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NUTRITIONAL COMPOSITION, IN VITRO DEGRADATION AND POTENTIAL FERMENTATION OF TREE SPECIES GRAZED BY RUMINANTS IN SECONDARY VEGETATION (ACAHUAL) OF DECIDUOUS FOREST

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ABSTRACT

Study conducted to know the nutritional composition, in vitro degradation and the potential fermentation of tree leaves species grazed by ruminants in secondary vegetation of a deciduous forest. Tree leaves were selected from 18 tree species that were subjected to in vitro fermentation. Fermentation variables were analyzed with a designed block repeated over time. The content of CP, NDF and ADF fluctuated among species, from 109 to 262, 391 to 641 and 322 to 579 g kg⁻¹of DM, respectively. The concentrations of condensed tannins (CT) presented a wide variation among species and ranged from 1.73 to 233.45 g kg⁻¹ DM. The significant differences (P < 0.05) observed among species in fermentation and digestibility. G. floribundum, M. lindeniana, V. gaumeri, H. barvensis, T. amygdalifolia and C. gaumeri had the highest gas volume (155 to 293.88 mL g⁻¹), total fermentation (379.45 to 677.39 mg g⁻¹), fermentation rate (0.031 to 0.038 h⁻¹), and soluble fraction (178.3 to 265 g kg of DM⁻¹). In addition, they had highest values of the rapid fermentation fractions (123.58 a 214.88 mg g⁻¹), medium fermentation (37.07 to 217.87 mg g⁻¹), and slow fermentation fractions (162.33 to 244.64 mg g⁻¹), and the highest IVDMD values (39.71 to 54.93%) and IVOMD (47.96 to 66.50%). The species H. albicans, P. piscipula, B. divaricata, L. rugosus, N. emarginata and M. bahamensis had the lowest potential fermented gas emission index (181.13, 181.19, 200.59, 206.36 and 217.24 mL g⁻¹MOD). It is concluded that the species G. floribundum, M. lindeniana, V. gaumeri, H. barvensis, T. amygdalifolia and C. gaumeri present in the secondary vegetation of the forest have a good potential in the feeding of ruminants due to their highest fermentability in the rumen.

Key words: IVOMD, fermentation kinetics, tree leaves, secondary metabolites.

INTRODUCTION

Tropical forest that is managed for agricultural purposes are crossed by different successional stages of secondary vegetation ("acahuales") and its composition is characterized by a diversity of trees, shrubs, grasses, creepers and herbaceous plants (González et al., 2014; López et al., 2014), which provides leaves, flowers, pods and edible fruits for ruminants (González et al., 2015). In the tropics, during the dry season, acahuales are a resource of high value for small producers because they use it as a natural silvopastoral management strategy for feeding their animals (Torres et al., 2016; Gómez, 2017), especially in southern Mexico (González et al., 2015). Its use in livestock systems allows a noticeable reduction in production costs, helps to adapt and mitigate climate change impacts (Dambe et al., 2015) and provides a variety of benefits and services to society and the ecosystem (Nahed et al., 2013). Mainly, because the acahual enhances a greater carbon capture and maintains a high diversity of plant species that is used in multiple purposes (Pearson *et al.*, 2017). However, despite the local knowledge related to the use and management of secondary vegetation (Nahed *et al.*, 2013), the high vegetal diversity present in the tropics and its contribution to ecosystem services (Chazdon, 2014). There is little researches done to study its potential as an animal feed source, both in the nutritional value of the different species and in terms of forage productivity (Giuburuncă *et al.*, 2014); with the purpose to incorporate promising tree species (Girma *et al.*, 2015) into specific animal production systems in association with grasses or to design a sustainable management of *acahuales* under grazing (Malézieux, 2012).

Plant species that have shown forage potential are notable for their high protein content and high ruminal fermentation of carbohydrates. In addition, they have a high concentration of secondary compounds (Hartmann, 2007), such as polyphenols, non-protein amino acids, cyanogen's, alkaloids and saponins (Patra

and Saxena, 2010). The concentration of these compounds varies among the species of plants according to the edaphic and climatic characteristics, and on the time harvested of the year (Bodas et al., 2008). Although it is not entirely clear what is the implications of secondary compounds on ruminant feed (Patra and Saxena, 2010), they have been shown to modulate microbial populations in the rumen (Bodas et al., 2012). Allowing an improvement in the fermentation and the use of nitrogen (N), and increase in the productivity of the animals (Piñeiro et al., 2016). Therefore, it is essential to evaluate the effect of the secondary metabolites and identify the main nutritional components that determine the digestibility and the in vitro fermentation characteristics, as indicators of the nutritional value of the beneficial plant species that consumed by cattle under grazing in the acahuales. In this study, it is hypothesized that plant species that have a high content of secondary metabolites and cell wall compounds will maintain less fermentation and in vitro organic matter digestibility. So that the objective of the study was to evaluate the nutritional composition, the in vitro degradation and potential fermentation of 18 tree species consumed by cattle under free grazing in a deciduous forest.

MATERIALS AND METHODS

Plant selection: Plant material was collected from 14 cattle ranches that representing 20% of the total production units located in the town of Tenabo. Campeche, Mexico. The ranches were chosen at random and permission was requested from the owners through a community assembly where the objective of the study was announced. The participating ranches were located among the meridians 90 ° 03 '10 " and 90 ° 29' 26" west longitude and among 19 $^{\circ}$ 48 '30 " and 20 $^{\circ}$ 08' 44" north latitude. In this region the predominant climate is warm semi humid, with annual average temperature and precipitation of 27.3 °C and 1200 mm as described by García (1973). The predominant vegetation is deciduous forest and the height of the trees varies among 6 and 12 meters (Miranda and Hernández, 1963) and their diameters among 10 and 30 cm as mentioned by Flores and Espejel (1994). The abundant species in this type of forest are Acacia gaumeri, Alvaradoa amorphoides, Bursera simaruba, Caesalpinia gaumeri, Cohniella vucatanensis, Ceiba aesculifolia, Diospyros cuneata, Gymnopodium floribundum, Hampea trilobata, Jatropha gaumeri, Neomillspaughia emargiata, Parmentiera aculeata, Piscidia piscipula, Randia longiloba, Sideroxylon americanum. These tree species were also reported in earlier literature (Flores and Espejel, 1994), as species in the secondary vegetation.

The plant material collections were carried out during the rainy season (August to October 2015) and to obtain the material, one kilometer transects were

established in each sampling unit (ranch) as reported by Jansson (2001). In each transect, the voluntary intake of five adult cows was monitored. In each cow, the selection and consumption of the species were observed during the grazing time and samples were taken from the leaves selected by the animals. Additionally, in each transect, botanical samples were obtained for the identification of the species in the herbarium. From the total tree species selected by cows, young and mature leaves of emargiata, Tabernaemontana Neomillspaughia amvgdalifolia, Piscidia piscipula, Gymnopodium floribundum, Havardia albicans, Lonchocarpus rugosus, Guazuma ulmifolia, Lysiloma latisiliquum, Luecaena leucocephala, Pithecellobium albicans, Haematoxylum campechianum, Mimosa bahamensis, Bursera simaruba, Caesalpinia gaumeri, Helicteres barvensis, Machaonia lindeniana, Vitex gaumeri, and Bauhinia divaricata were selected due to their highest consumption by animals. Leaves samples were dried at 60 ° C for 48 hours and ground in a hammer mill Willey at a particle size of 1

Nutrient Analysis

Chemical analysis: Total nitrogen content (N) of each forage sample was determined by combustion on a LECCO CN-2000 analyzer (Series 3740; LECCO Corporation); and organic matter (OM) by combustion of the samples in muffle at 600 ° C for 6 h (AOAC, 2006). The neutral detergent fiber (NDF), acid detergent fiber (ADF), hemicellulose, cellulose and lignin were measured according to Van Soest et al. (1991) and ethereal extract (EE) by AOAC method (AOAC, 2006). condensed tannins were determined spectrophotometry of the methanolic extracts of the samples where Catechin (5mg / mL) was used as a standard (Makkar et al., 2007). The determination of saponins was performed qualitatively from the aqueous extracts and using pure saponin as standard (Makkar et al., 2007). Cyanogenic glycosides and alkaloids were determined according to the technique described by Rosales (1989). An extraction was performed by adding 30 ml of a 9: 1 mixture of methanol-water, taking the lower or polar phase, and the Wagner reagent was used to identify the cocaine hydrochloride, tertiary ammonium and quaternary alkaloids.

In vitro gas production: in vitro gas production was determined using the gas production technique proposed by Menke and Steingass (1988) and modified by Theodorou et al. (1994). Experimental treatments were the leaves of the 18 tree species collected with six replicates per treatment. In each treatment 500 mg of dry and ground leaves and 90 mL of the ruminal inoculum were placed in amber bottles of 125 mL capacity. The bottles were kept under constant CO₂ flow and tightly sealed with rubber stopper and aluminum ring as

described by Theodorou et al. (1994) and placed in a water bath at 39 °C. The gas pressure was measured with a manometer (Metron, Mode: 63100, Mexico) at 0, 2, 4, 6, 8, 12, 16, 20, 24, 30, 36, 42, 48, 60 and 72 h of incubation (Blümmel and Ledzien, 2001). The gas pressure values were transformed to gas volume by a linear regression equation: $V = (P + 0.0186) (0.0237)^{-1}$ as reported by Elmasry et al. (2016). The ruminal inoculum consisted of a ruminal fluid (RF) sample of three Holstein cattle (450 kg of live weight) supplied with cannulas in their rumen and fed with a diet composed of 30% concentrated, 35% of Avena sativa straw and 35% Medicago sativa. Before the extraction of ruminal fluid, the animals were fasted for 14 hours. Then the ruminal fluid was filtered through eight layers of gauze and mixed of 1:9 ratios with a reduced mineral solution (Menke and Steingass, 1988; Krishnamoorthy et al., 2005).

In vitro gas fermentation kinetics and fermentable fractions: The maximum gas volume (mV; mL g-1), the fermentation rate (S; h-1) and the delay phase (L; h-1) of gas production was estimated with the logistic model Vo = $mV/(1+ e^{(2-4k (t-L))})$ (Schofield and Pell, 1995), and analyzed through the NLIN program (SAS, 2006). These gas volumes were also fractionated in time intervals from 0 to 8 (Vf₀₋₈), 8 to 24 (Vf₈₋₂₄) and 24 to 72 (Vf₂₄₋₇₂) hours of incubation. These volumes were used to estimate the rapid fermentation fractions (RF) (mg g-1 forage), medium fermentation fractions (MF) and slow fermentation fractions (SF) of forages, according to the linear regression equations proposed by Miranda et al. (2015): RF= fV_{0-8} /0.4266, MF= fV_{8-24} /0.6152, SF= fV_{24-} 72/0.3453. The sum of the three fractions made up the total fermentable fraction (TF). Additionally, a potential fermented gas emission index per gram of digestible organic matter (PFGEI; mL g⁻¹DOM) was estimated.

In vitro digestibility of dry matter (IVDMD) and organic matter (IVOMD): At the end of the *in vitro* fermentation period (72 h) the residues of each sample were obtained by filtration in a flask and a Buchner funnel with filter (Filter paper F / fast MOD.617 Code P.V.NO.1034), and *in vitro* dry matter digestibility (IVDMD) was estimated by drying at 60 ° C for 48 h. To determine the *in vitro* digestibility of organic matter (IVOMD), each waste material was incinerated at 500 °C and its ash content was determined. With the initial and residual dry matter the IVDMD (%) was calculated and with the organic matter in the initial DM and of the residue, the IVOMD (%) was calculated as reported by Monforte *et al.* (2005).

Soluble fraction (SolFrac): It was determined by the difference among the amount of dry matter (DM) contained in the samples prior to fermentation and the residual DM, after being subjected to a ten minutes stirring period under the same operating conditions as

described for the *in vitro* gas production technique (Modified from Orskov, 1982).

Statistical design and analysis: Fermentation variables (mV, S, L, SolFrac, RF, MF, SF, TF, IVDMD, IVOMD, and PFGEI) were analyzed with the general linear model using the SAS statistical package (version 9); the randomized block design employed six replicates per treatment. Two replicate blocks were made over time and in each block three replicates were performed for each treatment. Treatment averages were compared by Tukey's multiple comparisons and statistical tests were considered significant when P <0.05 (Montgomery, 2012). A Pearson correlation analysis was performed for the chemical components (CP, NDF, ADF, Hemicellulose, Cellulose, Lignin, EE and CT) and fermentation variables; and a linear regression analysis for in vitro digestibility of DM and total fermentable fraction was carried out. Through the multiple linear regressions determined the major chemical components that explain the IVDMD and the different fermentation fractions (RF, MF, SF, TF) using the statistical package Rstudio (version 3.3.2, 2016-10-31). The regression models were compared using the information criterion proposed by Akaike (AIC) (1974). Providing simple expression based on the relationship among the Chi-square statistic and the AIC index value based on the likelihood ratio. The models with lower AIC index value were chosen; thus indicating a better fitness (Greven et al., 2010).

RESULTS

Chemical composition: The crude protein content (CP) in the foliage of the tree species ranged from 109 to 262 g $kg^{-1}of$ DM. The species with high CP content were L. leucocephala, H. albicans, L. rugosus, G. ulmifolia and P. albicans (Table 1). NDF content ranged from 391 in H. campechianum to 641 g kg⁻¹ of DM in H. albicans and ADF ranged from 322 in T. amygdalifolia to 579 g kg⁻¹of DM in H. albicans. The leaves of N. emargiata, M. lindeniana, B. divaricata, G. floribundum, had the highest concentration of hemicellulose; and the highest cellulose content was observed in B. divaricata, M. lindeniana, B. simaruba, C. gaumeri, V. gaumeri (Table 1). The concentration of EE, of all species, with the exception of C. gaumeri and T. amygdalifolia, they had an averaged <50 g kg⁻¹DM (Table 1). The concentration of lignin ranged from 152 in C. gaumeri to 549.8 g kg-1 of DM in H. albicans. Also, it was found that T. amygdalifolia, and C. gaumeri (1.73 and 3.78 g kg⁻¹ of DM, respectively) had the lowest TC contents, while G. floribundum, B. simaruba, N. emargiata, M. bahamensis, presented the highest concentration (Table 1). The presence of cyanogenic glycosides was not found in any of the analyzed species, but in some species the presence of saponins was recorded (Table 2). The highest abundance

of saponins was found in *H. albicans*, *L. rugosus*, *M. bahamensis*, *B. divaricata*, and *P. piscipula*, and the lowest abundances in *N. emargiata* and *G. floribundum* (Table 2). The abundant and very abundant presence of alkaloids was detected in all tree species (Table 2).

In vitro gas fermentation kinetics: The maximum volume (mV) of gas production, fermentation rate (S), lag phase (L), and soluble fraction (SolFrac) (Table 3) differed significantly (P < 0.05) among tree species. The species with the highest mV were G. floribundum, M. lindeniana, V. gaumeri, H. barvensis, T. amygdalifolia and C. gaumeri (155.37, 217.42, 223.63, 234.02, 258.08 and 293.88 mL g⁻¹, respectively). Likewise, the tree species L. latisiliquum, P. albicans, P. piscipula, B. simaruba, L. leucocephala and G. ulmifolia were characterized by an average gas production (Table 3). While the species H. campechianum, N. emargiata, H. albicans, L. rugosus, M. bahamensis, B. divaricata produced a lower mV (71.00, 75.62, 76.02, 78.07, 79.67, 85.31 mL g⁻¹, respectively). Higher fermentation rates (S) were observed in T. amygdalifolia and C. gaumeri followed by M. bahamensis, C. gaumeri and B. divaricata (Table 3). While M. lindeniana, H. barvensis, L. leucocephala, L. latisiliquum, P. piscipula, and G. floribundum showed significantly similar intermediate S (Table 3). The lowest S were found in the species G. ulmifolia, P. albicans $(0.030, 0.027, h^{-1})$ followed by H. campechianum, B. simaruba, L. rugosus, H. albicans and N. emargiata, which showed similar S (0.026 h⁻¹). The lowest lag phase (L) was observed to be similar among H. albicans, P. albicans, L. rugosus, H. campechianum and L. latisiliquum (Table 3). Likewise, the intermediate delay phase was found to be similar among P. piscipula and L. leucocephala (2.73 and 2.97 h); while the major phases of delay were observed in V. gaumeri, T. amygdalifolia, H. barvensis, C. gaumeri, N. emargiata, G. ulmifolia, M. bahamensis, M. lindeniana, B. simaruba, B. divaricata, and G. floribundum (Table 3).

The largest soluble fraction (SolFrac) was observed in *M. lindeniana* (265 g kg⁻¹DM), followed by *T. amygdalifolia*, *C. gaumeri*, *G. floribundum*, *P. piscipula*, *L. leucocephala*, *L. latisiliquum*, *G. ulmifolia* and *V. gaumeri* (Table 3). In the same way, the intermediate SolFrac was similar among *B. simaruba*, *P. albicans*, *H. campechianum*, *L. rugosus*, *N. emargiata* and *H. albicans* (159.90, 149.00, 134.30, 130.00, 125.70 and 102.00 g kg⁻¹of DM). While *B. divaricata*, *M. bahamensis* and *H. barvensis* showed the lowest SolFrac (92.70, 89.70 and 66.60 g kg⁻¹DM).

Fermentable fractions, digestibility and potential fermented gas emission index: Among the leaves of the tree species it was found that the fraction of rapid fermentation (0-8 h) was significantly (P <0.05) higher in C. gaumeri, T. amygdalifolia, V. gaumeri, M. lindeniana, H. barvensis, L. leucocephala, G. floribundum, and P.

piscipula (Table 4). While the species G. ulmifolia, L. latisiliquum, P. albicans, B. simaruba (98.49, 94.38, 93.15 and 87.80 mg g⁻¹) showed a similar fermentation and the species B. divaricata, H. albicans, M. bahamensis, L. rugosus, H. campechianum and N. emargiata had the smallest fraction of rapid fermentation (Table 4). On the other hand, it was found that the medium fermentation fraction (8-24 h) also differed (P <0.05) among species. The foliage of C. gaumeri and T. amygdalifolia had the highest values (217.87 and 209.03 mg g^{-1}) followed by V. gaumeri, H. barvensis, and M. lindeniana (Table 4). Also a similar average fermentation (98.10, 95.82, 93.54, 86.98 and 75.85 mg g⁻¹) was observed among the species G. ulmifolia, L. leucocephala, G. floribundum, B. simaruba, and P. piscipula, and the species B. divaricata, L. latisiliquum, M. bahamensis, P. albicans, N. emargiata, L. rugosus, H. albicans and H. campechianum had a lower fermentation of DM (Table 4).

Regarding the fraction of slow fermentation (24-72 h), differences (P <0.05) were also found among plant species. The highest fermentation values were observed in the species *C. gaumeri* and *H. barvensis* (244.64 and 231.94 mg g⁻¹), followed by *M. lindeniana*, *B. simaruba*, *G. ulmifolia*, *T. amygdalifolia*, and *G. floribundum* (Table 4). While *L. leucocephala*, *V. gaumeri*, *P. piscipula*, *P. albicans* and *N. emargiata* had similar slow fermentation fractions (143.53, 137.44, 133.37, 118.13, 109.93 mg g⁻¹) and the species with lower fermentation values *L. latisiliquum*, *L. rugosus*, *H. campechianum*, *H. albicans*, *B. divaricata* and *M. bahamensis* (Table 4).

The forage tree that showed significantly the highest total fermentable fraction (TF) was *C. gaumeri* (677.39 mg g⁻¹), followed by *T. amygdalifolia*, *H. barvensis*, *M. lindeniana*, *V. gaumeri*, *B. simaruba*, *G. ulmifolia*, *G. floribundum*, *G. ulmifolia*, *L. leucocephala*, *B. simaruba* and *P. piscipula* that showed similar TF (Table 4). Likewise, *P. albicans*, *L. latisiliquum*, *B. divaricata*, *N. emargiata*, *L. rugosus*, *M. bahamensis*, *H. albicans* and *H. campechianum* showed the lowest total fermentable fractions (Table 4).

In vitro dry matter digestibility (IVDMD), in vitro organic matter digestibility (IVOMD), and potential fermented gas emission index (PFGEI) differed (P <0.05) among tree species (Table 4). The greatest IVDMD and IVOMD were observed in the foliage of C. gaumeri, T. amygdalifolia, V. gaumeri, H. barvensis, P. piscipula and M. lindeniana, (Table 4). While foliages of P. albicans, H. campechianum and L. latisiliquum showed the lowest IVDMD (21.50, 21.01, and 22.24%) and IVOMD (29.25, 27.26, and 27.68%, respectively) values. The species that had the lowest potential fermented gas emission index by organic matter fermentation (PFGEI) were M. bahamensis, L. rugosus, B. divaricata, H. albicans, and N. emargiata (217.24, 206.36, 200.59, 181.19 and 181.13 mL g-1 OMD). While the species that produced the

highest amount of gas per unit of fermented organic matter were *T. amygdalifolia*, *M. lindeniana*, *C. gaumeri*, *B. simaruba*, *H. barvensis*, *G. ulmifolia*, *L. latisiliquum*, *G. floribundum*, *P. albicans* and *L. leucocephala* (Table 4).

Relationship among nutrient composition and kinetics of *in vitro* gas production: The CP concentration of the foliage of the different species was negatively correlated with the delay phase (L) (-0.4760, P = 0.0458, Table 5); while cellulose concentration was positively correlated with IVDMD (0.5100, P = 0.0306). Also, EE was positively correlated with IVDMD, IVOMD, mV, S, RF, MF, TF, and PFGEI (Table 5). Lignin concentration had a negative correlated effect with SolFrac (-0.4856, P = 0.0410) and we found a tendency to correlate negatively with mV, S, L, RF, MF (Table 5). The concentration of CT was negatively correlated with the maximum volume of fermented gas (mV), with rapid fermentation fraction

(RF) and the total fermentable fraction (TF) (Table 5). Total fermentable fraction of the foliage (TF) showed a positive correlation with the IVDMD (correlation coefficient = 0.8200, P = 0.0001), however, due to a low coefficient of determination in the model ($R^2 = 0.6220$), TF obtained with gas production cannot predict the IVDMD (Figure 1). Due to the influence exerted by some tree species that despite having a low value of DM fermentation and gas production, they have a high digestibility (Figure 1, circle).

On the other hand, it was observed that both the IVDMD and the different fermentation fractions (RF, MF and TF) can be explained by the concentration of CP, NDF, ADF, EE, Lignin and CT contained in the foliage of the different species (Table 6) except for the variable SF that is only explained by the concentration of CP, NDF and EE (Table 6).

Table 1. Nutritional composition and condensed tannins of trees species consumed by cattle in *acahuales* of low deciduous forest.

Tr	DM	OM	CP	EE	NDF	ADF	Hemicellulose	Cellulose	Lignin	CT
Tree species						g kg-1 Dl	М			
Neomillspaughia										
emargiata	362.21	911.88	123.36	12.51	592.58	470.18	122.40	144.53	353.31	170.63
Tabernaemontana										
amygdalifolia	351.43	885.36	168.78	54.92	397.98	322.91	75.07	116.00	235.00	1.73
Piscidia piscipula	383.58	874.18	155.95	28.85	553.49	448.01	105.48	140.60	339.55	26.99
Gymnopodium										
floribundum	344.61	897.04	151.90	14.21	497.55	338.93	158.61	116.92	223.95	114.69
Havardia albicans	397.35	938.49	192.94	34.71	641.14	579.51	61.63	150.54	549.89	11.87
Lonchocarpus rugosus	321.12	937.25	192.36	11.76	551.22	441.08	110.13	165.33	309.62	99.30
Guazuma ulmifolia	380.83	906.35	170.73	29.75	596.96	490.47	106.49	158.34	340.71	21.51
Lysiloma latisiliquum	402.46	927.47	155.49	37.79	533.70	421.04	112.66	157.17	273.45	56.24
Luecaena leucocephala	300.93	919.17	262.14	29.04	477.74	371.56	106.18	121.43	266.63	16.53
Pithecellobium albicans	411.12	944.49	174.66	36.04	430.05	408.91	21.14	38.22	383.82	25.05
Haematoxylum										
campechianum	284.23	923.54	135.40	5.18	391.27	341.44	49.83	133.89	210.30	41.24
Mimosa bahamensis	398.51	936.17	141.19	20.86	447.43	352.38	95.05	94.91	257.47	233.45
Bursera simaruba	295.50	913.25	123.91	22.64	561.56	536.65	24.91	200.18	335.32	128.17
Caesalpinia gaumeri	278.71	948.70	141.99	54.68	475.40	356.05	119.34	206.17	152.78	3.78
Helicteres barvensis	312.67	914.61	148.42	32.77	548.01	448.61	99.40	145.24	342.79	13.07
Machaonia lindeniana	407.70	939.71	121.39	21.35	492.91	366.15	126.76	197.91	167.02	41.39
Vitex gaumeri	223.45	929.88	108.87	44.04	621.67	552.97	68.70	247.15	295.15	0.00
Bauhinia divaricata	549.10	917.04	157.23	15.16	561.42	425.51	135.91	192.63	228.99	38.28

DM: Dry matter; OM: Organic matter; CP: Crude protein; EE: Ethereal extract; NDF: neutral detergent fiber; ADF: acid detergent fiber; CT: Condensed tannins.

Table 2. Concentration of saponins, cyanogenic glycosides and alkaloids of trees species consumed by cattle in *acahuales* of low deciduous forest.

Tree species	Saponins	Cyanogenic glycosides	Alkaloids
Neomillspaughia emargiata	+	-	+++
Tabernaemontana amygdalifolia	-	-	++++
Piscidia piscipula.	++	-	++++
Gymnopodium floribundum	+	-	++++
Havardia albicans	+++	-	+++

Lonchocarpus rugosus	+++	-	+++
Guazuma ulmifolia	-	-	+++
Lysiloma latisiliquum	-	-	+++
Luecaena leucocephala	-	-	++++
Pithecellobium albicans	-	-	++++
Haematoxylum campechianum.	-	-	++++
Mimosa bahamensis	+++	-	+++
Bursera simaruba	-	-	++
Caesalpinia gaumeri	-	-	++++
Helicteres barvensis	-	-	+++
Machaonia lindeniana	-	-	++++
Vitex gaumeri	-	-	++++
Bauhinia divaricata	++	-	++++

^{- (}No presence); + (low in abundance); ++ (abundant); +++ (moderately abundant); ++++ (very abundant)

Table 3. Parameters of the kinetics of *in vitro* gas production of trees species consumed by cattle in *acahuales* of low deciduous forest.

Tree species	mV (mL g ⁻¹)	S (h ⁻¹)	L (h)	SolFrac (g kg ⁻¹ of DM)
Neomillspaughia emargiata	75.62 ^j	0.026e	5.09 ^{ab}	125.70 ^{ij}
Tabernaemontana amygdalifolia	258.08^{b}	0.047^{a}	5.59 ^a	230.00^{b}
Piscidia piscipula	$130.97^{\rm g}$	0.032^{c}	$2.73^{\rm cdefg}$	200.30^{cde}
Gymnopodium floribundum	155.37 ^e	$0.031^{\rm cd}$	3.53 ^{abcdef}	209.70^{bcd}
Havardia albicans	76.02^{j}	0.026^{e}	$0.74^{\rm g}$	102.00^{jk}
Lonchocarpus rugosus	78.07^{ji}	0.026^{e}	1.43^{fg}	130.0^{ij}
Guazuma ulmifolia	154.02 ^{ef}	0.030^{d}	4.76^{abc}	$179.70^{\rm ef}$
Lysiloma latisiliquum	$101.46^{\rm h}$	0.032°	2.35^{defg}	189.00^{def}
Luecaena leucocephala	153.75 ^{ef}	0.032°	2.97^{bcdefg}	199.30 ^{cde}
Pithecellobium albicans	104.92 ^h	$0.027^{\rm e}$	0.88^{g}	$149.00^{ m ghi}$
Haematoxylum campechianum	71.00^{j}	0.026^{e}	$1.89^{\rm efg}$	134.30^{hi}
Mimosa bahamensis	79.67^{ji}	$0.037^{\rm b}$	4.44abcd	89.70^{kl}
Bursera simaruba	145.72 ^f	0.026^{e}	4.19abcde	159.90^{fgh}
Caesalpinia gaumeri	293.88a	0.038^{b}	5.18 ^{ab}	228.70^{bc}
Helicteres barvensis	234.02°	0.033°	5.52a	66.60^{1}
Machaonia lindeniana	217.42 ^d	0.034^{c}	4.31 ^{abcd}	265.00 ^a
Vitex gaumeri	223.63 ^d	0.046a	5.82a	178.30 ^{efg}
Bauhinia divaricata	85.31 ⁱ	$0.038^{\rm b}$	3.61 ^{abcdef}	92.70^{kl}

a, b, c= Means along the same column with different superscripts are significantly different (P<0.05); mV= Maximum volume; S: Fermentation rate; L: Delay phase; SolFrac= Soluble fraction.

Table 4. Fermentation and *in vitro* digestibility of dry matter and organic matter and potential fermented gas emission index of the foliage of trees species consumed by cattle in *acahuales* of low deciduous forest.

Tree species	RF	MF	SF	TF	IVDMD	IVOMD	PFGEI
	$(mg g^{-1})$	$(mg g^{-1})$	$(mg g^{-1})$	$(mg g^{-1})$	(%)	(%)	(mL g ⁻
							¹ OMD)
Neomillspaughia emargiata	40.89^{h}	45.60^{gh}	109.93^{hi}	196.41 ^{hg}	34.23 ^{cde}	42.34 ^{bcdef}	181.19 ^e
Tabernaemontana amygdalifolia	210.76^{ab}	209.03a	162.33 ^{de}	582.13 ^b	49.54^{ab}	55.32ab	466.41a
Piscidia piscipula	113.71 ^{def}	75.85^{ef}	133.37^{fg}	322.94 ^{de}	44.27^{bc}	51.80 ^{bc}	264.08^{de}
Gymnopodium floribundum	123.58 ^{ed}	93.54^{de}	162.33 ^{de}	379.45^{d}	30.66^{defg}	41.88^{bcdef}	376.48^{abc}
Havardia albicans	68.47^{fgh}	37.07^{h}	82.56^{jk}	188.11 ^{gh}	31.35^{defg}	42.60^{bcdef}	181.13 ^e
Lonchocarpus rugosus	63.13 ^{gh}	38.78^{gh}	93.23^{ijk}	195.14 ^{gh}	29.42^{defg}	$39.03^{\rm cdefg}$	206.36 ^e
Guazuma ulmifolia	$98.49^{\rm efg}$	98.10^{d}	170.46 ^{cd}	367.05^{d}	28.33^{efg}	36.37^{defg}	425.30ab
Lysiloma latisiliquum	94.38^{efg}	58.75^{fg}	95.77^{hij}	248.90^{fg}	22.24^{fg}	27.68^{g}	376.73^{abc}
Luecaena leucocephala	127.28 ^{cde}	95.82 ^{de}	143.53 ^{ef}	366.63 ^d	33.61 ^{de}	41.87^{bcdef}	368.66 ^{abc}

Pithecellobium albicans	93.15 ^{efg}	53.61gh	118.13 ^{gh}	264.89ef	21.50 ^{fg}	29.25 ^{fg}	375.04 ^{abc}
Haematoxylum campechianum	56.14^{gh}	35.65^{h}	84.09^{jk}	175.87 ^h	21.01^{g}	27.26^{g}	278.96^{cde}
Mimosa bahamensis	$63.95^{\rm gh}$	55.61^{gh}	71.39^{k}	190.94gh	27.71^{efg}	36.77^{defg}	217.24 ^e
Bursera simaruba	$87.80^{\rm efg}$	86.97^{de}	186.72^{bc}	361.50^{d}	28.94^{efg}	34.14^{efg}	441.83 ^a
Caesalpinia gaumeri	214.88a	217.87a	244.64a	677.39 ^a	54.93a	66.50^{a}	442.40 ^a
Helicteres barvensis	148.67^{cd}	165.69°	231.94 ^a	546.29 ^{bc}	44.75^{ab}	53.51 ^{ab}	437.93 ^{ab}
Machaonia lindeniana	158.54 ^{cd}	148.86^{c}	202.98^{b}	510.37°	39.71^{bcd}	47.96^{bcd}	453.73 ^a
Vitex gaumeri	169.23 ^{bc}	186.50^{b}	137.44^{fg}	493.17°	45.05^{ab}	66.14 ^b	339.79^{bcd}
Bauhinia divaricata	76.29^{fgh}	58.75^{fg}	81.04^{jk}	216.07^{fgh}	31.80^{def}	43.55 ^{bcd}	200.59 ^e

^{a, b, c} Means along the same column with different superscripts are significantly different (P<0.05); RF: rapid fractions; MF: mean fractions; SF: slow fractions; TF: total fractions; IVDMD: *In vitro* digestibility of dry matter; IVOMD: *In vitro* digestibility of organic matter; PFGEI: potential fermented gas emission index per gram of digestible organic matter.

Table 5. Correlation matrices between the chemical composition, the gas production constants and *in vitro* digestibility of dry matter and organic matter.

	CP	NDF	ADF	Hemicell	Cellulose	Lignin	EE	CT
IVDMD	-0.1679 ^A	0.0629	-0.0601	0.2493	0.4203	-0.2929	0.6061	-0.3927
IVDIVID	$(0.5055)^{B}$	(0.8043)	(0.8126)	(0.3184)	(0.0820)	(0.2382)	(0.0077)	(0.1069)
IVOMD	-0.2043	0.1889	0.0562	0.2572	0.5100	-0.2496	0.5738	-0.3948
IVONID	(0.4160)	(0.4530)	(0.8247)	(0.3028)	(0.0306)	(0.3179)	(0.0128)	(0.1050)
SolFrac	-0.0149	-0.2678	-0.3552	0.2074	0.1834	-0.4856	0.3786	-0.3203
Soirtac	(0.9531)	(0.2827)	(0.1481)	(0.4089)	(0.4662)	(0.0410)	(0.1213)	(0.1951)
S	-0.1925	-0.1623	-0.2382	0.1734	0.2930	0.4682	0.6051	-0.2866
3	(0.4440)	(0.5199)	(0.3410)	(0.4913)	(0.2379)	(0.0501)	(0.0078)	(0.2488)
T	-0.4760	0.0683	-0.0653	0.2709	0.4222	-0.4518	0.3168	0.0552
L	(0.0458)	(0.7876)	(0.7967)	(0.2768)	(0.0809)	(0.0598)	(0.2002)	(0.8276)
mV	-0.1790	-0.1460	-0.1940	0.1150	0.3580	-0.4220	0.6980	-0.4920
111 V	(0.4784)	(0.5643)	(0.4404)	(0.6507)	(0.1451)	(0.0809)	(0.0013)	(0.0382)
RF	-0.0710	-0.2360	-0.2850	0.1240	0.2760	-0.4390	0.7650	-0.5630
Kr	(0.7787)	(0.3449)	(0.2515)	(0.6241)	(0.2669)	(0.0685)	(0.0002)	(0.0149)
MF	-0.2248	-0.1372	-0.1810	0.1042	0.3902	-0.4383	0.7171	-0.4665
IVII	(0.3698)	(0.5872)	(0.4724)	(0.6808)	(0.1094)	(0.0688)	(0.0008)	(0.0510)
SF	-0.1840	-0.0430	-0.1040	0.1300	0.3030	-0.3080	0.4390	-0.3440
Sr	(0.4655)	(0.8648)	(0.6817)	(0.6068)	(0.2214)	(0.2133)	(0.0680)	(0.1625)
TF	-0.1740	-0.1460	-0.2000	0.1260	0.3470	-0.4210	0.6820	-0.4850
11	(0.4904)	(0.5624)	(0.4260)	(0.6189)	(0.1587)	(0.0820)	(0.0018)	(0.0413)
PFGEI	-0.0890	-0.3120	-0.2520	-0.0960	0.0940	-0.3470	0.5260	-0.4040
FFGEI	(0.7262)	(0.2071)	(0.3138)	(0.7052)	(0.7092)	(0.1586)	(0.0250)	(0.0962)

A Correlation coefficient; Bp value (P<0.05); CP: Crude protein; EE: Ethereal extract; NDF: neutral detergent fiber; ADF: acid detergent fiber; Hemicell= Hemicellulose; CT: Condensed tannins; IVDMD: In vitro digestibility of dry matter; IVOMD: In vitro digestibility of organic matter; SolFrac: Soluble fraction; S: fermentation rate; L: delay phase; mV= Maximum volume; RF: rapid fractions; MF: mean fractions; SF: slow fractions; TF: total fractions; PFGEI: potential fermented gas emission index per gram of digestible organic matter.

Table 6. Comparison of information criterion (AIC) index and coefficients of determination for models.

Models	R ²	R ² adjusted	AIC	P(0.005) of the model
$IVOMD \sim CP + EE^{*1} + NDF^* + ADF + CT$	0.5902	0.4194	136.3149	0.0363
$TF \sim CP + NDF + EE * + ADF + Lignin + CT$	0.7233	0.5724	224.6847	0.0122
$RF \sim CP + NDF + EE *+ ADF + Lignin + CT$	0.8528	0.7726	173.4112	0.0005
$MF \sim CP + NDF + EE *+ ADF + Lignin + CT$	0.7940	0.6817	185.5398	0.0028
$SF \sim CP + NDF + EE$	0.2423	0.0799	203.9087	0.2598

¹Significant variable within the model (P<0.05); R²= coefficient of determination; R²adjusted= adjusted coefficient of determination; AIC=information criterion index Akaike; CP: Crude protein; EE: Ethereal extract; NDF: neutral detergent fiber; ADF: acid detergent fiber; CT: Condensed tannins; IVOMD: *In vitro* digestibility of organic matter; TF: total fractions; RF: rapid fractions; MF: mean fractions; SF: slow fractions.

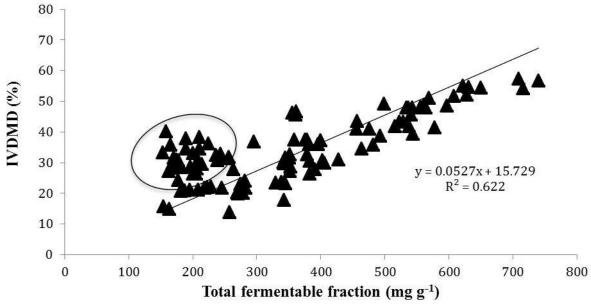


Figure 1. Regression model of in vitro dry matter digestibility (%) and total fermentable fraction (mg g-1)

DISCUSSION

Chemical composition: Crude Protein concentrations found in most of the foliage of tree species (Table 1) are above the threshold of crude protein requirements (110-120 g kg⁻¹of DM) for a mean level of grazing animal production (ARC, 1980; NRC, 2016) and exceeded the critical level (60-80 g kg⁻¹of DM) that negatively influences the voluntary intake (VI) in the animals and the microbial activity in the rumen (Van Soest, 1991; Orskov, 1982). With the exception of *V. gaumeri, M. lindeniana, B. simaruba, M. bahamensis, H. campechianum* and *N. emargiata*; all other species have a CP concentration (Table 1) above 150 g kg⁻¹of DM that potentially can meet the requirements of lactation and growth in ruminants as reported by Norton (1982).

The NDF content of H. campechianum, T. amvgdalifolia, P. albicans, M. bahamensis, and L. leucocephala, was below the concentration of 550 g kg ¹of DM that limits the voluntary intake and nutrient digestibility in animals (Van Soest, 1965). This allows them to be characterized as a high quality food, having a concentration close to 450 g kg⁻¹of DM of NDF as mentioned by Singh and Oosting (1992) and Girma et al. (2015). However, other species such as G. floribundum, C. gaumeri, M. lindeniana, P. piscipula, L. rugosus, B. divaricata, B. simaruba, N. emargiata, G. ulmifolia, H. albicans, V. gaumeri can be considered as medium quality forages for to have a concentration among 450 and 650 g kg⁻¹of DM of NDF (Table 1) (Singh and Oosting, 1992; Jolly and Wallace, 2007). In addition, these species (P. piscipula, L. rugosus, B. simaruba, N.

emargiata, H. albicans, and V. gaumeri) have high concentrations of ADF that could be influenced by the maturity stage of the plants at the time of cutting, together with the age of regrowth of the foliage (Apráez et al., 2012, Girma et al., 2015), and which was reflected in the concentration of lignin (Ku et al., 1999). The high concentrations of lignin found in all studied species exceed the concentration (100 g kg⁻¹of DM) considered critical that influence the voluntary intake of dry matter of ruminants as described by Reed (1995). This characteristic is common to be observed in tropical species that grow under high temperatures and low rainfall, as is characteristic of the deciduous forest where the study was carried out. Boufennara et al. (2012) reported that under these conditions, plants tend to increase the fraction of the cell wall and decrease soluble cell content.

The low concentrations of ether extract (EE) found in most of the tree species in this study indicate their low potential energy input for ruminants (Mayouf et al., 2015); except for C. gaumeri and T. amygdalifolia species, which can be considered as plants that improve energy intake in the ruminant diet, because the EE concentration is above 50 g kg⁻¹of DM (Odedire and Babayemi, 2008). The influence of plant secondary metabolites on the digestion and nutrient utilization by ruminants has been extensively studied by Kamra et al. (2015) and Patra et al. (2017). Thus, it has been found that the species G. floribundum, B. simaruba, N. emargiata, M. bahamensis, have the capacity to inhibit enzymatic activity (Kumar and Singh, 1984) and microbial activity (Makkar et al., 1989) in the digestion

of nutrients; because of its high CT content (> 100 g kg⁻¹ of DM, Table 1) (Gasmi-Boubaker *et al.*, 2005; Piñeiro *et al.*, 2016). While other trees species such *T. amygdalifolia*, *C. gaumeri*, *H. albicans*, *H. barvensis*, *P. piscipula*, *G. ulmifolia*, *L. leucocephala*, *P. albicans*, *H. campechianum*, *B. divaricata* and *M. lindeniana* (<50 g kg⁻¹ of DM) have a potential for use as a dietary supplement, with a low risk of compromising nutrient digestibility in ruminants (Bayssa *et al.*, 2016).

Additionally to condensed tannins, the presence and effect of other secondary metabolites present on tree species has been relatively little studied. In this respect, the presence of saponins alone has been reported for P. piscipula and G. ulmifolia (López et al., 2014). However, there are other forage species that possess these secondary compounds such as those found in this study, where we determined their presence in N. emargiata, G. floribundum, H. albicans, L. rugosus, M. bahamensis, and B. divaricata (Table 2). The saponins contained in these foliages may have advantages in animal feeding, it has been found that when applied at low doses (0.2 g / 1 or 13.5 a100 g kg-1 DM) the digestibility of the food can be improved (Patra et al., 2016; Albores et al., 2017). However, along with the presence of saponins and condensable tannins in tree foliage, it is possible to find the presence of alkaloids (Martello and Farnsworth, 1962); as we found in the present study. These compounds may interfere with the voluntary intake of animals when their dietary concentrations are above 0.1 mg, causing anorexia, miosis, and constipation as reported by Cheeke (1994).

In vitro fermentation kinetics: The highest fermentation and total fermentable fraction (mV, TF) observed in the species C. gaumeri, T. amygdalifolia, H. barvensis, V. gaumeri, M. lindeniana, and G. floribundum, could be related to the greater digestion of structural carbohydrates present in the foliage, which cause a slow onset of fermentation (L, Table 3) and a longer adhesion time of the microorganisms to the soluble fraction (SolFrac); though posterior to the breaking off of the lignin complexes, it increased the fermentation rate (S) by the microbial joining to the soluble fraction (SolFrac) (Table 3) (Kibon and Orskov, 1993). Additionally, the higher fermentation observed with these species could be related to the combination of a high CP content, a low CT content (Table 1) and alkaloids (Table 2), and the absence of saponins (Table 2) (Bhatta et al., 2013; Giuburuncă et al., 2014).

The low total gas production of some tree species such as *L. latisiliquum*, *P. albicans*, *P. piscipula*, *B. simaruba*, *L. leucocephala*, *G. ulmifolia* and *H. campechianum*, *N. emargiata*, *H. albicans*, *L. rugosus*, *M. bahamensis*, *B. divaricata* (Table 3) is related to a low concentration of SolFrac and a rapid onset of fermentation (Bueno *et al.*, 2005) due to their high CP

contents, which upon degradation release ammonium carbonate and ammonia which is used by bacteria for the synthesis of microbial protein (Osuga *et al.*, 2006), decreasing the amount of gas produced (Table 3) (González *et al.*, 1998). Also, it is probable that the different concentrations of CT (Table 1), saponins and alkaloids (Table 2) have affected the amount of OM that is fermented and therefore the gas production (Osuga *et al.*, 2006; Bayssa *et al.*, 2016). These secondary metabolites form complexes with proteins and carbohydrates (Barry and Duncan, 1986), causing protozoa population defaunation and decreasing gas production *in vitro* (Table 3) (Sirohi, 2014).

Fermentable fraction, digestibility and potential fermented gas emission index: The speed in the potential availability of nutrients contained in the foliage (RF, MF and LF; Table 4), is important for the synchronization in energy availability and NH3 release in the rumen. With the use of the diversity of tree leaves for animal feed, the synchronization indexes are chemically more complex and critical, compared to the more homogeneous foods (Rosales et al., 1999); and it is common to observe an excess of nitrogen and present a poor to moderate synchronization among fermentation of nitrogen and the fermentation of OM as presented by Nsahlai et al. (1995). In this sense, our findings on the rapid to moderate onset of the fermentation process of OM with V. gaumeri, T. amygdalifolia, C. gaumeri, M. lindeniana, and H. barvensis (Table 4) may be due to a further fermentation of its soluble fraction containing sugars, in addition to starch fermentation, cellulose and pectins (Miranda et al., 2015). Additionally, the absence of saponins and the low concentrations of CT and lignin could had favor the rapid microbial action and the beginning of the fermentation, which was maintained during the fermentation time (SF, TF) as a consequence of the cellulose concentration (Table 5) and the interaction of CP, NDF, ADF, EE and CT concentrations in the foliage (Table 6). The identification of forage species that only present a slow fermentation, as was the case of C. gaumeri, H. barvensis, M. lindeniana, B. simaruba, G. ulmifolia, T. amygdalifolia, and G. floribundum, it may be useful to incorporate them into balanced diets as a source of energy, and synchronize them in mixtures with other leaves that have a rapid fermentation to take advantage of the excess of NH₃ that they contribute (Table 4; Rosales et al., 1999).

The highest *in vitro* digestibility of DM (IVDMD) and OM (IVOMD) found in *C. gaumeri*, *T. amygdalifolia*, *V. gaumeri*, *H. barvensis*, *P. piscipula* and *M. lindeniana*, (Table 4) is related with its higher concentration of cellulose and fat content (EE) in the foliage (Tables 1 and 5) (Girma *et al.*, 2015). The higher energetic concentration (EE) of these foliages favored a

rapid onset of fermentation, sustaining high fermentation rates that resulted in a higher volume of total gas (Table 3). While the lowest IVDMD and IVOMD of the species *P. albicans, H. campechianum, L. latisiliquum, H. albicans, L. rugosus,* and *M. bahamensis* (Table 4) are associated with their higher proportion of NDF, ADF and lignin (Table 1) that limit fermentation activity (Table 3); because it chemically bonds to structural carbohydrates, limiting their digestion (Moore and Jung, 2001). Also, it could be attributed to the effect of microbial inhibition exerted by high concentrations of CT (Table 1), saponins, or alkaloids (Table 2) that decrease the population of protozoa and bacteria (Patra *et al.*, 2016) that affect degradation of DM and OM (Table 4) (Piñeiro *et al.*, 2016).

The potential gas emission index (PFGEI) is indicative of the efficiency in the degradability of OM (Miranda et al., 2015; Bayssa et al., 2016). In this study the species B. divaricata, H. albicans, N. emargiata, L. rugosus and M. bahamensis have a high potential to be used as a mitigation strategy in the gas production, since for each unit of OM fermented occurred the lowest amount of gas (Bodas et al., 2008; Vélez et al., 2015). This phenomenon can be explained by the low coefficient of determination (0.62) in the linear regression model of the total fermentable fraction (TF) obtained with gas production values in relation to IVDMD (Figure 1). Where the species of B. divaricata, H. albicans, N. emargiata, L. rugosus and M. bahamensis indicated in the circle (Figure 1) are those that showed high contents of secondary metabolites and high concentrations of cellular constituents (Tables 1 and 2) that affect the fermentation, possibly through the inhibition of microorganisms (bacteria, Archaea, protozoa, fungi) without affecting the enzymatic degradation on the organic matter (Carballa et al., 2015).

Considering the above, it can be concluded that the chemical composition and its correlation with the fermentation characteristics of the foliage of the tree species are useful criteria for the selection of plant species with potential for the feeding ruminants that grazing in the secondary vegetation (acahual) of tropical deciduous forest. Among the tree species that form part of the diversity of secondary vegetation, G. floribundum, M. lindeniana, V. gaumeri, H. barvensis, T. amygdalifolia and C. gaumeri are designated as species with high potential for use in nutrition of ruminants, due to their higher gas production, their high fermentation rates, high soluble fraction, their rapid onset of fermentation of hemicellulose and cellulose contained in their cell walls, and their greater digestibility of dry matter and organic matter. On the other hand, the species N. emargiata, H. albicans, L. rugosus, H. campechianum, M. bahamensis, B. divaricata, L. latisiliquum, P. albicans, P. piscipula, B. simaruba, L. leucocephala, G. ulmifolia could play an important role in greenhouse gas

mitigation strategies due to a higher concentration of condensed tannins, saponins, alkaloids and fiber concentration, which influence the lower gas production per unit of fermentable organic matter.

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