Am. Midl. Nat. 128:11–21

Soil Seed Bank of a Semiarid Texas Grassland Under Three Long-term (36-Years) Grazing Regimes

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ABSTRACT.—Species composition and density of the readily germinable soil seed bank of three long-term (36-yr) grazing treatments (heavy continuous, moderate deferred rotation and ungrazed exclosure) were determined for a summer and spring period for a semiarid grassland of the western Edwards Plateau, Texas. Total seed densities (2252 to 4409 seeds/m^2) did not differ among grazing treatments, but did vary seasonally. Species composition varied among treatments. Heavy continuous grazing had a high proportion of early-seral, annual-dicot taxa, whereas the ungrazed treatment had a high proportion of late-seral, perennial-monocot taxa. Seeds of late-successional midgrass species (*e.g.*, *Bouteloua curtipendula, Eriochloa sericea*) were not stored in the soil of any treatment and appeared to be transient. Many other species appeared to maintain persistent seed banks, including seeds of the current mid-successional dominant shortgrass, *Hilaria belangeri*. Similarity of composition between germinable seeds in the soil and existing plant communities was low. Soil seed bank is a primary control of secondary succession in these grasslands, and absence of late-successional species in the seed bank impairs the rate of succession.

INTRODUCTION

Species establishment following disturbance is dependent upon soil seed bank, persistence of vegetative structures and propagule immigration (Egler, 1954; Raynal and Bazzaz, 1973; Drury and Nisbet, 1973; Connell and Slatyer, 1977; Grime, 1981; Roberts, 1981). Soil seed banks are pools of viable seeds in the soil and on its surface (Roberts, 1981; Simpson, *et al.*, 1989) in which seeds may persist for brief or extended periods (Thompson and Grime, 1979). Grazing by large herbivores has been shown to alter composition and density of the seed bank (Lippert and Hopkins, 1950; Major and Pyott, 1966; Johnston *et al.*, 1969; Iverson and Wali, 1982) by altering species composition and abundance relationships of the plant community (Ellison, 1960), and subsequent seed output of each community component (Belsky, 1986). Thus, herbivory can modify successional processes.

Vegetation of the Edwards Plateau of Texas before settlement by Europeans was a savannah dominated by caespitose midgrasses (*e.g.*, *Bouteloua curtipendula, Stipa leucotricha, Eriochloa sericea, Schizachyrium scoparium*) with associated shortgrasses (*e.g.*, *Hilaria belangeri, Bouteloua trifida, Erioneuron pilosum*) and scattered clumps or individuals of *Quercus fusiformis, Q. pungens* var. *vaseyana, Juniperus ashei* and other woody species (Merrill and Young, 1959; Smeins and Merrill, 1988). Overgrazing by domestic livestock and elimination of fire have assisted in converting most areas to shortgrass communities dominated by the stoloniferous grass *Hilaria belangeri* and increased abundance of woody species (Smeins and Merrill, 1988). Reestablishment potential of midgrass species is largely a function of stored, viable, late-successional propagules in the soil seed bank.

We hypothesize that long-term herbivory by domestic livestock has altered the soil seed bank. Consequently, abundance and availability of late-successional midgrass propagules have been reduced. Lack of these species in the seed bank could significantly influence rates and patterns of secondary succession. Research objectives were to characterize the composition and abundance of the readily germinable soil seed bank present in three 36-yr grazing treatments, relate the seed bank to extant vegetation and assess the potential impact of altered seed banks on successional processes.

STUDY AREA

The study was conducted on the 1404 ha Texas Agricultural Research Station near Sonora, Texas. It lies within the southwestern portion of the Edwards Plateau Natural Region (Gould, 1975), 56 km S of Sonora (31°14′N, 100°10′W) with an approximate elevation of 735 m. Annual average precipitation is 577 mm with maximums occurring in May–June and September. Summers are hot and dry with average July temperatures of 27.7 C, while winters are generally mild with an average January temperature of 9.5 C. Soils are primarily clay and clay loam Mollisols over a fractured limestone substrate that produces shallow, rocky soils with great surface heterogeneity (Wiedenfeld and McAndrew, 1968).

The Station has a long history of heavy continuous grazing by large herbivores. Before 1900, grazing intensities were as high as 2 ha/animal unit/year (animal unit = 12 kg/day dry biomass requirement) by cattle, sheep and goats (Youngblood and Cox, 1922). From 1900 until 1948, stocking rates of approximately 3.7 ha/animal unit/year were common. In 1948, a series of experimental pastures were established to test the influence of stocking rate, grazing system, and combination of livestock on vegetation and animal responses (Merrill, 1959). Two replicates of three long-term grazing treatments were chosen for this study: a heavy continuous (HC) grazing treatment (32 ha each) maintained at 4.5–5.3 ha/animal unit/year; a moderate deferred rotation (MDR) grazing treatment (24 ha each) at 6.2 ha/animal unit/year until 1969 when the rate was changed to 7.7 ha/animal unit/year; and an ungrazed exclosure (EXC) treatment (16 ha each) with no livestock grazing. The HC treatments were grazed throughout the year, while the MDR received periodic, seasonally rotated rest periods. The ratio of cattle, sheep and goats in the grazed pastures was generally 60:20:20. One exclosure excluded white-tailed deer, but neither excluded small mammals. Deer had access to grazed pastures generally at densities of 1 deer/5 ha.

METHODS

Within each pasture a grass-dominated study site was selected on deep (>30 cm), fine-textured soils on flat terrain. Woody plants were not present within 10 m of the sites. Sites were fenced to prevent grazing during the study.

Foliar cover was estimated using a canopy cover method (Daubenmire, 1959). Within each replicate, ten 25 × 50-cm randomly located quadrats were inventoried on 10 July 1985 and 20 quadrats on 17 September 1986. These dates corresponded with greatest development of herbaceous vegetation. Because of drought, foliar cover estimates made on dates associated with seed bank sample periods were not representative of the extant communities. Taxonomic nomenclature follows Gould (1975) for grasses and Correll and Johnston (1970) for other taxa.

Twenty soil cores (7.6-cm diam, 5-cm deep) were collected in each replicate using a stratified random sampling design. Soil samples were collected on 18 June 1984 and 8 March 1985, air-dried and stored at room temperature and humidity. Seeds were germinated in a greenhouse, with germination of June 1984 samples initiated in July 1984, and germination of March 1985 samples initiated in July 1985. Germination continued through December of the respective years. This allowed seeds from each collection to be subjected to approximately the same regimes of photoperiod, temperature and moisture for germination.

Soil was sieved through a 4-mm mesh and subsamples (58% by volume) were placed in greenhouse flats divided by glass plates into six 7.5 × 21.5-cm sections. Samples were spread 1-cm deep over a 2-cm deep layer of vermiculite covered by filter paper. A sterile control medium was placed in one section of each flat to monitor extraneous seed contamination. Flats were subirrigated by placing them in trays of distilled water and were periodically fertilized with a 15:30:15 ratio of N:P:K plus trace elements. Four flats were used for each treatment replication, with soil samples and flats arranged in a randomized block design. Emerged seedlings, an estimate of germinable buried seeds, were counted weekly from 24 July through 31 December and removed once identified.

Analysis of variance was used to identify significant differences ($P \leq 0.01$) in foliar cover and seed density among grazing treatments and sample periods, and differences by life history or taxonomic groups (*e.g.*, longevity, dicots and monocots). Seed bank data were transformed [$\ln(x + 1)$] prior to analysis to normalize group distributions. A Student-Newman-Keuls mean separation test was used to separate significant main effects.

Seed bank spatial patterns were analyzed using seed density variance–mean ratios, and significance determined with a chi-square test ($P \leq 0.01$) (Greig-Smith, 1983). Species richness was considered as the total number of seed bank taxa occurring within all soil cores for each grazing treatment. Sorensen's coefficient for presence-absence of species (Greig-Smith, 1983) was used to express similarity of seed banks among grazing treatments, and within grazing treatments to express similarities between seed bank and extant vegetation.

RESULTS

Extant vegetation.—Forty-eight genera including 53 species appeared in the samples (Table 1). For all seasons and replicates, 30, 33 and 44 species were observed within the HC, MDR and EXC treatments, respectively. Of these, 16 species (30%) were perennial monocots, except the annual monocot *Cyperus aristatus. Hilaria belangeri, Aristida wrightii* and *Erioneuron pilosum* were present in all three treatments. Late-successional species (*e.g.*, *Eriochloa sericea*) (Smeins and Merrill, 1988) were limited to the EXC treatment. Total cover across all treatments was dominated by perennial grass species (*e.g.*, *Hilaria belangeri, Aristida wrightii* and *Eriochloa sericea*). Lowest foliar cover occurred in the HC treatment in July 1985, following 2 yr of drought conditions, with growing season precipitation 41% of mean. Cover was highest in the same treatment in September 1986, following favorable growing conditions with growing season precipitation 115% of mean. No significant grazing treatment effect on total cover or life history groups was found within a sample period, although dicots contributed relatively more foliar cover during drought periods and monocots contributed a greater proportion during non-drought periods.

Seed bank density and spatial pattern.—Total seed density ranged from 2252 seeds/m^2 in the HC treatment spring sample to 4409 seeds/m^2 in the EXC summer sample, with a mean density of 3749/m^2 for all samples (Table 2). Seed densities differed seasonally, but not among grazing treatments. No density differences for life history or taxonomic groups (annual, perennial, monocot and dicot) were observed among treatments, although densities of perennials and dicots were significantly lower in spring than in summer. Densities for seeds of individual species had similar proportional relationships between seasons, regardless of grazing intensity. Examples of similar seasonal proportions were found for *Valerianella stenocarpa* in which July densities were always higher than those for March, and for

TABLE 1.—Percent foliar cover (±1 SE) of selected species for two sample periods for sites subjected to three long-term grazing treatments

Species	Longevity/ Season[a]	Heavy continuous		Moderate deferred rotation		Exclosure	
		July 1985	Sept 1986	July 1985	Sept 1986	July 1985	Sept 1986
			Monocots				
Hilaria belangeri	P/W	15.9 (2.2)	75.2 (3.6)	29.9 (3.5)	78.5 (2.5)	8.1 (2.4)	31.6 (4.5)
Aristida wrightii	P/W	1.0 (0.6)	2.3 (1.4)	2.7 (1.0)	1.6 (0.5)	12.1 (4.3)	9.5 (2.7)
Erioneuron pilosum	P/W	2.5 (0.9)	0.2	0.4 (0.4)	0.5	0.4 (0.4)	0.2
Panicum hallii	P/W	0.4 (0.4)	4.4 (2.1)	1.0 (0.5)	0.2 (0.1)	2.2 (0.9)	1.3 (0.5)
Stipa leucotricha	P/C	—	0.1	2.3 (1.2)	—	0.8 (0.7)	1.0
Eriochloa sericea	P/W	—	—	—	—	3.4 (1.1)	24.3 (4.1)
Tridens muticus	P/W	—	—	—	—	0.5 (0.4)	6.8 (2.4)
Other monocots[b]		0.0	0.4	0.8	2.6	0.9	8.8
Total monocots		19.8 (2.4)	82.6 (3.4)	37.1 (3.4)	83.4 (2.2)	28.4 (4.9)	83.5 (3.9)
			Dicots				
Hymenoxys odorata	A/W	11.8 (3.9)	0.3 (0.04)	6.5 (1.6)	—	2.1 (1.1)	—
Verbena neomexicana	P/W	6.9 (1.8)	0.3 (0.2)	2.0 (0.5)	0.1 (0.04)	0.9 (0.4)	0.1 (0.1)
Sida procumbens	P/W	5.4 (2.1)	5.1 (0.9)	—	0.3 (0.2)	0.2 (0.2)	1.7 (0.7)
Croton monanthogynus	A/W	0.5	0.7	3.0	0.8	4.0	0.7
Argythamnia humilis	P/W	0.2	0.1	0.8	1.4	1.6	0.1
Euphorbia sp.	A/W	0.1	0.1	0.1	0.2	0.6	—

TABLE 1.—Continued

Species	Longevity/ Season[a]	Heavy continuous		Moderate deferred rotation		Exclosure	
		July 1985	Sept 1986	July 1985	Sept 1986	July 1985	Sept 1986
Aphanostephus ramossissimus	A/W	0.5 (0.2)	—	11.5 (1.6)	—	1.3 (0.9)	—
Hedeoma drummondii	P/W	0.7	—	0.9	—	0.1	—
Scutellaria drummondii	P/C	0.8	—	0.7	—	—	—
Oxalis amplifolia	P/W	—	2.8	—	0.9	—	0.2
Lesquerella gordoni	A/C	—	0.3	—	0.3	—	0.5
Plantago rhodosperma	A/C	—	0.2	—	0.2	—	0.4
Physalis lobata	P/W	—	0.1	0.1	—	—	—
Ratibida columnaris	P/W	—	—	5.5 (2.3)	—	17.9 (5.5)	0.03 (0.02)
Zexmenia hispida	P/W	—	—	—	—	0.1	1.5
Other dicots[b]		0.0	2.2	3.5	2.7	7.8	3.9
Total dicots		26.9 (5.1)	12.2 (1.7)	34.6 (3.2)	6.9 (2.0)	36.6 (7.0)	9.1 (1.7)
Total cover		46.7 (4.2)	94.8 (2.9)	71.7 (3.6)	90.3 (2.0)	65.0 (6.3)	92.6 (4.0)

[a] Longevity: P = perennial, A = annual; Season: W = warm season, C = cool season
[b] Pooled values of infrequently occurring species

TABLE 2.—Total germinable soil seed density per m^2 (±1 SE) in the surface 5 cm of soil for selected species for two sample periods for sites subjected to three long-term grazing treatments

Species	Longevity/ Season[a]	Heavy continuous		Moderate deferred rotation		Exclosure	
		July 1984	March 1985	July 1984	March 1985	July 1984	March 1985
				Monocots			
Hilaria belangeri	P/W	254 (54.0)	10 (9.4)	132 (34.0)	113 (95.6)	38 (25.8)	—
Cyperus aristatus	A/W	330 (106.0)	38 (22.6)	—	19 (19.0)	462 (198.0)	104 (46.0)
Stipa leucotricha	P/C	—	—	75 (36.0)	19 (19.0)	19 (13.2)	9 (9.0)
Panicum hallii	P/W	—	—	47 (30.0)	9 (9.0)	75 (34.0)	—
Aristida wrightii	P/W	—	—	10 (9.4)	10 (9.4)	160 (58.0)	19 (19.0)
Sisyrinchium angustifolium	P/C	9 (9.0)	—	—	—	122 (42.0)	57 (25.0)
Erioneuron pilosum	P/W	—	—	—	—	28 (20.8)	9 (9.4)
Other monocots[b]		0	47	9	66	65	47
Total monocots		593 (114.0)	95 (32.0)	273 (57.2)	236 (101.6)	969 (234.0)	245 (73.3)
				Dicots			
Valerianella stenocarpa	A/C	924 (168.0)	594 (109.5)	1846 (299.2)	1583 (366.0)	1912 (448.0)	1028 (210.0)
Verbena neomexicana	P/W	508 (107.6)	57 (21.6)	490 (154.0)	38 (22.6)	75 (27.6)	48 (20.0)
Evax multicaulis	A/C	311 (110.0)	339 (72.0)	490 (120.8)	414 (99.9)	28 (20.8)	38 (18.2)
Euphorbia sp.	A/W	142 (34.0)	330 (60.0)	19 (13.2)	48 (24.0)	57 (25.4)	104 (38.0)
Hymenoxys odorata	A/W	151 (40.0)	28 (15.8)	48 (20.5)	10 (9.4)	28 (20.8)	9 (9.0)

TABLE 2.—Continued

Species	Longevity/ Season[a]	Heavy continuous		Moderate deferred rotation		Exclosure	
		July 1984	March 1985	July 1984	March 1985	July 1984	March 1985
Aphanostephus riddellii	P/W	28 (15.8)	132 (44.0)	160 (78.0)	565 (88.4)	330 (78.0)	443 (78.0)
Sida procumbens	P/W	66 (26.6)	38 (22.6)	48 (20.0)	28 (15.8)	—	47 (24.0)
Hedeoma drummondii	P/W	28 (15.8)	10 (9.4)	47 (20.0)	48 (19.9)	48 (20.3)	28 (15.8)
Scutellaria drummondii	P/C	57 (22.0)	28 (20.8)	9 (9.0)	9 (9.0)	9 (9.0)	9 (9.0)
Plantago rhodosperma	A/C	47 (24.0)	—	114 (60.6)	28 (20.8)	104 (35.6)	19 (13.2)
Physalis lobata	P/W	10 (9.4)	—	499 (100.0)	—	170 (76.0)	28 (20.8)
Draba cuneifolia	A/C	—	123 (50.0)	85 (31.6)	94 (38.0)	264 (66.8)	132 (9.4)
Stellaria prostrata	A/C	—	56 (25.4)	56 (39.4)	19 (19.0)	47 (24.0)	20 (19.0)
Lesquerella gordoni	A/C	—	141 (48.0)	—	9 (9.0)	—	47 (20.0)
Mecardonia vandellioides	P/W	970 (260.0)	28 (20.0)	—	—	—	—
Sedum nuttallianum	A/C	9 (9.0)	19 (19.0)	84 (46.0)	—	—	—
Dalea lasiathera	P/W	10 (9.4)	10 (9.4)	28 (20.8)	—	—	—
Daucus carota	P/W	—	—	19 (18.8)	9 (9.0)	28 (15.8)	160 (72.0)
Croton monanthogynus	A/W	—	—	75 (36.0)	—	56 (34.6)	9 (9.2)
Chaetopappa bellioides	P/W	—	—	—	94 (35.0)	—	141 (46.0)
Other dicots[b]		27	224	19	885	142	1016
Total dicots		3288 (342.4)	2157 (235.6)	4136 (397.2)	3881 (352.0)	3298 (541.4)	3326 (306.4)
Total		3881 (374.4)	2252 (328.5)	4409 (390.4)	4117 (372.8)	4267 (562.5)	3571 (305.2)

[a] Longevity: P = perennial, A = annual; Season: W = warm season, C = cool season
[b] Pooled value of infrequently occurring species

Aphanostephus riddellii in which March densities were always highest, in all grazing treatments.

Variance–mean ratios for total seed density ranged from 49.4 to 148.3 which indicated a highly aggregated distribution of seeds in the soil. Individual species' variance–mean ratios ranged from 16 to 65, all significantly aggregated.

Seed bank composition and richness.—Thirty-nine genera, including a minimum of 42 species, were identified (Table 2). Sixteen species were present in all treatments, 14 occurred in two of three treatments,while nine occurred within only one treatment. Some species such as *Chaetopappa bellioides,* which was present only in spring, were present in only one of the two seasons sampled. Similarity of floristic composition between grazing treatments for July and March sample dates, respectively, were: HC-MDR, 70 and 64%; MDR-EXC, 78 and 76%; and HC-EXC, 60 and 58%.

Seeds of 29, 28 and 32 species were observed within the HC, MDR and EXC treatments, respectively (both seasons pooled). Based on species present, the EXC seed bank possessed a higher perennial–annual monocot ratio (4:1) than did the MDR (2.5:1) and HC (1:1). Perennial–annual dicot ratios were EXC (1.9:1), MDR (1.3:1) and HC (1.1:1). The overall dicot–monocot ratio was 2.4:1, 3:1 and 6.3:1 for the EXC, MDR and HC treatments, respectively. The EXC treatment had a high proportion of perennial monocot species whereas the HC had a high proportion of annual dicots. MDR ratios were intermediate.

Similarity between vegetation and seed bank.—Several species, including *Aphanostephus riddellii, Valerianella stenocarpa* and *Mecardonia vandellioides,* were abundant in the seed bank but not observed in the vegetation (Tables 1 and 2). Conversely, species such as *Eriochloa sericea* and *Tridens muticus* were prominent in the EXC vegetation, yet not detected as seeds. When species presence in the seed bank was compared with that of the extant vegetation, similarities for all combinations fell between 32 and 51%.

DISCUSSION

Total density of buried germinable seeds was within reported values for North American grasslands (Lippert and Hopkins, 1950; Rabinowitz, 1981; Iverson and Wali, 1982; Coffin and Lauenroth, 1989). These values underestimate the actual number of viable seeds in the soil because no single procedure can maximize germination for all species. In addition, the sample periods may not account for all transient species, that is, those which germinate within a year of dispersal (Thompson and Grime, 1979). The purpose of two sample dates, however, was to collect soil seeds at different periods to allow dormancy breaking conditions to occur in the field, and to sample transient (those seeds which germinate within a year of dispersal) and persistent (those seeds which remain viable in the soil until a second or later germination season) components of the seed bank. Further, timing of germination trials corresponded with probable periods of natural germination (summer through winter) in the field. Therefore, these results provide a reasonable estimate of readily germinable seeds, seedlings of which would be expected to enter successional processes.

The proportions of persistent and transient seeds within a seed bank can have important implications for succession. Grime (1981) hypothesized that species with certain kinds of persistent seed banks have the potential to rapidly expand populations into disturbed habitats, yet maintain a persistent seed bank when conditions are not immediately favorable for germination.

To determine which species have a persistent seed bank, seeds should be present in samples collected after germination but before dispersal of the next seed crop. The July and March sample periods permitted assessment of species with persistent seeds based on species-specific seed dispersal and germination times. However, the mild climate of the region and irregular occurrence of precipitation favor species with rapid seed production and germination, making assessment of production and germination timing difficult.

Time of seed production and germination with respect to seasonal seed densities can provide insights to seed persistence. Most species with seeds represented in the seed bank were present in each sampling period and appear to have persistent seeds. Late-successional grasses from EXC treatments (*e.g., Eriochloa sericea*) produced seed which was dispersed in a seed rain (Kinucan, 1987), but not detected in the seed bank, indicative of transient species. Many grassland species appear to germinate once moisture conditions are favorable, and do not form persistent seed banks (Roberts, 1981). This seems particularly true for late-successional grasses in the study sites. The seeds probably germinated soon after dispersal, or were lost to predation and pathogens (Fenner, 1985) and may in part account for the seasonal (summer and spring) difference in total seed density.

The aggregated distribution of seeds of each species was indicative of species-specific seed dispersal patterns (Harper, 1977) interacting with the heterogeneity of small topographical features (Reichman, 1984) of the sites. Aggregation of seed could be an important factor in succession, if vegetation disturbance patches are of a scale smaller than patches of seed. This would contribute to spatial clumping of species germinating on disturbed areas.

The nonsignificant grazing effect on total seed bank density contrasted with results from other studies in which total seed density increased with intensification of grazing and other disturbances (Lippert and Hopkins, 1950; Major and Pyott, 1966; Thompson, 1978; Thompson and Grime, 1979; Iverson and Wali, 1982). The absence of a grazing effect may have been a function of the proportion of persistent and transient seeds and time of sampling. Although absolute density of seeds can be important successionally, the composition of the seed bank may be more critical by dictating which species are present to interact in successional processes. Grazing treatment clearly influenced composition of the seed bank. Species richness among treatments was comparable, but floristic similarity among treatments was low. The HC treatment was dominated by early-seral annual dicot taxa, and the EXC treatment was dominated by mid- and late-seral perennial monocot taxa, while the MDR treatment was intermediate in composition. Studies in other grasslands have demonstrated that weedy dicot taxa were more prevalent in seed banks of heavily grazed than ungrazed sites (Major and Pyott, 1966; Iverson and Wali, 1982).

Heavy livestock grazing alters composition and structure of plant communities (Ellison, 1960; Austin *et al.*, 1981; Walker and Noy-Meir, 1982; Foran, 1986); and because propagule input is strongly associated with the nearby biotic assemblage (Harper, 1977; Cook, 1980; Bazzaz, 1983; Fenner, 1985), it is also reasonable to expect grazing disturbance to alter the seed bank. Because of the dominance of annual dicots in the HC, and to a lesser extent MDR treatments, early-seral communities on the grazed sites would be largely composed of these species. Early-seral communities in the ungrazed sites appear less likely to be dominated by annual dicots.

Seed bank input is strongly influenced by surrounding communities, but the relative abundance of existing vegetation and the soil seed bank are often poorly related (Major and Pyott, 1966; Thompson and Grime, 1979; Rabinowitz, 1981; Abrams, 1988), as was the case in this study (32–51% similarity between extant vegetation and seed bank). The weak relationship may reflect differences in seed production, dormancy and survival among species in the community (Roberts, 1981) and relative allocation to seed output by annuals and perennials. Species with abundant seed banks such as *Mecardonia vandellioides, Cyperus aristatus, Aphanostephus riddellii* and *Valerianella stenocarpa* were sparse or not present in the extant vegetation. These species have relatively small seeds which may be easily transported long distances by water and deposited on a site. They also have persistent seeds which may only germinate when environmental conditions are suitable. Species that possess this type of life history strategy may strongly influence community composition following disturbance. In contrast, species predominant in the vegetation (*e.g., Aphanostephus ramossissimus* and *Chaetopappa bellidifolia*) were poorly represented in the seed bank. *Hilaria belangeri* was common in the vegetation and relatively abundant in the seed bank which, with other life history traits, permit it to recover after disturbance and persist in areas subjected to intensive livestock grazing (Smeins and Merrill, 1988).

Egler (1954) hypothesized that individuals on a site, represented in large part by a seed bank, are likely to dominate that site after disturbance. On the sites studied, long-term grazing has altered vegetation and seed bank composition to that of an earlier successional flora. Many current seed bank floras are of early- and mid-seral species, and possess persistent seed. Late-successional midgrass seeds were not found in any treatment and if present are probably transient. Without a propagule source, succession within the grazed sites to a midgrass-dominated community would be slow or unlikely, particularly where few midgrasses exist in the current community and grazing restricts seed production. Within the exclosures, succession may also be slowed, depending on season of disturbance, because midgrass seeds are transient, and existing mid-successional species (*e.g., Hilaria belangeri*) are abundant and may inhibit establishment of other species (Kinucan, 1987; Smeins and Merrill, 1988).

Acknowledgments.—The authors gratefully acknowledge C. A. Taylor, Jr. and the staff of the Texas Agricultural Experiment Station at Sonora for their cooperation and support, and K. N. Gandhi at the TAMU Tracy Herbarium for assistance with plant identification. S. R. Archer, D. D. Briske, K. F. Kinucan, R. R. Hollander and several anonymous reviewers provided insightful comments at various stages in the preparation of the manuscript. Partial support for this study was provided by the TAMU Tom Slick Graduate Research Fellowship Committee and the Texas Agricultural Experiment Station.

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SUBMITTED 2 JANUARY 1991 ACCEPTED 5 MARCH 1992