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Reyes B Torres-Lugo
Autonomous University of Yucatan: Universidad Autonoma de Yucatan
Luis Ramírez-Avilés
Autonomous University of Yucatan: Universidad Autonoma de Yucatan
Juan C. Ku-Vera
Universidad Autónoma de Yucatán: Universidad Autonoma de Yucatan
Carlos F. Aguilar-Pérez
Universidad Autónoma de Yucatán: Universidad Autonoma de Yucatan
Jesús Jarillo-Rodríguez
Autonomous University of Yucatan: Universidad Autonoma de Yucatan
David Parsons
Swedish University of Agricultural Sciences - Umea Campus: Sveriges lantbruksuniversitet - Campus Umea
Jorge A. Hidalgo-Moreno
University of Georgia
Mario A. Santiago-Ortega
Universidad Autónoma de Yucatán: Universidad Autonoma de Yucatan
Jonathan Hernández-Pérez
Universidad Autónoma de Baja California: Universidad Autonoma de Baja California
Francisco Javier Solorio-Sánchez
ssolorio@correo.uady.mx

Universidad Autonoma de Yucatan Facultad de Medicina Veterinaria y Zootecnia
https://orcid.org/0000-0002-1384-8639

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In situ ruminal degradation kinetics of tropical *Urochloa* genotypes under shade and full sun in Yucatán, Mexico

Reyes B. Torres-Lugo[1] (0000-0002-9800-9753), Luis Ramírez-Avilés[1] (0000-0003-3340-8558), Juan C. Ku-Vera[1] (0000-0002-4384-9990), Carlos F. Aguilar- Pérez[1] (0000-0001-8102-1919), Jesús Jarillo-Rodríguez[2] (0000-0001-6010-5865), David Parsons[4] (0000-0002-1393-8431), Jorge Á. Hidalgo-Moreno[3] (0000-0002-0783-381X), Mario A. Santiago-Ortega[1] (0000-0001-6713-487X), Jonathan Hernández-Pérez[5] (0000-0002-8892-8115), Francisco J. Solorio-Sánchez[1]* (0000-0002-1384-8639).

[1] Facultad de Medicina Veterinaria y Zootecnia, Universidad Autónoma de Yucatán, Mérida 97300, Yucatán, México.

[2] Facultad de Medicina Veterinaria y Zootecnia, Universidad Nacional Autónoma de México, Tlapacoyan 93600, Veracruz, México.

[3] Department of Animal and Dairy Science, University of Georgia, Athens 30602, Georgia, United States of America.

[4] Department of Crop Production Ecology, Swedish University of Agricultural Sciences, Umeå 90183, Västerbotten, Sweden.

[5] Instituto de Ciencias Agrícolas, Universidad Autónoma de Baja California, Valle de Mexicali 21100, Baja California, Mexico.

*Corresponding author: ssolorio@correo.uady.mx

Abstract

Silvopastoral systems can modify forage nutritive value through changes in light availability; however, information on their effects on ruminal degradation kinetics of tropical *Urochloa* grasses remains limited. This study evaluated the influence of light environment and season on forage chemical composition and in situ ruminal dry matter degradability of five tropical *Urochloa* genotypes grown in Yucatán, Mexico. Forages were harvested under full sun and shade generated by scattered trees during the rainy, *nortes* (regional cool season), and dry seasons. Ruminal dry matter degradability was determined using the nylon bag technique in three rumen-cannulated cattle, and degradation kinetics were estimated using the Ørskov

and McDonald model. Shaded conditions significantly increased crude protein concentration across genotypes and seasons. The soluble fraction (*a*) was the degradation parameter most responsive to environmental conditions, showing significant effects of genotype ($p = 0.002$), light environment ($p < 0.001$), season ($p < 0.001$), as well as genotype × season ($p < 0.001$) and genotype × light × season ($p = 0.034$) interactions. In contrast, the potentially degradable fraction (*b*) and the fractional degradation rate (*c*) showed fewer and less consistent responses. Potential degradability ($a + b$) remained relatively stable across genotypes, light environments, and seasons. These results indicate that shade modified nutrient availability and ruminal degradation kinetics without affecting overall degradability potential. Moderate shade improved forage nutritional quality through increased crude protein concentration and changes in soluble fraction dynamics. The contrasting responses observed for the soluble fraction (*a*) among genotypes highlight the importance of genotype × environment interactions and support the selection of adapted *Urochloa* genotypes for tropical silvopastoral systems under seasonally variable conditions.

Key words

Urochloa; *in situ* ruminal degradability; degradation kinetics; crude protein; forage quality; tropical silvopastoral systems

Introduction

Tropical livestock production relies primarily on perennial grasslands as the main source of nutrients for ruminants. Among tropical forage grasses, species of the genus *Urochloa* (syn. *Brachiaria*) are widely used in tropical and subtropical regions because of their high dry matter production, strong regrowth capacity, and adaptation to acidic and low-fertility soils (Ferreira et al. 2021). These characteristics have enabled species such as *Urochloa brizantha*, *U. decumbens, U. humidicola*, and *U. ruziziensis* to occupy extensive pasture areas across Latin America, supporting economically important beef and dairy production systems (Morales-Ruiz et al. 2025).

Silvopastoral systems have been increasingly promoted as a sustainable alternative to conventional open pastures by integrating trees, forage, and livestock within the same productive area. These systems can improve microclimatic conditions, enhance biodiversity, and contribute to carbon sequestration without necessarily reducing animal productivity (Paciullo et al. 2014). Tree cover modifies radiation availability, temperature, and moisture conditions within the canopy, influencing forage growth and nutritive value

(Moreno et al. 2022; Monteiro et al. 2024). In tropical C4 grasses, moderate shade has frequently been associated with increased crude protein concentration and changes in plant structure, although responses in biomass production and forage quality vary according to species, management, and shade intensity (Santos et al. 2023).

In the Yucatán Peninsula, where shallow karst soils predominate, silvopastoral systems based on native tree species represent a promising strategy to improve the resilience and sustainability of livestock production. However, the response of *Urochloa* genotypes to the partial shade conditions characteristic of these systems remains poorly documented, particularly regarding forage nutritive value and ruminal degradation kinetics. Dry matter digestibility and ruminal degradation are key variables for estimating the effective supply of energy and protein to grazing animals and improving feeding efficiency in tropical pasture-based systems (Valles de la Mora et al. 2016).

The *in situ* ruminal degradation technique using nylon bags (*in sacco*) is a reference method for characterizing feed degradation kinetics in the rumen. By fitting nonlinear models such as that proposed by Ørskov and McDonald (1979), it is possible to estimate the soluble fraction (*a*), the potentially degradable fraction (*b*), and the fractional degradation rate (*c*), as well as overall degradability (Ørskov et al. 1980; Ferreira et al. 2016). This approach has been widely applied to tropical forages and provides a useful framework for comparing plant materials, management strategies, and growing environments (Woods et al. 2002; Despal et al. 2022).

Several studies have evaluated in situ ruminal degradation of *Urochloa* cultivars under monoculture and integrated production systems. For example, forage produced under silvopastoral conditions may exhibit changes in degradation kinetics compared with conventional monoculture, suggesting that shade can modify the availability of degradable fractions in the rumen (Silva et al. 2021). Likewise, Araújo et al. (2019) reported that dry matter and crude protein degradability may vary according to production system and plant morphological component. In Mexico, in situ degradability has also been documented for several tropical forage grasses, supporting the usefulness of this approach for characterizing forage quality under seasonal tropical conditions (Valles de la Mora et al. 2016).

Despite these advances, important knowledge gaps remain regarding how shade generated by scattered trees affects ruminal degradation kinetics of *Urochloa* genotypes adapted to tropical environments with marked seasonal variation. The interaction among genotype, light availability, and season may influence

chemical composition and structural traits, thereby modifying degradation parameters (*a*, *b*, and *c*) and the resulting potential degradability (*a* + *b*) that determine substrate availability for ruminal microorganisms (Ortega-Aguirre et al. 2015; Moreno et al. 2022).

In this context, the present study evaluated the *in situ* ruminal dry matter degradation kinetics and chemical composition of five *Urochloa* genotypes grown under moderate shade (average 57% reduction in incident radiation) and full sun across three seasonal periods in Yucatán, Mexico. The objective was to determine how light environment, season, and genotype influence forage chemical composition and ruminal degradation kinetics under tropical silvopastoral conditions. We hypothesized that shade would increase crude protein concentration and alter ruminal degradation kinetics, although the magnitude and direction of these responses would vary among genotypes and seasons.

Materials and methods

Study area and forage sampling

The forage samples evaluated in this study were obtained from a field experiment established at Kampepén Ranch, located in the San José Tzal area south of Mérida, Yucatán, Mexico. The site is located on a karst plain characterized by shallow, highly permeable stony soils locally known as *tzek'el* in the Mayan language, corresponding to Lithosols typical of the Yucatán Peninsula (Duch Gary 1988; Bautista 2021).

The region has a warm subhumid climate with summer rainfall (Aw climate according to the Köppen classification modified by García (2004)). Three seasonal periods were considered during forage sampling: rainy (June–October), *nortes* (November–January; the regional cool season associated with cold fronts in the Yucatán Peninsula), and dry (February–May). Mean annual precipitation ranges from 900 to 1100 mm, and mean annual temperature is approximately 26 °C, with average maximum temperatures close to 35 °C and minimum temperatures around 18 °C. Relative humidity ranges between 75 and 80% (Instituto Nacional de Estadística y Geografía (INEGI) 2023). The region also receives high solar radiation, averaging between 5.0 and 5.5 kWh m^{-2} day^{-1} (equivalent to approximately 18–19.8 MJ m^{-2} day^{-1}), which contributes to high evapotranspiration rates throughout the year (NASA 2024).

Five *Urochloa* genotypes were selected for the degradability study based on contrasting performance in a previous field evaluation conducted under the same experimental conditions (Torres-Lugo et al., manuscript under review). Four genotypes represented the highest forage yield under field conditions (GP1467, Mulato

II, GPNF3025-456, and GP1752), whereas genotype GP0423 was included as a contrasting low-yield control to represent a wider range of agronomic responses. Samples were collected under two light environments (full sun and shade) during the rainy, *nortes*, and dry seasons, resulting in 30 forage treatment combinations (5 genotypes × 2 light conditions × 3 seasons).

Chemical composition

Forage samples used for chemical composition analysis were obtained from the same material evaluated in the ruminal degradability trial. For each genotype × light × season combination, forage collected from the three field blocks was pooled to obtain one composite sample, resulting in 30 composite samples (5 genotypes × 2 light conditions × 3 seasons).

Samples were dried and ground to pass through a 2-mm screen prior to laboratory analysis. Dry matter (DM) and crude protein (CP) concentrations were determined according to standard procedures of AOAC (AOAC International 2019), whereas neutral detergent fiber (NDF) was determined following the method described by Van Soest et al. (1991). All chemical composition results were expressed on a dry matter basis. Detailed chemical composition values for each genotype × light × season combination are presented in Supplementary Table S1.

In situ ruminal dry matter degradability

In situ ruminal dry matter degradability was determined using the nylon bag technique described by Ørskov and McDonald (1979) at the Climate Change and Livestock Laboratory (LACCLIGA), Faculty of Veterinary Medicine and Animal Science, Universidad Autónoma de Yucatán (UADY), Mérida, Yucatán, Mexico.

Three rumen-cannulated crossbred cattle (*Bos taurus* × *Bos indicus*) with an average initial body weight of 430.5 ± 20.2 kg were used. All animal procedures were approved by the Bioethics Committee of the Campus de Ciencias Biológicas y Agropecuarias (CCBA), Universidad Autónoma de Yucatán (Approval No. CB-CCBA-D-2025-001), and were conducted in accordance with institutional guidelines for the care and use of animals in research.

Forage samples previously dried and ground to pass through a 2-mm screen were used for the in situ ruminal degradability evaluation. Before incubation, nylon bags were visually inspected to verify integrity and cleanliness, then dried at 55 °C for 10–15 min and weighed. Five grams of ground forage were placed into

in situ nylon bags (5 × 10 cm; 50 ± 10 µm porosity; Bar Diamond Inc., Parma, ID, USA), which were then sealed. Individual bags corresponding to each incubation time were grouped into larger synthetic mesh bags (45 × 60 cm) to facilitate insertion into and retrieval from the rumen.

Dry matter degradability was evaluated at 0, 12, 24, 48, 72, and 96 h. Samples corresponding to 12, 24, 48, 72, and 96 h were incubated in the dorsal sac of the rumen, whereas time 0 was determined outside the rumen by washing the bags with water, followed by the same drying and weighing procedure. After removal from the rumen, bags were carefully washed with water until the rinse water was clear. Bags were then dried at 55 °C for 48 h, weighed, returned to the oven for an additional 24 h, and weighed again until constant weight was achieved.

Dry matter degradability was calculated using the following equation:

$$\text{DM degradability (\%)} = \frac{[M - (PR - B)]}{M} \times 100$$

where:

M = dry sample weight before ruminal incubation

PR = bag plus residual sample weight after ruminal incubation

B = dry bag weight before incubation

Cattle were adapted to the experimental diet for 15 d before incubation. During the study, they were housed individually and fed once daily (08:30 h) with 12 kg of fresh elephant grass (*Pennisetum purpureum*) plus 600 g of a concentrate supplement composed of soybean meal, ground maize, urea, and mineral supplement. Water was available *ad libitum*. The chemical composition of the basal diet was determined according to AOAC (2019) procedures and Van Soest et al. (1991) fiber methodology and is presented in Supplementary Table S2.

Statistical analysis

For chemical composition variables (CP and NDF), genotype was included as a blocking factor, whereas light environment, season, and their interaction were considered fixed effects. These variables were analyzed using analysis of variance (ANOVA), and pairwise comparisons among light environments, seasons, and light × season combinations were performed using Tukey-adjusted tests.

Dry matter degradability data obtained at each incubation time were fitted to the nonlinear model proposed by Ørskov and McDonald (1979):

$$Y_t = a + b(1 - e^{-ct})$$

where Y_t is dry matter degradability at time t; a is the soluble fraction (%); b is the potentially degradable fraction (%); and c is the fractional degradation rate (h^{-1}). Potential degradability was calculated as $a + b$.

Model parameters were estimated separately for each genotype × light × season combination using nonlinear least squares with the nlsLM function from the minpack.lm package in R.

The estimated kinetic parameters (a, b, c, and $a + b$) were analyzed independently under a completely randomized design with a 5 × 2 × 3 factorial arrangement, consisting of genotype, light condition (full sun and shade), and season (rainy, *nortes*, and dry). The three rumen-cannulated cattle were considered biological replicates for each treatment combination.

The estimated kinetic parameters were subjected to analysis of variance (ANOVA) using the following fixed-effects linear model:

$$Y_{ijkl} = \mu + E_i + L_j + S_k + (E \times L)_{ij} + (E \times S)_{ik} + (L \times S)_{jk} + (E \times L \times S)_{ijk} + \varepsilon_{ijkl}$$

where:

Y_{ijkl} = observed value of the kinetic parameter (a, b, c, or $a + b$)

μ = overall mean

E_i = effect of the i^{th} genotype

L_j = effect of the j^{th} light condition

S_k = effect of the k^{th} season

$(E \times L)_{ij}$ = interaction effect between genotype and light condition

$(E \times S)_{ik}$ = interaction effect between genotype and season

$(L \times S)_{jk}$ = interaction effect between light condition and season

$(E \times L \times S)_{ijk}$ = three-way interaction effect among genotype, light condition, and season

ε_{ijkl} = residual error associated with each observation

$i = 1, \ldots, 5$ genotypes

$j = 1,2$ light conditions

$k = 1, \ldots, 3$ seasons

When significant effects were detected, means were compared using Tukey's significant difference test at $p \leq 0.05$. Means are presented as mean ± standard error. All statistical analyses and graphical visualizations were performed using R software (R version 4.5.3; R Core Team, Vienna, Austria).

Results

Chemical composition

Table 1 Least-squares means (LSMeans ± SE) of crude protein (CP) and neutral detergent fiber (NDF) concentrations as affected by light environment and season.

Variable	Factor	Level	LSMean ± SE	Group
CP	Light	Shade	12.64 ± 0.38	a
CP	Light	Sun	8.82 ± 0.38	b
NDF	Season	Rainy	67.4 ± 0.7	a
NDF	Season	*Nortes*	62.7 ± 0.7	b
NDF	Season	Dry	65.1 ± 0.7	ab

Note: Means within each variable followed by different letters differ significantly ($P \leq 0.05$) according to Tukey-adjusted pairwise comparisons. Crude protein (CP) and neutral detergent fiber (NDF) concentrations are expressed as percentage of dry matter (% DM).

Crude protein (CP)

Crude protein (CP) concentration was significantly affected by light environment ($p < 0.001$), whereas season and the light × season interaction were not significant ($p > 0.05$). Averaged across genotypes and seasons, CP concentration was greater under shade than under full-sun conditions (12.64 vs. 8.82% DM; Table 1).

Neutral detergent fiber (NDF)

Neutral detergent fiber (NDF) concentration was significantly affected by season ($p < 0.001$), whereas light environment and the light × season interaction were not significant ($p > 0.05$). Averaged across genotypes

and light environments, NDF concentration was greatest during the rainy season (67.4% DM), lowest during the *nortes* season (62.7% DM), and intermediate during the dry season (65.1% DM) (Table 1). Tukey-adjusted comparisons indicated that NDF concentration was greater during the rainy season than during the *nortes* season ($p < 0.001$), whereas the dry season did not differ significantly from either season.

In situ ruminal dry matter degradability

The kinetic parameters estimated from the Ørskov and McDonald model (*a*, *b*, *c*, and *a* + *b*) were analyzed independently using factorial ANOVA. A summary of ANOVA results for all degradation parameters is presented in Supplementary Table S3. Because the soluble fraction (*a*) exhibited the strongest response to genotype, light condition, and season, including significant two- and three-way interactions, it is presented in detail in Figure 1 and Table 2. The remaining kinetic parameters are summarized in Table 3.

Soluble fraction (*a*)

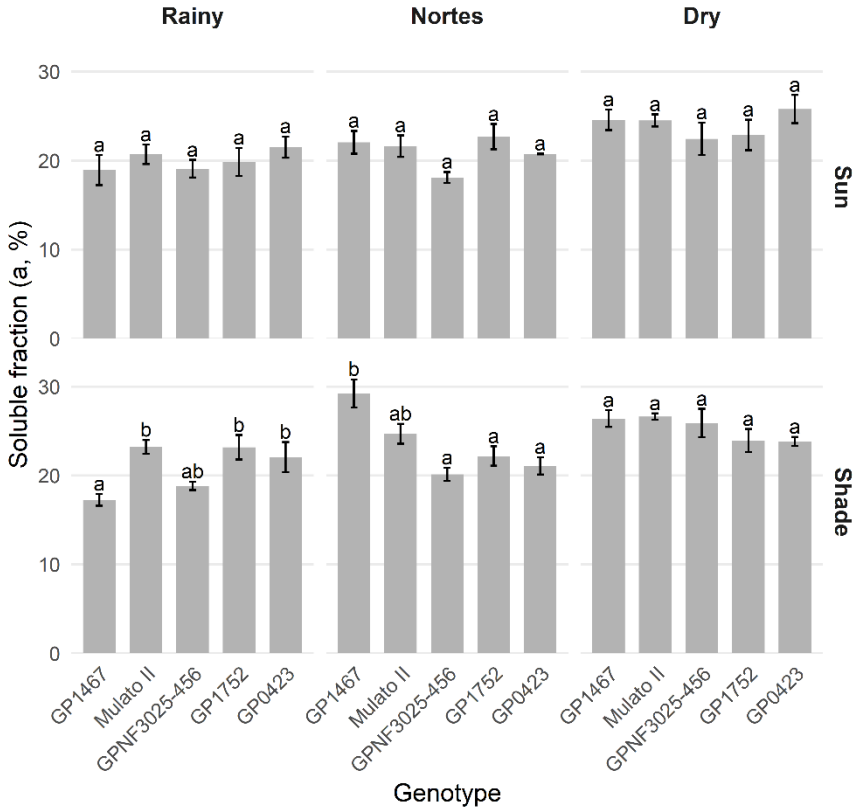


Fig. 1 Soluble fraction (*a*, %) of five tropical *Urochloa* genotypes evaluated under contrasting light environments (full sun and shade) across three seasons (rainy, *nortes*, and dry) in Yucatán, Mexico. Bars represent means ± SE (n = 3 cows). Different lowercase letters indicate significant differences among genotypes within each light × season combination according to Tukey's test ($P \leq 0.05$).

Analysis of variance showed significant effects of genotype ($p = 0.002$), light condition ($p < 0.001$), and season ($p < 0.001$) on soluble fraction (*a*) (Table 2). Significant genotype × season ($p < 0.001$) and genotype × light × season ($p = 0.034$) interactions were also detected, indicating that soluble fraction varied according to the combined effect of genotype, light environment, and season.

Under full-sun conditions, no significant differences among genotypes were detected in any season (Fig. 1). In contrast, shaded conditions revealed significant genotypes differences during the rainy and *nortes* seasons. During the rainy season, GP1467 showed lower soluble fraction values than several of the other genotypes under shade, whereas during the *nortes* season it exhibited the highest values and differed from most of the remaining genotypes. During the dry season, no significant differences among genotypes were observed under shade.

The significant genotype × light × season interaction indicates that differences among genotypes were expressed differently across light environments and seasons, resulting in distinct soluble fraction patterns across treatment combinations.

Table 2 Analysis of variance for the soluble fraction (*a*, %) of dry matter estimated using the Ørskov and McDonald model in five tropical *Urochloa* genotypes grown with or without shade during the rainy, *nortes*, and dry seasons in Yucatán, Mexico.

Source of variation	Numerator df	F	*p*
Genotype	4	4.74	0.002 **
Light	1	12.28	<0.001 ***
Season	2	31.39	<0.001 ***
Genotype × Light	4	1.46	0.227 ns
Genotype × Season	8	4.66	<0.001 ***
Light × Season	2	1.09	0.341 ns
Genotype × Light × Season	8	2.26	0.034 *
Residual	60		

ns = not significant; * $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

Potentially degradable fraction (*b*)

For parameter (*b*), light condition had a significant effect ($p = 0.045$), whereas genotype was not significant at the 0.05 level ($p = 0.079$). Season and all interaction terms were not significant ($p > 0.05$). Overall, *b* values tended to be slightly higher under full-sun than under shaded conditions. Values ranged from 35.31 to 57.38%.

Fractional degradation rate (*c*)

The fractional degradation rate (*c*) was significantly affected by season ($p = 0.025$), indicating seasonal variation in the degradation rate of the potentially degradable fraction. No significant effects of genotype or light condition were detected, and no significant interactions were observed among the evaluated factors ($p > 0.05$). Observed values ranged from 0.027 to 0.067 h^{-1}. Although seasonal differences were statistically significant, the magnitude of the variation was relatively small.

Potential degradability (*a* + *b*)

No significant main effects of genotype, light condition, or season were detected for total potential degradability (*a* + *b*), and no significant interactions among these factors were observed ($p > 0.05$). Values ranged from 60.92 to 77.22%, with no consistent pattern associated with genotype, light environment, or season.

Table 3 Mean values ± standard error of soluble fraction (*a*), potentially degradable fraction (*b*), fractional degradation rate (c), and potential degradability (*a* + *b*) estimated using the Ørskov and McDonald model in five tropical *Urochloa* genotypes grown under full sun and shade during the rainy, *nortes*, and dry seasons in Yucatán, Mexico.

Genotype	Light	Season	*a* (%)	*b* (%)	*c* (h^{-1})	*a* + *b* (%)
GP1467	Sun	Rainy	18.92 ± 1.69 a	46.23 ± 4.42 ab	0.031 ± 0.007 a	65.16 ± 5.24 ab
Mulato II	Sun	Rainy	20.70 ± 1.10 a	45.50 ± 2.56 ab	0.031 ± 0.004 a	66.20 ± 1.60 ab
GPNF3025-456	Sun	Rainy	19.07 ± 0.99 a	42.33 ± 2.82 a	0.039 ± 0.009 a	61.40 ± 3.79 a
GP1752	Sun	Rainy	19.84 ± 1.59 a	57.38 ± 12.51 b	0.027 ± 0.010 a	77.22 ± 13.45 b
GP0423	Sun	Rainy	21.51 ± 1.19 a	43.82 ± 5.50 ab	0.034 ± 0.012 a	65.32 ± 6.55 ab
GP1467	Shade	Rainy	17.25 ± 0.66 a	48.46 ± 0.38 a	0.030 ± 0.004 a	65.71 ± 0.71 a
Mulato II	Shade	Rainy	23.21 ± 0.77 b	44.88 ± 1.57 a	0.029 ± 0.001 a	68.08 ± 0.85 a
GPNF3025-456	Shade	Rainy	18.82 ± 0.48 ab	43.72 ± 3.59 a	0.030 ± 0.006 a	62.55 ± 3.79 a
GP1752	Shade	Rainy	23.16 ± 1.38 b	38.49 ± 2.53 a	0.041 ± 0.010 a	61.65 ± 1.77 a
GP0423	Shade	Rainy	22.05 ± 1.69 b	38.22 ± 2.31 a	0.037 ± 0.005 a	60.27 ± 0.65 a
GP1467	Sun	*Nortes*	22.05 ± 1.28 a	38.87 ± 0.97 a	0.041 ± 0.006 a	60.92 ± 1.36 a
Mulato II	Sun	*Nortes*	21.61 ± 1.21 a	44.00 ± 2.61 a	0.034 ± 0.011 a	65.61 ± 1.41 a
GPNF3025-456	Sun	*Nortes*	18.10 ± 0.62 a	49.60 ± 3.43 a	0.036 ± 0.004 a	67.70 ± 3.24 a
GP1752	Sun	*Nortes*	22.68 ± 1.41 a	41.89 ± 3.80 a	0.031 ± 0.002 a	64.56 ± 3.02 a
GP0423	Sun	*Nortes*	20.73 ± 0.05 a	43.08 ± 1.70 a	0.034 ± 0.005 a	63.81 ± 1.67 a
GP1467	Shade	*Nortes*	29.21 ± 1.58 b	39.57 ± 1.65 a	0.036 ± 0.011 a	68.77 ± 3.23 a
Mulato II	Shade	*Nortes*	24.68 ± 1.11 ab	46.65 ± 2.13 a	0.029 ± 0.003 a	71.33 ± 3.08 a
GPNF3025-456	Shade	*Nortes*	20.11 ± 0.75 a	43.99 ± 1.09 a	0.034 ± 0.004 a	64.10 ± 1.32 a
GP1752	Shade	*Nortes*	22.18 ± 1.09 a	41.85 ± 1.55 a	0.040 ± 0.005 a	64.02 ± 1.95 a
GP0423	Shade	*Nortes*	21.08 ± 0.98 a	41.22 ± 8.04 a	0.030 ± 0.013 a	62.29 ± 8.57 a
GP1467	Sun	Dry	24.57 ± 1.16 a	41.33 ± 4.17 a	0.041 ± 0.004 ab	65.90 ± 3.40 a
Mulato II	Sun	Dry	24.51 ± 0.68 a	48.07 ± 0.57 a	0.034 ± 0.002 a	72.58 ± 0.11 a
GPNF3025-456	Sun	Dry	22.44 ± 1.83 a	48.23 ± 2.31 a	0.027 ± 0.007 a	70.68 ± 3.62 a
GP1752	Sun	Dry	22.86 ± 1.72 a	46.91 ± 2.01 a	0.035 ± 0.005 a	69.78 ± 0.30 a
GP0423	Sun	Dry	25.78 ± 1.59 a	35.31 ± 2.55 a	0.067 ± 0.018 b	61.09 ± 1.09 a
GP1467	Shade	Dry	26.39 ± 0.94 a	40.77 ± 0.68 a	0.036 ± 0.005 a	67.15 ± 0.79 a
Mulato II	Shade	Dry	26.62 ± 0.35 a	36.81 ± 0.67 a	0.048 ± 0.005 a	63.43 ± 0.88 a
GPNF3025-456	Shade	Dry	25.89 ± 1.59 a	42.03 ± 2.27 a	0.034 ± 0.002 a	67.92 ± 2.38 a
GP1752	Shade	Dry	23.91 ± 1.29 a	46.30 ± 1.30 a	0.056 ± 0.008 a	70.21 ± 0.30 a
GP0423	Shade	Dry	23.81 ± 0.51 a	38.57 ± 0.96 a	0.037 ± 0.005 a	62.38 ± 1.47 a

Note: Values are presented as means ± SE (n = 3) for each genotype × light × season combination to facilitate biological interpretation. Statistical inference for each degradation parameter was based on the corresponding ANOVA results presented in Table 2 and Supplementary Table S3. Different lowercase letters within each light × season combination and within each parameter indicate significant differences among genotypes according to Tukey's test ($P \leq 0.05$).

Curves of dry matter degradability and model fit

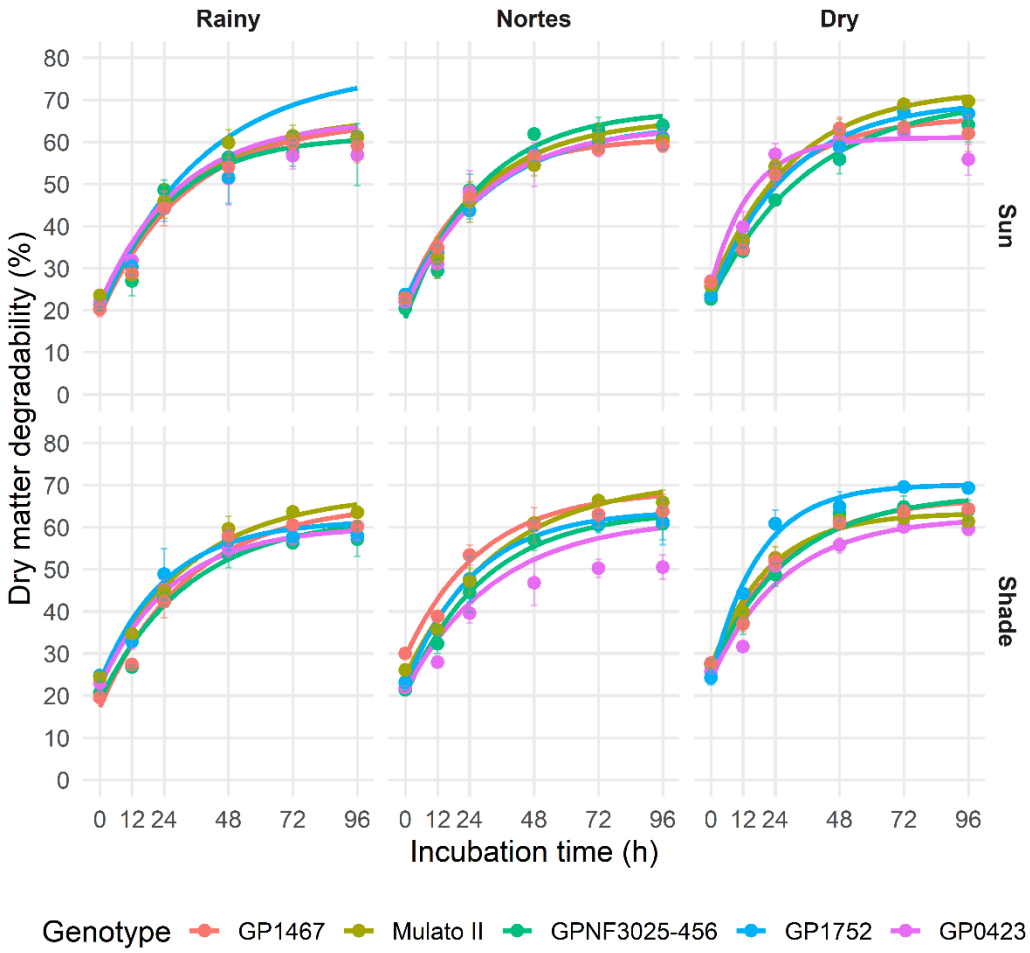


Fig. 2 *In situ* dry matter degradability (%), expressed as observed means (± SE; n = 3 cows) and fitted curves estimated using the Ørskov and McDonald model in five tropical *Urochloa* genotypes grown under two light conditions (full sun and shade) and three seasons (rainy, *nortes*, and dry) in Yucatán, Mexico.

Figure 2 presents the observed dry matter degradability values (mean ± SE) and the curves fitted using the Ørskov and McDonald model. Across genotypes, light environments, and seasons, degradability increased with incubation time following the expected asymptotic pattern. The fitted curves closely followed the observed data throughout the incubation period, indicating an adequate model fit across treatments. Differences among treatment combinations were primarily associated with variation in the estimated kinetic parameters presented in Tables 2 and 3.

Discussion

Shade and crude protein

The significant increase in crude protein concentration under shade across genotypes suggests a modification in plant nitrogen allocation under reduced radiation environments. Under reduced light availability, plants frequently decrease the accumulation of structural carbohydrates while increasing the relative concentration of nitrogen-containing compounds associated with light capture and photosynthetic efficiency, including components of the photosynthetic apparatus (Evans 1989; Lambers and Oliveira 2019). As a result, foliar nitrogen concentration per unit of dry matter often increases.

This physiological response has been widely documented in plant ecophysiology, where shading alters the carbon:nitrogen (C:N) balance and promotes the development of tissues with higher nitrogen concentration and lower structural density (Reich et al. 1997; Poorter and Evans 1998). Similar responses have recently been reported in tropical forage systems, including silvopastoral environments and *Urochloa* species, where microclimatic variation and partial shading were associated with improved nutritional quality and increased crude protein concentration (Murga-Orrillo et al. 2025; Narváez-Herrera et al. 2025).

From a nutritional perspective, increases in crude protein concentration are particularly relevant in tropical grazing systems because nitrogen availability frequently limits ruminal microbial activity and forage utilization. Therefore, the higher crude protein concentrations observed under shade may contribute to improved forage nutritive value and partially explain the changes observed in ruminal degradation dynamics.

Shade and soluble fraction (*a*)

The soluble fraction (*a*) was the kinetic parameter most responsive to the environmental conditions evaluated in the present study. Significant effects of genotype, light environment, and season, together with genotype × season and genotype × light × season interactions, indicate that the availability of rapidly degradable substrates was strongly influenced by both genetic background and environmental conditions. In contrast, the remaining kinetic parameters showed fewer responses, suggesting that environmental variation primarily affected the immediately available fraction rather than overall degradability potential.

The increase in crude protein concentration observed under shade coincided with higher soluble fraction values in several genotype × season combinations. According to the model proposed by Ørskov and McDonald (1979), fraction (*a*) represents the rapidly degradable portion of the forage. Thus, greater concentrations of soluble proteins and other cellular constituents under shaded conditions may explain the higher soluble fraction values observed in several genotypes. Similar relationships between forage composition and ruminal degradation dynamics have been reported in tropical grasses and other forage species (Wilson 1994; Vergara-López and Araujo-Febres 2006; Van Soest 2018).

The significant interactions detected for parameter a indicate that the influence of light environment varied according to genotype and season. For example, GP1467 exhibited comparatively low soluble fraction values under shade during the rainy season but the highest values during the *nortes* season, illustrating how environmental conditions can modify the expression of degradability traits. Similar genotype-dependent responses to shade have been reported in *Urochloa* species (Santiago-Hernández et al. 2016).

Seasonal influences on degradation kinetics

Seasonal conditions influenced ruminal degradation kinetics, particularly through changes in the soluble fraction (*a*) and, to a lesser extent, the fractional degradation rate (*c*). These responses suggest that seasonal variation affected the availability and degradation dynamics of forage constituents rather than overall degradability potential. Environmental conditions associated with the rainy, nortes, and dry seasons, particularly differences in precipitation, temperature, and water availability, may alter plant growth, tissue development, and the relative abundance of soluble and structural compounds, thereby influencing ruminal degradation characteristics (Santana et al. 2022).

The significant effects of season and the genotype × season interaction detected for parameter a indicate that seasonal responses were not uniform among genotypes. For example, GP1467 exhibited comparatively low soluble fraction values under shade during the rainy season but high values during the *nortes* season, illustrating how seasonal conditions can modify degradability traits. Similar seasonal variation has been reported in tropical forage grasses (Wilson and Hatfield 1997; Valles de la Mora et al. 2016; Sousa et al. 2017; Garay Martínez et al. 2022).

Season also affected the fractional degradation rate (*c*), although differences were relatively small. Because potential degradability (*a* + *b*) remained stable across seasons, these responses likely reflect changes in the timing and partitioning of degradable material rather than major alterations in total degradability potential.

Stability of potential degradability (*a* + *b*)

Potential degradability (*a* + *b*) remained stable across genotypes, light environments, and seasons. Unlike the responses observed for the soluble fraction (*a*) and, to a lesser extent, the fractional degradation rate (*c*), no significant effects of genotype, light condition, season, or their interactions were detected for this parameter. These results suggest that environmental conditions modified the distribution and availability of degradable substrates rather than the overall degradability potential of the forage.

According to the model proposed by Ørskov and McDonald (1979), parameters (*a*) and (*b*) represent complementary components of ruminal degradation; therefore, shifts in their relative contribution may occur without substantially affecting total degradability. The results indicate that moderate shade and seasonal variation may have altered the partitioning of degradable material, increasing the availability of rapidly degradable compounds under specific conditions while maintaining a stable degradation potential.

From a biological perspective, shade did not increase the maximum degradability of the forage but rather modified the timing and form of nutrient availability to ruminal microorganisms. Such changes may influence ruminal fermentation dynamics and nutrient synchronization even when overall degradability remains unchanged (Mertens 1997). Similar responses have been reported in tropical forage systems (Buxton and Fales 1994; Silva et al. 2021; Santos et al. 2023).

Implications for tropical silvopastoral systems

From a practical perspective, the increase in crude protein concentration and the enhancement of the soluble fraction (*a*) observed under shade suggest greater availability of degradable nutrients for ruminal microorganisms in silvopastoral systems. These changes may improve nitrogen utilization and synchronization between nitrogen release and fermentable energy, particularly in tropical forage-based systems where protein availability often limits microbial activity and animal performance (Hoover and Stokes 1991; Russell et al. 1992).

Moderate shade improved forage nutritive value without substantially altering potential degradability (*a* + *b*), a response also reported for tropical grasses grown under silvopastoral conditions (Malaquias Júnior et al. 2006; Gomes et al. 2022; Santos et al. 2023). This suggests that shaded environments enhance nutrient availability during ruminal fermentation without compromising overall degradation potential.

Responses of the soluble fraction (*a*) were not uniform among genotypes, highlighting the importance of genotype × environment interactions. The contrasting responses observed across seasons indicate that adaptation to silvopastoral conditions should be evaluated not only in terms of biomass production but also in terms of forage quality and ruminal degradation characteristics (Ortega-Aguirre et al. 2015; Torres Salado et al. 2020).

Overall, moderate shade generated by scattered trees improved forage nutritional quality through increases in crude protein concentration and modifications in the soluble fraction while maintaining stable degradability. These findings support the use of adapted *Urochloa* genotypes in tropical silvopastoral systems to enhance forage quality and the nutritional efficiency of grazing livestock production (Ibrahim et al. 2007; Mahecha-Ledesma et al. 2017; Pezo et al. 2018; Lima et al. 2019).

Future research directions

The present study demonstrated that moderate shade can modify forage chemical composition and ruminal degradation dynamics in tropical *Urochloa* genotypes, particularly through increases in crude protein concentration and modifications in soluble fraction dynamics. Future research should evaluate whether these responses translate into differences in voluntary intake, ruminal fermentation parameters, animal performance, and indicators of animal welfare under grazing conditions. Additional studies integrating forage chemical composition with variables such as acid detergent fiber, lignin concentration, methane emissions, voluntary intake, animal performance, and indicators of heat stress and animal welfare across contrasting shade intensities and multiple production cycles would further improve our understanding of the mechanisms underlying genotype-specific adaptation and support the design of nutritionally efficient tropical silvopastoral systems.

Conclusions

Moderate shade generated by scattered trees in tropical silvopastoral systems modified forage chemical composition and ruminal degradation dynamics of tropical *Urochloa* genotypes grown in Yucatán, Mexico. Across genotypes and seasons, shaded conditions consistently increased crude protein concentration and frequently increased the soluble fraction (*a*), indicating greater immediate availability of degradable nutrients for ruminal microorganisms.

The soluble fraction (*a*) was the kinetic parameter most responsive to the evaluated environmental conditions, showing significant effects of genotype, light environment, season, as well as genotype × season and genotype × light × season interactions. In contrast, the remaining degradation parameters showed fewer or less consistent responses. Although shade and season modified nutrient availability and degradation kinetics, potential degradability (*a* + *b*) remained relatively stable across treatments, indicating that environmental conditions affected the partitioning and timing of nutrient release rather than the overall degradability potential of the forage.

Overall, the results demonstrate that moderate shade can improve forage nutritional quality without compromising degradability potential. The contrasting responses observed for the soluble fraction (*a*) among genotypes highlight the importance of genotype × environment interactions and support the selection of adapted *Urochloa* genotypes that combine favorable forage quality and ruminal degradation characteristics for tropical silvopastoral systems in the Yucatán Peninsula and other seasonally variable tropical environments.

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Author contributions

Reyes B. Torres-Lugo: Conceptualization, methodology, investigation, project administration, formal analysis, data interpretation, visualization, Writing – original draft.

Francisco J. Solorio-Sánchez: Conceptualization, investigation, supervision, funding acquisition, Writing – review & editing.

Luis Ramírez-Avilés: Investigation, supervision, Writing – review & editing.

Juan C. Ku-Vera: Conceptualization, investigation, supervision, Writing – review & editing.

Carlos F. Aguilar-Pérez: Supervision, Writing – review & editing.

Jesús Jarillo-Rodríguez: Supervision, Writing – review & editing.

David Parsons: Methodology, formal analysis, supervision, Writing – review & editing.

Jorge Á. Hidalgo-Moreno: Formal analysis, supervision, Writing – review & editing.

Mario A. Santiago-Ortega: Writing – review & editing.

Jonathan Hernández-Pérez: Writing – review & editing.

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Data availability

The authors confirm that the data supporting the findings of this study are available within the article [and/or] its supplementary materials. Additionally, datasets generated and analyzed during the current study are available from the corresponding author upon reasonable request.

Declarations

Ethics approval

Ethical approval for all animal procedures was granted by the Bioethics Committee of the Campus de Ciencias Biológicas y Agropecuarias (CCBA), Universidad Autónoma de Yucatán (Approval No. CB-CCBA-D-2025-001). All procedures were conducted in accordance with institutional guidelines for the care and use of animals in research.

Competing interests

The authors have no financial or non-financial interests to disclose.

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