SURVIVAL OF MESQUITE SEEDLINGS EMERGING FROM CATTLE AND WILDLIFE FECES IN A SEMI-ARID GRASSLAND

B. A. KRAMP, R. J. ANSLEY, AND T. R. TUNNELL

Texas A&M Agricultural Experiment Station, P.O. Box 1658, 11708 HWY 70 South, Vernon, TX 76385

ABSTRACT—This study examined the potential of animals as vectors for mesquite seedling establishment via fecal deposition. Cattle, deer, and coyote fecal material containing emerging mesquite was located in May 1994 on a clay loam site in north Texas and assigned to two grass competition treatments (clipped to 3-cm height, or unclipped) and three moisture treatments (rainfall, rainfall + four 1.25-cm irrigations, or rainfall + one 10-cm irrigation). Except for a 2-week period in August 1993 when feces were deposited, cattle grazing was excluded from the site during the study and for several years prior to study initiation. Seedling emergence and survival were quantified throughout 1994, a dry year, and 1995, which had precipitation well above normal. By spring 1995, survival of 1994 seedlings (all treatments pooled) was 16.6, 9.3, and 1.3% at deer, cattle, and coyote fecal sites, respectively. Survival of 1994 seedlings was not affected by moisture or clipping treatments. New cohorts of emerging seedlings occurred from the same fecal sites during 1995. High rainfall during summer 1995 increased percent survival of 1995 seedlings when compared to survival of 1994 seedlings, even though grass growth was much greater in 1995 than in 1994. A strong trend emerged in which survival of 1995 seedlings appeared to be greater when surrounding perennial grasses were clipped (37.0% in clipped plots vs. 9.4% in unclipped plots), but this was not statistically significant ($P \leq 0.14$). By spring 1996, average number of seedlings emerged per site (1994 and 1995 cohorts combined) was 7.8, 5.2, and 4.5; number of established seedlings per site was 0.8, 0.6, and 0.3; and percent survival was 12.1, 13.5, and 6.5% at cattle, deer, and coyote sites, respectively. Mesquite seedlings were capable of establishing from feces of all three animal vectors within dense, ungrazed stands of perennial grass.

RESUMEN—Este estudio examinó el potencial de animales como vectores para el establecimiento de plántulas de mesquite via deposición fecal. Materia fecal de ganado, venado, y coyote conteniendo brotes de mesquite fue hallado en mayo de 1994 en un sitio de marga de barro en el norte de Texas y asignado a dos tratamientos de pasto (cortado a 3 cm de altura, o sin cortar) y a tres tratamientos de humedad (lluvia, lluvia + 1.25-cm de riego cuatro veces, o lluvia + 10-cm de riego una vez). Con exclusión de un período de dos semanas en agosto de 1993 cuando excrementos fueron depositados, pastar de ganado fue excluido del sitio durante el estudio y por varios años antes del inicio del estudio. El brote de las plántulas y la sobrevivencia fueron medidos durante 1994, un año seco, y 1995, que tuvo lluvia mucho más de lo normal. Para la primavera de 1995, la sobrevivencia de las plántulas de 1994 (todos los tratamientos juntos) fue de 16.6, 9.3, y 1.3% en sitios fecales de venado, ganado, y coyote, respectivamente. La sobrevivencia de plántulas de 1994 no fue afectada por tratameintos de humedad o corte. Grupos nuevos de brotes de plántulas emergieron de los mismos sitios fecales durante 1995. Mucha lluvia en el verano de 1995 aumentó el porcentaje de sobrevivencia de plántulas de 1995 comparada con la sobrevivencia de plántulas de 1994, aunque el crecimiento del pasto fue mucho más en 1995 que en 1994. Una fuerte tendencia apareció en que la sobrevivencia de las plántulas de 1995 fue aparentemente mejor cuando pastos perenes alrededor fueron cortados (37.0% en sitios cortados vs. 9.4 en sitios sin cortar), pero esto no fue estadisticamente significativo ($P \leq 0.14$). Para la primavera de 1996, el número promedio de brotes de plántulas por sitio (los grupos de 1994 y 1995 combinados) fue 7.8, 5.2, y 4.5; el número de plántulas establecidas por sitio fue 0.8, 0.6, y 0.3; y el porcentaje de sobrevivencia fue 12.1, 13.5, y 6.5% en sitios de venado, ganado y coyote, respectivamente. Las plántulas de mesquite fueron capaces de establecerse de excrementos de los tres animales vectores en sitios de pasto denso perene sin pastar de ganado.

Recent theories suggest that encroachment of mesquite (*Prosopis* sp.) into grasslands has been accelerated by dispersal of seed via livestock (Brown and Archer, 1987; Archer et al., 1995). Mesquite legumes contain up to 30% sugar and are readily consumed by cattle and many wildlife species (Vines, 1960). Scarification of mesquite seed, which is required for rapid germination, occurs during mastication and ruminant digestion (Scifres and Brock, 1972; Brown and Archer, 1989). Dispersal of mesquite propagules away from point of origin is facilitated by consumer movement during digestion (Reynolds and Glendening, 1949; Wilson, 1993). Relative importance of animals as vectors of mesquite may be determined by access to and preference for mesquite pods, population density of the animal, season of grazing, and/or home range size and habitat utilization (Archer and Pyke, 1991; Leopold and Krausman, 1991).

Conditions necessary for germination and early survival of mesquite seedlings are well documented (Scifres and Brock, 1969, 1971, 1972). Imo and Timmer (1992) demonstrated that in nitrogen-deficient media, mesquite seedling root growth is stimulated at the expense of shoot development. Brown and Archer (1990) concluded that mesquite roots rapidly penetrate to deep soil layers not utilized by competing grasses and thereby avoid competition for moisture and nutrients. Although relatively small rainfall events are necessary to germinate mesquite, survival may be more closely linked to multiple precipitation events (Roundy et al., 1993).

Competitive effects of surrounding vegetation may be more important than soil properties in influencing establishment (Ueckert et al., 1979). In a series of greenhouse experiments, Van Auken and Bush (1987, 1988, 1990), concluded that mesquite requires gaps formed by disturbance to establish in grass stands but is able to compete when gaps close because of rapid root elongation at the expense of early shoot growth. Existing herbaceous vegetation may limit mesquite establishment during short term drought, but extended droughts which reduce grass cover may enhance mesquite recruitment (Ueckert et al., 1979).

Schupp and Fuentes (1995) suggested the need for information that links seed dispersal by animals to adult recruitment. Although it is well known that seeds of many species, including mesquite, emerge from animal feces, seedling survival at fecal sites is not well understood (Schupp, 1993). Much is known regarding requirements for germination and establishment of mesquite seedlings in soil, but studies are needed which quantify factors that affect survival of fecal-emerged mesquite.

Our objective was to contrast survival of mesquite seeds deposited by a domestic ruminant (cattle; *Bos taurus*), a native ruminant (white-tailed deer; *Odocoileus virginianus*), and a non-ruminant (coyote; *Canis latrans*). In addition, we studied the effect of moisture patterns and competition by neighboring perennial grasses on seedling emergence and survival from each fecal type. We also evaluated over-winter survival. A secondary objective was to relate the effect, if any, of short-term climatic anomalies imposed by our treatments to historic episodic pulses of mesquite encroachment in the southwest.

METHODS AND MATERIALS—Sites were located on 2 ha of native grassland in northwest Texas. Mean annual rainfall of 66.5 cm is bimodally distributed, peaking in May (11.9 cm) and September (7.7 cm). Mean monthly air temperatures range from a maximum of 36°C in July to a minimum of −2.5°C in January (NOAA, 1994). Dominant woody vegetation is honey mesquite (*Prosopis glandulosa* Torr.) with 30% canopy cover. Understory species include C_4 buffalograss (*Buchloe dactyloides* [Nutt.] Englem.) and C_3 Texas wintergrass (*Nasella leucotricha* [Trin. and Rupr.] Pohl). Soils are Tillman clay loams (Thermic Typic Paleustolls–Koos et al., 1962).

The study area was located within a larger 160-ha exclosure that had been protected from livestock grazing since 1987. A wildfire on 24 August 1993 destroyed a 200-m section of the exclosure fence and allowed cattle from adjacent pastures to graze within the exclosure for 2 weeks before they were removed and the fence repaired. During that time a considerable amount of cattle feces was deposited within the exclosure. Deer and coyotes were not excluded from the research site prior to the wildfire. However, because most of the area surrounding the exclosure had been burned, wildlife were also concentrated in the area, as evidenced by numerous sightings, tracks, and fresh feces. Mesquite outside the exclosure prior to the wildfire had produced a heavy bean crop that was mature and beginning to drop to the ground. Fecal deposits during the week following the wildfire contained large numbers of mesquite seeds. Following spring rainfall in 1994, we observed mesquite seedlings emerging from most of the cattle feces as well as from coyote and white-tailed deer feces. Because the area had been excluded from grazing for 5 years prior to the wildfire, we are reasonably certain that cattle feces with emerging mesquite were less than 8 to 9 months old. Other than the 2-week fecal deposition period in August 1993, cattle grazing was excluded from the area during the study.

On 17 May 1994, 72 fecal sites (24 each of cattle, deer, coyote) containing emerging mesquite were identified, permanently marked and hereafter referred to as site. Each site was described by estimating amount of feces, noting dominant vegetation within a 0.25-m^2 area surrounding feces, and counting the number of live mesquite seedlings present. All fecal sites selected for the study contained cotyledonary mesquite and no older mesquite seedlings.

Seedling emergence and survival were observed biweekly throughout 1994 and 1995 growing seasons. Identity of the initial cohort of seedlings (Cohort A) was maintained throughout the 1994 growing season and the first evaluation date in spring 1995. All subsequent cohorts of seedlings that emerged in 1994 were identified individually as B_1, B_2, etc., and collectively as Cohort B. During the first spring 1995 evaluation date (23 May 1995), all live seedlings that had emerged during 1994 (Cohorts A and B) were marked with a colored wire and, subsequent to this date, were evaluated collectively as Cohort "AB." Seedlings emerging during 1995 were identified as Cohort C. Cohorts A, B, and C were referred to collectively as Cohort ABC. Number of live seedlings of each cohort was recorded at each fecal site on each sample date. A final seedling evaluation was taken on 1 June 1996.

Total seeds per fecal site were quantified indirectly by collecting an additional 10 cattle dung pats and 10 deer pellet groups that resembled the experimental fecal sites. Dimensions and volume of cattle pat and deer pellet were measured and feces were oven-dried at 60°C for 24 h, and weighed. Oven-dried fecal material was passed though a sieve and number of mesquite seeds counted. We found only enough coyote scats for the treatments and were therefore unable to estimate total number of mesquite seeds per coyote site.

Treatments—To evaluate effects of animal vector (i.e., fecal type), surrounding grass competition and moisture availability on mesquite seedling survival, the study was designed as a split-plot. Animal vectors (cattle, deer, coyote) were treated as main plots, with herbaceous competition (two levels), and moisture treatments (three levels) assigned as completely randomized subplots within each vector. There were four replicates per treatment for a total of 72 sites. The competition levels consisted of (1) high, with surrounding vegetation intact, and (2) low, with vegetation within a 0.25-m radius of each site clipped to 3-cm height on 02 June 1994 and on 21 June 1995. To estimate herbaceous standing crop of the high competition level, six 0.25-m^2 quadrats each of Texas wintergrass and buffalograss were clipped to 3-cm height, oven dried and weighed four times each year. Sample points were in monoculture patches that occurred within 100 m of, but no closer than 10 m from, the fecal sites. Moisture treatments consisted of (1) rainfall only, (2) rainfall plus four small irrigations of 1.25 cm each, and (3) rainfall plus one large 10-cm irrigation. The 1.25-cm irrigations were applied on 13 June, 22 June, 19 July, and 3 August 1994. The single 10-cm irrigation was applied 19 July 1994. Irrigations were hand applied between 0700–0900 h by sprinkling the 0.25-m^2 sites with a pre-measured volume of water. Irrigation treatments were not applied in 1995 because of high rainfall. Fecal sites that were irrigated in 1994 were retained as part of the study, however, to increase vector and competition treatment replication. Soil moisture was not measured at any fecal sites, but precipitation was measured at the research site during the study.

Statistical Analyses—Single-date analyses were performed on individual cohorts (A, B, or C) or cohort groups (AB, ABC) using analysis of variance (ANOVA) or general linear models (GLM) to assess main effects of vector (cattle, deer, coyote), and subplot combinations of competition (clip, no clip) and irrigation (none, 4 small, 1 large) and their interactions on percent seedling survival (number of live seedlings/total emerged seedlings) and number of live seedlings per site (SAS Institute Inc., 1988). Single-date analyses were performed at end of growing season or at study termination (1 June 1996). When irrigation was included in the model (as with Cohorts A and AB in 1994), replicate sample size was 4. Because irrigation treatments were imposed in 1994 only, Cohorts AB and ABC were analyzed without irrigation as a source of variation in 1995–1996. Fecal sites irrigated in 1994 were retained in the study, however, increasing replicate sample size to 12.

Thirty-seven of the original 72 fecal sites produced Cohort B seedlings during 1994 which occurred in most vector, competition, and irrigation treatments, although treatment replication was unbalanced. A split-plot GLM analysis was performed for Cohort B seedlings at the end of 1994 (n from 1 to 4) with vector as main plot and competition and irrigation as subplots. Only cattle and deer vectors were included in the analysis because coyote fecal sites produced an insufficient number of Cohort B seedlings for analysis. Similarly, 39 of the original 72 fecal sites produced Cohort C seedlings in 1995. Single-date analysis was performed on Cohort C using a split-plot GLM, with vector (coyote included) as main plot and competition as subplot (n from 4 to 8).

Effect of date on percent survival was analyzed using a repeated measures ANOVA or GLM, with vector as main plot, and competition, irrigation, and date as subplots. Main effects of date and all associated interactions were tested using full model residual. Specific dates used in these analyses varied with cohort or cohort group. Starting date of each cohort (when survival of all replicates was 100%) was not included in any analysis. To quantify effects of the first winter following emergence on seedling survival, analyses included a fall sample date at first growing season end, and a spring sample date the following year. GLM analysis was used for Cohorts B and C, which had unequal replicates.

Percent seedling survival values were arcsin-transformed prior to analysis following a Bartlett's test for homogeniety of variance (Steel and Torrie, 1980). A value of $25/n$ was substituted for 0 percent, and 100 $-$ $25/n$ for 100 percent. Means were separated by the LSD test at $P \leq 0.10$ (SAS Institute Inc., 1988). Means reported in figures, tables, and text are actual, not transformed, means.

RESULTS—Seed condition in deer and cattle feces was similar, with pods and outer seed coats removed during acid digestion. Conversely, beans and pods often made up the bulk of fecal matter in mesquite mast found at coyote sites. Seed coats and pod fragments remained undigested. It appeared that mastication was largely responsible for scarification of mesquite seed by coyotes. Data from non-treated fecal sites (cattle and deer only) indicated that the average dung pat at each cattle fecal site was 25 cm in diameter, occupied 444 cc volume, weighed 183 g, and contained 15 mesquite seeds. Total mesquite seed per cattle site was variable, ranging from 0 to 121 seeds. The average deer site contained 37 fecal pellets, which averaged 0.1 cc and 0.4 g per pellet. Ten mesquite seeds were found per deer site, or about one seed for every three to four pellets.

Precipitation Patterns and Herbaceous Growth—Precipitation was above normal during February and April and below normal from May through September 1994 (Fig. 1). Following above normal rains in September and October 1994, precipitation remained below normal until June 1995. Several large precipitation events occurred during June to October 1995. June to August rainfall in 1994 and 1995 was 41% of, and 286% greater than, the 30-year average, respectively.

Texas wintergrass and buffalograss standing crop paralleled each other during 1994 and 1995 and responded to precipitation trends. Texas wintergrass standing crop remained about 100 to 150% greater than buffalograss. Winter and spring (January to April) standing crop of both species was greater during 1994 than during the same period in 1995. However, summer and fall (May to October) standing crop of both species was much greater in 1995. For example, Texas wintergrass end-of-season standing crop was 1,613 kg/ha in 1994 and 2,994 kg/ha in 1995.

Mesquite Seedling Emergence and Survival—The initial cohort of mesquite seedlings (Cohort A) emerged in May 1994 as a result of above normal rainfall in April. Cattle fecal sites averaged 3.5 (range 1 to 7) seedlings per site (Table 1). Deer and coyote sites averaged 2.9 (range 1 to 8) and 3.3 (range 1 to 12) Cohort A seedlings per site, respectively. Based on the indirect estimate of total seed per site, Cohort A represented 23% (3.5/15) of available seed from each cattle site and 29% (2.9/10) from each deer site. This percentage was not determined for coyote sites.

Number of live Cohort A seedlings declined during the 1994 growing season (Fig. 2). As many as 60% of all seedlings died between the initial observation date in May and the second date on 13 June 1994. All but 2% of seedlings from coyote sites died by 13 June. Following this initial mortality, analysis indicated a second significant decline in Cohort A seedling survival at cattle and deer sites from 19 July to 27 September 1994 after a brief period of survival stability from 13 June to 19 July. There was a significant date by vector interaction (Table 2), indicating that seedling survival declined only at cattle and deer sites during this period and not coyote sites, which were already near zero (Fig. 2).

Three rainfall events of 2.4 cm or more in June, July, and August 1994 (data not shown) stimulated emergence of three new seedling cohorts (Cohorts B_1, B_2, B_3). These cohorts collectively (i.e., Cohort B) produced nearly as many seedlings as Cohort A at cattle sites (2.9 vs. 3.5 seedlings per site), but produced fewer seedlings than Cohort A at deer or coyote sites (Table 1).

By the end of the first growing season (27 September 1994), Cohort A percent survival was 14.5, 14.9, and 1.4% at cattle, deer, and coyote sites, respectively (Fig. 2). Percent sur-

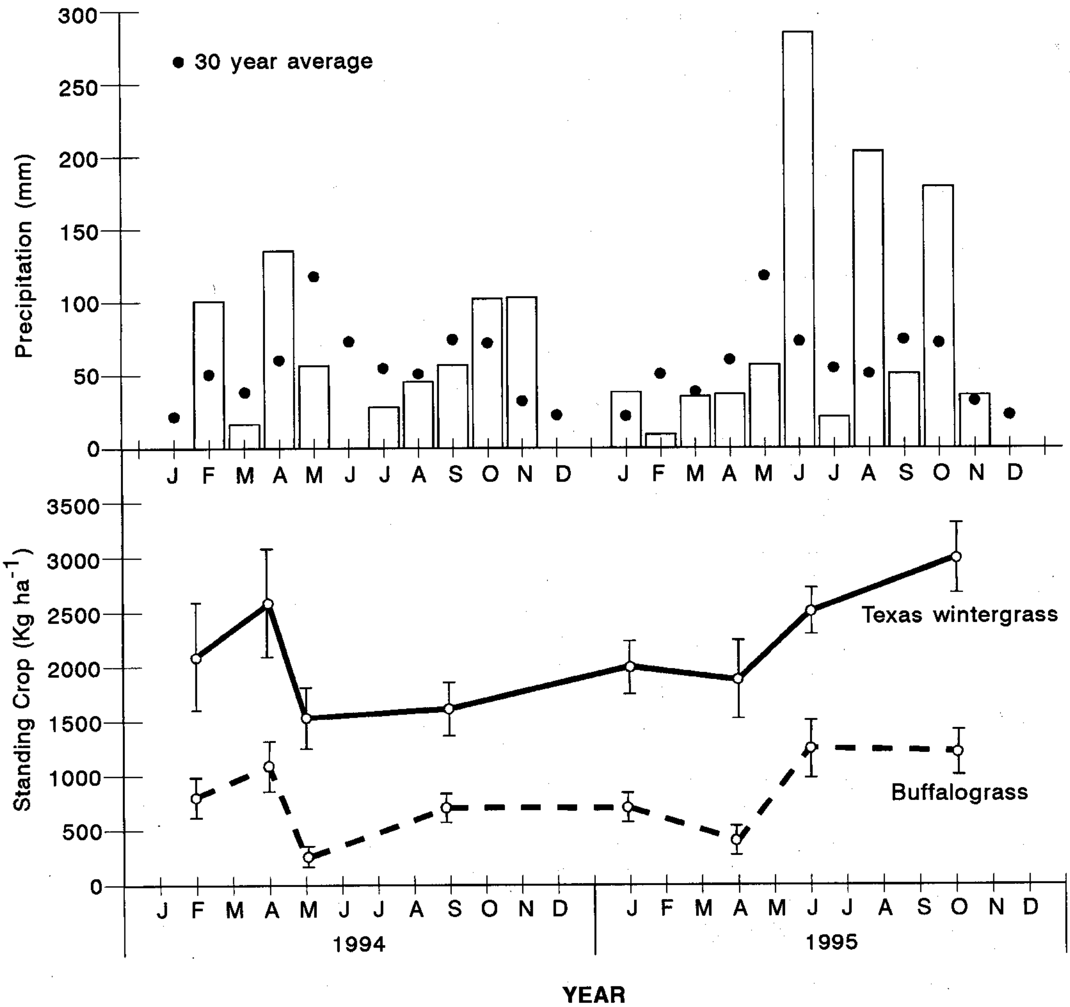

FIG. 1—Monthly precipitation (bars) compared to the 30-year NOAA average (solid circle, top) and standing crop of Texas wintergrass and buffalograss (kg ha^{-1}) during 1994 and 1995 at the research site, Rolling Plains, north Texas.

vival of Cohort B seedlings at cattle and deer sites was 18.7 and 20.1%, respectively. Fifty percent of Cohort B seedlings from coyote sites were alive by September 1994, but this represented only two of four seedlings.

End-of-first-growing season analysis of Cohort A survival indicated a significant ($P \leq 0.10$) vector main effect (Table 3). Differences in vector were attributed to lower survival at coyote than at cattle or deer sites (Fig. 2). Herbaceous competition and/or irrigation treatments had no significant effects on Cohort A survival in 1994. Significant competition by irrigation ($P \leq 0.10$) and vector by competition by irrigation ($P \leq 0.05$) interactions occurred (Table 3). Greatest seedling survival at cattle sites (29.2%) occurred at clipped plots treated with the single large irrigation event. In contrast, greatest survival at deer sites occurred at unclipped sites that had no irrigation (47.5%), or at clipped sites treated with four small irrigations (29.2%).

End-of-first-growing-season analysis of Cohort B (with coyote vector excluded) indicated main effects of vector or irrigation were not significant but there was a significant vector by irrigation interaction. Cohort B percent survival at cattle sites was greatest within irrigated

TABLE 1—Number of emerged mesquite seedlings per fecal site, organized by cohort and animal vector. Cohorts B and C averaged over 24 sites per vector.

Cohort	Date emerged	Emerged seedlings per site		
		Cattle	Deer	Coyote
A	May 1994	3.5	2.9	3.3
B	June–September 1994	2.9	1.6	0.2
B_1	01 June–13 June 1994	0.3	0.5	0.1
B_2	14 June–19 July 1994	1.7	0.8	0
B_3	20 July–27 September 1994	0.9	0.3	0.1
AB	1994	6.4	4.5	3.5
C	May–June 1995	1.4	0.7	1.0
ABC	1994–1995	7.8	5.2	4.5

treatments, whereas greatest survival at deer sites was at non-irrigated sites (data not shown). Cohort B, which emerged during the time of irrigations, appeared to be more sensitive to irrigation treatments than was Cohort A. We were unable to statistically compare responses of Cohorts B_1, B_2, and B_3. End-of-season analysis of the combined Cohort AB indicated a significant ($P \leq 0.05$) vector main effect and significant vector by irrigation and vector by competition by irrigation interactions (data not shown).

By spring 1995, first-winter survival of Cohort A seedlings was 14.9, 9.6, and 1.4% at deer, cattle, and coyote sites, respectively (Fig. 2). These values are lower than those reported by Gibbens et al. (1992), who found in Arizona that 19% of spring-emerged honey mesquite seedlings survived to the following year. Analysis indicated that survival of Cohort A seedlings declined significantly ($P \leq 0.10$) over the 1994/1995 winter (Table 2), which had below normal precipitation and temperatures. Percent survival of Cohort B seedlings did not decline significantly at cattle and deer sites during the 1994/1995 winter (Fig. 2). The few Cohort B seedlings that occurred at coyote sites, which were not included in analysis, died during the 1994/1995 winter. First-winter survival of all 1994 seedlings (Cohort AB) was 16.6, 9.3, and 1.3% at deer, cattle, and coyote sites, respectively (Fig. 3).

Above normal rainfall during the 1995 growing season stimulated emergence of new mesquite seedlings (Cohort C) from original fecal sites in all vector types, although number of emerged Cohort C seedlings per site was much lower than those found in Cohort AB (Table 1). Nearly 80 to 85% of the total emergence of Cohort ABC occurred as Cohort AB in the first year. The remaining 15 to 20% of mesquite seeds maintained dormancy for at least 2 years following fecal deposition prior to germinating. This percentage was consistent among the three vector types.

Cohort C survival by the end of the first growing season (12 October 1995) was 43.9, 27.8, and 44.9% at cattle, deer, and coyote sites, respectively (Fig. 2). These differences were not significant ($P > 0.10$) among vectors, but represented a considerable increase in end-of-first-season survival when compared to Cohort A in 1994. Analysis indicated a significant decline in Cohort C survival during the 1995/1996 winter, and this occurred in all vector-types. However, first-winter percent survival was greater in Cohort C than in Cohort A or B, and especially at cattle and coyote sites.

Percent survival of Cohort AB declined significantly at all vector sites from 27 September 1994 to 12 October 1995, but stabilized after that (Fig. 3). Most Cohort AB seedlings that survived the first winter (1994/1995) survived until June 1996. From 23 May 1995 to 1 June 1996, Cohort AB survival declined from 9.3 to 8.2% at cattle sites and from 16.6 to 12.9% at deer sites. Analysis indicated that the only factors which significantly affected Cohort AB survival during this interval were main effects of vector and date (data not shown). Survival of Cohort ABC declined at cattle and coyote sites from October 1995 to June 1996 (Fig. 3), pri-

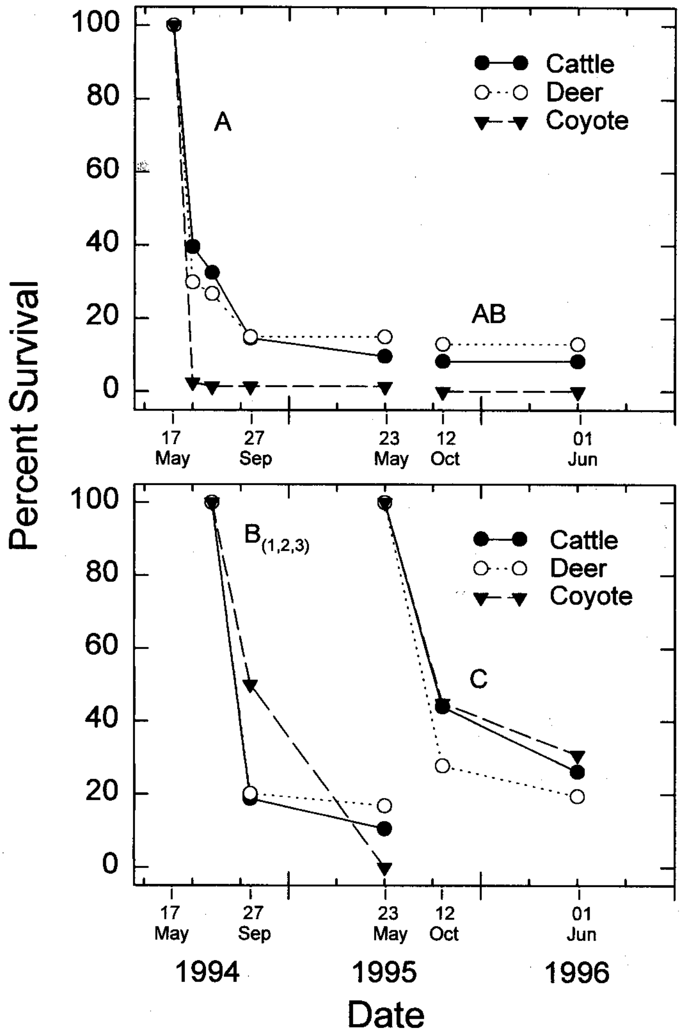

FIG. 2—Percent mesquite seedling survival of Cohorts A, B, C and AB within each fecal vector type from May 1994 to June 1996. Data were pooled across all clipping and watering treatments. Cohort B is the combined response of Cohorts B_1, B_2 and B_3. Standard error bars were omitted for clarity.

marily due to death of Cohort C seedlings (Fig. 2).

Effect of Clipping Treatments—Single-date analysis at study termination (1 June 1996) indicated that, although vector significantly affected Cohort AB percent survival and competition did not, an opposite trend was found for Cohort C (Table 4). Effect of vector was not significant, yet effect of competition was nearly ($P \leq 0.14$) significant. When vectors were pooled, reduction of grass competition by clipping in the wet year (1995) increased percent survival of Cohort C seedlings nearly four-fold (37.0 vs. 9.4%) by 1 June 1996 (Fig. 4, Table 5). This trend was consistent within each vector (data not shown). In contrast, reduction of grass competition by clipping in the dry year (1994) had no effect on Cohort AB seedling survival (Table 5). Opposite responses of Cohort AB and Cohort C to vector and competition effects caused these sources of variation to have insignificant effects on percent survival when the entire population (Cohort ABC) was analyzed at study termination.

In comparing percent survival at end-of-first-growing season of Cohort AB at unclipped sites

TABLE 2—Repeated measures ANOVA for percent survival of Cohort A seedlings during the first summer (13 June to 27 September 1994), and over the first winter (27 September 1994 to 23 May 1995).

Source	Summer 1994			Over-winter 1994/1995		
	df	*F*	Pr > *F*	*df*	*F*	Pr > *F*
Vector	2	9.52	0.006**	2	2.45	0.14
Ea = Rep(Vector)	9			9		
Comp	1	0.01	0.95	1	0.07	0.79
Irrig	2	0.01	0.99	2	0.53	0.59
Irrig × Comp	2	0.45	0.64	2	2.98	0.06*
Comp × Vector	2	0.51	0.60	2	1.22	0.30
Irrig × Vector	4	0.51	0.73	4	2.25	0.08*
Irrig × Vector × Comp	4	1.63	0.18	4	2.91	0.03*
Eb = Irrig × Comp × Rep(Vector)	45			45		
Date	2	11.39	0.0001**	1	2.94	0.09*
Date × Vector	4	2.93	0.02*	2	2.94	0.06*
Date × Comp	2	0.29	0.75	1	0.47	0.50
Date × Irrig	4	0.31	0.87	2	1.09	0.34
Date × Vector × Comp	4	0.20	0.94	2	0.47	0.63
Date × Vector × Irrig	8	0.31	0.96	4	1.09	0.37
Date × Comp × Irrig	4	0.65	0.63	2	0.21	0.81
Date × Vector × Comp × Irrig	8	0.62	0.76	4	0.21	0.93
EC = Error	108			54		
Total	215			143		

(11.4%) with survival at end-of-first-growing-season of Cohort C at unclipped sites (28.0%; Fig. 4), it appeared that the wet summer of 1995 alone accounted for an increase in percent seedling survival when compared to the dry summer. However, this difference between cohorts on unclipped sites disappeared after the 1995/1996 winter such that, by 1 June 1996, percent survival of Cohorts AB and C on unclipped sites was 7.4 and 9.4%, respectively.

Cohort ABC Summary—By study termination, percent emergence (number of emerged seedlings per site/total seed per site) of Cohort ABC was 52% at both cattle (7.8/15) and deer (5.2/10) sites. Percent survival was 12.1, 13.5, and 6.5% in cattle, deer, and coyote, respectively, with coyote significantly different from deer (Table 5). With all sources of variation pooled, survival was 10.7%.

Number of live seedlings per site averaged 0.58 and was slightly greater at cattle (0.83) than at deer (0.58) or coyote (0.33) sites. Establishment efficiency (i.e., number of live seedlings per site/total seed per site) was similar between cattle (0.055) and deer (0.058) sites. The clipping treatment significantly affected number of live seedlings per site. Cohort ABC had more live seedlings per site at clipped (0.81) than at unclipped (0.36) sites when pooled across vectors. This trend was consistent within each vector (data not shown). At study's end, greatest percent survival was at unclipped deer sites (14.2%, *SE* = 8.5), and greatest number of live seedlings per site was at clipped cattle sites (1.08, *SE* = 0.43).

Of the 24 cattle sites initially identified with emerging mesquite seedlings in May 1994, 10 sites, or 42% produced at least one established

TABLE 3—End-of-first-growing-season ANOVA for percent survival of Cohort A seedlings on 27 September 1994.

Source	*df*	*F*	Pr > *F*
Vector	2	3.03	0.09*
Ea = Rep(Vector)	9		
Comp	1	0.16	0.69
Irrig	2	0.66	0.52
Irrig × Comp	2	2.53	0.09*
Comp × Vector	2	1.32	0.28
Irrig × Vector	4	1.77	0.15
Irrig × Vector × Comp	4	2.68	0.04*
Eb = Error	45		
Total	71		

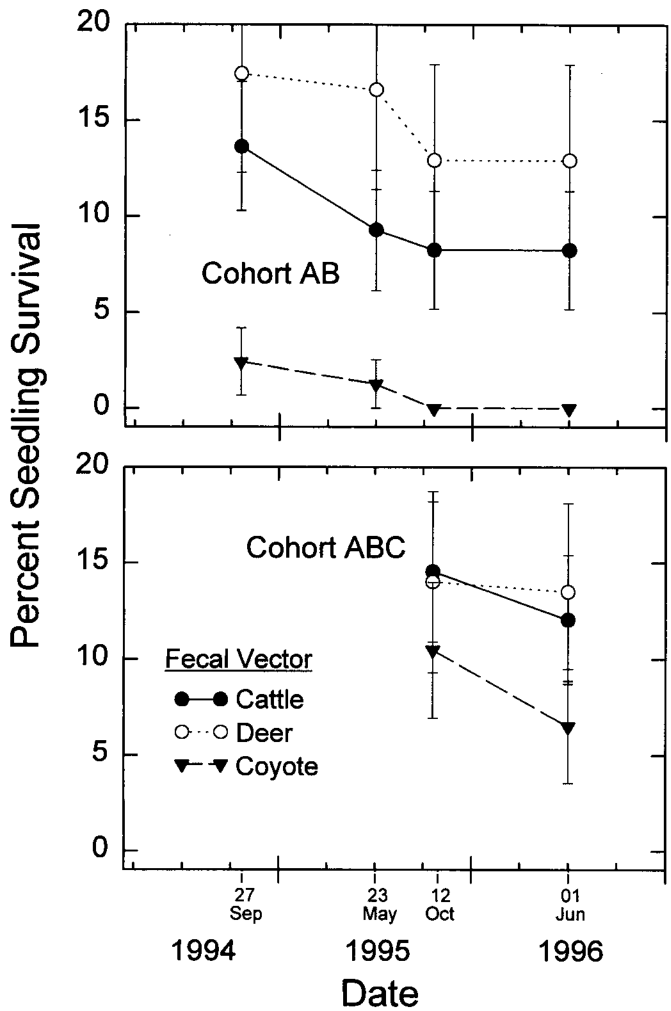

FIG. 3—Percent mesquite seedling survival of Cohorts AB and ABC within each fecal vector type from 27 September 1994 to 1 June 1996. Data were pooled across all clipping and watering treatments. Vertical bars are ±1 standard error.

mesquite plant by June 1996. Of all deer and coyote sites, 42 and 21%, respectively, produced at least one established mesquite seedling.

DISCUSSION—Successional shifts from grasslands to woodlands traditionally have been attributed to changes in fire and domestic grazing patterns as influenced by humans (Archer et al., 1995). Although native ungulates and rodents consume, digest, and disseminate mesquite seed, grazing by domestic livestock is believed to accelerate this process (Reynolds and Glendening, 1949; Archer and Pyke, 1991).

Domestic animals commonly travel 0.6 to 1.8 km or more in a single day and may retain mesquite seed in their intestines for 2 to 8 days (Glendening and Paulsen, 1950). White-tailed deer commonly reside in a fairly stable home range of approximately 24 to 350 ha. However, deer may travel several miles as a result of environmental perturbation such as wildfires (Marchinton and Hirth, 1984). Average home range of coyotes is 4 to 5 km^2. Distance traveled by an individual coyote in a 24-h period ranges from 7 to 10 km (Andelt, 1985). Movement patterns, combined with a propensity to consume mesquite pods, suggest that all of

TABLE 4—Single-date ANOVA or GLM for percent survival of Cohort AB and C seedlings on 01 June 1996.

Source	*df*	*F*	Pr > *F*
	Cohort AB (ANOVA)		
Vector	2	5.01	0.01**
Ea = Rep(Vector)	33		
Comp	1	0.03	0.87
Comp × Vector	2	0.19	0.83
Eb = Error	33		
Total	71		
	Cohort C (GLM)		
Vector	2	0.39	0.68
Ea = Rep(Vector)	20		
Comp	1	2.42	0.14
Comp × Vector	2	0.40	0.68
Eb = Error	13		
Total	38		

these animals have potential to disperse mesquite into grasslands if a seed source is available. Wildlife movement is not limited by conventional cattle fences; thus, wildlife can carry mesquite seeds to most areas.

In this study, a 1993 wildfire left the research site as one of the few unburned areas for several kilometers. We believe cattle and wildlife concentrated on this site and provided an atypically high density of mesquite-filled feces. For this reason, we did not attempt to quantify, or make conclusions regarding, fecal site demographics (i.e., density per vector, percent containing mesquite seed, percent with emerging mesquite, etc.). In general, one would expect a greater density of cattle fecal sites relative to wildlife sites in this region of north Texas, because cattle stocking densities are typically higher than are wildlife densities. This study offered a rare opportunity to observe emergence and survival of mesquite seedlings from feces that were naturally deposited within a

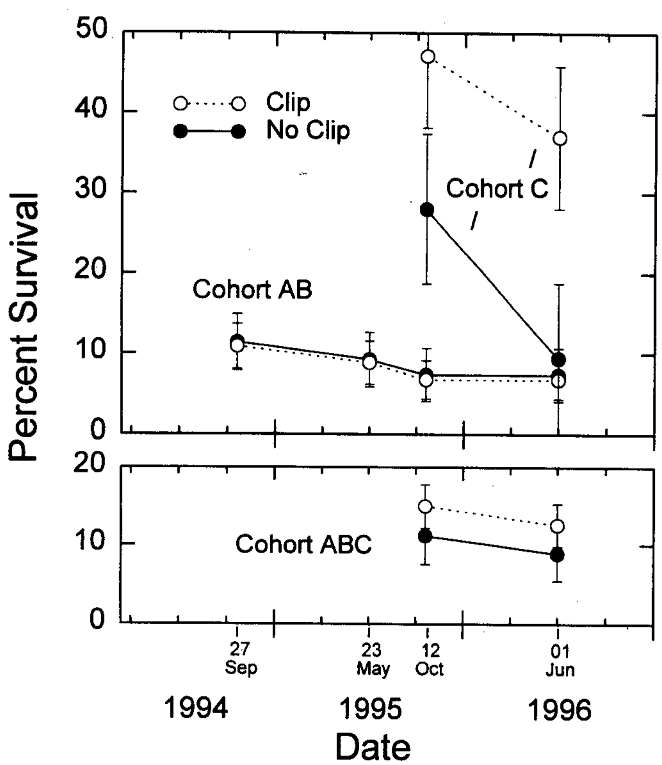

FIG. 4—Mesquite seedling survival in clipped and unclipped plots for Cohort AB and Cohort C (top) and Cohort ABC (bottom). Data were pooled across all three animal vector types and watering treatments. Vertical bars are ±1 standard error.

TABLE 5—Effect of vector and competition on percent survival and number of live seedlings per site for Cohorts AB, C and ABC on 01 June 1996. Standard errors in parentheses following means.

		Percent survival			Live seedlings per site		
Fecal vector	Comp Trt	Cohort AB	Cohort C	Cohort ABC	Cohort AB	Cohort C	Cohort ABC
Cattle	Pooled	8.2 (3.1)	26.2 (9.8)	12.1 (3.3)	0.46 (0.19)	0.57 (0.20)	0.83 (0.26)
Deer	Pooled	12.9 (5.0)	19.4 (11.2)	13.5 (4.6)	0.43 (0.13)	0.33 (0.19)	0.58 (0.16)
Coyote	Pooled	0	30.8 (12.2)	6.5 (3.0)	0	0.62 (0.27)	0.33 (0.15)
Pooled	No Clip	7.4 (3.3)	9.4 (6.8)	8.9 (3.4)	0.25 (0.09)	0.19 (0.13)	0.36 (0.12)
Pooled	Clip	6.8 (2.4)	37.0 (8.9)	12.5 (2.7)	0.33 (0.13)	0.74 (0.18)	0.81 (0.19)
Pooled	Pooled	7.1 (2.0)	25.6 (6.3)	10.7 (2.1)	0.29 (0.08)	0.51 (0.12)	0.58 (0.11)

known time-frame, and were of sufficient concentration on the same soil type for a replicated study. Because of such a unique situation precipitated by a surrounding wildfire, it was not possible to repeat this study on another site or in subsequent years.

Cattle, deer, and coyotes contribute to mesquite seedling establishment on native grasslands. Cattle appeared to be a slightly better disseminator of mesquite than deer or coyotes primarily because cattle sites contained more seed. However, we found much fewer seed per cattle site ($\bar{X}$ = 15) than the 1,671 seeds per cattle pat found in Arizona by Glendening and Paulsen (1955). The overall 52% emergence relative to total seed at cattle and deer sites was consistent with a study by Fisher (1947), who found that 45% of honey mesquite seed recovered from cattle droppings germinated. Seedling survival, as a percentage of total emergence, was slightly greater in deer than in cattle or coyote feces, perhaps because of quicker contact of the radicle with the soil surface at deer sites. Overall, an equal number of cattle and deer fecal sites produced established mesquite plants, whereas coyote sites produced fewer established seedlings.

It has been hypothesized that reduction of perennial grass stands and changes in soil characteristics resulting from cattle grazing have accelerated establishment and spread of mesquite from seed (Hastings and Turner, 1965). Glendening and Paulsen (1955) found that the average number of velvet mesquite seeds needed to produce a single live seedling at the end of one growing season was 16 times greater in areas with grass cover as compared to bare areas. Greenhouse studies by Bush and Van Auken (1987, 1990, 1991) suggested that management of an adequate grass cover will reduce mesquite establishment. Conversely, in a south Texas study, Brown and Archer (1989) found that honey mesquite were capable of establishing from (non-fecal deposited) seed in thick swards of grass.

Mesquite seedlings in our study established in ungrazed, perennial grass stands during both a dry and a wet year, which tends to support findings of Brown and Archer (1989), although our seeds were fecal-deposited. Although establishment was higher in the wet year (1995) when pooled across all treatments and vector types (Cohort AB = 7.1% vs. Cohort C = 25.6%; Table 5), it was only during that year, when vigorous perennial grass growth occurred, that clipping neighboring vegetation showed a strong trend toward increasing mesquite seedling survival (37.0% vs. 9.4%; Fig. 4, Table 5). Thus, our results from the wet year agree with studies by Glendening and Paulsen (1955) and Bush and Van Auken (1987, 1990, 1991). Below normal rainfall during the 1994 summer months limited herbaceous growth which minimized competitive effects of surrounding grasses and reduced differences between clipped and unclipped treatments. Hot, dry conditions also reduced effectiveness of irrigation treatments because water evaporated within a few hours after it was applied. This occurred even when the 10-cm irrigation treatment was applied on 19 July 1994.

Our results suggest that, assuming an adequate seed source and spring moisture, some mesquite recruitment occurs that is independent of summer climatic anomalies or neighbor competition. Years with significant spring rainfall to stimulate emergence, followed by summer drought, are as likely to promote seedling establishment as are years with wet springs and wet summers. However, overgrazing during wet years may stimulate pulses of maximum mesquite establishment. Our data suggest that overgrazing during wet years can potentially increase establishment by two-fold over normal wet-year recruitment rates, and by four-fold over dry-year recruitment rates.

In ancillary support of our hypothesis, we have recently observed mesquite establishment in many historically agronomic, grazing-excluded CRP (Conservation Reserve Program) areas which are unlikely to have had any viable soil bank of mesquite seed. Non-domestic animals are certain to have been responsible for dissemination of this seed after the CRP grasses were established. On these sites vigorous, perennial grass stands that have been protected from grazing did not preclude mesquite establishment.

CONCLUSIONS—Some mesquite recruitment will occur regardless of the vigor of a stand of grass, if the seed is disseminated into the stand. However, maintaining a high level of perennial grass cover during wet years may help reduce pulses of maximum mesquite establishment. Increasingly, resource management plans will include multiple-use needs of both domestic livestock and wildlife. Such plans should include an awareness of potential impacts by deer and other wildlife populations in addition to livestock grazing on mesquite seed dispersal. Mesquite recruitment will likely increase with increasing wildlife populations. Movement of livestock from mesquite-infested areas, when pods are available, to areas of low mesquite density should be carefully monitored and avoided if possible (Glendening and Paulsen, 1955).

This research was funded by a grant from the E. Paul and H. Buck Waggoner Foundation, Vernon, Texas, and the University Lands-Surface Interests, University of Texas System, Midland. We thank the W. T. Waggoner Estate for providing the research site for this project. D. Jones and G. Schulz assisted with field data collection. B. Pinchak, K. Owens, J. Huddle, and J. Cox reviewed earlier drafts of the manuscript.

LITERATURE CITED

ARCHER, S., AND D. A. PYKE. 1991. Plant-animal interactions affecting plant establishment and persistence on revegetated rangeland. Journal of Range Management 44:558–565.

ARCHER, S., D. S. SCHIMEL, AND E. A. HOLLAND. 1995. Mechanisms of shrubland expansion: land use, climate or CO_2? Climate Change 29:91–99.

ANDELT, W. F. 1985. Behavioral ecology of coyotes in south Texas. Wildlife Monographs 94:1–47.

BROWN, J. R., AND S. ARCHER. 1987. Woody plant seed dispersal and gap formation in American subtropical savanna woodland: the role of domestic herbivores. Vegetatio 73:73–80.

BROWN, J. R., AND S. ARCHER. 1989. Woody plant invasion of grassland: establishment of honey mesquite (*Prosopis glandulosa* var. *glandulosa*) on sites differing in herbaceous biomass and grazing history. Oecologia 80:19–26.

BROWN, J. R., AND S. ARCHER. 1990. Water relations of a perennial grass and seedling vs adult woody plants in a subtropical savanna, Texas. Oikos 57: 366–374.

BUSH, J. K., AND O. W. VAN AUKEN. 1987. Light requirements for growth of *Prosopis glandulosa* seedlings. Southwestern Naturalist 32:469–473.

BUSH, J. K., AND O. W. VAN AUKEN. 1990. Growth and survival of *Prosopis glandulosa* seedlings associated with shade and herbaceous competition. Botanical Gazette 151:234–239.

BUSH, J. K., AND O. W. VAN AUKEN. 1991. Importance of time of germination and soil depth on growth of *Prosopis glandulosa* (Leguminosae) seedlings in the presence of a C_4 grass. American Journal of Botany 78:1732–1739.

FISHER, C. E. 1947. Present information on the mesquite problem. Texas Agricultural Experiment Station Progress Report 1056, 7 pp.

GIBBENS, R. P., R. F. BECK, R. P. MCNEELY, AND C. H. HERBEL. 1992. Recent rates of mesquite establishment in the northern Chihauhuan desert. Journal of Range Management 45:585–588.

GLENDENING, G. E., AND H. A. PAULSEN. 1950. Recovery and viability of mesquite seeds fed to sheep receiving 2,4-D in drinking water. Botanical Gazette 111:486–491.

GLENDENING, G. E., AND H. A. PAULSEN. 1955. Reproduction and establishment of velvet mesquite as related to invasion of semidesert grasslands. United States Department of Agriculture, Forest Service Technical Bulletin No. 1127, 50 pp.

HASTINGS, G. J., AND R. M. TURNER. 1965. The changing mile: an ecological study of vegetation change with time in the lower mile of an arid and semi-arid region. University of Arizona Press, Tucson.

IMO, M., AND V. R. TIMMER. 1992. Nitrogen uptake of mesquite seedlings at conventional and exponential fertilization schedules. Soil Science Society of America Journal 56:927–934.

KOOS, W. M., J. C. WILLIAMS, AND M. L. DIXON. 1962. Soil survey of Wilbarger County, Texas. United States Department of Agriculture, Soil Conservation Service, Soil Survey Series 1959 No. 18, Ft. Worth, Texas.

LEOPOLD, B. D., AND P. R. KRAUSMAN. 1991. Factors influencing desert mule deer distribution and productivity in southwestern Texas. Southwestern Naturalist 36:67–74.

MARCHINTON, R. L., AND D. H. HIRTH. 1984. Behavior. In: Halls, L. K., R. E. McCabe, and L. R. John, editors. White-tailed deer ecology and management. Stackpole Books, Harrisburg, Pennsylvania. Pp. 129–168.

NOAA (NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION) 1994. Climatogical data, Texas. Volume 99, No. 13.

REYNOLDS, H. G., AND G. E. GLENDENING. 1949. Merriam kangaroo rat a factor in mesquite propagation on southern Arizona range lands. Journal of Range Management 2:193–197.

ROUNDY, B. A., V. K. WINKEL, J. R. COX, A. K. DOBRENZ, AND H. TEWOLDE. 1993. Sowing depth and soil water effects on seedling emergence and root morphology of three warm-season grasses. Agronomy Journal 85:975–1082.

SAS INSTITUTE INC. 1988. SAS/STAT User's Guide, Release 6.03 Edition. SAS Institute Inc., Cary, North Carolina.

SCHUPP, E. W. 1993. Quantity, quality and effectiveness of seed dispersal by animals. Vegetatio 107/108:15–29.

SCHUPP, E. W., AND M. FUENTES. 1995. Spatial patterns of seed dispersal and the unification of plant ecology. Ecoscience 2:267–275.

SCIFRES, C. J., AND J. H. BROCK. 1969. Moisture-temperature interrelations in germination and early seedling development of mesquite. Journal of Range Management 22:334–337.

SCIFRES, C. J., AND J. H. BROCK. 1971. Thermal regulation of water uptake by germination honey mesquite seeds. Journal of Range Management 24:157–158.

SCIFRES, C. J., AND J. H. BROCK. 1972. Emergence of honey mesquite seedlings relative to planting depth and soil temperature. Journal of Range Management 25:217–219.

STEEL, R. G. D., AND J. H. TORRIE. 1980. Principles and procedures of statistics—a biometrical approach. McGraw-Hill, Second ed. New York.

UECKERT, D. N., L. L. SMITH, AND B. L. ALLEN. 1979. Emergence and survival of honey mesquite seedlings on several soils in west Texas. Journal of Range Management 32:284–287.

VAN AUKEN, O. W., AND J. K. BUSH. 1987. Interspecific competition between *Prosopis glandulosa* Torr. (honey mesquite) and *Diospyros texana* Scheele (Texas persimmon). American Midland Naturalist 118:385–392.

VAN AUKEN, O. W., AND J. K. BUSH. 1988. Competition between *Schizachyrium scoparium* and *Prosopis glandulosa*. American Journal of Botany 75:782–789.

VAN AUKEN, O. W., AND J. K. BUSH. 1990. Importance of grass density and time of planting on *Prosopis glandulosa* seedling growth. Southwestern Naturalist 35:411–415.

VINES, R. A. 1960. Trees shrubs and woody vines of the southwest. University of Texas Press, Austin, Texas.

WILSON, M. 1993. Mammals as seed-dispersal mutualists in North America. Oikos 67:159–176.