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Consumption and dispersion of mesquite seeds by ruminants

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Abstract

Consumption of mesquite (*Prosopis glandulosa* Torr. var *glandulosa*) fruit by ruminants is an important component of seed dispersal. Two experiments were conducted to estimate the role of livestock and wildlife in the dispersion of mesquite fruit. In Experiment 1, 3 trials were conducted to determine preference for mesquite fruit by different species of livestock, intake relative to fruit maturity, and seed survival of digestion. Cattle, sheep, and goats were offered immature (IM), mature off the tree (MT), or mature off the ground (MG) fruit to quantify intake and seed survival of digestion. Germination of seeds surviving digestion was also assessed. Experiment 2 assessed rate of pod disappearance from pastures with and without livestock grazing and attempted to quantify seed loss to wildlife. In Experiment 1, livestock consumed more ($P < 0.05$) mature than immature fruit; sheep and goats consumed more fruit than cattle on a body weight basis. Seed survival was greater ($P < 0.05$) from cattle than from sheep or goats. The number of seeds remaining intact after digestion was greater for mature fruit. Germination of seeds surviving digestion was similar ($P > 0.05$) to seeds that experienced natural weathering for 6 months. In Experiment 2, the presence or absence of livestock did not affect the disappearance of seeds; seeds disappeared from the ground within 3 weeks in 1999 and 5 weeks in 2000 presumably by wildlife. Deer, raccoons, skunks, bobcats, turkeys, and other birds visited plots with fresh mesquite fruit. Collectively, these results suggest that cattle readily consume and disperse viable mesquite seeds; sheep and goat consumption of mesquite fruit may reduce the number of viable seeds; and mesquite fruit may only remain on the ground for a short period of time even without livestock grazing because of consumption by wildlife.

Key Words: *Prosopis, germination*, digestion, fecal dispersal, phenology, encroachment

Resumen

El consumo de los frutos del mezquite (*Prosopis glandulosa* Torr. var *glandulosa*) por los rumiantes es un componente componente de la dispersión de semilla. Se condujeron dos experimentos para estimar el papel del ganado doméstico y la fauna silvestre en la dispersión de frutos de "Mesquite". En el experimento 1 se realizaron 3 ensayos para determinar la preferencia del fruto de "Mesquite" por diferentes especies de ganado, el consumo en relación a la madurez del fruto y la sobrevivencia de la a la digestión. A bovinos, caprinos y ovinos se les ofreció frutos inmaduros (IM), frutos maduros tomados del árbol (MT) y frutos maduros tomados del suelo (MG) para cuantificar el consumo y sobrevivencia a la digestión. El experimento 2 evaluó la tasa de desaparición de vainas de potreros con y sin apacentamiento de ganado y se intento cuantificar la perdida de semilla para la fauna silvestre. En el experimento 1 el ganado consumió mas frutos maduros que inmaduros ($P < 0.05$), los caprinos y ovinos consumieron mas frutos que los bovinos, esto expresado en base al peso corporal. La sobrvivencia de la semilla fue mayor ($P < 0.05$) en los bovinos que en los ovinos o caprinos. El número de semillas que permanecieron intactas después de la digestión fue mayor en los frutos maduros. La germinación de las semillas sobrevivientes a la digestión fue similar ($P > 0.05$) a la de semillas expuestas a intemperización natural por 6 meses. En el experimento 2 la presencia o ausencia de ganado doméstico no afectó la tasa de desaparición de semillas, las semillas desaparecieron del suelo en 3 semanas en 1999 y en 5 semanas en el 2000, esto presumiblemente por efecto de la fauna. Venados, mapaches, zorrillos, pumas, pavos y otras aves visitaron las parcelas con frutos frescos de "Mesquite". Estos resultados sugieren que el ganado bovino si consume y dispersa semillas viables de "Mesquite", el consumo de frutos de "Mesquite" por ovinos y caprinos puede reducir el número de semillas viables y el fruto del "Mesquite" puede permanecer en el suelo solo por un periodo corto de tiempo, aun sin apacentamiento de ganado, debido al consumo de este por la fauna silvestre.

Across Texas, an ever-increasing density of mesquite (*Prosopis glandulosa* Torr. var. *glandulosa*) has reduced herbaceous production on rangelands (Bedunah and Sosebee 1984, Cuda and DeLoach 1998). Mesquite infests about 22 million ha of rangeland in Texas (Jacoby et al. 1990a), and control of mesquite is a major concern for ranchers (Ueckert 1974, Heitschmidt and Dowhower 1991). Herbicide application is the most common method for controlling large areas of mesquite, but most treatments only last for a few years (e.g., 5-10) because some mesquite trees resprout after herbicide treatment and seedlings readily establish (Jacoby et al. 1982, 1990b, Teague et al. 1997).

Encroachment and reinvasion of mesquite into grasslands is accelerated by livestock consuming and then dispersing seeds (Gibbens et al. 1992, Lerner and Peinetti 1996, Kramp et al. 1998). Mesquite produces a seed pod with 10–20 seeds/pod depending on growing conditions. Seeds are encapsulated in a hard coat that must be scarified before rapid germination will

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occur; passage of seeds through the ruminant digestive tract apparently enhances seed germination potential (Scifres and Brock 1969, 1972, Cuda and DeLoach 1998), and livestock are a likely primary dispersal vector for mesquite (Kramp et al. 1998).

Little information is available on when livestock consume mesquite fruit relative to fruit maturity and on seed survival from different stages of fruit maturity. The relative importance of animals as dispersal agents of mesquite seeds may depend on intake patterns relative to seed availability and maturity (Kramp et al. 1998). This study quantified intake and survival of digestion of mesquite seeds from different stages of fruit maturity by 3 species of livestock. In addition, we identified disappearance rate of fruit from pastures with and without the presence of livestock, and we attempted to identify other species that may consume and disperse mesquite fruit.

Methods

This research was conducted at the Angelo State University Management, Instruction, and Research (MIR) Center located in the Rolling Plains region of Texas, 9.7 km north of San Angelo, Tex (30°N, 100°W). Five freshly weaned Angus/Beefmaster crossbred steers (5 months-old, weight 250 kg), 5 castrated Ramboullet sheep (4 months-old, weight 40 kg), and 5 castrated Boer/Spanish goats (3 months-old, weight 25 kg) were placed in individual pens and offered current growing season mesquite fruit from different stages of maturity on a daily basis. Sheep and goats were placed in 1.5 x 1.5 m metabolism stalls to facilitate fecal collections for Experiment 1. Steers were individually placed in 4 x 7 m pens and fecal collection bags were attached to the steers. Fecal bags were emptied twice daily because of the volume of feces produced. Fecal samples for each steer were combined to estimate daily fecal production/animal. All animals were fed (1.5% BW) an alfalfa hay/concentrate basal ration (CP% 12.3, TDN 61%, DE 2.7 mcal kg^{-1}) to meet maintenance requirements (NRC 1981, 1984, 1996). Fresh water and a calcium/phosphorus mineral with trace elements were provided ad libitum. All animals were housed in the same open-air research facility under similar environmental conditions.

Experiment 1

To assess intake of mesquite fruit from different stages of maturity, fruit was collected daily from several randomly selected trees on the MIR Center. Fruit was arbitrarily categorized as immature attached to the tree (IM), mature attached to the tree (MT), and mature on the ground (MG). Immature fruit was identified as green pods with seeds that appeared underdeveloped. Mature attached to the tree (MT) were pods that were beginning to change from the immature green color to a mature red-brown color. The fruit was filled out and seeds appeared fully developed. Mature on the ground (MG) represented the mature fruit that had completely changed to the red-brown color and had recently fallen to the ground. Any fruit that appeared mature and fell to the ground during harvesting was classified as MG.

Intake of 3 classes of mesquite fruit was determined in Trial 1. Livestock (cattle, sheep, and goats) were fed a single class of mesquite fruit (0.5% BW) at 0800 hours each morning for 10 min over 7 days. Feeding level was based on the amount of beans consumed in a similar feeding trial (Kneuper and Scott 1998). The trial was divided into 3 phases. In the first 7 days, individual steers, sheep, and goats were fed IM fruit. Phase 2 consisted of feeding MT fruit. Mature on the ground fruit was fed during phase 3. Refusals were weighed to determine intake of each class of fruit. After each class of fruit was fed individually, all 3 stages of fruit development were fed simultaneously in separate containers to quantify preference. Individuals were offered a choice between fruit classes for 10 min each day for 7 days. If fruits from any maturity stage were completely consumed during the preference trial, all remaining fruit was removed immediately.

In Trial 2, the percent of intact seeds in feces from different stages of maturity was determined by feeding seeds and collecting feces. Each stage of seed maturity was fed once and total fecal collections were utilized to recover seeds for 4 days thereafter. Before feeding seeds from a particular maturity stage, a 5-day rest period was used to ensure any seeds already in an individual's digestive system had passed. Other studies have shown that seeds will pass up to 4 days post-ingestion (Armke and Scott 1999). The number of seeds fed was based on feeding 0.1% BW of fruit to an animal. This level was sufficient for seed recovery in feces in a previous study (Kneuper and Scott 1998). Before feeding each stage, representative samples of each stage were weighed and the number of seeds were counted. The average number of seeds fed was used to calculate the percent of intact seeds surviving digestion.

Feces were collected twice daily for cattle and once daily for sheep and goats, and total fecal weight was recorded. Subsamples were taken to estimate the number of seeds surviving digestion. Fecal subsamples were washed through a series of screens and seeds were separated; whole seeds that were found, with or without an exocarp, constituted survival of digestion.

In Trial 3, germination was determined for seeds that had remained on the ground and weathered for 6 months, unweathered seeds, and for MT and MG seeds collected from cattle, sheep, and goat feces from Trial 2. One hundred and twenty seeds were used in the study, 15 seeds from each treatment. Immature seeds (IM) were excluded from this trial because few were collected from feces. Seeds from the ground that had weathered were kept in cages to prevent loss to herbivory.

Seeds that were sealed in dry containers and stored in the laboratory were included in the trial as an unweathered control. One half of the unweathered seeds were dissected and the exocarp was removed to assess seed germination without the presence of the exocarp. All seeds were stored at 5°C from time of collection until initiation of the germination test.

Fifteen seeds of each treatment were placed between sheets of moistened filter paper in petri dishes, with 5 seeds/dish. Samples were placed in na oven set at 30°C (Scifres and Brock 1969, 1972). Seeds were checked daily for germination for 21 days. Once seeds germinated, they were removed from the petri dishes. Filter paper was moistened as needed to maintain imbibition.

Experiment 2

This study was conducted for 2 years. In 1999, we determined the length of time that fruit remained on the ground. Ten mature Angus cows, 40 Rambouillet ewes, and 50 Boer-Spanish cross nannies were placed in separate 30 ha pastures at a stock density of 1 AU/10 ha. One additional pasture was ungrazed by livestock. Each pasture was dominated by an overstory of mesquite and an understory of sideoats grama (*Bouteloua curtipendula* (Michx.) Torr.), buffalograss (*Buchloe dactyloides* (Nutt.) Engelm.), threeawns (*Aristida* sp. L), and K.R. bluestem (*Bothriochloa ischaemum* L.). In each pasture, 2 transects 250 m in length were randomly established with six, 0.33 m^2 plots at 50 m spacings on each transect. Twenty-five mesquite pods were placed in each plot and monitored weekly for 4 weeks to determine disappearance rates of fruit. There were only 4 pastures available for this experiment. Thus, class of livestock as a treatment effect was not replicated.

In 2000, the rate of fruit disappearance and consumption of mesquite fruit by other animal species was assessed. Sixteen, 1-m diameter plots containing 20 fresh mature mesquite pods each were placed throughout the MIR Center. Plots were placed adjacent to existing dirt roads, 0.5 km apart, and 20 m from the edge of the road. The pathway was systematically chosen to represent all of the major vegetation types on the MIR Center. Crushed lime was evenly spread across the plot on every third plot (n = 5 plots). The crushed lime was checked daily for 2 consecutive days to identify tracks of animals visiting the mesquite pod plots (Woods 1959).

Statistical analysis

For Experiment 1, Trial 1 (intake and preference of maturity classes) and Trial 2 (seed survival), data were analyzed using analysis of variance for repeated measures (Hicks 1993). Stage of maturity and species of livestock were the main effects, and day of data collection was the repeated measure. Individual animals served as replications nested within species of livestock and maturity class. Differences in germination were assessed in Trial 3 using analysis of variance with replications (petri dishes) nested within livestock species and maturity class of seeds. Differences among means were separated using a least significant difference when $P < 0.05$ (Gomez and Gomez 1984). Data was analyzed using the statistical computer package JMP (SAS 1994).

For Experiment 2, average disappearance rate of fruit was calculated. The percent of visitation by different species of wildlife was also calculated in 2000. Traditional statistical comparisons were not appropriate for Experiment 2 because treatment effect was not replicated and because the experimental protocol differed between years.

Results

Experiment 1, Trial 1

Intake of mesquite fruit differed by class of livestock and stage of maturity resulting in a significant ($P < 0.05$) class of livestock by stage of maturity interaction (Table 1). All 3 classes of livestock ate less immature fruit. However, sheep consumed more immature attached to tree (IM) fruit than goats which consumed more IM than cattle. Sheep and goats also consumed more mature attached to tree (MT) and mature on ground (MG) fruit than cattle on a body weight basis. When comparing intake of the 2 mature stages of fruit (MT and MG), there were no differences across species of livestock. Intake was similar across days of collection.

When livestock were offered a choice of the 3 maturity stages of fruit, cattle, sheep, and goats ate no immature fruit. Intake of MT and MG was similar among all 3 species of livestock ($P > 0.05$; 0.2 vs. 0.2 g kg^{-1} BW).

Table 1. Intake (g kg^{-1} BW) of 3 maturity classes of mesquite fruit by 3 species of livestock. Livestock were offered 0.5% BW of each maturity class singly for 10 min daily for 7 days to determine intake.

	Stage of development			
Livestock Species	IM	MT	MG	Across Maturity Classes
	(g kg^{-1} BW)			
Cattle	0.4^e	2.7^{cd}	2.4^d	1.8^B
Sheep	3.8^b	5.0^a	4.7^a	4.5^A
Goats	3.0^c	4.6^a	5.0^a	4.2^A
Across Livestock Species		2.4^B	4.0^A	4.0^A

$^{a-e}$Values within columns and rows with different superscripts differ ($P < 0.05$).
$^{A-B}$Values for different stages of fruit maturity or for different classes of livestock with different superscripts differ ($P < 0.05$).

Experiment 1, Trials 2 and 3

We were unable to estimate seed survival of IM fruit for cattle because they ate few IM fruits in Trial 1. Roughly equal proportions of seeds were retrieved from feces in each of the first 3 days for each animal species and maturity class (data not shown). There was almost no survival of seeds from IM and MT fruit among sheep and goats (Table 2). Survival of MT and MG seeds was greater after passing through cattle than through sheep or goats (Table 2). Twenty-two percent of MT seeds and 92% of MG seeds survived cattle digestion (Table 2). Sheep and goats had a lower ($P < 0.05$) survival rate of mature seeds than cattle with less than 12% of the seeds surviving. Seed survival was similar between species and stage of maturity for sheep and goats.

Table 2. The percent (%) of each maturity class of seed that was found intact in the feces of 3 species of livestock. The percent of intact seeds in feces was determined by feeding each maturity class of fruit separately (0.1% BW) and separating seeds from feces for 4 days.

	Stage of development		
Livestock Species	IM	MT	MG
	(%)		
-			
Cattle	--	22.1^b	92.3^a
Sheep	0.3^c	0.8^c	11.3^c
Goats	0.0^c	0.0^c	9.2^c

*Survival of IM was not determined for cattle.
$^{a-c}$Values within columns and rows with different superscripts differ ($P < 0.05$).

In Trial 3, germination rates were similar among seeds that survived digestion in cattle and sheep and for seeds that had weathered on the ground (Table 3). No seeds with the exocarp intact or seeds that passed through goats germinated.

Table 3. Percent (%) of seeds that germinated after undergoing digestion or weathering. Unweathered seeds were included as a control. Percent germination represents the number of seeds from each treatment that germinated.

Treatment	Germination
	(%)
Unweathered (with exocarp)	0.0
Dissected (without exocarp)	26.7
Weathered	13.3
Cattle MT	0.0
Cattle MG	13.3
Sheep MG	13.3
Goats MG	0.0

Germination of MT seeds for sheep and goats were not assessed because of the low survival rate.

Experiment 2

In 1999, 96% of the mesquite fruit placed in plots had disappeared from each pasture after 1 week, regardless of the livestock species or absence of livestock (data not shown), indicating that both livestock and wildlife were eating the pods. In 2000, some mesquite pods remained on the ground for up to 6 weeks, but few seeds remained after week 4 (Table 4).

Table 4. Percent (%) of mesquite pods remaining on the ground each week without the presence of livestock grazing in 2000.

Week	Remaining	SEM
	(%)	
1	90.0	4.3
2	68.8	5.5
3	53.1	7.9
4	38.1	7.2
5	38.0	7.6

Raccoons, skunks, deer, bobcats, and turkeys visited mesquite pod plots during the first 2 days (Table 5). Deer visited more frequently than any other species.

Table 5. Percent (%) visitation rate by different wildlife species to plots containing mesquite pods. Observations were recorded for 2 consecutive days in 2000.

Species	Total Visitations
	(%)
Deer	41.9
Raccoon	26.4
Bobcat	15.7
Skunk	10.6
Turkey	5.4

Discussion

Intake and seed survival

Intake of mesquite fruit increased with fruit maturity. Sheep and goats consumed more mesquite fruit on a body weight basis than cattle, and they ate immature fruit when offered alone. Fewer seeds survived sheep and goat digestion which suggests that sheep and goats function mainly as predators of mesquite seeds. No seeds germinated after passing through goats which suggests that goats should reduce the number of viable mesquite seeds across the landscape .

Cox et al. (1993) also reported greater seed survival following cattle digestion (28–31%) versus sheep digestion (2–8%). Based on our results, an animal unit (i.e., 1 cow, 4 sheep, or 5 goats), of sheep or goats would consume almost twice as many seeds as cattle (10,000 seeds compared to 5,000 seeds), but cattle would disperse 4 times as many seeds as sheep or goats given cattle's higher seed survival (4,500 compared to 1,200). These results and others (Kramp et al. 1998) illustrate that cattle probably contribute more to seed dispersal than other livestock species.

Mechanisms of seed loss

Physiological differences among ruminant species affect the digestibility of diets that vary in composition and quality (Huston et al. 1986). Cattle have a larger reticulo-omasal orifice and omasum than sheep and goats, and larger particles, including whole mesquite seeds, are more likely to pass through cattle than sheep or goats (Hofmann 1988). Other variations in digestive physiology, such as differences in mastication times between species of livestock may also influence the ability to digest mesquite seeds. Mastication times of cattle have been observed to range from 15 to 45 sec. while that of sheep ranged from 2 to 7 min (Cox et al. 1993). As mastication time increases, seed damage should also increase.

Germination after ingestion

Seeds with an exocarp intact did not germinate in Trial 3 regardless of seed origin (feces, weathered, unweathered). Weathered seeds germinated when the exocarp was damaged, but germination rates were lower than the rates reported for mesquite seeds when seeds are artificially scarified (80% germination) (Scifres and Brock 1969, 1972, Ueckert et al. 1979). Scarification naturally occurs through weathering or by digestive activities after consumption by livestock, which may explain why germination rates were the same for weathered seeds and seeds collected from cattle feces.

Bruchid larvae feed inside mesquite pods, and damage some seeds in the process (Impson and Hoffman 1998, Impson et al. 1999). Weathered seeds used in germination trials for this research showed no evidence of bruchid damage.

Experiment 2

Fruit did not remain on the ground for long periods in either year. Most fruit disappeared within 1 week in 1999 irrespective of the species of livestock present. In 2000, most the fruit (90%) remained after 1 week but disappeared quickly thereafter; 62% of fruit disappeared after 3 weeks. Fruit also quickly disappeared in South Texas on grazed and ungrazed plots (Owens unpubl. data), while in North Texas fruit remained on the ground for several weeks when cattle grazing was excluded (Ansley unpubl. data). Differences in fruit production could explain these differences. In 1999, few mesquite pods were produced. Fruit was collected off site and placed in each pasture and disappeared within 1 week. In 2000, when fruit production was greater, some fruit remained on the ground for 6 weeks. These data suggest that the rate of predation of mesquite fruit is dependent on overall abundance and availability of fruits.

Predation of fruits by livestock and wildlife restricts the potential for human-managed biological control of mesquite. Bruchid beetles are able to damage up to 90% of mesquite seeds when fruit remains on the ground for 6 months in South Africa (Hoffmann et al. 1993). When pods are quickly eaten by herbivores, bruchids are unable to colonize pods and damage most seeds (Impson et al. 1999).

Information is lacking on the combined effect of livestock and insect damage. Preliminary data indicated that bruchid-damaged seeds survived digestion but would not germinate after digestion (Kneuper and Scott 1998); however, bruchid-damaged seeds were not used in this study. It is possible that insect herbivory, when combined with livestock consumption, could further reduce the number of seeds surviving digestion. Bruchids bore a hole through the pod exocarp as the larvae escape the fruit (Watts et al. 1989). Damaged exocarps may allow rumen fluid and other digestive juices to surround the seed for additional damage and digestion.

Mesquite encroachment into grasslands and an increase in mesquite density coincide with the development of the livestock industry. Before the introduction of livestock, mesquite was restricted on most ranges because of dispersal limitations (Archer 1994). Livestock transport seeds away from existing trees, and livestock grazing opens interspaces among grass plants allowing mesquite to establish. However, mesquite also establishes in non-grazed areas with substantial grass cover (Archer 1994, Weltzin et al. 1998). Undoubtedly, the establishment of mesquite on ungrazed rangelands is impacted by seed dispersal from wildlife species. Wildlife movement is typically not limited by conventional livestock fences, thus wildlife can disperse mesquite seeds to grazed and ungrazed areas. Although different wildlife species consume and disperse mesquite seeds, livestock grazing probably accelerates the process because of greater livestock densities on most rangelands throughout Texas (Kramp et al. 1998).

Implications

Sheep and goat grazing during the early stages of fruit development should reduce the number of viable mesquite seeds. Sheep and goats appear to act as predators to mesquite because of their consumption of immature attached to the tree (IM) fruit, and lower seed survival of digestion. Additional research should be conducted to determine if sheep and goats will consume IM fruit in the field with other forages available. In addition, it may be possible to manipulate behavioral patterns of sheep and goats to increase intake of mesquite fruits. Recent advances in behavior modification have illustrated that preferences can be formed through pairing nutrients with forages (e.g., immature fruit) (Banner et al. 2000). Supplemental nutrients (e.g., propionate, starch) could be paired with consumption of IM fruit to increase intake. If sheep and goats will consume IM mesquite fruit on rangelands, fewer mature fruits would be available for consumption by cattle and wildlife which should reduce dispersal of viable seeds.

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