimental Design and Statistical Analysis

The proposed study can be formalized through a test of hypotheses based on two random factors, taxa (*Tabebuia aurea* and *T. ochracea*) and habitat (Pantanal and cerrado). This basic model is an unbalanced design, where *T. aurea* is completely confounded with "Pantanal." Therefore, the analysis output is equivalent to a one-way comparison between the three populations (hereafter *T. aurea*/Pantanal, *T. aurea*/cerrado, and *T. ochracea*), and conclusions are

based on contrasts by Bonferroni simple interval (Sokal & Rohlf 1995).

Phenotypic variability

Due to a strong heteroscedasticity of the leaf data, a Kruskal-Wallis non-parametric ANOVA was used to compare leaf area. Mean crown values for leaf area were used to test differences between populations. Since SLA was homoscedastic and normally distributed, a Nested ANOVA was used to explore the variance of SLA among individual trees within each of the populations. Variance among populations was tested using the lower level, i.e., the Mean Square of trees within populations.

Canopy herbivory

Variance in insect herbivory among tree branches was tested for each population separately. In the cerrado, both species may be affected by habitat fragmentation, thus been divided in subpopulations. Three-level Nested ANOVAs were run for each population, having mean leaf area lost per branch nested within trees, and trees nested within each subpopulation (except *T. aurea*/Pantanal, for which a two-level Nested ANOVA was run). A general linear model procedure (GLIM) was used for this analysis (Crawley 1993), and run on a UNIX computing system.

The variance in insect herbivory among sites in the cerrado was tested by including subpopulations as random blocks. These analyses were generated in the ANOVA factorial procedure in SPSS (SPSS Advanced Statistics™ 6.1), and a full factorial design was chosen as in a mixed Model 2 (sensu Newman et al. 1997; or Scheffé model [Simms & Triplett 1994, Sokal & Rohlf 1995]). In this case, both "population" and "subpopulation" factors were tested against residual plus error terms, and the role of the latter factor was merely to control the level of variance (Newman et al. 1997).

The probability distribution of geometric mean leaf area lost per tree, taken from arcsine data transformation, was normal and homoscedastic. Leaf area lost within and between trees also matched a normal distribution after arcsine transformation, but a certain heteroscedasticity in its distribution was observed. However, as the number of leaves sampled in each branch (units of comparison) were equal and large, an ANOVA test may be robust enough to handle this deviation from homoscedasticity (Zar 1984).

Finally, a one-way ANCOVA, testing populations covaried with genetic dissimilarity, which was estimated from an Unweighted Pair Group Method using Arithmetic averager

TABLE 1. Significant variances in herbivory rates (total herbivory, chewing or mining) for branches within trees, and trees within sites of *Tabebuia aurea*/Pantanal, *T. aurea*/cerrado, and *T. ochracea*. No significant variance was observed among sites in any situation. Nested ANOVA outputs are given in Appendix 1.

Populations	Leaf cohort 1		Leaf cohort 2	
	Among trees	Within trees	Among trees	Within trees
<i>T. aurea</i> /Pantanal	Total herbivory	—	—	Total herbivory
	Chewing	Chewing	—	Chewing
	Mining	—	—	—
<i>T. aurea</i> /cerrado	—	—	—	Total herbivory
	—	Chewing	—	Chewing
	—	Mining	Mining	—
<i>T. ochracea</i>	Total herbivory	—	—	Total herbivory
	Chewing	—	—	Chewing
	Mining	Mining	—	Mining

(UPGMA), and a simple linear regression were developed to test the relationship between population genetic diversity and individual resistance to herbivory. The dissimilarity distances among trees were generated by clustering presence/absence of observed polymorphic DNA fragment bands (from a RAPD analysis) (Ribeiro 1999). The matrix of dissimilarity was then averaged per individual to produce trees' mean genetic distance.

Herbivory and plant growth

Since reproductive success was strongly influenced by climatic conditions, the effect of herbivory on vegetative bud growth was taken as a measure of insect impact on plant performance. A model II multiple regression was used to test the effect of herbivory rates on bud growth. Leaf area lost from leaves developed before and after the measurement of bud length were entered into the model in a stepwise method. The effect of populations was tested by adding species and habitat as two dummy variables.

RESULTS

Leaf phenotypic variability

Leaf area varied independently of species among the three populations. *Tabebuia aurea* had the largest mean leaf area ($39.19 \text{ cm}^2 \pm 5.6$) in the cerrado, but also the smallest in the Pantanal ($17.93 \text{ cm}^2 \pm 0.74$). Therefore, this species had either larger or smaller leaves than *T. ochracea* ($23.52 \text{ cm}^2 \pm 2.0$) according to its habitat (Kruskal-Wallis, $\kappa^2_{0.05;2} = 14.57$, $P < 0.05$). The variability in leaf size of *T. aurea*/cerrado (CV = 43%) was greater than that of *T. ochracea* (CV = 34%), and these were both much greater than the variability of *T. aurea*/Pantanal (CV = 16%).

SLA varied significantly among trees within

each population (Nested ANOVA, $F_{35,799} = 6.4$, $P < 0.0001$), but there was no difference in SLA among populations (overall mean SLA = 0.021 mg/cm^2 , $F_{2,35} = 3.0$, $P > 0.05$). Similarly for leaf size, SLA was more variable in individuals from the cerrado than from the Pantanal. However, in this case, the coefficient of variance of *Tabebuia ochracea* (CV = 22%) was greater than that of *T. aurea* (cerrado: CV = 17%; Pantanal: CV = 0.07%).

Canopy herbivory

Insect chewing was predominantly by several species of Chrysomelidae, mainly Alticinae (e.g., up to five species of *Oedionychus*), but also by unidentified species of Cassidinae, Galerucinae, Eumopinae, Hispinae, and Megascelinae. A total of 10 morphospecies (five on *Tabebuia ochracea*, five on *T. aurea*/cerrado, and only two on *T. aurea*/Pantanal) were identified in the rainy season of 1996.

Herbivory varied significantly between branches within trees of both species and in both habitats. Chewing damage showed the most consistent pattern, varying within trees of the three populations in both leaf cohorts, the exception being *Tabebuia ochracea* in the first cohort (TABLE 1). Mining varied only within trees of *T. ochracea* (for both leaf cohorts) and *T. aurea*/cerrado in the first leaf cohort (TABLE 1). Variance between individual trees within subpopulations was observed for *T. ochracea* (chewing) and *T. aurea*/Pantanal (chewing and mining) in the first leaf cohort, and for *T. aurea*/cerrado in the second cohort (mining, TABLE 1). Nested ANOVA tables are found in Appendix 1.

Leaf area lost by chewing insects was higher in the cerrado than in the Pantanal, and higher on *Tabebuia aurea* than on *T. ochracea* in the cerrado, for both leaf cohorts (FIGURE 1, ANOVA $F_{2,34} = 6.61$, $P < 0.01$; $F_{2,36} = 6.07$, $P < 0.05$, respectively). Loss of leaf area by mining

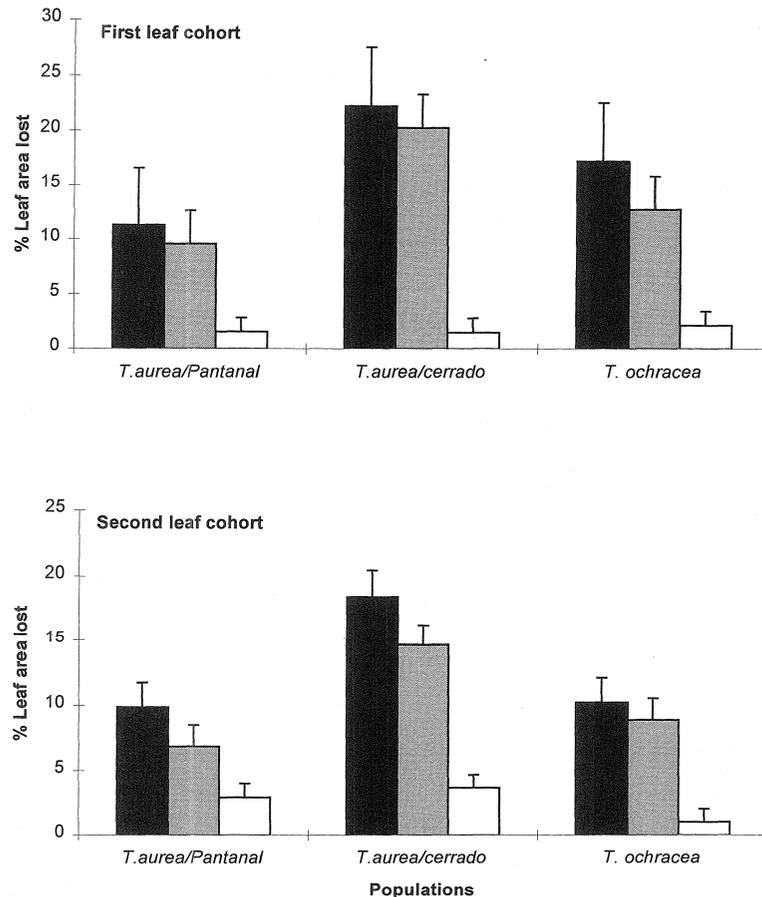


FIGURE 1. Percentage of leaf area lost (arcsine transformed) by herbivory in the two leaf cohorts of 1996, for two populations of *Tabebuia aurea* and one of *T. ochracea* (cerrado). First column is total herbivory, followed by chewing and mining. Error bars are Least Significant Difference (LSD) based on within + residual MS value from the respective ANOVAs. Detailed ANOVA tables in appendices.

was less than by chewing, and showed a less consistent pattern between leaf cohorts. There was no difference in leaf area lost by mining among populations after the first leaf flush, but there was less damage on *T. ochracea* than on *T. aurea* (independent of habitat) in the second leaf cohort (FIGURE 1, $F_{2,31} = 2.12$, $P = 0.14$; $F_{2,36} = 4.32$, $P < 0.01$, respectively). Therefore, in respect to total leaf area lost, *T. aurea/cerrado* was more attacked than *T. aurea/Pantanal* and *T. ochracea*, which were similar. This pattern was consistent for both leaf cohorts (FIGURE 1, $F_{2,31} = 6.08$, $P < 0.05$; $F_{2,34} = 15.72$, $P < 0.001$, respectively). In any situation, leaf area lost did not differ significantly between subpopulations in the cerrado, as the variances were high. In some models (i.e., total leaf area lost in both leaf cohorts, and chewing in the second leaf cohort), the variance absorbed by subpopulations masked

a significant difference between populations, which was detected by the full model. For these cases, a model simplification procedure was applied, and non significant factors were excluded sequentially, until the one responsible for the significance was found. In all three cases, the significant factor was "population." Details of ANOVAs found in the Appendix 2.

To test individual susceptibility to insect attack, the total leaf area lost after the second leaf flush was tested against populations and covaried with dissimilarity index (UPGMA) among individuals, based on polymorphic DNA bands. The analysis showed a highly significant effect of population and a marginally significant correspondence between attack and genetic distance ($P < 0.052$, TABLE 2). In other words, there was a trend towards lower insect damage on leaves of individuals more genetically different. This

TABLE 2. ANCOVA of total leaf area lost in the second leaf cohort, tested against populations and having mean genetic dissimilarity between individuals within populations (percentage disagreement distances) as covariate.

Source	SS	df	MS	F-test	P
Within + residual	701.96	37	18.97		
Regression	76.80	1	76.80	4.05	0.0520
Populations	572.32	2	286.16	15.08	0.0001
Model	629.89	3	209.96	11.07	0.0001
Total	1331.85	40	33.30		

pattern was obviously influenced by the difference between the two species. *Tabebuia ochracea*, a genetically polymorphic species, had consistently low herbivory rates among its individuals, while genetically more homogeneous *T. aurea*/cerrado had high levels of leaf damage. To test this hypothesis, a simple linear regression, using only data from cerrado trees, was produced. There was a highly significant decrease in insect damage as a function of genetic dissimilarity ($r^2 = 0.48$, $F_{1,24} = 22.74$, $P < 0.0001$), which was strongly influenced by the differences between the species (FIGURE 2). Separated regressions for each species were not significant (*T. ochracea*: $F_{1,13} = 0.97$, $P = 0.34$; *T. aurea*: $F_{1,9} = 2.65$, $P = 0.14$).

Herbivory and plant growth

Stem growth did not vary significantly between sites or populations ($F_{2,36} = 0.28$, $P = 0.75$). Thus, pooling the whole data set to test

the direct impact of herbivory on individual growth rates was an acceptable procedure. Mean stem growth per tree was negatively correlated with leaf area lost in the previous leaf cohort, in a stepwise multiple regression ($F_{1,35} = 6.48$, $P < 0.05$, $r^2 = 0.15$, FIGURE 3).

DISCUSSION

Phenotypic variability was high for both species of *Tabebuia*. For both species, the number of leaflets varied from three to seven within a tree, though five was described as the commonest value (Gentry 1992). Normally, each main branch had leaves with a similar number of leaflets, which may be related to polyploidy (M. B. Lobato, UFMG, pers. comm.). However, the trait that varied most within a single tree was leaf area. Despite strong genetic similarities (=common lineage) between *T. aurea*/Pantanal and / cerrado (S.P. Ribeiro & V.K. Brown, unpubl.

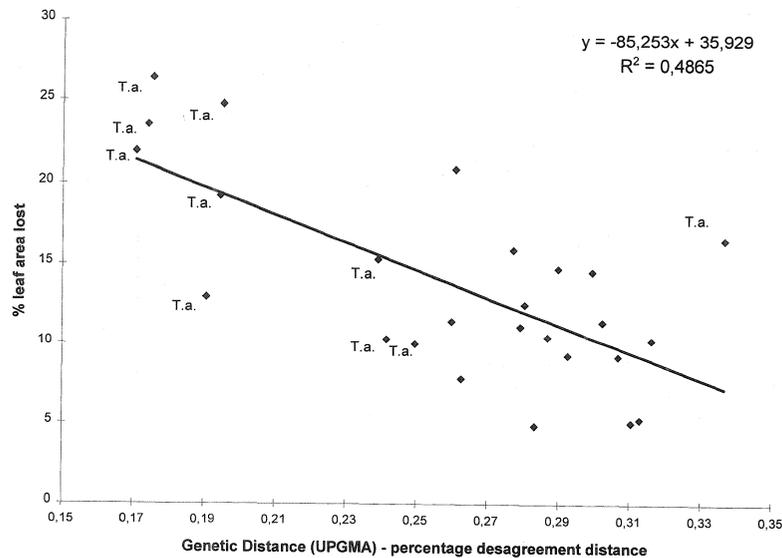


FIGURE 2. Simple linear regression of leaf area lost against genetic distance between individual trees of *Tabebuia aurea* and *T. ochracea* in the cerrado ($r^2 = 0.48$, $F_{1,24} = 22.74$, $P < 0.0001$). (♦ + T.a.) = *T. aurea*; (♦) = *T. ochracea*.

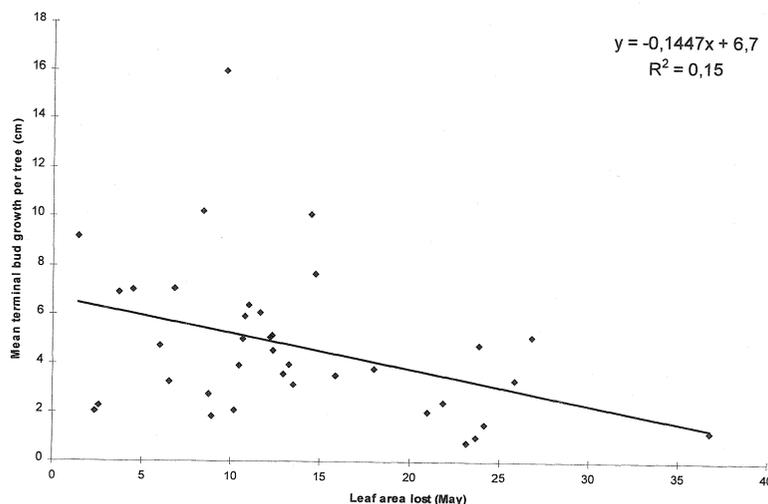


FIGURE 3. Simple linear regression of mean terminal bud growth per tree against leaf area lost in the previous leaf cohort ($r^2 = 0.15$, $F_{1,35} = 6.48$, $P < 0.015$). The three populations were pooled as no difference was found in bud growth among sites or populations.

data), the latter had a greater variability in leaf area, and also the largest leaves. The coefficient of variation of leaf area and SLA for *T. aureal* cerrado was more similar to that found in *T. ochracea* than for the former species' population in the Pantanal. Despite habitat heterogeneity among the cerrado sites, the highly significant within-individual variance suggests common selective pressures in the cerrado compared with the Pantanal, leading to a greater phenotypic differentiation between individuals.

For *Tabebuia ochracea*, which has very hairy leaves (covered with stellate aciculate trichomes above a basal layer of glandular trichomes), the variability in leaf size has a direct impact on insects. In a previous work, Ribeiro et al. (1994) showed that the density of trichomes is inversely correlated with leaf size on *T. ochracea*, and that density of sap-feeding insects on the adult trees is positively correlated with leaf size. An immediate consequence of this mechanical defense is that young leaves (preferred by chewing insects, but less so by specialist sap-feeders) are protected against herbivory in the first days of expansion, by a very dense indumentum. Besides this, a whole sector of the tree may be saved from intense herbivory by having leaf size varying between branches, as shown by Edmund and Alstad (1982) and Whitham (1983).

The existence of chewing and mining varied significantly among branches within trees of *Tabebuia ochracea* and *T. aureal* cerrado. Since leaf-mining insects establish on already expanded leaves, they may reflect a response to leaf size variability rather more. Leaf miners oc-

curred in different densities among branches of *T. ochracea* in both leaf cohorts. However, in the second leaf cohort, in November 1996, when the damage by leaf miners on *T. aureal* cerrado was the highest recorded, no significant variation was observed within trees. In the Pantanal, leaf-miners were distributed evenly within a tree. Although variability per se can be an indicator of resistance, there was no evidence of an association between toughness (SLA) and levels of herbivory. It is difficult to infer a functional reason for such a variance in leaf size for *T. aurea*. Nevertheless, variability in components of plant size is a neglected, though important, component of resistance to herbivory (Clarke & Clarke 1985, Gange & Brown 1989), as was initially described for temperate trees (Whitham & Slobodchikoff 1981, Edmund & Alstad 1982, Whitham 1983).

Coley (1983) and Coley and Aide (1991) showed that annual herbivory rates are around 10% in the tropics, which approaches the annual mean values found for *T. ochracea* and *T. aureal* Pantanal. The similar value for *T. aureal* cerrado was 18%, which approached the maximum observed for ten tree species, from habitats of different successional status in Papua New Guinea (Basset & Hoefl 1994). Similarly, high herbivory rates are difficult to find in tropical habitats. One exception is the Mexican tropical deciduous forest, where Filip et al. (1995) described an average leaf area loss of 17%, mainly due to extremely high herbivory rates on six out of 16 species studied. Dry forests generally have higher herbivory than wet forests (Coley & Barone

1996). High rates of damage (up to 48%) are also common on gap specialists, which are, according to Coley and Barone (1996), a minority of the trees in tropical forest.

High susceptibility to insect attack is commonly observed in monospecific patches. However, this pattern is normally confounded with temperate and homogeneous, versus tropical and heterogeneous forests (Selman and Lowman 1983, Lowman 1995). Apart from the fact that most examples come from the temperate zone, there is a lack of comparative studies for the Neotropical region (Lowman 1995). One particular example of high insect attack on a tropical monodominant was provided by Nascimento and Proctor (1994), who found that, in a specific year, $\frac{2}{3}$ of individuals of *Peltogyne gracilipes* in a monodominant forest had 50 to > 90% defoliation, contrasting with the low attack on trees of this species in a nearby heterogeneous forest, in the Northern Amazon.

Leaf damage can erode fitness, when persisting for a certain period of time (Marquis 1984, 1992). The present results suggest significant insect herbivory pressure, mainly on some highly vulnerable individuals of *Tabebuia aurea*/cerrado. For the two years of study, *T. aurea*/cerrado had consistently the highest levels of leaf loss by insect damage, a trend related to the negative relationship between stem growth and total herbivory, and also to low reproductive success (Ribeiro 1999, S.P. Ribeiro & V.K. Brown, unpubl. data). The high genetic dissimilarity among individuals of *T. ochracea* correlated negatively with leaf damage, contrasting with an opposite trend in both genetic polymorphism and attack on *T. aurea*/cerrado. Conversely, there was a similar leaf damage between *T. ochracea* and *T. aurea*/Pantanal. Low damage on Pantanal trees, however, seems to be more related to the low richness and abundance of herbivores in this habitat (Ribeiro 1999).

Although *Tabebuia aurea*/Pantanal forms a monodominance in a savanna system, leaf area loss in this species happens to be higher on isolated and scarce subpopulations in the cerrado. A previous pilot study carried out in 1994 confirmed the pattern found for the two leaf cohorts sampled in 1996: viz., levels of herbivory in the Pantanal are extremely low. Of course, this is a short time period to evaluate the probability of insect outbreaks, but even if outbreaks do occur, they seem to have little or no impact on the maintenance of the species' monodominance, or on the fitness of individual trees (Ribeiro 1999). Since the reproductive rate seems to be high for this species in the Pantanal, a sporadic defoliation would hardly have any evolutionary or ecological consequence, bearing in mind it is an it-

eroparous species. In addition, an array of unpredictable and disruptive climatic and biotic conditions described for the Pantanal may cause a high and frequent mortality of insects (Ribeiro 1999). Therefore, these severe conditions may have positively influenced the establishment of *T. aurea* as a monodominant stand, by decreasing herbivory. The eventual absence of frequency and density-dependent selective forces, such as those likely to be caused by herbivory, may have favored plants with faster growth rate and higher seed production. Hence, a pioneer tree population can become very robust in an environment constantly under the influence of disturbance.

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APPENDIX 1. Nested ANOVAs for each population. Leaf area lost against branches, trees, and sites.

Source	SS	df	MS	F-test	P
1.0—First leaf cohort					
<i>Tabebuia aurea</i> /Pantanal—Total leaf area lost					
Trees	34788	14	2484.9	6.21	0.001
Branches	10397	26	399.9	1.54	ns
Total	173734	669	259.7		
<i>Tabebuia aurea</i> /Pantanal—Leaf area lost by chewing					
Trees	31355	14	2239.6	5.23	0.001
Branches	11143	26	428.6	1.9	0.050
Total	150643	669	225.2		
<i>Tabebuia aurea</i> /Pantanal—Leaf area lost by mining					
Trees	1321	14	94.4	1.18	ns
Branches	2080	26	80.0	1.83	0.05
Total	29187	669	43.6		
<i>Tabebuia aurea</i> /cerrado—Total leaf area lost					
Sites	6455	2	3227.5	5.06	ns
Trees	7659	12	638.2	2.19	ns
Branches	6715	23	292.0	1.61	ns
Total	60623	334	181.5		
<i>Tabebuia aurea</i> /cerrado—Leaf area lost by chewing					
Sites	5573	2	2786.5	3.69	ns
Trees	9065	12	755.4	2.35	ns
Branches	7381	23	320.9	1.87	0.05
Total	57364	334	171.7		
<i>Tabebuia aurea</i> /cerrado—Leaf area lost by mining					
Sites	34.6	2	17.3	0.26	ns
Trees	808.5	12	67.4	1.63	ns
Branches	951.3	23	41.4	1.82	0.05
Total	7574.4	334	22.7		
<i>Tabebuia ochracea</i> —Total leaf area lost					
Sites	6690	2	3345.0	2.61	ns
Trees	14077	11	1279.7	7.11	0.001
Branches	46.79	26	180.0	1.15	ns
Total	82775	527	157.1		

APPENDIX 1. Continued.

Source	SS	df	MS	F-test	P
<i>Tabebuia ochracea</i> —Leaf area lost by chewing					
Sites	3654	2	1827.0	1.15	ns
Trees	17490	11	1590.0	14.66	0.001
Branches	2819	26	108.4	0.81	ns
Total	70924	527	134.6		
<i>Tabebuia ochracea</i> —Leaf area lost by mining					
Sites	664	2	332.0	1.41	ns
Trees	2576	11	234.2	2.70	0.05
Branches	2255	26	86.7	2.03	0.01
Total	22546	527	42.8		
2.0—Second leaf cohort					
<i>Tabebuia aurea</i> /Pantanal—Total leaf area lost					
Trees	8477	14	605.5	2.16	ns
Branches	7297	26	280.6	2.09	0.01
Total	58416	434	134.6		
<i>Tabebuia aurea</i> /Pantanal—Leaf area lost by chewing					
Trees	7143	14	510.2	2.21	ns
Branches	6014	26	231.3	2.37	0.01
Total	42364	434	97.6		
<i>Tabebuia aurea</i> /Pantanal—Leaf area lost by mining					
Trees	1736	14	124.0	1.68	ns
Branches	1917	26	73.7	1.37	ns
Total	23330	434	53.7		
<i>Tabebuia aurea</i> /cerrado—Total leaf area lost					
Sites	1138	2	569.0	0.61	ns
Trees	8404	9	933.8	2.07	ns
Branches	8105	18	450.3	2.08	0.05
Total	76049	351	216.7		
<i>Tabebuia aurea</i> /cerrado—Leaf area lost by chewing					
Sites	1417	2	708.5	1.48	ns
Trees	4310	9	478.89	1.50	ns
Branches	5756	18	319.78	2.28	0.01
Total	49157	351	140.05		
<i>Tabebuia aurea</i> /cerrado—Leaf area lost by mining					
Sites	554.4	2	277.2	0.88	ns
Trees	2849	9	316.5	3.36	0.05
Branches	1693	18	94.05	0.96	ns
Total	34201	351	97.44		
<i>Tabebuia ochracea</i> —Total leaf area lost					
Sites	725.3	3	241.77	0.58	ns
Trees	4600.0	11	418.18	0.87	ns
Branches	8207.0	17	482.76	4.48	0.001
Total	45697.0	424	107.77		
<i>Tabebuia ochracea</i> —Leaf area lost by chewing					
Sites	1217	3	405.67	12.5	0.010
Trees	357	11	32.45	0.11	ns
Branches	4922	17	289.53	3.32	0.001
Total	37034	424	87.34		
<i>Tabebuia ochracea</i> —Leaf area lost by mining					
Sites	339.4	3	113.13	0.54	ns
Trees	2291.0	11	208.27	1.3	ns
Branches	2720.0	17	160	6.42	0.001
Total	10571.0	424	24.93		

APPENDIX 2. Factorial ANOVAs. Leaf area lost against populations randomly distributed in sites.

Source	SS	df	MS	F-test	<i>P</i>
1.0—First leaf cohort					
Total leaf area lost					
Within + residual	1582.03	31	51.03		
Populations	182.23	2	91.11	1.79	ns
Sites	149.82	3	49.94	0.98	ns
Model	769.05	5	153.81	3.01	0.025
Total	2351.08	36	65.31		
Leaf area lost by chewing					
Within + residual	1560.01	31	50.32		
Populations	195.65	2	97.82	1.94	ns
Sites	97.29	3	32.43	0.64	0.59
Model	741.47	5	148.29	2.95	0.03
Total	2301.49	36	63.93		
Leaf area lost by mining					
Within + residual	96.66	31	3.12		
Populations	13.23	2	6.62	2.12	ns
Sites	17.77	3	5.92	1.90	ns
Model	20.41	5	4.08	1.31	ns
Total	117.07	36	3.25		
2.0—Second leaf cohort					
Total leaf area lost					
Within + residual	717.56	36	19.93		
Populations	394.03	2	197.02	9.88	0.0001
Sites	64.12	3	21.37	1.07	ns
Model	674.36	5	134.87	6.77	0.0001
Total	1391.93	41	33.95		
Leaf area lost by chewing					
Within + residual	565.24	36	15.70		
Populations	190.65	2	95.33	6.07	0.005
Sites	27.93	3	9.31	0.59	ns
Model	408.14	5	81.63	5.20	0.001
Total	973.38	41	23.74		
Leaf area lost by mining					
Within + residual	218.9	36	6.08		
Populations	52.48	2	26.24	4.32	0.02
Sites	28.9	3	9.63	1.58	ns
Model	93.32	5	18.66	3.07	0.02
Total	312.22	41	7.62		