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Phenological changes in the nutritive value of honey mesquite leaves, pods, and flowers in the Chihuahuan Desert

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Abstract

Honey mesquite [*Prosopis glandulosa* (Torr.) *glandulosa*] is a potential foraging resource in southwestern United States rangelands and in other semi-arid rangelands. Yet, intake by ruminants is limited. We conducted an in vitro digestion experiment to assess phenological changes in nutrient value and relative digestibility of honey mesquite leaves, pods, and flowers throughout the 2012 growing season. Crude protein (CP) content of leaves decreased ($P < .001$) during the year, while acid detergent fiber (ADF) and neutral detergent fiber (NDF) increased ($P < .05$). Crude protein content of pods decreased ($P = .009$) over time, but we did not detect ($P > .10$) any phenological changes in ADF or NDF levels during the study. A cubic response was observed with in vitro gas production and Julian date for both leaves and pods ($P \leq .01$). Gas production from leaves collected in spring and early summer were lower than during late summer and early fall. Gas production and nutrient content values suggest that concentration of secondary compounds of mesquite leaves may decrease in late summer. Gas production values of mesquite leaves were lowest in early and mid-summer when CP levels were high and fiber levels were low. Mesquite flowers and pods can be valuable forage resources for cattle. Although mesquite leaves contain nutrients, secondary compounds likely limit intake, especially in late spring and early summer when the CP in mesquite leaves would be most beneficial because quality of herbaceous forages in southwestern United States rangelands at that time is usually low.

1 | INTRODUCTION

Honey mesquite (*Prosopis glandulosa* [Torr.] *glandulosa*) is a highly invasive species found on rangelands across the world including the southwestern regions of the United States and Australia (Meyer, Morton, Haas, Robison, & Riley, 1971; Robinson, Van Klinken, & Metternicht, 2008). It is the most prevalent mesquite species in the southwestern United States, occurring mainly in Texas and New Mexico (Ansley, Huddle, & Kramp, 1997). Gibbens, McNeely, Havstad, Beck, and Nolen (2005) indicate that honey mesquite has become the predominant plant in the Jornada Basin of New Mexico over the past 150 yr. Honey mesquite can outcompete desirable forage species and reduce potential stocking rates (McDaniel, Brock, & Haas, 1982). Control methods such as mechanical and chemical removal are usually not cost effective

Abbreviations: ADF, acid detergent fiber; CDRRC, Chihuahuan Desert Rangeland Research Center; CP, crude protein; DM, dry matter; IVDMD, in vitro dry matter digestibility; NDF, neutral detergent fiber.

(Holechek & Hess, 1994). Therefore, using mesquite as a forage resource in southwestern rangelands could increase the sustainability of livestock operations by providing forage during periods when herbaceous forage is limited or low in quality (Witmore, 2009). Potentially, mesquite could be a valuable forage resource in the spring and early summer due to its high crude protein (CP) content. However, presence of plant secondary compounds (PSMs) such as alkaloids, (Cates & Rhoades, 1977) flavonoids, (Solbrig et al., 1977) condensed tannins and phenolics (Witmore, 2009) may limit its consumption by ruminants.

There is limited information on nutrient content of mesquite. Based on these few studies, nutrient levels of honey mesquite leaves and pods are higher than levels of grasses that are often dormant prior to the monsoon season in the southwestern United States. Baptista (1996) reported that the CP content of honey mesquite leaves was 17% in May and 10% in November. In the same study, Baptista (1996) found that honey mesquite leaves had relatively low fiber levels, neutral detergent levels (NDF) levels of 32–43% and acid detergent levels (ADF) levels of 23–33%). Forage quality of mesquite pods is relatively high. Meyer et al. (1986) examined the nutritive values of velvet mesquite (*P. velutina* Whooton) bean. Whole beans had 12% CP and 22% crude fiber. Becker and Grosjean (1980) compared the nutritive values of honey and velvet mesquite pods. Their results indicated that pods of both species were high in CP: 32% CP for honey mesquite pods and 33% CP for velvet mesquite pods. Harden and Zolfaghari (1988) indicated that CP of honey mesquite pods decreased from 28 to 13% throughout the growing season.

These studies suggest that honey mesquite potentially can be used by livestock to improve diet quality during periods in late spring and early summer in the southwestern United States when mesquite is actively growing and grasses are dormant. However, our understanding of phenological changes in nutrients and secondary compounds of honey mesquite during the growing season is limited. The objective of this study was to evaluate the phenological changes of honey mesquite leaves, pods, and flowers throughout the growing season. We used in vitro gas production as an indicator of secondary compound impacts on forage value, because these metabolites adversely affect rumen fermentation (Estell, 2010). We hypothesized that in vitro gas production would not track changes in nutrient levels because of changes in concentrations of secondary compounds.

Core Ideas

- Honey mesquite provides relatively high crude protein and low fiber levels.
- Nutrient levels of honey mesquite forage decline over the summer months.
- Secondary compound impacts in honey mesquite leaves appear to be greater in early summer.
- Honey mesquite flowers appear to be a good forage source in early summer.

2 | MATERIALS AND METHODS

2.1 | Sample collection

Samples of honey mesquite leaves, flowers, and pods were collected from the Chihuahuan Desert Rangeland Research Center (CDRRC), located approximately 37 km North of Las Cruces (32°31′48″ N; 106°48′39″ W) in South central New Mexico. The CDRRC has an arid climate. Average daily temperatures range from 14 °C in January to 35 °C in July with an average of 200 frost-free days (Western Regional Climate Center, 2015). Mean annual precipitation at the CDRRC is 233 mm and rainfall peaks at August of 47 mm (Western Regional Climate Center, 2015). Samples were collected in 2012, which was an exceptionally dry year with only 109 mm of annual precipitation. The drought conditions of 2012 were compounded by low precipitation in 2011 (155 mm of annual precipitation).

Soils of the CDRRC belong to the Harrisburg (coarse-loamy, mixed, superactive, thermic Typic Petrocalcids) and Wink (coarse-loamy, mixed, superactive, thermic Petronodic Haplocalcids) soil series (USDA, 2014). Both series are found on gentle slopes (1–15%) and are fine sandy loam soils that are moderately deep to deep and well drained (USDA, 2014).

Honey mesquite leaves, flowers, and pods were collected approximately every 3–4 wk from April 2012 to December 2012 at the CDRRC. The sample area had gentle terrain (≤1% slope) and fine sandy loam soils. Mesquite samples were hand-picked in the field from multiple mature shrubs (>2 m in height) and placed in plastic freezer bags. Shrubs that were sampled appeared typical for the size and phenological stage of mesquite at the sampling site. Entire petiole of bipinnate mesquite leaves were removed and included the rachis and leaflets. Mesquite leaves were collected nine times (every 4 wk from 15 Apr. 2012 to 16 Dec. 2012). Mesquite flowers were collected two times (29 May 2012 and 18 June 2012) and were completely removed from the branch. Mesquite pods were collected every 4 wk from 15 July 2012 to 16 Oct. 2012). Pods were also completely removed from the branch. Leaves, pods, and flowers were collected from several shrubs at each sampling date. For transportation from the field to the laboratory, samples were stored in coolers with ice. Afterwards, samples were stored at −20 °C. Dormant dropseed grass (*Sporobolus* spp.) was also collected at the CDRRC in June 2012, prior to

the monsoon precipitation. Dropseed grass is the dominant forage at the CDRRC and has been used as a standard in other mesquite studies (Witmore, 2009).

The amount of mesquite flowers collected in 2012 was not sufficient to complete the nutrient analyses and the in vitro studies. Consequently, honey mesquite flowers used for nutrient analyses were collected in May 2013 rather than 2012. Although mesquite flowers used for nutrient analyses were collected in a different year, the 2013 flower collection was collected at the same site and at the same time of the year and should be reflective of the 2012 collections. Annual precipitation was slightly higher in 2013 (120 mm) than in 2012 (109 mm), and January to April precipitation in both years was less than 7 mm. Mesquite leaves were also collected in May 2013 to use as a standard in the in vitro studies to ensure there was a sufficient amount for the analyses.

2.2 | Forage analyses

Mesquite leaves, flowers, and pods as well as dormant dropseed were dried at 50 °C for 48 h and ground with a Wiley mill (Thomas Scientific) using a 1-mm screen. Ground material was used for chemical analyses: CP, NDF, and ADF. Nutrient analyses were conducted at SDK Labs (Hutchinson, KS) using wet chemistry (Association of Official Analytical Chemists, 2006) and Ankom filter bag method 5 (ADF) and method 6 (NDF) at SDK.

For all in vitro experiments, rumen inoculum was collected from four cannulated cows located at the New Mexico State University campus farm. Cows were fed a low-quality beardless wheat hay for 7 d prior to rumen collection to allow them to adapt to the diet. For every rumen fluid collection, inoculum was obtained from two randomly selected cows. Rumen fluid was collected at approximately 0900 h and strained through three layers of cheesecloth. Previously warmed insulated containers were used to preserve anaerobic conditions and optimal rumen temperature (39 °C). Rumen fluid was mixed with McDougall's buffer (Galyean, 1997) in a 1:1 solution. Individual 250 ml Erlenmyer flasks were filled with 150 ml of the mixture of McDougall's solution and rumen fluid and 2.3 g dry matter (DM) of sample forage. Frozen mesquite samples (flowers, pods, and leaves) were ground with dry ice in a Micro-Mill Grinder (Bel-Art Scienceware 372500000) to an average length of 2 mm (Witmore, 2009) and then added to the Erlenmeyer flask. Flasks were incubated for 48 h at 39 °C in a forced air Lab Line Orbit Environ shaker system with a 24-flask capacity (referred to as a batch). Each combination of sample date and plant part (leaves, pods, and flowers) and standards were run in triplicate (three flasks), which allowed a comparison of eight types of samples per batch (24 flasks). Locations of flasks in the shaker system were randomized for each batch. Tubes from the sealed flasks were placed in inverted burets to collect the gas produced from the flasks. Gas production was recorded every 4 h for 48 h as displaced water in inverted burets. Although we recorded and evaluated gas production of each 4-h reading, we report only the 24-h readings. Statistical analyses from readings at other times yielded similar results, and the 24-h reading appeared to be representative and were consistent with other readings across sample collection dates. After incubation, contents of each flask were stored in a plastic container at −20 °C for later analyses.

Each batch had a total of three types of standards and five sample date–plant part combinations. The standards were (a) a mix of 70% grass and 30% mesquite leaves from a separate sampling date (31 May 2013) on a DM basis, (b) 100% grass, and (c) a blank (flasks containing only the mixture of rumen fluid and McDougall's solution). The purpose of mixing mesquite leaves with dormant grass for a standard was to simulate a ruminant's diet of grass and mesquite. Witmore (2009) used the same mixture of mesquite leaves and grass to evaluate the effects of activated charcoal, polyethene glycol, and other supplements on gas production and in vitro digestibility. The dropseed grass had been used on previous studies as a standard for mesquite studies (Witmore, 2009). The allocation of forage samples (plant part and sampling date) to batches (1–3) was randomized.

Similar to Menke and Steinglass (1988), we used a standard to adjust gas production values for variation among the three batches. We used the mix of mesquite leaves and dropseed grass as the standard for adjustments because it included both mesquite leaves and the dominant livestock forage at the CDRRC (dropseed grass).

Within the same batch, gas production from the three mesquite/grass standards were averaged. The lowest average for a batch of the three batches was used as the base. Next, this base was subtracted from average grass/mesquite standard values from each trial. This difference between the base and batch standard (average of the triplicates) was used as the adjustment for that batch to standardize among the three batches. The corresponding adjustments were subtracted from the original gas production values of all mesquite samples (leaves, flowers, or pods). The adjustments allowed comparisons of sample collection dates across the batches.

The residual material and fluid from the in vitro gas production experiment from each flask was thawed. All contents were removed with deionized water and poured into two plastic centrifuge bottles (pairs). Prior to centrifugation, samples were weighed and arranged in pairs. Samples were centrifuged at 14,000 × *g* for 20 min in a Beckman Coulter Centrifuge. Afterwards, samples were filtered using Whatman 54 paper inside Buchner funnels using suction. Once all fluid was removed, residues and filter paper were dried at 105 °C for

48 h and weighed to determine disappearance (in vitro dry matter disappearance, IVDMD).

Average weight of residual material was calculated for the three blank standards in each trial and then subtracted from the residual weight of the other samples in that batch. Percentage of ingestible material was obtained dividing the weight of the residual solids (adjusted for the blanks) by the weight of the original sample (2.3 g) and multiplying by hundred. Percent disappearance was calculated by subtracting the percentage of indigestible material from 100.

2.3 | Statistical analyses

A pooled sample of leaves or pods from each collection date was used as a sample for linear and polynomial regression analyses of nutrient content. For gas production and IVDMD, each flask from each date of sampling was used as a sample for regression analyses for a total of three samples for each combination of sampling date and mesquite part (flowers, pods, and leaves). Gas production values were adjusted for the grass and mesquite standards to a similar base level for the three batches (see above). The adjustments allowed us to evaluate data from different batches in the same regression model (Menke & Steingass, 1988).

Nutrient content, gas production, and IVDMD were evaluated as dependent variables in linear and polynomial regression analyses using PROC MIXED of SAS 9.3 (SAS Institute, 2012). Sample date (Julian date) was used as a continuous independent variable and linear, quadratic and cubic relationships were evaluated. Corresponding analyses of leaves, pods, and flowers were conducted separately. No statistical analyses were conducted on the CP, ADF, and NDF of mesquite flowers because the flower nutrient content sample was collected once in May of 2013.

3 | RESULTS AND DISCUSSION

3.1 | Nutrient composition

The forage quality of the dormant dropseed grass used as a standard (in a mixture with mesquite leaves and alone) was very poor (Table 1). Crude protein content of mesquite leaves decreased linearly ($P < .001$) from April to December (Table 1). The ADF level in mesquite leaves varied during the growing season and displayed a cubic response ($P < .001$). The ADF in mesquite leaves increased from April to May, then stabilized from May through August, and decreased slightly in November and December (Table 1). A cubic relationship was also detected ($P < .001$) for NDF of mesquite leaves. The NDF levels increased through July, then decreased until October, and then increased in November and December.

TABLE 1 Collection dates of mesquite leaves, flowers, and pods and crude protein (CP) concentration, acid detergent fiber (ADF), and nutrient detergent fiber (NDF) associated with each collection date and plant part. Nutrient values of the dormant dropseed grass used as a standard are also presented

Item	Date	CP	ADF	NDF
		%		
Grass standard	28 June	1.58	51.7	69.0
Flowers	25 May 2013[a]	24.03	16.65	31.51
Leaves	29 April	25.39	14.80	22.42
Leaves	13 May	18.05	23.80	35.76
Leaves	29 May	18.50	31.14	45.36
Leaves	18 June	18.04	31.31	44.01
Leaves	3 July	18.48	29.88	43.68
Leaves	25 July	18.55	32.11	40.25
Leaves	10 August	17.69	30.95	39.41
Leaves	26 August	16.82	30.68	38.70
Leaves	15 September	17.28	29.17	37.25
Leaves	2 October	15.34	28.88	35.11
Leaves	16 October	15.73	28.64	34.99
Leaves	2 November	14.48	24.99	35.33
Leaves	19 November	12.55	27.86	39.39
Leaves	3 December	10.81	33.92	47.01
Leaves used in the standard	24 May 2013[a]	16.65	35.67	47.67
Pods	25 July	21.03	32.07	47.28
Pods	10 August	18.37	34.11	48.98
Pods	26 August	14.54	30.45	45.24
Pods	15 September	14.64	18.99	27.72
Pods	2 October	14.87	21.95	32.61
Pods	2 November	10.85	28.35	42.42

[a]Flowers and leaves used for the mesquite/grass standard were collected in 2013. All other samples were collected in 2012.

Crude protein content of flowers collected in May 2013 was 24.0% (Table 1). Crude protein content of pods decreased linearly from July to December ($P = .009$) (Table 1). No patterns in seasonal changes of ADF and NDF levels were detected ($P > .10$) in pods.

Mesquite leaves, flowers, and pods had much higher nutritive levels than dormant dropseed grass that provided most of the herbaceous forage at the CDRRC from April to July 2012. Nutrient levels of dormant grass were well below cattle requirements when sampled in late June, prior to the monsoon season (NRC, 1996). In contrast, mesquite flowers contained relatively high levels of CP and low fiber levels. Mesquite leaves and pods contain similar amounts of CP and fiber. Crude protein levels decreased throughout the season for both mesquite leaves and pods. Baptista (1996) reported a similar decline in CP in mesquite leaves from 17% in May to 10% in November. Crude protein levels and fiber levels (ADF and NDF) of mesquite leaves observed in this study are similar

to values reported by Witmore (2009). Observed changes in ADF levels in our study are similar to patterns observed by Baptista (1996). The ADF values increased in late spring and then remained relatively stable from June to September and then slowly declined. Baptista (1996) suggests that faster rates of maturation and development of leaves after flowering could explain the increase in ADF from May to June.

3.2 | Gas production

A cubic response was detected for gas production of mesquite leaves with Julian date ($P < .01$). From April through July, gas production was lower than later in the year (Figure 1). Gas production began to increase in August and peaked in September and October, and then declined in November and December. Gas production of mesquite flowers increased linearly ($P = .003$) from May to June (Figure 1). Gas production of mesquite pods exhibited a cubic response to Julian date ($P \leq .01$), increasing from July to September and then decreasing in October (Figure 1).

3.3 | In vitro dry matter disappearance

In vitro dry matter disappearance of leaves ranged from 30 to 80% (Figure 2). The IVDMD displayed a cubic relationship with Julian date ($P < .001$) with leaves sampled in early spring having higher values and decreasing during the season except for an increase in September and October. The IVDMD of mesquite flowers ranged from 68 to 72% (Figure 2). No differences in sampling date were detected for IVDMD ($P = .97$) for mesquite flowers in May and June.

3.4 | Phenological changes in Mesquite leaves

Similar to the nutrient level data, results for IVDMD (Figure 2) also suggest forage quality of mesquite leaves declined from April (77%) to December (32%). Baptista (1996) observed a decrease in IVDMD during the summer from 79% in May to 69% in November. Early in the season, fiber levels are relatively low and the decrease in IVDMD is likely a consequence of increasing fiber levels. However, gas production from leaves was greater during August through November. This suggests that rumen fermentation may have been more adversely affected by the presence of secondary compounds during late spring and early summer (April and May) than during late summer and autumn (August–October). Lyon, Gumbmann, and Becker (1988) observed that phenolic compounds are 2.3–6.5 times greater in mesquite leaves than in alfalfa (*Medicago sativa* L.), which may decrease enzymatic digestibility. Cates and Rhoades (1977) mention that young mesquite leaves have the highest alkaloids concentrations, but levels decline as they reach maturity. Bryant, Reichardt, and Clausen (1992) suggest that compounds such as alkaloids play a pivotal role in the defense of immature plants due to their mobility and low molecular weight. The adverse effect of mesquite leaves on rumen fermentation was demonstrated by Witmore (2009). In her in vitro study, gas production and IVDMD decreased as the proportion of mesquite increased in a simulated diet with grass from 0% mesquite (100% grass) to 100% mesquite (0% grass).

In late spring and early summer, grasses and other herbaceous forages typically contain low levels of CP and are poor quality forages in the Chihuahuan Desert and other parts of the southwestern United States. Potentially, mesquite leaves could be a valuable CP source for livestock during these periods. Unfortunately, results from this study suggest that impacts of secondary compounds in mesquite leaves (either levels or activity) may be greater in late spring and early summer, which likely makes the leaves less palatable. During late summer and autumn when impacts of secondary compounds in mesquite leaves appear to decline, forage quality of grasses and other preferred forages normally are high because monsoon precipitation stimulates new growth.

Mesquite leaves can be a forage source in the southwestern United States, but intake is usually low. Baptista and Launchbaugh (2001) reported that sheep can tolerate inclusions up to 5% mesquite leaves in their diet. Likewise, Mayagoitia (2015) found that lambs will consume mesquite leaves (mean intake of 3.7% of the diet). Cows can consume up to 5% of their diet as mesquite leaves before showing signs of negative postingestive feedback (Altangerel et al., 2017). Microhistological analyses by Hakkila, Holechek, Wallace, Anderson, and Cardenas (1987) revealed that honey mesquite pods were consumed in August and October, and dead leaves were consumed in March. De Alba Becerra, Winder, Holechek, and Cardenas (1998) also reported that honey mesquite made up about 5% of cattle diets during June in the Chihuahuan Desert. Shrubs can make up over half of the diets of goats in the Chihuahuan Desert (Mellado, 2016).

3.5 | Mesquite flowers

Mesquite flowers have relatively high nutritive levels and are potentially a valuable forage resource in late spring and early summer. Gas production from flowers were higher than corresponding values for mesquite leaves, suggesting that impacts of secondary compounds in mesquite flowers are likely less than mesquite leaves during late spring and early summer. Staff from the CDRRC (Calvin Bailey, personal communication, 2015) and the authors have observed cattle consuming honey mesquite flowers. Consumption of mesquite flowers may be one strategy by which cattle

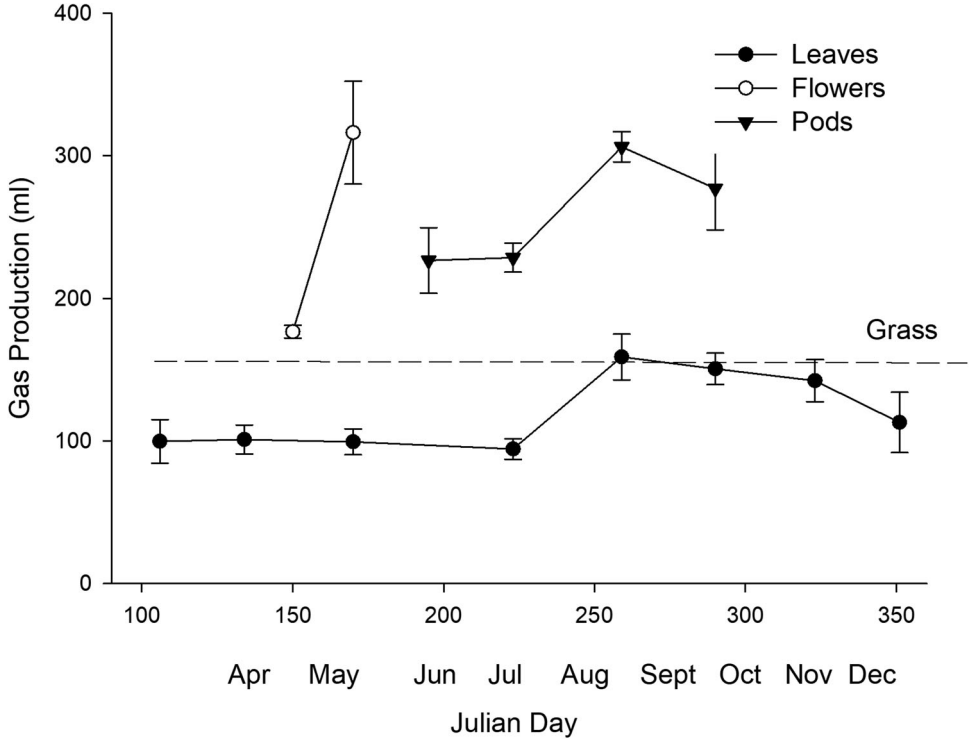

FIGURE 1 In vitro gas production at 24 h of honey mesquite (*Prosopis glandulosa* Torr.) leaves, flowers, and pods. As a reference to available dormant herbaceous forage at the study site, gas production of the dormant dropseed grass that was used as a standard and was available for livestock in June 2012 (year of study) is shown as a dashed line. Error bars represent standard deviations

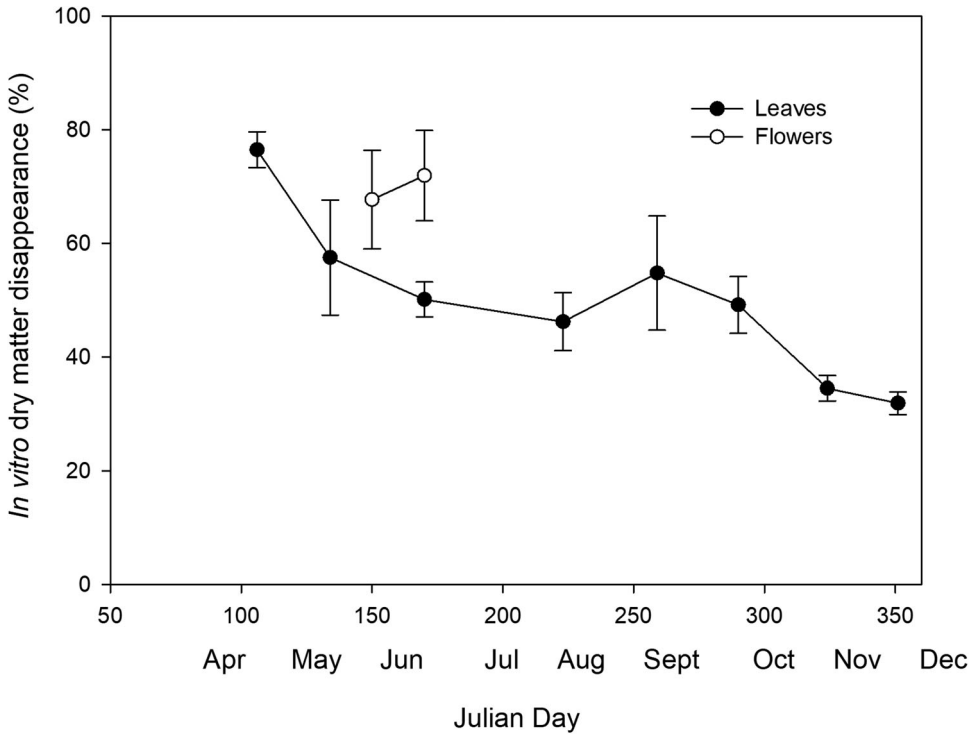

FIGURE 2 In vitro dry matter disappearance (IVDMD) of honey mesquite *(Prosopis glandulosa* Torr.) leaves and flowers. Error bars represent standard deviations. The IVDMD of the dormant dropseed grass standard was 50%, which provides reference to the quality of the dormant herbaceous forage at the study site

improve the quality of their diets during late spring and early summer in the Chihuahuan Desert and other parts of southwestern United States when grasses and other herbaceous are normally dormant and low in quality.

3.6 | Mesquite pods

Mesquite pods exhibited a similar pattern to mesquite leaves in that the highest CP content was observed in early summer and gas production peaked in late summer (Figure 1 and Table 1). Similarly, Harden and Zolfaghari (1988) found that CP of honey mesquite pods declined from 28% when pods were immature to 12% for mature pods. These CP values for pods are somewhat higher than those from our research (21% for immature pods in July and 11% for mature pods in November, Table 1). The ADF and NDF levels of pods decreased in September and October, which may help explain the increase in gas production in those months. In addition, levels of secondary compounds in immature pods could potentially decline as pods mature. These factors may help explain cattle preference for mature pods over immature pods (Kneuper, Scott, & Pinchak, 2003).

3.7 | Implications

To our knowledge, no other research has examined nutrient content, gas production, and IVDMD of honey mesquite leaves, flowers, and pods throughout the year. Although crude protein levels were high and fiber levels were low at the beginning of the growing season (May–July), gas production was lower than levels later in the season, August–November. These findings suggest that the impact of secondary compounds on rumen fermentation of mesquite leaves may be greater in late spring and early summer, which could limit livestock consumption of mesquite leaves during a period when grasses and other forages in the southwestern United States are often dormant and low in quality. In late summer and autumn, impact of secondary compounds in mesquite leaves on rumen fermentation may decline since crude protein levels decreased and fiber levels increased, but gas production increased. However, quality and quantity of grasses and other forages is much greater during this period because of monsoon precipitation, which negates the need for mesquite leaves as a forage source in late summer and autumn. Mesquite flowers are a potential forage resource for livestock. Flowers have high levels of protein and low fiber levels and observed fermentation rates suggest that secondary compounds in mesquite flowers have less impact than in mesquite leaves. Mesquite pods are known to be a valuable forage resource for livestock during late summer and autumn. Fiber levels of mesquite pods (and beans) was lower in September and October and CP was still above 14%. Consumption of honey mesquite may allow adapted livestock to obtain needed nutrients during periods when grasses are dormant and forage quality is low and during droughts when forage quantity is limited. However, more research is needed to evaluate the levels of secondary compounds in honey mesquite and the impact on palatability and intake by livestock.

CONFLICT OF INTEREST

This manuscript has not been published and is not under consideration for publication elsewhere. We have no conflicts of interest to disclose.

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