Herbivoria de dossel e sucessão em uma floresta tropical sazonalmente seca no Brasil

Canopy herbivory and succession in a Brazilian tropical seasonally dry forest

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RESUMO

O padrão geral de herbivoria ao longo da sucessão foi descrito principalmente a partir de estudos em florestas temperadas e, principalmente, no sub-bosque. Este é um dos poucos estudos a documentar a herbivoria do dossel em relação aos estágios sucessionais de uma floresta tropical sazonalmente seca. A diversidade de herbívoros de vida livre (mastigadores e sugadores de seiva) e danos nas folhas causados por guildas de insetos (folívoros, minadores e galhadores) foram quantificados na copa de 117 árvores distribuídas em três áreas de estágios intermediário e três de estágio tardio de sucessão de uma floresta tropical sazonalmente seca, na Serra do Cipó, Minas Gerais. A riqueza de mastigadores e sugadores foi maior no estágio de sucessão tardia. A abundância de herbívoros sugadores de seiva também foi maior no estágio tardio, enquanto os insetos mastigadores foram mais abundantes na sucessão intermediária. O dano global das folhas foi maior no estágio intermediário de sucessão. Folivoria foi o tipo mais frequente de dano foliar em ambos os estágios de sucessão, sendo observada em 92,33% das folhas, seguido de mina foliar em 14,58% das folhas e galhas em 5,27% das folhas. Folivoria não mostrou diferença entre os estágios de sucessão, enquanto os minadores de folhas e as galhas

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apresentaram frequências mais altas no estágio intermediário. Esses resultados corroboram em grande parte o padrão anteriormente documentado para as florestas temperadas, de crescente diversidade de herbívoros e de diminuição do dano das folhas ao longo da sucessão. Estudos mais específicos em florestas tropicais, no entanto, não corroboraram o padrão encontrado em regiões temperadas. O presente estudo enfatiza a importância da amostragem através do dossel de múltiplas espécies de plantas e analisando as guildas de herbívoros individualmente para melhor compreensão da herbivoria de dossel em estágios sucessionais de florestas tropicais sazonalmente secas.

PALAVRAS-CHAVE: Estratificação da floresta, floresta decídua, folivoria, guildas herbívoras, regeneração natural.

ABSTRACT

The general pattern of herbivory throughout succession has been drawn chiefly from temperate forest studies and mainly at the understorey. This is one of the very few studies to document canopy herbivory in relation to successional stages of tropical seasonally dry forests. Diversity of free-feeding herbivores (chewing and sap-sucking) and leaf damage caused by insect guilds (folivores, leaf miners and galling insects) were quantified in the canopy of 117 trees distributed in three areas of intermediate stages and three of late stage of succession of a tropical seasonally dry forest, in Serra do Cipó, Minas Gerais, Brazil. The richness of the chewing and sap-sucking guilds of herbivores was higher in late succession stages. The abundance of sap-sucking herbivores was also higher in the late stage, whereas chewing insects were more abundant in the intermediate succession. Overall leaf damage was higher in the earlier stage of succession. Folivory was the most frequent type of leaf damage in both succession stages and was present in 92.33% of the leaves, followed by leaf mining in 14.58% of the leaves, and galls in 5.27% of the leaves. Folivory showed no difference between successional stages, while leaf miners and gallers showed higher frequencies in the intermediate stage. These results largely corroborate the pattern earlier documented for temperate forests, of increasing diversity of herbivores and decreasing leaf damage across succession. More specific studies in tropical forests, however, did not corroborate the pattern found in temperate regions. The present study emphasises the importance of sampling across canopy of multiple plant species and analysing herbivore guilds individually for better understanding herbivory in tropical dry forests.

KEYWORDS: Deciduous forest, folivory, forest layers, herbivore guilds, natural regeneration.

INTRODUCTION

Tropical dry forests (TDFs) are the major and most threatened of all tropical forests (Janzen, 1988; Sánchez-Azofeifa *et al.*, 2005), and are recognized as biodiversity "hotspots" (Miles *et al.*, 2006). Yet, they remain the least studied ecosystem at the tropics (Quesada *et al.*, 2009). TDFs present fertile soils and are valuable source of timber (Espírito-Santo *et al.*, 2009), therefore, these ecosystems have been historically preferred areas for agriculture and human settlement in Mesoamerica, the Caribbean, and South America (Murphy & Lugo, 1986; Maass, 1995; González, 2003).

In Latin America nearly 66% of TDFs have already been lost (Miles *et al.*, 2006; Quesada *et al.*, 2009), and mosaics of forests at different successional stages are the most frequent scenarios (Sanchez-Azofeifa *et al.*, 2005; Quesada *et al.*, 2009). Therefore, there is an urgent need for understanding the regeneration processes of TDFs (Quesada *et al.*, 2009). However, current knowledge on secondary succession of tropical forests regards mostly to plant diversity and composition (Corbet, 1995; Quesada *et al.*, 2009). Least understood remain the changes in insect composition and diversity throughout successional stages (Edwards-Jones & Brown, 1993; Siemann *et al.*, 1999).

Most previous works claim that insect diversity increases throughout succession following increments in plant diversity, habitat structural complexity and resource availability (Southwood *et al.*, 1979; Strong *et al.*, 1984; Corbet, 1995; Siemann *et al.*, 1999; Lewinsohn *et al.*, 2005). In the same way, herbivore population density and leaf damage decreases with succession due to increasing quantitative plant defenses and natural enemies (Feeny, 1976; Godfray, 1985; Edwards-Jones & Brown, 1993; Lewinsohn *et al.*, 2005), and decreasing leaf nitrogen content (Coley *et al.*, 1985). Three aspects concerning this general pattern call for further investigation, and they were the motivation for the present study. The first one is that current knowledge on herbivore distribution and herbivory patterns throughout succession derives mostly from temperate forest studies, and may not apply to TDFs (Quesada *et al.*, 2009; Silva *et al.*, 2011). The second is that a general pattern may be unrealistic as different insect guilds can exhibit different responses to the successional process according to specialization on their host plants and responsiveness to habitat changes (Golden & Crist, 1999; Godfray & Lawton, 2001; Crist *et al.*, 2006; Martinko *et al.*, 2006; Neves *et al.*, 2010a; Silva *et al.*, 2011, Neves *et al.* 2014). The third aspect is that the pattern discussed here was mainly drawn from understorey surveys. Yet, the canopy-understorey gradient affects herbivores distribution (Parker, 1995; Basset, 2001; Basset *et al.*, 2003; Novotny *et al.*, 2003, Neves *et al.* 2014) and, as it is less intense in earlier stages of succession, comparisons of herbivory between successional stages based on understorey data may be biased.

The aim of the present study was to analyse, in a TDF, canopy herbivory by different guilds (chewing, sap-sucking, leaf miners and galls) and distribution of herbivore insects in trees of different successional stages. Specifically, (i) determine how the richness and abundance of different insect guilds (chewing, sap-sucking) are affected by succession; (ii) determine how the levels of herbivory by different insect guilds (folivores, leaf miners and gallers) are affected by succession.

Methods

Study site: Fieldwork was carried out in April 2009, at the end of the wet season, in Serra do Cipó, Minas Gerais, Brazil. This region is located at the southern portion of the Espinhaço Mountain Range, which is dominated by Cerrado (Savannah-like vegetation) and rupestrian grasslands, a rocky outcrop vegetation (Eiten, 1978; Giulietti *et al.*, 1987). The climate is marked by dry winters and rainy summers (Schulz & Machado, 2000). Fragments of secondary dry forests are usually found surrounded by pasturelands or, at the highest elevations, mixed with rupestrian grasslands. We compared two natural fragments of TDFs (2.5 ha per site) of different successional stages (elevation c. 900m asl, 19°20'S, 43°36'W; 19°19'S, 43°36'W). The fragments formerly comprised a single unit that was separated by anthropogenic activities. These forests were primarily used for logging and mining in the past, and currently are in processes of natural regeneration. Successional stages were identified based on land use history (see Nassar *et al.*, 2008) and confirmed by floristic composition and structure (Coelho *et al.*, 2012). The earlier succession fragment is about 15 years old, comprised 23 tree species (11 families) with average height of 6.30 (± 1.62 SD) and basal area of 17.8 $m^2 \cdot ha^{-1}$ forming a single forest layer. The fragment in late stage of succession has been under protection for nearly 30 years, presented 38 tree species (18 families) with average height of 7.77 (±2.93 SD) and basal area of 29.3 $m^2 \cdot ha^{-1}$ (Coelho *et al.*, 2012). In the older fragment, the canopy and understory layers are fairly well distinguishable and emergent trees of up to 20 meters were frequently found, in opposition to the fragment of earlier succession.

Sampling of free-feeding herbivores: To compare the richness and abundance of the free-feeding herbivores between the successional stages, chewing and sap-sucking insects were sampled through the beating method (see Basset *et al.*, 1997; Neves *et al.*, 2010b), at the upper forest canopy, combining single-rope and free climbing techniques to access the treetops (Perry, 1978; Lowman & Wittman, 1996). The beating method consists of vigorously beating with a wooden stick 10 times on each of three branches haphazardly chosen around the crown of each tree, totaling 30 hits per individual plant. In each of the two successional stages, three plots of 20 x 50 m (0.1 ha each) were established (for details see Nassar *et al.*, 2008). Plots of the same successional stage were located 0.2-0.5 km apart from each other. Based on the plant-insect interactions literature, this distance is considered long enough to avoid pseudo-replication between plots (see Silva *et al.*, 2011). Each successional plot of the same age was located under similar topographic, microclimatic and soil characteristics (See Madeira *et al.*, 2009), thus reducing variation in physical conditions that could affect succession. In each plot, 17 to 20 trees (>15 cm dbh) of different heights were arbitrarily chosen for sampling regardless of species. In total, 117 trees were sampled, 57 at the earlier stage (10 species) and 60 at the late stage (17 species). The collected herbivorous insects were sorted into sap-sucking and chewing guilds (see Weis & Berenbaum, 1989) and identified to family level (Borror *et al.*, 2002). The sap-feeding guild comprised all adults and juveniles of the Hemiptera herbivore families (Auchenorryncha, Sternorryncha and Heteroptera; see Moran & Southwood, 1982). Juveniles of Lepidoptera and adults and juveniles of Coleoptera and Orthoptera composed the chewing guild of herbivores (see Moran & Southwood, 1982). Herbivores were separated into morphospecies using external morphological characters. All collected insects were submitted to the thematic zoological collection of the Laboratório de Biologia da Conservação, at the Universidade Estadual de Montes Claros. Insect species richness per tree was estimated by counting the number of morphospecies, while abundance was estimated through the accumulated number of individuals per tree

Leaf damage assessment: To quantify leaf damage caused by different insect guilds (i.e. folivores, leaf miners and galls), 30 mature leaves were randomly collected from three branches around the crown of each tree (10 leaves per branch). The frequency of damaged leaves was quantified by counting the number of leaves “substantially damaged” (>10% of leaf area lost; following Coley & Aide, 1991), leaves presenting galls, and leaves with mines.

Logistic regression analyses using GENMOD were performed to test the effect of successional stages (independent variable) on the richness and abundance of sap-sucking and chewing herbivores and on the frequency of leaf damage (dependent variables). Because the distribution of these variables did not follow a normal distribution, we used a Poisson or Binomial distribution for the dependent variables, with a logarithmic link function using the GENMOD procedure from SAS (Stokes *et al.*, 2000). A LSMeans test was used for a posteriori comparisons (SAS, 2000).

Results

Richness and abundance of free-feeding herbivores: In total, 356 free-feeding herbivore insects (276 chewers and 80 sap-sucking), belonging to 16 families, were collected, on an average of 3.86 (± 0.37 SE) insects per tree. The most abundant families were Cicadelidae and Curculionidae, for sap-suckings and chewing respectively. There was a significant increase in richness of both chewing and sap-sucking herbivores with succession ($x^2 = 4.5$; d.f. = 1, $P < 0.03$; Figure 1). Chewing insects were more abundant in the earlier stage of succession ($x^2 = 7.6$; d.f. = 1, $P< 0.005$; Figure 2). On the other hand, the abundance of the sap-sucking guild was higher in the later stage ($x^2 = 7.6$; d.f. = 1, $P < 0.005$; Figure 2).

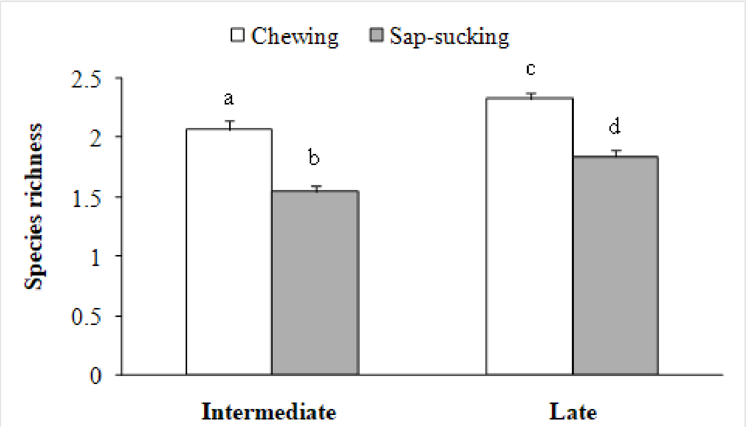

Figure 1 - Average richness of the chewing (white bars) and sap-sucking (grey bars) guilds of free-feeding insect herbivores in trees from intermediate and late successional stages of a tropical dry forest, in Minas Gerais, Brazil. Different letters indicate statistically significant *post hoc* differences ($P < 0.05$).

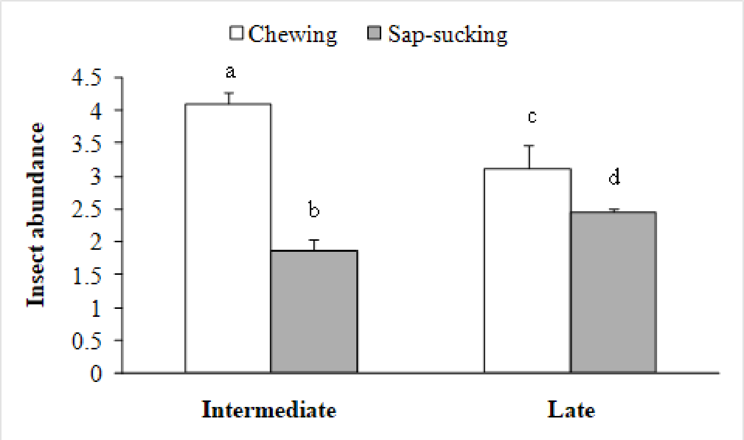

Figure 2 - Average abundance of the chewing (white bars) and sap-sucking (grey bars) guilds of free-feeding insect herbivores in trees of intermediate and late successional stages of a tropical dry forest, in Minas Gerais, Brazil. Different letters indicate statistically significant *post hoc* differences ($P < 0.05$).

Leaf damage: Very few leaves (5.64%) were completely free from damage by insect. Folivory was the most frequent type of leaf damage in both succession stages ($x^2 = 243.5$; d.f. = 2, $P < 0.0001$; Figure 3), and it was observed on 92.33% of the sampled leaves, followed by miners (14.58%) and galls (5.27%). There was a higher frequency of the overall leaf damage (folivory, galls, and miners combined) in the earlier stage of succession ($x^2 = 5.2$; d.f. = 1, $P = 0.02$; Figure 3), and higher frequencies of leaf miners and galls in this stage than in the later successional stage ($x^2 = 243.5$; d.f. = 2, $P < 0.0001$; Figure 3). Folivory did not differ between successional stages (Figure 3).

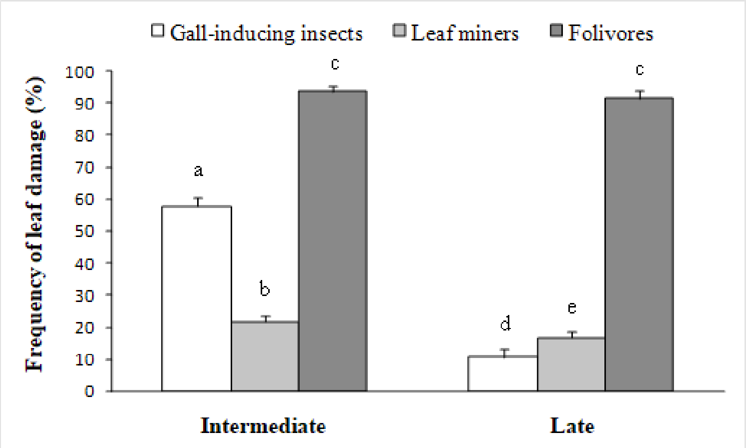

Figure 3 - Average percentage of leaves damaged by gall inducing insects (white bars), leaf miners (light grey bars) and folivores (grey bars) in trees of intermediate and late successional stages of a tropical dry forest in Minas Gerais, Brazil. Different letters indicate statistically significant *post hoc* differences ($P < 0.05$).

Discussion

The increase in richness of both chewing and sap-sucking herbivores with succession corroborates the general trend identified for temperate forests (Southwood *et al.*, 1979; Strong *et al.*, 1984; Corbet, 1995; Siemann *et al.*, 1999; Lewinsohn *et al.*, 2005). Because each plant species potentially represents a different resource for herbivores, insect richness is expected to track changes in plant-species richness (Southwood *et al.*, 1979; Strong *et al.*, 1984; Corbet, 1995; Denno & Perfect 1994; Siemann *et al.*, 1999; Cuevas-Reyes *et al.*, 2004). However, factors correlated to plant species diversity, such as structural complexity and vertical stratification, are likely be the underlying causes of the observed pattern (Southwood *et al.*, 1979; Corbet, 1995; Siemann *et al.*, 1999; Basset *et al.*, 2003; Madeira *et al.*, 2009). Forest vertical stratification increases with succession as canopy is shaped (Guariguata & Ostertag, 2001; Basset *et al.*, 2003; Lewinsohn *et al.*, 2005; Madeira *et al.*, 2009). Differences in illumination, temperature, relative humidity and water condensation between upper canopy and lower layers of a forest create different vertical strata. This leads to increased niche diversity and influences vertical distribution of herbivore insects (Parker, 1995; Basset, 2001; Basset *et al.*, 2003; Novotny *et al.*, 2003, Neves *et al.* 2014). Consequently, sampling only in understory underestimates richness and abundance of late succession forests. Comparisons of herbivory between successional stages of tropical forests ought to include canopy data.

The higher abundance of chewing insects in the earlier stage of succession is in accordance with the "resource availability hypothesis" (Coley *et al.*, 1985): plants in earlier succession stages would have greater growth rates and lower levels of defence compared to later stages, allowing specialist herbivores to have greater intrinsic rate of increase (Lawton & McNeill, 1979; Godfray, 1985; Edwards-Jones & Brown, 1993). Also, the increase in abundance of natural enemies throughout succession intensifies top-down limitation to herbivore population size (Lewinsohn *et al.*, 2005). On the other hand, higher abundance of sap-sucking guild in the later stage is most likely because sap-sucking insects are not much affected by chemical defences as they feed directly on sap assimilates (Strong *et al.*, 1984). Apparently, different guilds can exhibit different responses to succession (Neves *et al.*, 2010b; Silva *et al.*, 2011, Neves *et al.* 2014). Some herbivore insects are especially responsive to ontogenetic alterations in nutritional and defensive traits of their hosts across succession (Campos *et al.*, 2006; Fonseca *et al.*, 2006; Costa *et al.*, 2011), while others respond mainly to changes in plant size, phenology and architecture (Strong *et al.*, 1984; Espírito-Santo *et al.*, 2007).

Folivory rates were very high in both succession stages. TDFs usually suffer greater folivory than wetter forests, apparently as a result of a lower investment in chemical defences in their short-lived leaves (Dirzo & Boege, 2008). In spite of the greater abundance of chewers in the earlier stage of succession, folivory did not differ between stages. The higher frequency of the overall leaf damage (folivory, galls, and miners combined) in the earlier stage of succession is therefore due to higher frequencies of leaf miners and galls in this successional stage.

Discrete measurements can lead to a considerable underestimation of the leaf damage levels (Lowman, 1984). Nevertheless, for TDFs, this could possibly be less problematic than for other tropical forest types since that most plant species flush the new leaves simultaneously at the beginning of the wet season, with virtually no posterior production, and tend to retain them until the next dry season (Ackerly, 1996; Kikuzawa, 1983; Morellato *et al.*, 2000). As a result, most leaf damage occurs in synchrony at the beginning of the season, when the soft young leaves are launched (Janzen & Waterman, 1984; Filip *et al.*, 1995; Boege, 2005). Thus, a discrete measurement of the accumulated damage at the end of the season should account for most of the herbivory.

In general, the results reported here largely corroborate earlier studies carried out in temperate forests, reporting greater diversity (Southwood *et al.*, 1979; Strong *et al.*, 1984; Corbet, 1995; Siemann *et al.*, 1999) but lower frequency of leaf damage and lower density of herbivore insects (Godfray, 1985; Edwards-Jones & Brown, 1993) in the later stages of succession. Conversely, more specific studies on herbivory across tropical forest succession found different trends (Brown & Ewel, 1987; Lepš *et al.*, 2001; Poorter *et al.*, 2004; Silva *et al.*, 2011, Neves *et al.* 2014). This disparity may be an outcome of differences in the methods applied: samples here were taken at the canopy of multiple host plant species and the herbivore insect guilds were approached separately.

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References

Ackerly, D.D. (1996) Canopy structure and dynamics: integration of growth processes in tropical pioneer trees. In: Mulkey, S.S.; Chazdon, R.L.; Smith, A.P. (Ed.) *Tropical forest plant ecophysiology*. New York: Chapman and Hall, p. 619-658.

Basset, Y.N.D., Springate, Aberlenc, H.P., Delvare, G. (1997) A review of methods for sampling arthropods in tree canopies. In: Stork, N.E.; Adis, J.; Didham, R.K. (Ed.) *Canopy Arthropods*. London: Chapman and Hall, p. 619-658.

Basset, Y.N.D. (2001). Communities of insect herbivores foraging on mature trees vs. seedlings of *Pourouma bicolor* (Cecropiaceae) in Panama. *Oecologia*, 129: 253-260.

Basset, Y.N.D., Hammond, P.M., Barrios, H., Holloway, J.D., Miller, S.E. (2003). Vertical stratification of arthropod assemblages. In: Basset, Y.; Novotny, V.; Miller, S.E.; Kitching, R.L. (Ed.) *Arthropods of tropical forests – spatio-temporal dynamics and resource use in the canopy*. Cambridge: Cambridge University Press, p. 17-27.

Boege, K. (2005). Herbivore attack in *Casearia nitida* influenced by plant ontogenetic variation in foliage quality and plant architecture. *Oecologia*, 143: 117-125.

Borror, D.J., Triplehorn, C.A., Johnson, N.F. (2002). *An introduction to the study of insects*. Philadelphia: Saunders College Publishing.

Brown, B.J., Ewel, J.J. (1987). Herbivory in Complex and Simple Tropical Successional Ecosystems. *Ecology*, 68: 108-116.

Campos, R.I., Vasconcelos, H.L., Ribeiro, S.P., Neves, F.S., Soares, J.P. (2006). Relationship between tree size and insect assemblages associated with *Anadenanthera macrocarpa*. *Ecography*, 29: 442-450.

Coelho, M.S., Almada, E.D., Quintino, A.V., Fernandes, G.W, Santos, R.M., Sanchez-Azofeifa, G.A., Espírito-Santo, M.M. (2012). Floristic composition and structure of a seasonally dry tropical forest at different successional stages in the Espinhaço mountains, southeastern Brazil. *Interciencia*, 37: 190-196.

Coley, P.D., Bryant, J., Chapin III, F. (1985). Resource availability and plant antiherbivore defense. *Science*, 230: 895-899.

Coley, P.D., Aide, T.M. (1991). Comparison of herbivory and plant defense in temperate and tropical broad-leaved forests. In: Price, P.W.; Lewinsohn, T.M.; Fernandes. G.W.; Benson, W.W. (Ed.) *Plant animal interactions: evolutionary ecology in tropical and temperate regions*. New York, John Wiley and Sons, pp. 25–49.

Corbet, S.A. (1995). Insects, plants and succession: advantages of long-term set aside. *Agriculture, Ecosystems & Environment*, 53: 201-217.

Costa, F.V., Neves, F.S., Silva J.O., Fagundes, M. (2011). Relationship between plant development, tannin concentration and insects associated with *Copaifera langsdorffii* (Fabaceae). *Arthropod-Plant Interactions*, 5: 9-18.

Crist, T.O., Pradhan-Devare, S.V., Summerville K.S. (2006). Spatial variation in insect community and species responses to habitat loss and plant community composition. *Oecologia*, 147: 510-521.

Cuevas-Reyes, P., Hanson, P., Dirzo, R., Oyama, K. (2004). Diversity of gall-inducing insects in a Mexican tropical dry forest: The importance of plant species richness, life forms, host plant age and plant density. *Journal of Ecology*, 92: 707-716.

Denno, R.F., Perfect, T.J. (1994). *Plant hoppers: their ecology and management*. New York: Chapman and Hall.

Dirzo R., Boege K. (2008). Patterns of herbivory and defense in tropical dry and rain forests. In: Carson, W.; Schnitzer, S.A. (Ed.) *Tropical forest community ecology*. West Sussex: Blackwell Science, p. 63-78.

Edwards-Jones, G., Brown, V.K. (1993). Successional trends in insect herbivore population densities: a field test of a hypothesis. *Oikos*, 66: 463-471.

Eiten, G. (1978). Delimitation of Cerrado concept. *Vegetation*, 36: 169-178.

Espírito-Santo, M.M., Neves, F.S., Andrade-Neto, F.R., Fernandes, G.W. (2007). Plant architecture and meristem dynamics as the mechanisms determining the diversity of gall-inducing insects. *Oecologia*, 153: 353-364.

Espírito-Santo, M.M., Sevilha, A.C., Anaya F.C., Barbosa, R., Fernandes, G.W., Sanchez-Azofeifa, G.A., Scariot, A., Noronha, S.E., Sampaio, C.A. (2009). Sustainability of tropical dry forests: Two case studies in southeastern and central Brazil. *Forest Ecology and Management*, 258: 922-930.

Feeny, P.D. (1976). Plant appearance and chemical defence. *Recent Advances in Phytochemistry*, 10: 1-40.

Filip, V., Dirzo, R.J., Maass, M., Sarukhán, J. (1995). Within- and among-year variation in the levels of herbivory on the foliage of trees from a Mexican tropical deciduous forest. *Biotropica*, 27: 78-86.

Fonseca, C.R., Fleck, T., Fernandes, G.W. (2006). Processes driving ontogenetic succession of galls in a canopy tree. *Biotropica*, 38: 514-521.

Giulietti, A.M., Menezes, N.L., Pirani, M.M., Wanderley, M.G.L. (1987). Flora da Serra do Cipó, Minas Gerais: caracterização e lista das espécies. *Boletim de Botânica*, 9: 1-151.

Godfray, H.C.J. (1985). The Absolute Abundance of Leaf Miners on Plants of Different Successional Stages. *Oikos*, 45: 17-25.

Godfray, H.C.J., Lawton, J.H. (2001). Scale and species numbers. *Trends in Ecology and Evolution*, 16: 400-404.

Golden, D.M., Crist, T.O. (1999). Experimental effects of habitat fragmentation on old-field canopy insects: species, guild, and community responses. *Oecologia*, 118: 371-380.

González, V. (2003). Bosques secos. In: Aguilera, M.; Azócar, A.; González-Jimánez, E. (Ed.) *Biodiversidad en Venezuela*, Tomo II. Caracas: Fundación Polar y Editorial ExLibris, p. 734-744.

Guariguata, M.R., Ostertag, R. (2001). Neotropical secondary forest succession: changes in structural and functional characteristics. *Forest Ecology and Management*, 148: 185-206.

Janzen, D.H., Waterman, P.G. (1984). A seasonal census of phenolics, fibre and alkaloids in foliage of forest trees in Costa Rica: some factors influencing their distribution and relation to host selection by Sphingidae and Saturniidae. *Biological Journal of the Linnean Society*, 21: 439-454.

Janzen, D.H. (1988). Tropical dry forests: the most endangered major tropical ecosystem. In: Wilson, E.O. (Ed.) *Biodiversity*. Washington, DC: National Academy Press, p. 130-137.

Kikuzawa, K. (1983). Leaf survival of woody plants in deciduous broadleaved forests. Tall trees. *Canadian Journal of Botany*, 62: 2551-2556.

Lawton, J.H., McNeil, S. (1979). Between the devil and the deep blue sea: on the problems of being a herbivore. In: Anderson, R.M.; Turner, B.D.; Taylor, L.R. (Ed.) *Population dynamics*. Oxford: Blackwell, p. 223-244.

Lepš, J., Novotny, V., Basset, Y. (2001). Habitat and successional status of plants inrelation to the communities of their leaf-chewing herbivores in Papua New Guinea. *Journal of Ecology*, 89: 186-199.

Lewinsohn, T.M., Novotny, V., Basset, Y. (2005). Insects on plants: diversity of herbivore assemblages revisited. *Annual Review of Ecology, Evolution, and Systematics*, 36: 597-620.

Lowman, M.D. (1984). An assessment of techniques for measuring herbivory: Is rain forest defoliation more intense than we thought? *Biotropica*, 16(4): 264-68.

Lowman, M.D., Wittman, P.K. (1996). Forest canopies – methods, hypotheses and future directions. *Annual Review of Ecology, Evolution, and Systematics*, 27: 55-81.

Maass, J.M. (1995). Conversion of tropical dry forest to pasture and agriculture. In: Bullock, S.H.; Mooney, H.A.; Medina, E. (Eds.)

Seasonally Dry Tropical Forests. New York: Cambridge University Press, p. 399-422.

Madeira, B.G., Espírito-Santo, M.M., D'ÂngeloNeto, S., Nunes, Y.R.F., Sánchez-Azofeifa, A.S., Fernandes, G.W., Quesada, M. (2009). Changes in tree and lianas communities along a successional gradient in a tropical dry forest in southeastern Brazil. *Plant Ecology*, 201: 291-304.

Martinko, E.A., Hagen, R.H., Griffith, J.A. (2006). Successional change in the insect community of a fragmented landscape. *Landscape Ecology*, 21: 711-721.

Miles, L., Newton, A.C., Defries, R.S., Ravilious, C., May, I., Blyth, S., Kapos, V., Gordon, J.E. (2006). A global overview of the conservation status of tropical dry forests. *Journal of Biogeography*, 33: 491-505.

Moran, C.V., Southwood, T.R.E. (1982). The guild composition of arthropod communities in trees. *Journal of Animal Ecology*, 51: 289-306.

Morellato, L.P.C., Talora, D.C., Takahasi, A., Bencke, C.C., Romera, E.C., Ziparro, V.B. (2000). Phenology of Atlantic rain forest trees: a comparative study. *Biotropica*, 32: 811-823.

Murphy, P.G., Lugo, A.E. (1986). Ecology of tropical dry forest. *Annual Review of Ecology, Evolution, and Systematics*, 17: 67-88.

Nassar, J.M., Rodríguez, J.P., Sánchez-Azofeifa, A., Garvin, T., Quesada, M. (2008). *Manual of Methods: Human, Ecological and Biophysical Dimensions of Tropical Dry Forests*. Caracas: Ediciones IVIC Instituto Venezolano de Investigaciones Científicas.

Neves, F.S., Braga, R.F., Espírito-Santo, M.M., Delabie, J.H.C., Fernandes, G.W., Sánchez-Azofeifa, G.A. (2010a). Diversity of arboreal ants in a Brazilian Tropical Dry Forest: Effects of seasonality and successional Stage. *Sociobiology*, 56: 177-194.

Neves, F.S., Araújo, L.S., Fagundes, M., Espírito-Santo, M.M., Fernandes, G.W., Sánchez-Azofeifa, G.A., Quesada, M. (2010b). Canopy herbivory and insect herbivore diversity in a dry forest-savanna transition in Brazil. *Biotropica*, 42: 112-118.

Neves, F.S., Silva, J.O., Fernandes, G.W. (2014). Insect Herbivores and Leaf Damage along Successional and Vertical Gradients in a Tropical Dry Forest. *Biotropica* 46: 14-24.

Novotny, V., Basset, Y., Kitching, R. (2003). Herbivore assemblages and their food resources. In: Basset, Y.; Novotny, V.; Miller, S.; Kitching, R. (Ed.) *Arthropods of Tropical Forests: Spatio-Temporal Dynamics and Resource Use in the Canopy*. Cambridge: Cambridge University Press, p. 40-53.

Parker, G.G. (1995). Structure and microclimate of forest canopies. In: Lowman, M.D.; Nadkarni, N.M. (Ed.) *Forest canopies*. San Diego: Academic Press, p. 431-455.

Perry, D.R. (1978). A method of access into the crowns of emergent and canopy trees. *Biotropica*, 10: 155-157.

Poorter, L., Van de Plassche, M., Willems, S., Boo, R.G.A. (2004). Leaf traits and herbivory rates of tropical tree species differing in successional status. *Plant Biology*, 6: 746-754.

Quesada, M., Sánchez-Azofeifa, G.A., Alvarez-Añorve, M., Stoner, K.E., Avila-Cabadilla, L., Calvo-Alvarado, J., Castillo, A., Espírito-Santo, M.M., Fagundes, M., Fernandes, G.W., Gamon, J., Lopezaraiza-Mikel, M., Lawrence, D., Morellato, L.P.C., Powers, J.S., Neves, F.S., Rosas-Guerrero, V., Sayago, R., Sanchez-Montoya, G. (2009). Succession and management of tropical dry forests in the Americas: Review and new perspectives. *Forest Ecology and Management*, 258: 1014-1024.

Sánchez-Azofeifa, G.A., Quesada, M., Rodríguez, J. P., Nassar, J.M., Stoner, K.E., Castillo, A., Garvin, T., Zent, E.L., Calvo-Alvarado, J.C., Kalacska, M.E.R. (2005). Research priorities for Neotropical dry forests. *Biotropica*, 37: 477-485.

SAS (2000). Categorical data analysis using the SAS system. Cary: SAS Institute.

Schulz, R., Machado, M. (2000). *Uebelmannia and their environment*. São Paulo: Schulz Publishing.

Siemann, E., Haarstad, J., Tilman, D. (1999). Dynamics of plant and arthropod diversity during old field succession. *Ecography*, 22: 406-414.

Silva, J.O., Espírito-Santo, M.M., Melo, G.A. (2011). Herbivory on *Handroanthus ochraceus* (Bignoniaceae) along a successional gradient in a tropical dry forest. *Arthropod-Plant Interaction*, 6: 45-57.

Southwood, T.R.E., Brown, V.K. & Reader, P.M. (1979). The relationships of plant and insect diversity in succession. *Biological Journal of the Linnean Society*, 12: 327-348.

Stokes, M.E., Davis, C.S., Koch, G.G. (2000). *Categorical data analysis using the SAS system*. Second Ed. Cary: SAS Institute.

Strong, D.R., Lawton, J.H., Southwood, T.R. (1984). *Insects on Plants: Community Patterns and Mechanisms*. London: Blackwell Scientific Publication.

Weis, A.E., Berenbaum, M.R. (1989). Herbivorous insects and green plants. In: Abrahamson, W.G. (Ed.) *Plant-Animal Interactions*. New York: Mc Graw-Hill, p. 123-162.