Biological and physical factors influencing *Acacia constricta* and *Prosopis velutina* establishment in the Sonoran Desert

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Abstract

Over the past century woody plants have increased in abundance on sites formerly occupied by grasslands in the Sonoran Desert. Woody plant invasion has been associated with a multitude of biological and physical factors. This study was conducted to determine temperature, soil, fire, rodent, and livestock effects on the germination and establishment of whitethorn acacia (*Acacia constricta* Benth.) and velvet mesquite (*Prosopis velutina* (Woot.) Sarg.]. Optimum germination temperatures for both shrubs ranged from 26 to 31° C, and seedling emergence was greatest from seed sown at 1 to 2 cm depths in sandy loam soil. Merriams kangaroo rats *(Dipodomys merriami)* fed seeds in the laboratory removed seed coats and planted embryos at 2 to 4 cm depths in a sandy loam soil. Prescribed fire killed 100% of seed placed on the soil surface but had no measurable effect on the germination of seed planted at 2 cm. After passage by sheep, about 6% of the *A. constricta* and 13% of the *P. velutina* seeds germinated while after passage by cattle, only 1% of the *A. constricta* and 3% of the *P. velutina* seed germinated. Embryo planting by rodents may improve survival efficiencies for these leguminous shrub seedlings, but seed consumption and passage by sheep and cattle appear to adversely affect seed germination. *Dipodomys merriami*, rather than domestic livestock, may be responsible for the spread of these shrubs in the Sonoran Desert.

Key Words: whitethorn acacia, velvet mesquite, germination, soil texture, planting depth, fire, rodents, cattle, sheep semidesert grasslands, North America

Vegetation changes concern both livestock producers who depend on perennial grass forage and land managers who are responsible for natural resource conservation. Of particular concern is the increasing abundance of native shrubs, such as white-thorn acacia (*Acacia constricta* Benth.) and velvet mesquite [*Prosopis velutina* (Woot.) Sarg.]. Since the 1800's these shrubs have spread from riparian lowlands to adjacent semidesert grasslands (Hastings and Turner 1972, Humphrey 1958). Shrub invasion is followed by a reduction in perennial grass densities and accelerated soil erosion (Cooke and Reeves 1976).

Griffith (1901), Bryan (1925), Humphrey (1958), and York and Dick-Peddie (1969) documented the shrub invasion and Cable and Tschirley (1961) and Morton et al. (1990) developed technology to chemically and mechanically reduce *A. constricta* and *P. velutina* populations. There are, however, few studies which identify climatic, edaphic, and biological factors that cause vegetation change (Glendening and Paulsen 1955) and address interactions (Brown and Heske 1990). Yet, the development of basic information which identifies processes and process interactions, and their incorporation in management practices, may be the only acceptable approach for reducing shrub populations.

This paper addresses the effects of temperature, soil texture and planting depth, rodents, fire, and livestock on the germination and seedling growth of *A. constricta* and *P. velutina*. Historical observations of range management practices are included, and a discussion centers around strategies to limit shrub invasion through rodent and livestock management.

Materials and Methods

Between August and October 1983 and 1984, seed from *A. constricta* and *P. velutina* trees were collected along the Pantano Wash and the Santa Cruz River in southeastern Arizona. Elevations range from 965–1,000 m and slopes are 2–6%. Soils are recent alluvium, weathered from granitic rocks, and are moderately acid (pH = 6.2–6.9); depths range from 1–5 m (Richardson et al. 1979). Average annual precipitation is 400 mm and has ranged from 140–665 mm in the past 80 years (Sellers and Hill 1974, National Oceanic and Atmospheric Administration 1982).

Seed from the 1983 and 1984 collections were retained as separate lots. *A. constricta* seed were cleaned by hand and *P. velutina* seed were processed through a mechanical thresher. Mean seed weights were 20 ± 3 g for *A. constricta* lots and 45 ± 5 g for *P. velutina* lots. Chipped, distorted, and light seed were omitted and only apparently undamaged seed used in the study.

Temperature Effects on Germination

A hard pericarp surrounds the endosperm of the seed of these leguminous shrubs, and pericarp scarification is necessary to insure germination (Glendening and Paulsen 1955). Twenty scarified seed of either *A. constricta* or *P. velutina* were placed on 2 layers of Whatman's #3 filter paper in a plastic petri dish. Approximately 10 ml of distilled water was added and seed germinated at 16, 21, 26, 31, or 38° C on a thermogradient plate (Larsen 1962). These temperatures were selected because soil temperature at 2 cm usually varies from 16–38° C in spring, summer, and fall at 2 locations in the Chihuahuan and 3 locations in the Sonoran deserts (unpublished data, USDA-ARS, Tucson, Ariz.). Germination was considered complete when the seed radicle was 2 cm in length.

Dishes were arranged in a stratified randomized complete block design because temperature was constant across the thermogradient plate. One petri dish was used for each species at each temperature and the experiment was repeated 4 times for seed collected in 1983 and in 1984. Total germination was determined by accumulating the number of germinated seed over the 14-day period. Germination values for the respective shrubs were compared at the same rate for 5 temperatures with analysis of variance (ANOVA). When F-values were significant ($P \leq 0.05$), data were tested for normality and variance homogeneity, and means were separated with a Tukey's HSD test (Sokal and Rohlf 1981).

Planting Depth and Soil Textural Effects on Emergence and Seedling Growth

Soil with textural characteristics common to desert regions of the Southwestern United States and Northern Mexico (Hendricks 1985) were collected in southeastern Arizona. These soils were Pima silty clay loam, Sonoita silty clay loam, and Comoro sandy loam. The soils are classified as thermic Typic Torrifluvents. The clay content of both the Pima and Sonoita silty clay loam soil varies from 20-30%; however, the clay fraction of the Pima is 60% montmorillonite and the Sonoita is 80% kaolinite (Cox and Martin-R. 1984).

Soils were collected from 0-15 cm depths, screened to 1 cm to remove rocks, thoroughly mixed, and added to 15- by 15-cm tapered plastic pots to 6, 10, 12, 13, and 14 cm depths above the pot base. Ten pure live seed (scarified) of 1 shrub species were sown on the surface in each pot. Soils were added to 14 cm depths in all pots; thus, seed were planted at 0, 1, 2, 4, and 8 cm depths below the soil surface. Pots were sub-irrigated with distilled water continuously for 7 days, and thereafter for 8 hours on days 14 and 21. Sub-irrigation was used to minimize soil disturbance and seed movement, and surface soil was moist for at least 72 hours after each sub-irrigation.

Glasshouse relative humidity varied from 58-80%, and temperatures ranged from 23-32° C. Day length was 12 hours and no supplemental light was added. Twenty-five percent Hoagland's solution was added with distilled water on days 7, 14, and 21.

Seedling emergence was considered complete when the first leaf was 2 cm above the soil surface, and the seedling radicle had penetrated the soil surface in pots where seed were surface sown. Emergence was measured 28 days after the experiment began.

Pots were arranged in a randomized complete block design, with a 3 by 2 by 5 factorial arrangement. There were 6 blocks and each contained 3 soils, 2 species, and 5 planting depths. The experiment was repeated twice: once for seed collected in 1983 and once for seed collected in 1984. Seed seedlings did not emerge from all depths in the 3 soils, data were arcsin transformed and subjected to ANOVA with unequal sample numbers. When F-values were significant ($P \leq 0.05$), means were separated with Tukey's HSD Test (Sokal and Rohlf 1981).

Kangaroo Rat Predation Effects on Germination

In August 1985 and September 1986, 6 *D. merriami* males were trapped in a creosotebush (*Larrea tridentata* (DC.) Cov.)-*A. constricta-P. velutina* community on the Santa Rita Experimental Range in southeastern Arizona. Animals were transferred to a holding room and a series of feeding trials conducted to determined (1) the quantity of seed coat removal and its effect on seed germination and (2) depths in soil where seed are most frequently planted.

Six *D. merriami* were individually housed in 40- by 40- by 15-cm wire cages. Cages were fitted with 39- by 39- by 10-cm pans, and pans filled with sandy loam soil. On 5 consecutive nights, 200 seed of either *A. constricta* or *P. velutina* were provided to each rat. Each morning soil was removed from the pan at 1-cm intervals and

passed through a 5-mm sieve. Seed were separated, with a dissecting scope, in 3 categories: (1) no seed coat removal, (2) partial seed coat removal (teeth marks), and (3) complete seed coat removal. Remaining unburied seeds were counted.

A. constricta or *P. velutina* seed from the 3 categories were placed on 2 layers of Whatman's #3 paper in a plastic petri dish and germinated in distilled water at 30° C for 7 days. Hard seed were scarified on day 8 and observed for an additional 6 days. Germination was considered complete when the seed radicle was 2 cm in length.

The experiment was repeated twice for seed collection in 1983 and in 1984. Total germination was determined by accumulating the number of germinating seed in each category over the 14-day period. The 6 *D. merriami* were considered blocks and the 4 feeding trials were replications. Germination values for the respective shrubs were compared at the 3 levels of seed coat removal with ANOVA. When F-values were significant ($P \leq 0.05$) means were separated with a Tukey's HSD Test (Sokal and Rohlf 1981).

Fire Effects on Germination

A 6-ha stand of dense, shrub-free Lehmann lovegrass *(Eragrostis lehmanniana)* on the Santa Rita Experimental Range was fenced to exclude livestock. Twelve 15- by 15-m plots were established in January 1984, with 4 plots in each of 3 blocks. One plot in each block was randomly selected and *E. lehmanniana* was harvested at the soil surface in ten 25- by 25-cm quadrats. Aboveground biomass was separated into either standing (live and dead) or litter components. Biomass was weighed, dried at 105° C for 48 hours and reweighed. Dry weight (fuel load) and fine fuel water content (expressed as a percent of dry weight) were averaged by plot.

Prior to burning, 1 plot in each block was randomly selected, and all plots were divided into 4 equal quarters. In each quarter a 25- by 25-cm frame was centered over a randomly selected point. At the 4 corners, 25 seed of either *A. constricta* or *P. velutina* were either sown on the soil surface or hand planted at about 2 cm beneath the soil surface. In each plot there were a total of 100 seeds of each species at 2 soil depths. Seed were planted or sown 5-10 min. before the burn. Three plots were burned with a headfire in mid-June 1984, 1985, 1986, and 1987; no plot was reburned during the experiment.

Mid-June burning was selected because soils are dry, most above-ground biomass is dead, and daytime temperatures exceed 38° C (Cox 1988). During this period lightning frequency peaks (Osborn 1983) and naturally occurring fires would be most common (Hastings and Turner 1972). The time from fire ignition to total herbage removal was recorded by plot. During each burn, wind speed and air temperature were recorded at 10-s intervals. Near each random point, 2 thermocouples were installed to measure soil temperature extremes at 0 and 2 cm depths.

Following the burn, seed of either *A. constricta* or *P. velutina* collected at the 2 depths were placed on 2 layers of Whatman's #3 paper in a plastic petri dish, and germinated in distilled water at 30° C for 7 days. Hard seed were scarified on day 8 and observed for an additional 6 days. Again germination was considered complete when the seed radicle was 2 cm in length.

The experiment was repeated twice for seed collected in 1983 (1984 and 1985 burns) and twice for seed collected in 1984 (1986 and 1987 burns). Total germination was determined by accumulating the number of germinating seed at each depth over the 14-day period. Experimental design was a randomized complete block with 3 replications in 4 years. Because seed on the soil surface failed to germinate, germination of seed planted at about 2 cm was subjected to ANOVA. When F-values were significant ($P \leq 0.05$) means were separated with Tukey's HSD Test (Sokal and Rohlf 1981).

Livestock Digestion Effects on Germination

Four Suffolk ewes *(Ovis aries)* and 4 Angus cows *(Bos taurus)* were fed in individual feeding cages at the University of Arizona-Campbell Avenue Farm. Animals had free access to water, and each group was fed a predetermined daily quantity of alfalfa cubes; ewes received 3.2 kg/day and cows received 6.4 kg/day. During four 15-day feeding trials, animals were fed either *A. constricta* or *P. velutina* seed. On day 1, each ewe received 1,000 *A. constricta* seed, and on day 30, 3 of the same ewes and a substitute received 1,000 *P. velutina* seed. On day 15, each cow received 2,500 *P. velutina* seed, and on day 45, the same cows received 2,500 *A. constricta* seed. Seed were mixed in a 1.5 kg ration of milo and sorghum (50:50).

Fecal collections were made twice daily for 13 days. After each collection ewe feces were soaked for 15 min. in tap water and massaged with a wooden spatula, and cow feces were soaked for 30 min. and liquefied in a commercial dough blender. Fluid was passed through 10-, 5-, and 2-mm sieves, and sieve surfaces sprayed with tap water to remove herbage fragments. Seed were separated, with a dissecting scope, in 3 categories: (1) no seed coat removal, (2) partial seed coat removal (chips), and (3) complete seed coat removal. Some seed in each category had imbibed (swollen) moisture during passage through livestock, hence, a second separation of each category.

Hard and imbibed *A. constricta* and *P. velutina* seed from the 3 categories were placed on 2 layers of Whatman's #3 paper in a plastic petri dish and germinated under the conditions described in the 2 preceding studies. Germination was considered complete when the seed radical was 2 cm in length.

The experiment was conducted in 1985. The 1983 and 1984 seed lots, for the respective species, were combined to obtain adequate seed numbers. Experimental design was a split-plot, animals were main plots, and shrub seed were subplots. Data were subjected to repeated measures ANOVA. When F-values were significant ($P\leq0.05$) means were separated with a Tukey's HSD Test (Sokal and Rohlf 1981).

Results and Discussion

Temperature Effects on Germination

Germination characteristics of *A. constricta* and *P. velutina* seed collected in 1983 and 1984 were similar ($P\leq0.05$) and the data were pooled (data not shown). For both species seed germination began on day 5 at 26 and 31° C, and on day 9 at 21 and 38° C. Seed of *A. constricta* began to germinate on day 12 at 16° C and at the same temperature seed of *P. velutina* failed to germinate in 14 days (Table 1).

Table 1. Mean germination (%) of *Acacia constricta* (A.C.) and *Prosopis velutina* (P.V.) seed at 5 constant temperatures during a 14-day germination trial.

Species	Day	Temperature (° C)
		16	21	26	31	38
		%
A.C.	7	0	0	89a[1]	85a	0
P.V.		0	0	81a	95a	0
A.C.	14	27d	54c	98a	97a	34d
P.V.		0	77b	95a	95a	15d

[1]Means within days are not significantly different (P≤0.05) when followed by the same letter.

Optimal germination of *A. constricta* and *P. velutina* occurred at 26 and 31° C, and percentages declined above or below these temperatures (Table 1). Cotyledons and radicles of seed germination at 21, 26, and 31° C appeared healthy and normal. At 16°C, 10% of the *A. constricta* seedlings had either chlorotic or wrinkled

cotyledons, whereas, *P. velutina* failed to germinate after 14 days. At 38° C, 15% of *A. constricta* and 65% of *P. velutina* seedlings had stunted radicles and black abscesses on the root tip.

Germination of *A. constricta* across all temperatures suggests that this species may be adapted over a wider environmental gradient than *P. velutina*. Thus, *A. constricta* might be expected to germinate following both cool- and warm-season moisture. Cox et al. (1987) suggested *P. velutina* would most likely germinate in August when rainfall amounts peak and surface soil temperatures decline from 40 to 30° C. These germination characteristics may partially explain the abundance of *A. constricta* at higher elevations (1,000–1,500 m) and *P. velutina* at lower elevations (900–1,000 m) in the Sonoran desert (Hastings and Turner 1972).

Planting Depth and Soil Textural Effects on Emergence and Seedling Growth

There were no differences ($P\leq0.05$) in *A. constricta* and *P. velutina* seed lots, thus data were pooled (data not shown). Germination of seed placed on the soil surface averaged 95-100% for the 2 species. Radicles of *A. constricta* seedlings grew horizontally and they died within 48 hours because radicles were unable to penetrate soil surfaces. About 20% of the *P. velutina* radicles penetrated the soil surfaces. *P. velutina* radicles, however, elevated the endosperm above the surface soil, and seedlings with exposed radicles died in 3 to 6 days.

A. constricta seedlings failed to emerge when planted at any depth in the silty clay loam (Sonoita and Pima) soils, and emergence was less than that of *P. velutina* at all depths in the sandy loam (Comoro) soil (Table 2). Radicles of *A. constricta* seedlings

Table 2. Mean emergence (%) of *Acacia constricta* (A.C.) and *Prosopis velutina* (P.V.) seed sown at 5 depths in 3 soils after a 14-day trial.

Planting depths	Soils and species				
	\multicolumn{2}{c}{Comoro}	\multicolumn{2}{c}{Sonoita}	\multicolumn{2}{c}{Pima}
	A.C.	P.V.	A.C.	P.V.	A.C.	P.V.
(cm)	%				
0	0	0	0	0	0	0
1	77b[1]	100a	0	37d	0	67bc
2	57c	95a	0	42d	0	57c
4	10	50cd	0	0	0	0
8	0	15e	0	0	0	0

[1]Means followed by the same letter in both columns and rows are not significantly different (P≤0.05).

excavated from Sonoita and Pima soils were similar in amount and distribution to those from Comoro soils. In the coarse-textured Comoro soil, the epicotyl and cotyledons of emerging *A. constricta* seedlings were protected by the seed coat. Excavations of the 2 fine-textured soils, and the greater depths in Comoro soil, suggest that the seed coat was shed before emergence. Seed coat removal before emergence appears to damage either the epicotyl or hypocotyl and limit *A. constricta* survival. In contrast, seed coat removal before emergence did not appear to effect *P. velutina* seedlings.

Emergence of *A. constricta* and *P. velutina* seedlings peaked between days 6 and 9, and seedling recruitment appeared complete by day 11. However, additional *P. velutina* seedlings emerged when sub-irrigation was discontinued. As soils dried, 3 cm deep cracks appeared in Pima soil. Between days 13 and 15, seedlings from *P. velutina* seed planted at 1 and 2 cm depths emerged from cracks. *A. constricta* seedlings apparently died before the Pima soil cracked because additional seedlings failed to emerge after day 11.

Kangaroo Rat Predation Effects on Germination

Seed collection years, 1983 and 1984, had no apparent effects ($P\leq0.05$) on the germination characteristics of *A. constricta* and *P.*

Table 3. Effects of seed coat removal by *Dipodomys merriami* on mean germination (%) of *Acacia constricta* (A.C.) and *Prosopis velutina* (P.V.). Numbers in parentheses indicate total germination after further scarification.

| Species | Seed coat removal | | |
	None	Partial	Complete
	- - - - - - - - - - - - - - - - - % - - - - - - - - - - - - - - - -		
A.C.	59b (95)	92a[1]	95a
P.V.	35c (98)	57b (78)	85a

[1]Means followed by the same letter in both columns and rows are not significantly different ($P \leq 0.05$).

velutina seed fed to *D. merriami* in 1985 and 1986. As the amount of seed coat removal increased, germination increased (Table 3) and the time to germination decreased. Embryo's with all seed coat removed began to germinate in 24 hours and germination was complete in 60 hours. Nonscarified seed germinated between days 4 and 6.

During nights 1 and 2, *D. merriami* consumed 30% (60 ± 43) of the 200 seed and planted 10% (22 ± 8). The trend reversed on nights, 3, 4, and 5, and for health concerns we provided fleshy fruits on night 5. Approximately 87% of the lighter *A. constricta* seed were excavated between 2 and 3 cm depths, while 84% of the heavier *P. velutina* seed were found between 3 and 4 cm depths (Table 4). Our most important finding is that 90% of the seed

Table 4. Mean quantities of *Acacia constricta* (A.C.) and *Prosopis velutina* (P.V.) seed buried at several soil depths by *Dipodomys merriami* in laboratory feeding trials.

| Depth | Species | |
	A.C.	P.V.
(cm)	- - - - - - - - - - - - - number - - - - - - - - - - - - -	
1	3	5
2	80	20
3	50	100
4	10	58
5	5	3
6-10	2	2

buried between 2 and 4 cm had the seed coat completely removed and 85 to 95% of the seed germinated in less than 60 hours (Table 3).

Fire Effects on Germination

Aboveground phytomass (standing biomass plus litter) was highly variable among burned plots during the 4-year study, and varied from 3,890 to 5,600 kg/ha (Table 5). Fuel water content varied from 10 to 55%, and the forage in each plot was consumed by the fire in about 44 sec. Ambient air temperatures were 1 to 4° C cooler than temperatures at 2 cm depths during the fire. During the

12 fires, peak surface temperatures near the seed varied from 380° C in June 1987 to 535° C in June 1986.

Fire blackened the seed coat of surface sown *A. constricta* and *P. velutina* seed, and after scarification seed failed to germinate. In contrast, the fire had no effect on germination of seed sown at 2 cm soil depths; mean germination of nonscarified *A. constricta* and *P. velutina* was 55 and 33%, respectively. Germination of scarified seed exceeded 90% for both species.

Livestock Digestion Effects on Germination

Total recovery of ingested *A. constricta* and *P. velutina* seed varied from 2-8% in sheep and from 28-31% in cattle (Table 6). There was considerable variability in seed passage, but in most instances viable seed were passed before day 8 by sheep and day 9 by cattle. Seed passage by sheep and cattle primarily occurred on days 1 through 5, a pattern previously reported by Burton and Andrews (1984) and Simao Neto et al. (1987).

Seed passage in this study is about half that reported by Fisher (1947) and Glendening and Paulsen (1955). Differences may occur because we removed seed damaged by insects and light seed before feeding. Differences may also be attributed to livestock class, and passage rates of caged versus free roaming livestock.

The recovery of the smaller *A. constricta* seed from sheep was about 3 times greater than the larger *P. velutina* seed: 82 versus 25, respectively. Since *A. constricta* (770 seed) recovery from cattle was similar to *P. velutina* (703), seed size had no apparent effect on passage. The greater seed recovery from cattle compared to sheep is related to initial mastication and rumination. We observed that cattle chewed on seed of both shrubs for 15 to 45 sec. before swallowing. Sheep, in contrast, chewed on smaller *A. constricta* seed for 2 to 3 min. and larger *P. velutina* seed for 5 to 7 min. The passage of ingesta from the rumen is determined by particle size reduction during mastication and rumination (Van Soest 1982). Since the reticulo-omasal orifice in cattle is larger than in sheep, more large particles can be expected to pass from cattle. Hence, the passage of more seed by cattle (Table 6).

Of the 1,000 seed of each species ingested by sheep, only 56 (5.6%) *A. constricta* and 13 (1.3%) *P. velutina* seed germinated after passage through the digestive tract (Table 6). Of the 2,500 seed ingested, only 48 (1.9%) *A. constricta* and 81 (3.2%) *P. velutina* seed germinated after passage through cows. Considering the number of viable seed that survive after passage through cows and sheep, there is no reason to believe that germination is enhanced by domestic livestock (Janzen 1981).

D. merriami may remove hard seed from livestock dung (Reynolds 1958). Although most seed are eaten, the few remaining seed, with the seed coat removed, might be planted at 1 to 4 cm. This process may aid in the establishment of recruitment trees which serve as collection and dispersal centers (Brown and Archer 1987, 1989).

Conclusions

Prior to 1890, *A. constricta* and *P. velutina* commonly occurred

Table 5. Fuel characteristics, burn time, and environmental conditions during burning in summers of 1984, 1985, 1986, and 1987.

| Year | Fuel load | | Fuel water content | Burn time | Wind speed | Temperature (Max) during burn | | |
| | Standing | Litter | | | | Air | Soil | |
							Surface	2cm
	- - - - - - - - kg/ha - - - - - - - - -		(%)	(sec)	(km/h)	- - - - - - - - - - - - - - - - - - ° C - - - - - - - - - - - - - - - -		
1984	1,890	2,000	10	35	10	30	480 ± 50	33
1985	4,350	1,205	30	45	10	29	410 ± 90	31
1986	3,950	900	25	45	10	31	470 ± 65	32
1987	3,600	1,600	55	50	10	29	390 ± 110	33

Time after feeding seed	Sheep				Cattle			
	Imbibed seed		Hard seed		Imbibed seed		Hard seed	
	A.C.	P.V.	A.C.	P.V.	A.C.	P.V.	A.C.	P.V.
Days					No.			
1	1 (1)	2 (1)	9 (8)	0	10 (2)	4 (3)	6 (5)	1 (1)
2	4 (2)	3 (0)	23 (18)	2 (2)	310 (25)	378 (26)	15 (8)	11 (10)
3	4 (3)	1 (1)	10 (9)	4 (3)	250 (20)	124 (9)	25 (10)	22 (20)
4	2 (1)	0	10 (8)	4 (3)	86 (6)	72 (4)	16 (7)	6 (5)
5	0	0	7 (6)	3 (2)	20 (2)	17 (2)	9 (8)	15 (14)
6	0	0	3 (3)	4 (3)	5 (1)	8 (2)	5 (4)	9 (9)
7	0	0	4 (2)	2 (0)	0	4 (0)	9 (4)	4 (4)
8	0	0	3 (2)	0	0	4 (0)	4 (2)	13 (11)
9	0	0	2 (0)	0	0	3 (0)	0	6 (6)
10	0	0	0	0	0	1 (0)	0	1 (1)
11	0	0	0	0	0	0	0	0
12	0	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0
Total	11 (7)	6 (2)	71 (56)	19 (13)	681 (56)	615 (46)	89 (48)	88 (81)

as trees and their populations were largely limited to riparian zones (Hastings and Turner 1972). Seed dispersal occurred when floods carried seed downstream but frequent fires killed seed and seedlings. Humphrey (1958) was one of the few ecologists who regarded fire as an evolutionary force in semiarid Sonoran desert grasslands. Recent interpretations of historical evidence (Bahre 1985) supports Humphrey's hypotheses that large, destructive wildfires burned at 2-3-year intervals between 1859 and 1890. These uncontrolled fires were feared by federal land managers, who promoted overgrazing by domestic livestock as a tool to reduce timber losses by wildfire (Leopold 1924).

Our data suggest that increases in *A. constricta* and *P. velutina* during the past century may be attributed to a multiplicity of natural and man-made causes. The failure of surface sown seed to germinate after fire indicates wildfire was important in limiting shrub distribution on former semidesert grasslands. The inability of surface sown seed to establish on bare soil (Table 2), the destruction of most viable seed during mastication and passage through cattle and sheep (Table 6), and seed coat removal and seed embryo planting by *D. merriami* at depths ideal for seedling emergence in soil (Tables 2 and 3) do not support the commonly accepted belief that domestic livestock were solely responsible for shrub invasion. It could be argued that domestic livestock act primarily as seed predators, while *D. merriami* functions as predator, distributor, and planter. The identification of *D. merriami* as a primary mechanism responsible for maintaining and increasing shrub populations (Reynolds 1958) is supported by studies which show similar shrub populations in grazed and nongrazed enclosures where kangaroo rat populations were uncontrolled (Smith and Schmutz 1975, Wright 1982).

Little work has been done to identify the processes responsible for brush invasion. Research has emphasized chemical and mechanical treatments designed to reduce shrub populations and seed introduced grasses to restore grassland productivity (Stoddart et al. 1975). Today, the use of herbicides is less acceptable, mechanical treatments are costly, and there is more concern over introduced grasses. Hence there is a growing need to develop environmentally sound strategies to limit shrub encroachment on existing grasslands.

Because the studies presented in this paper were conducted in the laboratory, greenhouse, and at a few field locations, the results may not be applicable over vast areas. The results do suggest that frequent fires before 1890 probably controlled the abundance of

both species. The abundance of cattle and sheep after 1890, and their preference for pods of leguminous species, contributed to seed spread from lowland to upland areas (Glendening and Paulsen 1955). As livestock numbers increased, perennial forage crop declined and rat densities increased on semidesert grasslands (Norris 1950). Rats harvested seed from trees and livestock dung piles and stored seed at ideal planting depths. The number of germinating leguminous seed is directly related to rat populations, and rats may transport seed 30 m from the seed source (Reynolds 1958).

Cattle and sheep grazing is known to affect plant species composition, but vegetation change has yet to be detected when their numbers are reduced or excluded (Barns 1982, Stoddart et al. 1975). In contrast, kangaroo rat exclusion may be followed by perennial grass establishment, plant litter accumulation, soil disturbance reductions, and the return of a semidesert grassland ecosystem (Brown and Heske 1990). Selective foraging by kangaroo rats for large seed (Brown et al. 1979) and their apparent inability to locate all seed caches (Glendening and Paulsen 1955) appear to be, at least partially, responsible for the shrub invasion in semidesert grasslands.

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