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Research Paper

Seasonal nutritive value and in vitro fermentation kinetics of foliage of some multipurpose shrub species in northeastern Mexico

Valor nutritivo estacional y cinética de fermentación in vitro del follaje de algunas especies de arbustos multipropósito en el noreste de México

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Abstract

This study aimed to determine the seasonal variation in chemical composition, metabolizable energy (ME) concentration, in vitro gas production patterns, in vitro organic matter digestibility (IVOMD) and in vitro true organic matter digestibility (IVTOMD) of foliage from 5 native shrub species (*Celtis pallida, Croton suaveolens, Forestiera angustifolia, Guaiacum angustifolium* and *Parkinsonia aculeata*) growing in semi-arid areas of northeastern Mexico between July 2018 and June 2019 at 2 research sites. Crude protein (CP) concentrations (>13.2 % DM) found in leaf material should meet or exceed the requirements for maintenance of small ruminants; *C. pallida* provided the highest CP% (20.8–29.3 %). While CP% varied with season and site, species had a greater effect than either of those factors overall. ME concentrations ranged between 1.2 and 2.0 Mcal/kg DM. Neutral detergent fiber and acid detergent fiber concentrations ranged from 29.8 to 51.7 % DM and 9.8 to 33.0 % DM, respectively. Data obtained for IVOMD (34.5–58.8 %) and IVTOMD (64.1–88.7 %) demonstrate the high nutritive potential of leaf of browse species under study, especially *C. pallida*, as useful feed supplements for small ruminants in the semi-arid region of northeastern Mexico. Further studies could examine DM yields of browse from the various species, acceptance by small ruminants and their sustainability under regular defoliation by grazing animals.

Keywords: Browse, chemical composition, digestibility, gas production, ruminants, season.

Resumen

Este estudio tuvo como objetivo determinar la variación estacional en la composición química, concentración de energía metabolizable (EM), parámetros de producción de gas in vitro, digestibilidad in vitro de la materia orgánica (DMO) y la digestibilidad verdadera in vitro de la materia orgánica (DVIVMO) del follaje de 5 especies arbustivas nativas (*Celtis pallida, Croton suaveolens, Forestiera angustifolia, Guaiacum angustifolium* y *Parkinsonia aculeata*) que crecen en las regiones semiáridas del noreste de México, en dos sitios, entre julio del 2018 y julio del 2019. La concentración de proteína cruda (PC) (>13.2 % de MS) que se encontraron en el material foliar cumple o supera los requisitos para el mantenimiento de los pequeños rumiantes. *C. pallida* presento el contenido de PC % más alto (20.8–29.3 %). Si bien el % de PC varió con la estación y el sitio, las especies tuvieron un efecto mayor que cualquiera

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de de los otros dos factores. Las concentraciones de EM oscilaron entre 1.2 y 2.0 Mcal/kg MS. Las concentraciones de fibra detergente neutra (FDN) y fibra detergente ácida (FDA) oscilaron entre 29.8 y 51.7 % de MS y entre 9.8 y 33.0 % de MS, respectivamente. Los datos obtenidos para DMOIV (34.5–58.8 %) y DVMOIV (64.1–88.7 %) demostraron el alto potencial nutritivo de las hojas de las especies arbustivas en este estudio, especialmente *C. pallida*, como un suplemento alimenticio útil para pequeños rumiantes en las regiones semiáridas del noreste de México. Futuros estudios podrían examinar los rendimientos de MS bajo condiciones de ramoneo de diversas especies, así como su aceptación por parte de los pequeños rumiantes y su sostenibilidad bajo defoliación frecuente por animales en pastoreo.

Palabras clave: Composición química, digestibilidad, estación; producción de gas, ramoneo, rumiantes.

Introduction

Shrub species have an important role as feed resources for small ruminants in arid and semi-arid agro-pastoral areas and rangelands (Cerrillo et al. 2006; Habib et al. 2016; Oliveira et al. 2018). The leaves of browse shrubs can be used as protein and fiber supplements by small ruminants grazing according to the season and fodder availability in the rangeland, especially during dry seasons in extensive areas, such as semi-arid regions of northeastern México (Foroughbakhch et al. 2013). Pal et al. (2015) and Piñeiro-Vázquez et al. (2017) reported that leaves of some shrubs and fodder trees may also lower methane production and contribute to methane mitigation in small-ruminant production systems in developing countries. However, leaves of leguminous trees and shrubs contain a wide range of plant secondary compounds (PSCs), which can represent a challenge to their value as feed resources (Ramírez et al. 2000) by limiting digestibility of metabolizable energy and protein (Camacho et al. 2010). On the other hand Soliva et al. (2008) argued that these components did not affect protein degradation of tropical foliage from shrubs and trees to an excessive extent.

Since chemical analysis does not reflect the effects of these PSCs, it is important to choose additional methods of analysis to assess the nutritional quality of native shrubs in rangelands. In vitro gas production, measured using pressure transducers and gas syringes (Getachew et al. 2005), can be used to quantify the nutritional quality of foliage of shrubs and fodder trees (Larbi et al. 1998). It is sensitive to the presence of PSCs in foliage (Sebata et al. 2011), since those compounds, such as condensed tannins (CT), in browse species could limit in vitro fermentation (Guerrero et al. 2012a). The Daisy^{II} incubator is adaptable and efficient in determining forage digestibility (Holden 1999) and is reliable when compared with in sacco tests, but with a minimal number of ruminants needed as rumen liquor donors (Buthelezi et al. 2019).

Native shrub species grown in the Tamaulipan thornscrub plant ecosystem, in northeastern Mexico, have been studied to determine their potential as a source of minerals, protein and digestible dry matter for small ruminants (Domínguez-Gómez et al. 2011; Guerrero-Cervantes et al. 2012b; Chávez-Espinoza et al. 2020). However, to date there is limited information about the kinetics of ruminal fermentation, as well as the metabolizable energy of browse species throughout the year. Thus, the objectives of this study were to determine seasonal chemical composition, metabolizable energy (ME), in vitro fermentation parameters, in vitro organic matter digestibility (OMD) and in vitro true organic matter digestibility (IVTOMD) plus nutritional potential for small ruminants, of foliar tissue of common native shrub species in northeastern México, including *Celtis pallida* Torr. (Cannabaceae), *Croton suaveolens* Torr. (Euphorbiaceae), *Forestiera angustifolia* Torr. (Oleaceae), *Guaiacum angustifolium* Engelm. (Zygophyllaceae) and *Parkinsonia aculeata* L. (Leguminosae).

Materials and Methods

Study research sites

The research was carried out at 2 sites in the counties of Linares and Los Ramones, state of Nuevo León, Mexico, briefly described as follows:

Site 1 - Linares: Located in the Experimental Campus of the School of Forest Sciences, Universidad Autónoma de Nuevo León, in Linares County (24°47'45" N, 99°32'31" W; 350 masl). The climate is semi-arid and subtropical with a warm summer (González-Rodríguez et al. 2004). Average air temperature during the experimental period varied from 14.1 °C in January to 30.4 °C in August and 554 mm rainfall was received.

Site 2 - Los Ramones: Located in "El Abuelo Ranch" in Los Ramones County (25°39'46" N, 99°27'51" W; 200 masl). The climate is semi-arid with a warm summer

(González-Rodríguez et al. 2004). Average monthly air temperature during the study ranged from 14.3 °C in January to 31.5 °C in August and rainfall was 667 mm.

Foliage sampling and preparation

At each site, 3 representative experimental plots (50 × 50 m) were randomly demarcated without disturbance, and both young and mature leaves of *Celtis pallida*, *Croton suaveolens*, *Forestiera angustifolia*, *Guaiacum angustifolium* and *Parkinsonia aculeata* were randomly and manually collected, at a browsing height of 1.5 m from 5 representative plants (repetitions) of each species in each plot. Leaves were sampled monthly in summer (June and August 2018 and July 2019), autumn (October–November 2018), winter (December 2018–February 2019) and spring (March–May 2019). The collected leaf tissue was transferred to the Chemistry Laboratory of the School of Forest Sciences, where samples were partially dried at 55 °C for 24 h using a forced-air oven (Felisa®, Model FE-292AD, Mexico). Thereafter, leaf tissue was ground in a Thomas Wiley mill (Thomas Scientific Apparatus, Model 3383, USA) using a No. 60 mesh (1 × 1 mm) and stored in zip-lock plastic bags.

Chemical analyses

Ground leaf tissue was dried at 100 °C for 24 h in a forced-air oven. Organic matter (OM%) was determined by incinerating a dried sample at 550 °C for 3.5 h in a furnace (Thermo Scientific, Model F48010, USA), (Method no. 942.05; AOAC 2011); crude protein (CP%) from N concentration, obtained by a CHNS/O analyzer (2400 series II, Perkin Elmer) (Method no. 990.03; AOAC 2011); neutral detergent fiber (NDF%), acid detergent fiber (ADF%) and lignin (%) according to procedures described by Van Soest et al. (1991); and ether extract (EE%) by extracting lipids with petroleum ether, using an Ankom^{XT15} extractor (AOCS AM 5-04). All analyses were performed in triplicate.

In vitro gas production determinations

In vitro gas production of collected leaf tissue was determined at the School of Veterinary Medicine, Universidad Juárez del Estado de Durango, Durango, Mexico, using the technique proposed by Menke and Steingass (1988). Briefly, 500 mg DM samples in triplicate were placed in 100 mL calibrated glass syringes. Ruminal fluid was collected from 3 rumen-fistulated Dorper wethers (45 kg body weight), fed with alfalfa hay and commercial concentrate (75:25, respectively). To prepare the inoculum, ruminal liquid was mixed with a sodium buffer solution and ammonium bicarbonate (35 g $NaHCO_3$ and 4 g NH_4HCO_3 per liter) in a ratio of 1:2 (v/v). Each syringe was inoculated with 40 mL of this buffer solution and placed in an upright position in a water bath at 39 °C. Three syringes containing only 40 mL of inoculum served as Controls. Gas production was registered at 0, 3, 6, 9, 12, 24, 48, 72 and 96 h after inoculation. Data were adjusted using the non-linear equation proposed by Orskov and McDonald (1979), $p = a + b\ (1\text{-}e^{ct})$, and effective degradability of DM (EDDM) was calculated using the equation proposed by McDonald (1981), $EDDM = (a+b)\ c/(c+k)\ (e\text{-}^{(ct)LT})$, where:

p is the gas produced at time 't';

a is gas production from the immediately soluble fraction (mL);

b is gas production from the insoluble fraction (mL);

c is gas production rate constant for the insoluble fraction (b);

t is incubation time (h);

k is the rumen outflow rate assumed to be 0.05/h, i.e. 5 %/h; and

LT is the lag time (h).

Since in vitro production of gas is proportional to degraded DM (Menke et al. 1979), net gas yield at 24-h incubation of the substrate (mL/200 mg DM) was used to calculate metabolizable energy (ME) and in vitro organic matter digestibility (OMD%), using equations proposed by Menke et al. (1979) and Menke and Steingass (1988), respectively:

$ME\ (Mcal/kg\ DM) = [2.20 + 0.136(GP_{24h}) + 0.057(CP) + 0.0029(EE^2)]/4.184$ and $OMD\ (\%) = 14.88 + 0.889 \times GP_{24h} + 0.45 \times CP + 0.0651 \times ash$,

where:

GP_{24h} = gas production after 24 h of incubation (mL gas/200 mg DM);

CP = crude protein (% DM);

EE = ether extract (% DM); and

ash = ash concentration (%).

In vitro true organic matter digestibility

In vitro true organic matter digestibility (IVTOMD) was determined using a Daisy^{II} incubator (ANKOM Technology, Macedon, NY, USA) in the Laboratory of Animal Nutrition and Feed Quality at the School of Agronomy, Universidad Autónoma de Nuevo León, Mexico. Foliar samples (approximately 250 mg DM), in triplicate, were placed in multilayer polyester filter bags

(F57; 5.0 × 5.5 cm, ANKOM Technology Corp., Macedon, NY, USA) previously washed with acetone and dried in a forced-air oven at 60 °C for 2 h. Inoculum was prepared by diluting ruminal fluid from 2 Saint Croix wethers, provided with a ruminal cannula and fed a concentrate:forage ration (80:20) (not containing foliar tissue from the studied browse species), with a buffer solution in a ratio of 1:4. Inoculum was added to jars containing the filter bags, which were purged with CO_2 and placed in an incubator for 48 h at 39 °C. Jars were then removed from the incubation chamber and the bags were washed with distilled water. Thereafter, the bags were placed in the Ankom^{200} fiber analyzer (ANKOM Technology Corp., Macedon, NY, USA) and treated with neutral detergent solution for 75 min, according to the manufacturer's specifications and guidelines. The bags were rinsed with hot water and acetone, before being dried at 55 °C for 24 h. IVTOMD was calculated as the difference between OM incubated and residue after neutral detergent treatment.

Environmental variables

To measure temperature and precipitation at each site, automated HOBO sensors (HOBO Pro Temp/RH Series, Forestry Suppliers Inc., Jackson, MS, USA) were used to record environmental variables such as relative humidity (%) and air temperature (°C) every hour. Daily rainfall (mm) was measured using a Davis brand automated rain gauge, connected to a HOBO Event Onset recorder.

Statistical analyses

The effects of site (2), season (4) and species as well as their double (site × season, site × species and season × species) and triple (site × season × species) interactions on chemical analyses, in vitro gas production parameters and digestibility data were determined via analysis of variance using a completely randomized design with a factorial arrangement (Montgomery 2004). Pearson correlation analyses were performed between chemical composition, digestibility and environmental variables recorded during the experimental period. The SPSS (Statistical Package for the Social Sciences) software package (Version 22.0 for Windows, SPSS Inc., Chicago, IL, USA) was used for all statistical analyses.

Results

The effects of season, site and species and their respective double and triple interactions on OM, NDF, ADF, lignin, CP and EE concentrations are shown in Table 1. OM, NDF, ADF, lignin, CP and EE concentrations were significantly affected ($P<0.05$) by both season and species ($P<0.001$). The interaction season × site was significant ($P<0.05$) for only lignin and CP concentrations, while the interaction season × species was significant ($P<0.001$) for all chemical components. Interaction site × species was significant ($P<0.001$) for OM, NDF, ADF and EE concentrations. For triple interaction, season × site × species, significant differences were found for OM ($P<0.001$) and NDF ($P<0.05$) concentrations.

While there was marked variation between species at all sites in most seasons, overall *C. pallida* showed consistently lowest OM concentration, followed by *G. angustifolium*, with the remaining species higher. On the other hand, *C. pallida* showed the highest CP concentration of all species in summer and autumn. Overall CP% was highest in autumn (seasonal mean 26.0 %) and lowest in summer (19.7 %). Overall OMD was highest in spring (49.3 %) and lowest in summer (41.4 %), while IVTOMD did not vary markedly between seasons. (75.3–76.7 %) (Table 2). *C. pallida* was consistently highest for both parameters.

The 96-h cumulative in vitro gas production (GP_{96}) patterns for the 5 shrub species during summer, autumn, winter and spring at the 2 research sites are shown in Figure 1. Overall, GP_{96} values in spring samples were higher than in other seasons, while *C. pallida* consistently registered the highest, and *G. angustifolium* the lowest gas production values. *P. aculeata* consistently had highest gas production during the first 12 hours of incubation, while *C pallida*, *C. suaveolens* and *F. angustifolia* produced much more gas during the following 36 hours.

Table 1. Chemical composition (% DM; n = 9) of leaves from 5 shrub species collected at 2 sites in each season during 2018–2019.

Season	Species	OM[1]		NDF		ADF		Lignin		CP4		EE	
		S1[2]	S2	S1	S2	S1	S2	S1	S2	S1	S2	S1	S2
Summer	*C. pallida*	80.2	79.4	46.5	51.3	11.0	12.2	2.3	2.7	20.9	24.5	2.7	3.0
	C. suaveolens	93.0	91.8	41.5	38.9	23.5	22.3	5.8	5.5	16.3	17.8	3.1	2.3
	F. angustifolia	92.2	93.3	29.8	31.3	15.8	16.1	7.6	8.6	13.4	16.2	2.2	2.1
	G. angustifolium	83.0	86.3	39.6	39.3	26.0	25.4	14.3	15.2	20.9	21.3	3.6	5.6
	P. aculeata	90.4	92.4	45.3	48.9	27.4	30.1	9.6	9.5	18.2	18.8	3.0	2.7
	Site mean	87.8	88.6	40.5	41.9	20.8	21.2	7.9	8.3	18.0	19.7	2.9	3.1
	s.e.m.	0.3	0.3	0.8	0.8	0.4	0.4	0.3	0.3	0.6	0.6	0.1	0.1
	Season mean	88.2		41.2		21.0		8.1		18.8		3.0	
	s.e.m.	0.2		0.6		0.3		0.2		0.2		0.1	
Autumn	*C. pallida*	79.1	79.0	44.4	50.8	11.7	10.7	2.4	2.2	29.3	29.2	2.3	2.8
	C. suaveolens	91.7	91.7	48.0	40.9	24.6	26.3	7.3	9.2	25.7	25.9	1.4	1.4
	F. angustifolia	93.3	93.2	37.5	38.9	17.7	18.3	8.6	10.1	22.9	23.5	2.5	2.0
	G. angustifolium	81.0	85.2	36.6	41.1	24.7	24.6	14.7	14.1	23.7	26.7	4.8	6.0
	P. aculeata	90.4	92.8	44.3	49.6	25.5	29.0	9.1	10.7	24.9	27.6	2.4	1.9
	Site mean	87.1	88.4	42.1	44.3	20.9	21.8	8.4	9.2	25.3	26.6	2.7	2.8
	s.e.m.	0.3	0.3	0.8	0.8	0.4	0.4	0.3	0.3	0.6	0.6	0.1	0.1
	Season mean	87.7		43.2		21.3		8.8		26.0		2.8	
	s.e.m.	0.2		0.6		0.3		0.2		0.2		0.1	
Winter	*C. pallida*	76.7	78.7	32.0	47.0	9.9	10.2	2.2	1.9	24.5	20.8	1.8	1.9
	C. suaveolens	91.8	92.3	40.4	39.6	22.8	22.1	8.7	7.4	23.4	21.0	1.6	1.7
	F. angustifolia	92.2	91.5	34.7	32.1	17.9	16.3	9.2	7.9	20.6	18.1	1.8	1.9
	G. angustifolium	82.5	82.4	37.9	34.6	24.1	21.6	13.8	12.7	23.1	22.6	5.0	5.1
	P. aculeata	91.3	93.6	47.5	51.5	28.3	33.0	10.2	11.7	21.7	23.8	2.3	2.4
	Site mean	86.9	87.7	38.5	40.9	20.6	20.6	8.8	8.3	22.7	21.3	2.5	2.6
	s.e.m.	0.3	0.3	0.8	0.8	0.4	0.4	0.3	0.3	0.6	0.6	0.1	0.1
	Season mean	87.3		39.7		20.6		8.6		22.0		2.5	
	s.e.m.	0.2		0.6		0.3		0.2		0.2		0.1	
Spring	*C. pallida*	78.2	81.1	38.5	46.8	9.8	10.4	2.0	1.6	23.4	22.1	2.2	2.0
	C. suaveolens	91.9	92.0	41.6	43.9	21.9	18.2	5.5	4.5	24.5	23.6	2.7	2.5
	F. angustifolia	93.9	93.7	36.2	34.6	20.3	19.3	12.0	11.3	12.8	13.6	2.0	2.1
	G. angustifolium	89.1	89.9	40.8	35.3	26.7	23.0	14.1	12.5	21.9	21.6	2.7	3.1
	P. aculeata	94.0	94.4	46.2	51.7	24.3	29.1	7.4	8.5	26.3	19.5	2.8	2.3
	Site mean	89.4	90.2	40.7	42.5	20.6	20.0	8.2	7.7	21.8	20.0	2.5	2.4
	s.e.m.	0.3	0.3	0.8	0.8	0.4	0.4	0.3	0.3	0.6	0.6	0.1	0.1
	Season mean	89.8		41.6		20.3		7.9		20.9		2.4	
	s.e.m.	0.2		0.6		0.3		0.2		0.2		0.1	
Factors P-value	Season	<.001		<.001		0.047		0.002		<.001		<.001	
	Site	<.001		0.001		0.453		0.763		0.955		0.384	
	Species	<.001		<.001		<.001		<.001		<.001		<.001	
	Season × Site	0.754		0.922		0.238		0.020		0.006		0.657	
	Season × Species	<.001		<.001		<.001		<.001		<.001		<.001	
	Site × Species	<.001		<.001		<.001		0.057		0.891		<.001	
	Season × Site × Species	<.001		0.009		0.176		0.143		0.120		0.069	

[1]OM = organic matter; NDF = neutral detergent fiber; ADF = acid detergent fiber; CP = crude protein; EE = ether extract.
[2]S1 = Site 1 (Linares); S2 = Site 2 (Los Ramones).

Table 2. In vitro gas production at 24 h of incubation (mL/200 mg DM), metabolizable energy (Mcal/kg DM), gas production parameters (a, b, c, a+b and EDDM/500 mg DM), in vitro organic matter digestibility (g/100 g) and in vitro true organic matter digestibility (g/100 g) of leaves of 5 shrub species (n = 9) collected at 2 sites for each season of the year during 2018–2019.

Season / Species	GP_{24}[1]		ME		(a)		(b)		(a+b)		(c)		EDDM		IVOMD		IVTOMD	
	S1[2]	S2	S1	S2	S1	S2	S1	S2	S1	S2	S1	S2	S1	S2	S1	S2	S1	S2
Summer																		
C. pallida	26.8	24.5	1.7	1.7	-20.5	-19.2	137.3	122.5	116.8	103.3	0.05	0.04	41.4	35.1	49.4	49.1	85.2	84.5
C. suaveolens	23.3	18.5	1.5	1.4	-11.8	-9.0	123.3	107.3	111.6	98.3	0.04	0.03	38.7	30.6	43.4	39.9	71.1	73.4
F. angustifolia	14.6	13.4	1.2	1.2	1.5	1.9	125.8	137.6	128.7	139.5	0.02	0.01	30.1	26.9	34.4	34.5	77.9	78.3
G. angustifolium	14.3	12.0	1.3	1.2	-6.9	-6.4	58.7	55.2	51.8	48.8	0.07	0.06	24.7	20.3	38.1	36.0	76.1	75.1
P. aculeata	23.8	22.8	1.6	1.5	-3.9	-0.7	82.5	76.4	78.7	75.7	0.07	0.07	42.6	42.2	44.8	44.0	72.3	69.9
Season mean	19.4		1.42		-7.5		102.7		95.3		0.05		33.3		41.4		76.4	
s.e.m.	0.6		0.0		0.5		1.4		1.4		0.00		1.0		0.6		0.4	
Autumn																		
C. pallida	14.2	20.3	1.4	1.6	-12.9	-15.9	124.1	110.5	111.2	94.5	0.02	0.04	24.8	29.6	42.1	47.5	83.4	84.2
C. suaveolens	18.7	16.7	1.5	1.4	-6.3	-4.1	100.3	90.0	94.0	85.9	0.03	0.03	31.5	29.3	43.6	41.9	68.9	66.2
F. angustifolia	14.2	16.6	1.3	1.4	3.2	8.4	141.1	130.9	144.9	138.5	0.01	0.01	27.8	32.1	38.2	40.7	75.2	77.4
G. angustifolium	12.6	13.4	1.3	1.4	-3.0	-1.8	51.0	50.9	48.0	49.2	0.05	0.05	22.1	23.1	38.0	39.8	79.0	78.3
P. aculeata	20.5	16.9	1.5	1.5	-3.4	2.6	83.1	78.8	79.7	82.2	0.05	0.04	36.6	32.6	45.0	42.8	72.7	68.3
Season mean	16.4		1.42		-3.3		96.1		92.8		0.03		28.9		42.0		75.3	
s.e.m.	0.6		0.0		0.5		1.4		1.4		0.00		1.0		0.6		0.4	
Winter																		
C. pallida	29.4	36.8	1.8	2.0	-14.1	-18.9	118.1	132.3	104.0	113.3	0.05	0.07	46.9	55.8	53.6	58.3	88.2	88.7
C. suaveolens	26.5	31.4	1.7	1.8	-8.7	-9.1	112.8	116.4	104.1	107.3	0.05	0.05	46.3	50.6	49.5	52.7	71.1	70.2
F. angustifolia	19.6	22.0	1.4	1.5	3.0	5.9	120.5	114.2	123.5	120.1	0.03	0.03	43.5	43.3	42.1	43.1	75.4	76.3
G. angustifolium	15.1	16.7	1.3	1.4	-5.7	-5.2	55.5	53.7	49.8	48.5	0.07	0.09	26.0	29.3	39.8	41.0	78.4	79.6
P. aculeata	24.5	26.2	1.6	1.7	0.1	6.1	78.5	71.4	78.6	77.5	0.07	0.09	45.6	51.2	47.0	49.3	70.1	64.1
Season mean	24.8		1.6		-4.7		97.3		92.7		0.06		43.9		47.7		76.2	
s.e.m.	0.6		0.0		0.5		1.4		1.3		0.00		1.0		0.6		0.4	
Spring																		
C. pallida	31.5	36.8	1.9	2.0	-18.7	-21.2	123.1	135.5	104.4	114.2	0.06	0.07	45.7	55.7	54.8	58.8	85.2	84.5
C. suaveolens	32.7	33.1	1.9	1.9	-10.0	-10.8	115.5	118.0	105.6	107.2	0.06	0.06	54.8	54.6	55.5	55.4	73.3	76.2
F. angustifolia	18.9	19.4	1.3	1.3	13.2	9.6	135.5	136.3	148.7	146.0	0.01	0.02	41.2	40.6	37.8	38.7	74.6	74.4
G. angustifolium	20.4	20.2	1.5	1.5	-1.7	-7.3	60.5	63.6	58.8	56.3	0.10	0.11	38.7	36.4	43.5	43.2	74.1	77.9
P. aculeata	31.4	29.9	1.9	1.8	1.3	2.0	88.4	82.6	89.7	84.6	0.10	0.10	59.5	57.4	55.1	50.6	77.3	69.2
Season mean	27.4		1.7		-4.4		105.9		101.5		0.07		48.5		49.3		76.7	
s.e.m.	0.6		0.0		0.5		1.4		1.3		0.00		1.0		0.6		0.4	
Factors P-value																		
Season	<.001		<.001		<.001		<.001		<.001		<.001		<.001		<.001		0.070	
Site	0.233		0.241		0.215		0.073		0.241		0.321		0.666		0.321		0.076	
Species	<.001		<.001		<.001		<.001		<.001		<.001		<.001		<.001		<.001	
Season × Site	0.009		0.081		0.003		0.032		0.081		0.009		0.013		0.111		0.903	
Season × Species	<.001		<.001		<.001		<.001		<.001		<.001		<.001		<.001		<.001	
Site × Species	0.059		0.079		0.001		0.603		0.079		0.470		0.340		0.093		<.001	
Season × Site × Species	0.848		0.882		0.373		0.029		0.882		0.776		0.727		0.904		0.049	

[1]GP_{24} = In vitro gas production at 24 h; ME = metabolizable energy; (a) = immediately fermented fraction; (b) = slowly fermentable fraction; (c) = constant rate of gas production fraction; (a+b) = potential gas production fraction; EDDM = effective degradability of DM; IVOMD = in vitro organic matter digestibility; IVTOMD = in vitro true organic matter digestibility. [2]S1 = Site 1 (Linares); S2 = Site 2 (Los Ramones).

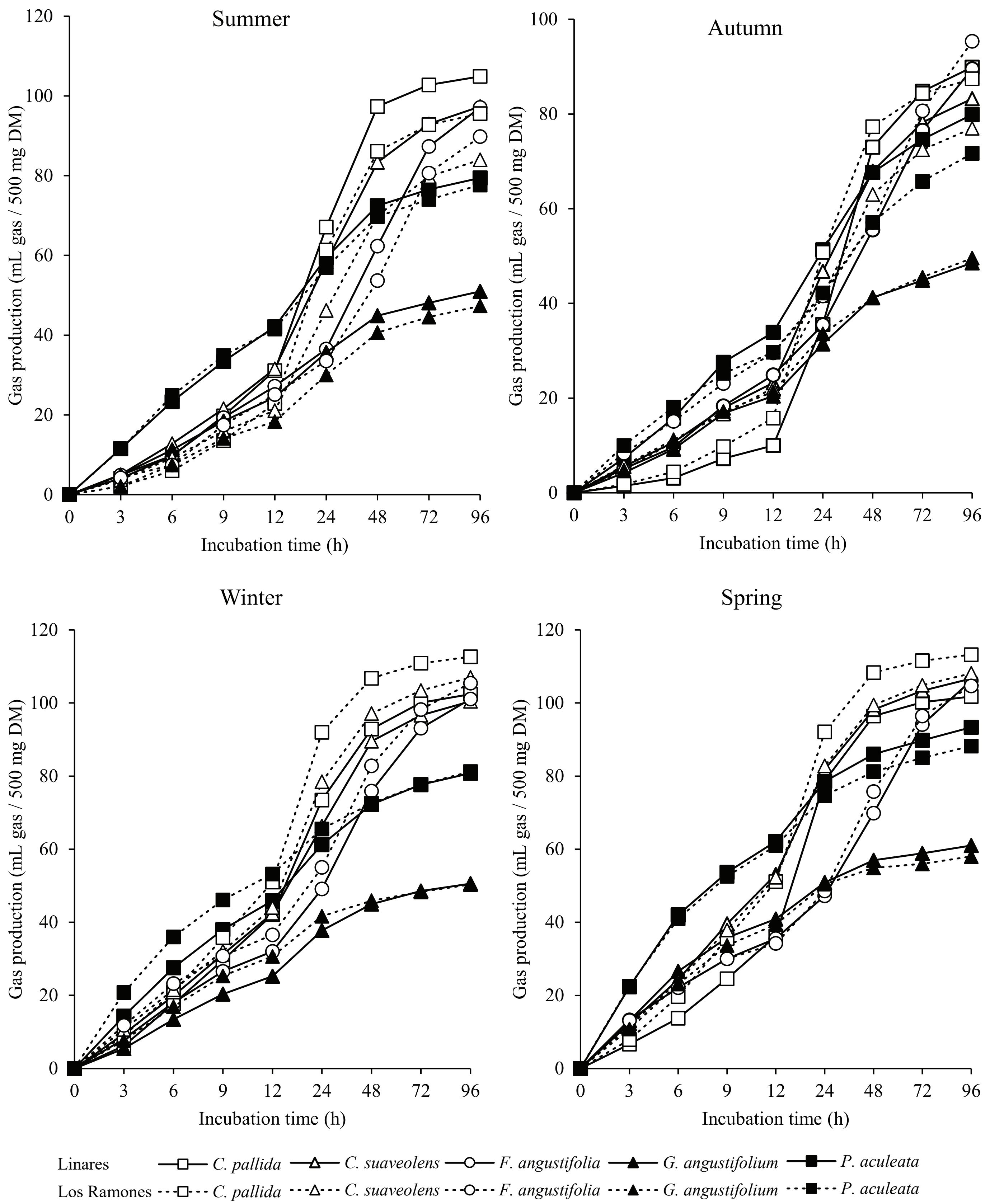

Figure 1. In vitro gas production at 96 h (n = 9) of leaves of 5 native shrub species collected at 2 sites for each season of the year during 2018–2019.

Discussion

This study has provided valuable information on nutritive value of some common browse species during different seasons in semiarid northeastern Mexico. Results suggest that these species could be a useful source of forage for browsing small ruminants in all seasons of the year.

Although differences were seen in nutrient concentrations in leaves of *C. pallida*, *C. suaveolens*, *F. angustifolia*, *G. angustifolium* and *P. aculeata*, seasonal mean CP concentrations in leaf samples ranged from 18.8 to 26.0 %, which far exceeds the requirements of 7–10 % (NRC 2007) for maintenance and growth of white-tailed deer, adult range goats and sheep, with *C. pallida* providing the highest CP concentration. Ramírez et al. (2000) and Domínguez-Gómez et al. (2011) reported that this species contains relatively low levels (<7.5 % DM) of condensed tannins (CT), indicating that CT concentrations in these plants should not affect CP digestibility by these animal species. Observed metabolizable energy (ME) concentrations (1.5–2.0 Mcal/kg DM) in *C. pallida* were somewhat inferior to ME in alfalfa hays (2.1 Mcal/kg DM) and maize silage (2.2 Mcal/kg DM) as an energy source according to Kara (2019). However, it would provide adequate energy to support small ruminants.

Mean NDF concentrations in the various seasons ranging from 40.9 to 43.2 % DM and ADF concentrations of 20.3–21.3 % are well below levels at which fiber becomes a limiting factor for intake. Similar findings have been documented by Hassen et al. (2007) in *Indigofera* shrub species and by Domínguez-Gómez et al. (2013) in native shrubs of northeastern Mexico. All evaluated species in this study showed NDF concentration lower than 60 %, levels which can be adequately managed by ruminants without affecting DM intake.

Low lignin concentrations in *C. pallida* (range 1.6–2.7 %) support its value as a useful forage source, while high lignin concentrations (12.5–15.2 %) in *G. angustifolium* suggest that it would be of lower feed value. Bouazza et al. (2012) reported that high lignin concentrations (>12 % DM basis) were associated with low digestibility in foliage of fodder trees and shrubs from Algerian arid and semi-arid rangelands. While lignin concentration tended to vary with seasons with lower values in spring, differences between seasons were not great and were unlikely to affect intake and nutritive value of most species in all seasons. Lignin concentrations in the current study (range 2.2 % for *C. pallida* to 13.9 % for *G. angustifolium*) range from low to high according to Anele et al. (2009) and Kara (2019). Further studies should examine biomass production of available forage to assess the potential of these feed sources for maintenance of small ruminants in rangelands of northeastern Mexico.

In vitro gas production following incubation of leaves in rumen fluid showed *C. pallida* produced highest amounts of gas, while *G. angustifolium* showed lowest gas production, in agreement with reports (Salem et al. 2014) of low total phenol and saponin concentrations in *C. pallida*. Higher levels of tannins and polyphenols may be responsible for lower gas production and in vitro digestibility in *G. angustifolium*.

In vitro gas production of shrub species at 24 h (GP_{24}) was positively influenced (r = 0.97; P<0.01) by ME concentration. GP_{24} from leaf was inversely proportional to lignin and EE concentrations. Interestingly GP_{24} values in the present study (12.0–36.8 mL/200 mg DM) were lower than those reported by Kara (2019) for fibrous feedstuffs (36.7–75.8 mL/200 mg DM) determined using rumen fluid of Damascus goats. Negative values for gas production from the immediately fermented fraction (a) (as low as -21.5 mL/200 mg DM), recorded in this study, are in accordance with those reported (from -3.0 to -1.7 mL/200 mg DM) in shrubs by Selmi et al. (2010) in north Tunisia. In contrast, *F. angustifolia* produced positive values (1.5–13.2 mL/200 mg DM). Gas production from the slowly fermentable fraction (b) was similar to or lower than values reported by Garcia-Montes de Oca et al. (2011) (89.5–187.3 mL/500 mg DM) from legume browse species in subtropical areas of Mexico, and higher than those (31–179 mL/500 mg) found by Larbi et al. (1998) in a study of fodder trees and shrubs from West Africa. Fraction (b) was negatively affected by concentrations of ADF (r = -0.62; P<0.01), lignin (r = -0.53; P<0.01) and EE (r = -0.49; P<0.01) and positively by ME concentration (r = 0.23; P<0.01) as reported by Domínguez-Gómez et al. (2011). Results for fraction (c) (constant rate of gas production) in the present study varied from 0.01 to 0.11 %/h, and are similar to the averages (0.03–0.11 %) reported by El Hassan et al. (2000) for foliage of some African multipurpose trees, but lower than those reported by Cerrillo et al. (2006) (6.1–6.4 %) for diets consumed by grazing goats in semi-arid regions of north Mexico, where plant species with high CP% and high DM digestibility were present. Potential gas production, fraction (a+b), varied considerably (48.0–148.7 mL/500 mg DM) and was higher than reported by Selmi et al. (2010) (26.1–66.6 mL/500 mg DM) for shrubs in north Tunisia, but similar to values reported by Domínguez-Gómez et al. (2011) (51–126 mL/500 mg DM), even though polyethylene glycol (PEG) was fed with forage in both of those studies.

Jančík et al. (2011) suggest that in vitro gas production can be useful in ranking forages on the basis of nutritional value.

IVOMD in this study was positively associated with ME concentration (r = 0.98; P<0.01) but negatively affected by lignin concentration (r = -0.50; P<0.01). Results reported herein were higher than those observed for leaf of *Detarium microcarpum* (32.1 %) and *Afzelia africana* (49.1 %), browse plants from Nigeria (Okunade et al. 2014), as well as those reported for *Quercus rugosa* leaves in western Mexico (Carrillo-Muro et al. 2018) and non-leguminous forage trees in tropical regions of southern Mexico (Rojas-Hernández et al. 2015). High values recorded for *C. pallida*, *C. suaveolens* and *P. aculeata* may be associated with their NDF concentrations. Future studies should consider analyzing NDF disappearance rate, since Kara (2019) showed positive correlation between NDF disappearance rate and DM digestibility, when it is determined with this method. IVTOMD values were negatively affected by ADF and lignin concentrations (r = -0.82; P<0.01; r = -0.50; P<0.01, respectively), in agreement with previous studies on litter fall reported by Rodríguez-Santillán et al. (2015). Trujillo et al. (2010) demonstrated that the Daisy^{II} incubator underestimated NDF disappearance values, compared with in situ methods. The absence of seasonal variations or spatial differences in IVTOMD indicates that differences among species are associated with their individual chemical compositions. Differences between the estimated IVOMD and IVTOMD values for individual assessments (range from 14.8 to 44.5 %) could be attributed to the longer incubation period of 48 h with the Daisy^{II} incubator, as IVOMD is calculated from GP_{24} data, with only 24 h of incubation time. According to Norman et al. (2010) leaves of some shrubs need to be incubated for more than 72 h in order to achieve an accurate estimation of in sacco digestibility. According to chemical composition and nutrient concentration data, IVOMD values appeared to be more realistic, as data for IVTOMD appear to possibly overestimate the feed potential of leaf of browse species under study. The moderate to high values in both OMD and IVTOMD demonstrate the high nutritive potential of leaf of browse species as a source of forage for small ruminants on smallholder farms in the semi-arid region of northeastern Mexico.

Conclusions

Browse plants studied appear to have potential for contributing significantly to diets of small ruminants in all seasons in Tamaulipan thornscrub in northeastern Mexico. Leaf material appears to have efficient rumen fermentation thereby providing adequate metabolizable energy and high CP for grazing stock. While *C. pallida* appears to provide the best quality browse in terms of CP, all species evaluated provided good quality forage. Further studies could be devoted to determining biomass production of the browse species under study and their sustainability under regular defoliation throughout the year. Feeding studies would indicate the acceptability to small ruminants of the various species.

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