Woody plant seed dispersal and gap formation in a North American subtropical savanna woodland: the role of domestic herbivores

J. R. Brown[1] & Steve Archer

Department of Range Science, Texas A&M University, College Station, TX 77843-2126, USA
[1]*Present address: Soil Conservation Service, 625 Merchant, Emporia, KS 66801, USA*

Abstract

The relationship between domestic cattle and vegetation change in a savanna woodland was evaluated with respect to dung deposition and the dispersal and establishment of mesquite (*Prosopis glandulosa* var. *glandulosa*, Mimosaceae), a cosmopolitan woody invader of grasslands in the southwestern USA. Dung deposited in autumn disintegrated rapidly, leaving patches of bare ground ranging from 50 to 900 cm^2. Herbaceous cover on gaps created by dung deposition recovered to levels comparable to neighboring vegetation by the end of the following growing season. Vegetation colonizing gaps consisted primarily of grasses not found in the surrounding vegetation. Dung deposition increased species diversity and spatial heterogeneity of the herbaceous vegetation and contributed to the development of a fine-grain mosaic of small patches of varying successional age-states.

The role of cattle in facilitating the ingress and establishment of mesquite has broader implications with regard to the conversion of grasslands to woodlands. On the site with cattle, mesquite seedlings were found in 75% of dung pats surveyed in September (mean = 4.2 seedlings per pat; maximum = 50). Although seedling survival in dung (79%) was only 16% greater than that of mesquite emerging from seeds experimentally sown away from dung, no seedlings were found on areas without cattle. Mean ($\pm$ SE) density of mesquite seedlings ranged from 12 ± 2 to 15 ± 2 m^{-2} on the site with cattle. Seed densities away from parent plants averaged 10.7 m^{-2} and 0.0 m^{-2} on areas with and without cattle, respectively. Seed densities beneath adult plants were comparable between sites.

The high density of seedlings on areas with cattle, in contrast to absence of seedlings on the area without cattle, suggests rates of invasion of grasslands by mesquite would have increased substantially in North America following the settlement and introduction of domestic ungulates. Prior to the introduction of livestock, poor seed dissemination and germination may have limited its Holocene spread.

Nomenclature follows Correll & Johnston, 1979.

Introduction

Increased abundance of mesquite (*Prosopis glandulosa* var. *glandulosa* Torr., Mimosaceae) and other woody plants in grasslands of the southwestern United States in the past century appears to have been coincident with the introduction of domestic livestock (Buffinton & Herbel 1965; Blackburn &

Tueller 1970; Herbel *et al.* 1972; Madany & West 1983). Climatic change, overgrazing and reductions in fire frequency and intensity have been cited as reasons for the increased abundance of mesquite in many areas (Hastings & Turner 1965). Implicit in such arguments are the assumptions that (1) native fauna were effectively disseminating viable seeds of this arborescent legume into grasslands; but (2) establishment was low because of interference from herbaceous vegetation; and (3) grazing by introduced livestock alleviated constraints on establishment. In this paper we explore an alternative hypothesis: low densities of mesquite in southwestern grasslands prior to the introduction of livestock resulted from limited dispersal rather than constraints on establishment. Livestock subsequently facilitated the ingress and establishment of mesquite into grasslands by serving as a new and effective agent of seed dispersal.

The relative effectiveness of a given agent of seed dispersal is difficult to evaluate, since there is no necessary correlation between numbers of seeds distributed by a particular agent and the value of that form of dispersal (Davidson & Morton 1984). Dissemination of mesquite has been observed for a wide array of native herbivores, including rodents, coyotes (*Canis* spp.), peccary (*Dicotyles* spp.) and numerous ungulates (Bogusch 1952). Large numbers of mesquite and *Acacia* spp. seedlings have been observed in cattle, sheep and horse dung in North America (Glendening & Paulsen 1950; Paulsen 1950), South America (Guitierrez & Armesto 1981), Australia (Harvey 1981) and Africa (Lamprey *et al.* 1974). However, little is known of the relationship between seed dissemination and subsequent seedling establishment.

Mesquite pods are palatable and domestic livestock (cattle, sheep, horses) have been observed to consume them in large quantities (Mooney *et al.* 1977). Relative to rodents, a high percentage of seeds in pods consumed by ungulates escape mastication and are scarified in the digestive tract, improving their germinability two to threefold (Glendening & Paulsen 1950; Haas *et al.* 1973). Many seeds thus consumed would be transported away from parent plants harboring host-specific seed predators (e.g. Webb & Wilson 1985) and deposited in dung, a

moist, nutrient rich microhabitat that may facilitate germination and seedling establishment. Given their widespread distribution, large numbers and high concentrations, domestic livestock could constitute a potentially effective vector of mesquite dispersal absent from North America until the late Holocene.

To address the role of cattle in mesquite dispersal and establishment, areas with and without cattle were surveyed for seeds and seedlings. Seedlings encountered were marked and their survival followed for one year. Over the same period, mesquite seedling establishment and herbaceous vegetation change on microsites with and without dung was also quantified.

Study site

Contiguous areas with similar densities of adult mesquite plants were monitored during 1984 and 1985 at the Texas Agricultural Experiment Station, La Copita Research Area in Jim Wells County near Alice, Texas (27°40′N; 98°12′W) in the eastern Rio Grande Plains of the Tamaulipan Biotic Province. The study site was a savanna woodland with discrete clusters of woody plants organized beneath mesquite. The site had been grazed by cattle since the late 1800's and woody plant cover has increased 23% since 1941, the result of mesquite invasion (Archer *et al.* 1988). Herbaceous vegetation between shrub clumps was dominated by C4 grasses such as *Paspalum setaceum, Setaria geniculata, Bouteloua rigidiseta* and *Chloris cucullata.*

Climate is subtropical with warm winters and hot summers. Mean annual rainfall is 68 cm with maxima in May and September. Mean annual temperature is 22.4°C with a growing season of 289 days. Soils on the study site are upland Runge fine sandy loams derived from sandstones. Elevation ranged from 75 to 90 m.

Materials and methods

The influence of cattle dung on herbaceous vegetation and its role in mesquite seedling emergence and establishment was quantified by permanently mark-

ing 40 randomly selected fresh dung pats in September 1984. Mesquite trees were producing pods at this time and cattle had been observed consuming them. Emergence and growth of mesquite seedlings and changes in herbaceous cover by species on each dung pat were quantified using a gridded frame (0.25 × 0.25 m) placed over a permanent stake. Color-coded wire loops were used to identify each cohort of mesquite seedlings emerging since the last inventory. Emergence on sites not subject to dung deposition was monitored on permanent 0.25 m² plots paired with the dung plots. Survival of mesquite seedlings emerging from dung was compared to that of 180 scarified seeds placed on the soil surface of nearby, non-dunged sites. Emergence of the sown seeds was coincided with emergence of the first cohort of seedlings from dung. Species composition on dung-free sites was determined by estimating aerial cover in 60, 0.25 m² plots located at 5 m intervals along 4 transects.

The extent to which cattle disseminated seeds of mesquite was quantified by comparing seed bank and seedling densities in contiguous areas with and without cattle. A four strand barbed wire fence 1.3 m in height was constructed in April 1984 within a large pasture to deny cattle access to a subset of the area. Thirty-six cattle roamed freely on the other portion of the pasture. We assumed the abundance of rodents, lagomorphs, whitetail deer (*Odocoileus virginianus*) and predators was comparable in and out of the exclosure.

On each area, 30 permanent plots (0.25 m²) were placed at 2 m intervals along each of two 90 m transects. The proportion of samples beneath mesquite tree canopies was comparable in each area (7.5% on area with cattle; 9.2% on area without cattle). Herbaceous species composition and standing crop, estimated by clipping twenty 0.25 m² plots in each site, were similar (229 ± 29 versus 242 ± 38 g·m⁻² on areas with and without cattle, respectively). Seedlings encountered in plots were marked with colored wire loops to aid in relocation and identification of cohorts. Density of mesquite seeds in soils of each area was estimated by extracting 300 soil cores (5 cm diameter) to a depth of 5 cm at regular intervals along transects. Soils were dried, sieved and seeds obtained were tested for viability with tetrazolium (Grabe 1970).

Chi-square tests were used to determine if survival differed among cohorts. Analysis of variance was used to compare seed and seedling densities between grazed and protected areas and beneath mesquite trees versus interstitial areas. All statistical tests were conducted at $P < 0.05$. Foliar cover data of herbaceous plant species on dunged microsites and adjacent non-dunged sites were ordinated with detrended correspondence analysis (DCA, Hill 1979) after an octave transformation.

Results

Gap phase succession

Dung deposited in September disintegrated rapidly and left patches of bare ground that began to revegetate the following spring. Areas bared by dung ranged from 50 to 900 cm² in size (mean ± SE = 229 ± 29 cm²). Herbaceous cover on microsites impacted by dung recovered to·levels comparable to that of adjacent non-dunged spots within one year (Fig. 1a), but species composition was altered (Ta-
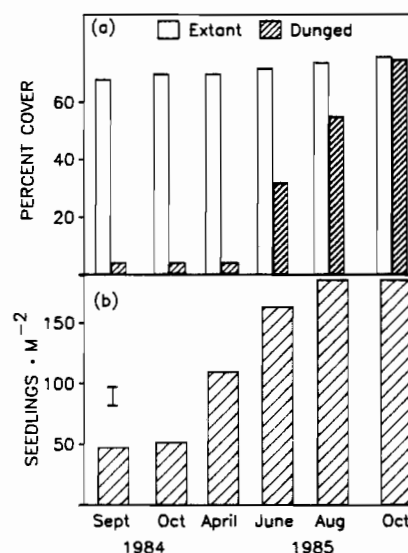

Fig. 1. *(a)* Herbaceous foliar cover (absolute, %) of dung-free extant vegetation (*n* = 60; clear bars) versus that on sites impacted by dung (*n* = 40; shaded bars) on a savanna woodland site and *(b)* mean cumulative seedling density of *Prosopis* on dunged microsites. Vertical line represents mean SE (*n* = 40). Mesquite seedlings were only encountered in dung. (See Table 1 for composition and Table 2 for seedling emergence and survival.)

Table 1. Species composition and dominance on dunged (n = 40) and non-dunged (n = 60) patches in August, 1985. Dung was deposited in September 1984, creating unvegetated gaps through April, 1985 (see Fig. 1).

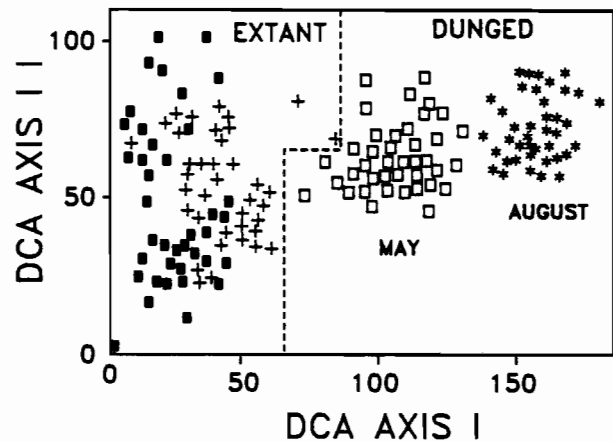| Category	Cover (%)		Frequency (%)	
	Dunged	Non-Dunged	Dunged	Non-Dunged
Grasses				
Dicanthelium				
oligosanthes	27 ± 3	0 ± 0	100	0
Cenchrus				
incertus	18 ± 2	18 ± 1	95	90
Paspalum				
setaceum	17 ± 2	0 ± 0	90	0
Aristida				
longespica	0 ± 0	14 ± 2	0	90
Bouteloua				
hirsuta	0 ± 0	14 ± 1	0	97
Leptoloma				
cognatum	0 ± 0	5 ± 1	0	45
Setaria				
geniculata	0 ± 0	6 ± 1	0	70
Other				
grasses	6 ± 1	8 ± 1	–	–
Forbs	7 ± 1	8 ± 1	80	97
Bare ground	24 ± 2	26 ± 1	100	100

Fig. 2. Distribution of vegetation samples from dunged (*n* = 40) and non-dunged (*n* = 60) plots within the plane defined by the first two axes of detrended correspondence analysis. Dung had been deposited in September. Samples were ordinated using percent foliar cover by species on permanent plots read the following May (+ = extant; □ = dunged) and August (■ = extant; * = dunged).

ble 1). Perennial grasses such as *Bouteloua hirsuta, Setaria geniculata,* and *Aristida longespica* that dominated the study site in areas free of dung were absent from spots impacted by dung. In contrast, dunged spots were dominated by weak perennials such as *Dicanthelium oligosanthes* and *Paspalum setaceum* not encountered in the surrounding vegetation. Axis I of the DCA ordination produced a temporal gradient reflecting the compositional changes caused by deposition of dung (Fig. 2). During the season following dung deposition, samples from the extant vegetation formed a distinct cluster exhibiting some seasonal fluctuation between May and August. In contrast, vegetation on dunged microsites demonstrated rapid divergence from non-dunged sites.

Mesquite dispersal and establishment

Mesquite seedlings emerged from 75% of the dung pats. The mean (± SE) number of seedlings per pat

was 4.2 ± 1.4 (maximum = 50). Most seedlings emerged during fall 1984 and spring 1985, coincident with the bimodal precipitation pattern (Fig. 1b). No additional recruitment was noted after June 1985. No mesquite seedlings emerged in permanent plots located in the vicinity of dung pats. Mortality of seedlings was low, regardless of date of emergence and did not differ significantly among cohorts (Table 2).

Table 2. Recruitment (count) and survival (%) of *Prosopis* seedlings emerging on 40 cattle dung pats on a savanna woodland in 1984 – 1985. Survival of seedlings emerging from scarified seeds sown on non-dunged sites in October 1984 was 63% at the end of the observation period. No seedlings were observed in 40 permanent plots located in the vicinity of dung pats.

Cohort	Date						%
	1984		1985				
	Oct	Nov	Apr	June	Aug	Oct	Survival
I	52	49	47	43	41	41	79
II	–	–	58	52	50	50	86
III	–	–	–	53	50	50	94
IV	–	–	–	–	22	21	95
Total	52	49	105	148	163	162	–

When seedling survival was regressed against size of gap created by dung, no significant correlation was observed ($R^2 = 0.27$; $P = 0.49$). Subsequent increases in herbaceous ground cover in gaps (Fig. 1a) had little effect on survival of later cohorts. Over 52% of the scarified mesquite seeds sown in non-dung plots in 1984 emerged. At the end of 1985, survivorship was 63% for these seedlings, significantly (16%) lower than that of the first cohort of seedlings which emerged from dung at the same time (Table 2).

Surveys of areas with and without cattle indicated the importance of livestock in dispersal of mesquite. Mesquite seedlings were absent from the area without cattle but numbered as high as 40 m^{-2} on the area with cattle (Table 3). As with seedlings in dung pats, mortality was low (Table 4) and not significantly different among cohorts. On the area with cattle, seedling densities were comparable beneath and away from adult plants even though seed densities were three times higher beneath adult mesquite plants. Mesquite seed densities were comparable beneath adult plants whether livestock were present or not (Table 3). However, no seeds were found away from adult plants on the area protected from grazing, while seed density on the area with cattle averaged 10.7 m^{-2}. Over 90% of the seeds collected from both sites tested positive with tetrazolium.

Table 3. Mean ($\pm$ SE) mesquite seed and seedling density and frequency in areas with and without cattle on a fine sandy loam site in a Texas savanna woodland in August 1985. Canopy refers to seeds and seedlings encountered beneath adult mesquite plants; open refers to occurrences in interstitial zones.

| | With cattle | | Without cattle | |
	Canopy	Open	Canopy	Open
Area sampled (%)	8	92	9	91
Seedlings m^{-2}	12 ± 2a*	15 ± 2a	0 ± 0b	0 ± 0b
Seeds m^{-2}	33 ± 7a	11 ± 2b	33 ± 8a	0± 0c
Seed Frequency (%)	60a	20b	50a	0c
Seedling Frequency (%)	70a	85b	0c	0c

* Means or percentages within row followed by different letters differed significantly at p < 0.05.

Table 4. Number of *Prosopis* seedlings (count) and survival (%) in areas with cattle on four dates in 1984 – 1985. Data are from 60 permanent plots regularly distributed along transects through each area. No seedlings were encountered along transects in the area without cattle.

| | Date | | | | |
| | *1984* | *1985* | | | |
Cohort	Oct	Apr	Jul	Sept	Survival
I	187	182	180	175	94
II	–	9	7	7	78
III	–	–	46	40	87
Total	187	191	233	222	–

Discussion

Gap phase succession

Species composition on microsites experiencing dung deposition will depend on the degree of vegetative regeneration among remaining or nearby plants and the expression of seeds in soil and dung (Welch 1985). Herbaceous cover in gaps created by dung quickly recovered to pre-disturbance levels (Fig. 1a). However, composition shifted to an assemblage of more opportunistic species (Table 1). Artificially created gaps in North Carolina grasslands (Fowler 1981) and disturbances associated with gopher and badger mounds (Platt 1975; Hobbs & Hobbs 1987) and buffalo wallows (Collins & Barber 1985) responded in a manner similar to our dung-generated gaps. The altered species composition on dunged microsites (Fig. 2) persisted after dung had decomposed and contributed to the species diversity and spatial heterogeneity of the herbaceous vegetation.

Cattle may defecate as many as 14 times in a 24-h period (Weeda 1967). Thus, substantial portions of landscapes can be impacted by dung, depending upon the number of animals and their temporal and spatial patterns of movement (Senft *et al.* 1980; Welch 1985). In contrast to larger-scale, infrequent disturbances characterizing grasslands and savannas (e.g. drought, fire) frequent, small-scale perturba-

tions associated with dung deposition would contribute to the development of fine-textured mosaics of varying successional age-states. On a large scale abiotic factors (e.g. climate) may dictate vegetation dynamics in arid and semi-arid systems (MacMahon 1980). However, grasslands are patchy (Belsky 1983) and broad-scale climatic factors cannot account for the existence of small-scale patterns. Thus, as spatial and temporal frames of observation are diminished and resolution increased, biotic processes assume greater importance (Prentice 1986). Ungulate contributions to patchiness include localized grazing (Bakker *et al.* 1983), altered competitive interactions resulting from the differential utilization of plants variously tolerant of grazing (Archer & Tieszen 1986) and dung deposition. Interpreting the structure of the herbaceous component of this subtropical savanna woodland is therefore contingent upon understanding the interactive role of multiple-scale disturbances (e.g. Loucks *et al.* 1985; Collins & Barber 1985).

Mesquite dispersal and establishment

While dung deposition influenced the structure of herbaceous vegetation, the role of cattle in facilitating the ingress and establishment of mesquite has broader implications with regard to the conversion of grasslands to woodlands. In this system, previous research had demonstrated that mesquite trees serve as recruitment foci for bird-disseminated seeds of numerous woody species (Archer *et al.* 1988). Thus, a knowledge of factors regulating its recruitment into grasslands is of central importance to understanding the large-scale, long-term vegetation dynamics.

Densities of viable seeds were comparable beneath adult mesquite plants on areas with and without cattle (Table 3). However, no seedlings were found on the site without cattle even though herbaceous composition and biomass were generally similar on both sites. If we assume that herbaceous competition, granivory and seedling predation were comparable in each area, the lack of seedlings beneath parent plants on the site without cattle (Table 3) would most likely reflect poor germination. It has been es-

tablished that germination of mesquite seeds is increased by a factor of 2 to 3 because of scarification during passage through ungulate digestive tracts (Glendening & Paulsen 1950; Mooney *et al.* 1977). In contrast, only 12% of mesquite seeds in fresh coyote (*Canis latrans*) scat germinated compared to 85% in a control group (Meinzer *et al.* 1975). On areas without cattle, other potential agents of scarification (small and large native herbivores, microbes, etc.) were apparently ineffective. Survival was >60% among seeds germinating away from dung (Table 2) and seeds were found away from adult plants only on the area with cattle. Together, these facts indicate the lack of seedlings away from parent plants on areas without cattle (Table 3) resulted from dispersal rather than establishment limitations.

We anticipated germination of mesquite seeds in dung would facilitate seedling establishment relative to germination in non-dunged sites. Emergence of most mesquite seedlings occurred while dung pats were intact and aboveground interference from herbaceous vegetation greatly reduced (Fig. 1 and Table 2). However, survival of seedlings emerging in dung was only 16% higher than that of seedlings emerging at the same time on vegetated, non-dunged microsites, a modest response to nutrient enrichment (Weeda 1967) and reduced competition associated with dung deposition. In addition, neither gap size nor subsequent development of herbaceous vegetation in gaps appeared to have any discernible effect on survival of mesquite, a large-seeded plant with high growth rates (Haas *et al*, 1973) (Fig. 1; Table 2). This contrasts other seedling establishment trials which have shown available area and gap size to be critical to emergence and survival (Schultz *et al.* 1955; Mithen *et al.* 1984).

Historical accounts indicate conversions of grassland to shrub- or woodlands were very recent in North America and coincided with the introduction of livestock (Bogusch 1952; Humphrey 1958; Inglis 1964). Other observations have indicated more specifically, that the spread of mesquite in recent history has been lateral, from drainage and riparian zones to upland prairies (Tharp 1926; Johnston 1963). It is generally assumed that herbaceous competition and fire kept mesquite densities low in grasslands

prior to the introduction of livestock. However, mesquite is capable of high levels of establishment in grass stands protected from grazing or receiving moderate defoliation (Smith & Schmutz 1975; Meyer & Bovey 1982) and mortality following extremely hot fires is less than 20% once seedlings reach two to three years of age (Wright *et al.* 1976). In addition, the plant is capable of establishing on a wide range of soil types having a variety of physical and chemical properties (Ueckert *et al.* 1979), moisture regimes (Scifres & Brock 1969) and light regimes (Scifres *et al.* 1973). The potential to symbiotically fix nitrogen (Shearer *et al.* 1983) would further enhance its ability to successfully invade new sites. Such observations suggest that the apparently low densities of mesquite in grasslands prior to settlement may have been a consequence of limited dispersal or germination rather than biotic or abiotic constraints on establishment.

Prosopis fruits are thought to have evolved with large native mammals of North and South America (Mooney *et al.* 1977) most of which became extinct at the end of the Pleistocene (Martin 1967). The loss of megafauna known to utilize mesquite [e.g. Shasta ground sloth (Long *et al.* 1974)] in the New World may have subsequently restricted the spread of this woody plant into grasslands until the introduction of domestic livestock. Relative to the native Holocene fauna known to disperse mesquite [e.g. rodents, deer, peccary, coyotes, etc. (Bogusch 1952; Reynolds 1954)] cattle were much more effective vectors of mesquite dispersal in our study, as evidenced by the absence of seedlings on areas without livestock (Table 3). It might be argued that native Holocene herbivores absent from our site may have played an important role in mesquite dispersal prior to the arrival of domestic livestock. We would counter that these may have been highly localized, transient and inconsistent vectors. For example, *Bison* were not abundant in southern Texas and other parts of the southwest and extensive periods of absence from the southern plains have been quantified (Dillehay 1974). Pronghorn (*Antilocapra americana*) utilization of mesquite in wooded habitats seems unlikely, given the strong behavioral preference of this animal for open areas. Deer (*Odocoileus* spp.) may have disseminated mesquite seeds within wooded zones but not into the plains. Thus, the hypothesis that lack of effective dispersal may have limited the Holocene spread of arborescent legumes such as *Prosopis* and *Acacia* into New World grasslands prior to the introduction of domestic livestock warrants further consideration. For natural resource managers seeking to curtail the invasion of mesquite into grasslands, strategies for reducing domestic livestock seed dispersal must be devised.

Acknowledgements

References

Archer, S., Scifres, C. J., Bassham, C. R. & Maggio, R. 1988. Autogenic succession in a subtropical savanna: rates, dynamics and processes in the conversion of a grassland to a thorn woodland. Ecol. Monogr. (In press).

Archer, S. & Tieszen, L. L. 1986. Plant response to defoliation: hierarchical considerations. In: Gudmundsson, O. (ed.), Grazing Research at Northern Latitudes, pp. 45 – 59. Plenum Publ. Corp, New York.

Bakker, J. P., de Leeuw, J. & van Wieren, S. E. 1983. Micropatterns in grassland vegetation sustained by sheep grazing. Vegetatio 55: 153 – 161.

Belsky, A. J. 1983. Small-scale pattern in grassland communities in the Serengeti National Park, Tanzania. Vegetatio 55: 141 – 155.

Blackburn, W. H. & Tueller, P. T. 1970. Pinyon and juniper invasion in black sagebrush communities in east-central Nevada. Ecology 51: 841 – 848.

Bogusch, E. R. 1952. Brush invasion in the Rio Grande Plains of Texas. Texas J. Sci. 4: 85 – 91.

Buffington, L. C. & Herbel, C. H. 1965. Vegetational changes on a semidesert grassland range from 1858 to 1963. Ecol. Monogr. 35: 139 – 164.

Collins, S. L. & Barber, S. C. 1985. Effects of disturbance on diversity in mixed-grass prairie. Vegetatio 64: 87 – 94.

Davidson, D. W. & Morton, S. R. 1984. Dispersal adaptations of some *Acacia* species in the Australian arid zone. Ecology 65: 1038 – 1051.

Dillehay, T. D. 1974. Late quaternary bison population changes on the Southern Plains. Plains Anthropol. 19: 180 – 196.

Fowler, N. 1981. Competition and coexistence in a North Carolina grassland. J. Ecol. 69: 843–854.

Glendening, G. E. & Paulsen, H. A. 1950. Recovery and viability of mesquite seeds fed to sheep receiving 2,4-D in drinking water. Bot. Gaz. 103: 486–491.

Grabe, D. F. (ed.) 1970. Tetrazolium testing handbook. Assoc. Official Seed Analysis Contribution 29.

Gutierrez, J. R. & Armesto, J. J. 1981. El rol del ganado en la dispersion de las semillas de *Acacia caven* (Leguminosae). Ciencia Invest. Agrar. 8: 3–8.

Haas, R. H., Meyer, R. E., Scifres, C. J. & Brock, J. H. 1973. Growth and development of mesquite. In: Scifres, C. J. *et al.* (eds), Mesquite: growth and development, management, economics, control, uses, pp. 10–19. Texas Agr. Exp. Sta. Res. Monogr. 1, College Station.

Harvey, G. J. 1981. Recovery and viability of prickly acacia (*Acacia nilotica* spp. *indica*) seed ingested by sheep and cattle. In: Proc. Sixth Austr. Weeds Conf., Vol. I, pp. 197–201.

Hasting, J. R. & Turner, R. M. 1965. The changing mile: an ecological study of vegetation change with time in the lower mile of an arid and semi-arid region. Univ. Arizona Press, Tucson.

Herbel, C. H., Ares, F. N. & Wright, R. A. 1972. Drought effects on a semidesert grassland range. Ecology 53: 1084–1093.

Hill, M. O. 1979. DECORANA: a Fortran program for detrended correspondence analysis and reciprocal averaging. Cornell Univ., Ithaca, NY. 47 pp.

Hobbs, R. J. & Hobbs, V. J. 1987. Gophers and grassland: a model of vegetation response to patchy soil disturbance. Vegetatio 69: 141–146.

Humphrey, R. R. 1958. The desert grasslands: a history of vegetational change and an analysis of causes. Bot. Rev. 24: 193–252.

Inglis, J. 1964. A history of vegetation on the Rio Grande Plains. Texas Parks and Wildlife Dep. Bull. 45, Austin, TX. 122 pp.

Johnston, M. C. 1963. Past and present grasslands of southern Texas and northeastern Mexico. Ecology 44: 456–466.

Lamprey, N. F., Halevy, G. & Makacha, S. 1974. Interactions between *Acacia*, burchid seed beetles, and large herbivores. E. Afr. Wildl. J. 12: 81–85.

Long, A., Hansen, R. M. & Martin, P. S. 1974. Extinction of the Shasta ground sloth. Geol. Soc. Am. Bull. 85: 1843–1848.

Loucks, O. L., Plumb-Mentjes, M. L. & Rogers, D. 1985. Gap processes and large-scale disturbances in sand prairies. In: Pickett, S. T. A. & White, P. S. (eds), The ecology of natural disturbance and patch dynamics, pp. 71–83. Academic Press, Inc. New York.

MacMahon, J. A. 1980. Ecosystems over time: succession and other types of change. In: Waring, R. (ed.), Forests: fresh perspectives from ecosystem analyses, pp. 27–58. Oregon State University Press, Corvallis.

Madany, M. H. & West, N. E. 1983. Livestock grazing-fire regime interactions within montane forests of Zion National Park, Utah. Ecology 64: 661–667.

Martin, P. S. 1967. Prehistoric overkill. In: Martin, P. S. & Wright, H. E. (eds), Pleistocene extinctions: the search for a cause, pp. 75–120. Yale Univ. Press, New Haven, Conn.

Meinzer, W. P., Ueckert, D. N. & Flinders, J. T. 1975. Food niche of coyotes in the Rolling Plains of Texas. J. Range Manage. 28: 22–27.

Meyer, R. E. & Bovey, R. W. 1982. Establishment of honey mesquite and huisache on a native pasture. J. Range Manage. 35: 548–550.

Mithen, R., Harper, J. L. & Weiner, J. 1984. Growth and mortality of individual plants as a function of available area. Oecologia 62: 57–60.

Mooney, H. A., Simpson, B. B. & Solbrig, O. T. 1977. Phenology, morphology, physiology. In: Simpson, B. B. (ed.), Mesquite: Its biology in two desert ecosystems, pp. 26–45. Dowden, Hutchinson and Ross, Inc., Stroudsberg, PA.

Paulsen, H. A. 1950. Mortality of velvet mesquite seedlings. J. Range Manage. 3: 281–286.

Platt, W. J. 1975. The colonization and formation of equilibrium plant species associations on badger disturbances in tall-grass prairie. Ecol. Monogr. 45: 385–405.

Prentice, I. C. 1986. Vegetation response to past climatic variations. Vegetatio 67: 131–141.

Reynolds, H. G. 1954. Some interrelations of the Merriam Kangaroo Rat to velvet mesquite. J. Range Manage. 7: 176–180.

Reynolds, H. G. & Glendening, G. E. 1949. Merriam Kangaroo Rat as a factor in mesquite propagation on southern Arizona rangelands. J. Range Manage. 2: 193–197.

Scifres, C. J. & Brock, J. H. 1969. Moisture-temperature interrelations in germination and early seedling development of mesquite. J. Range Manage. 22: 334–337.

Scifres, C. J., Kienart, C. R. & Elrod, D. J. 1973. Honey mesquite seedling growth and 2,4,5-T susceptibility as influenced by shading. J. Range Manage. 26: 58–60.

Schultz, A. M., Launchbaugh, J. L. & Biswell, H. H. 1955. Relationship between grass density and brush seedling survival. Ecology 36: 226–238.

Senft, R. L., Rittenhouse, L. R. & Woodmansee, R. G. 1980. Predicting patterns of cattle behavior on shortgrass prairie. Proc. Amer. Soc. Animal Science 31: 276–279.

Shearer, G., Kohl, D. H., Virginia, R. A., Bryan, B. A., Skeeters, J. L., Nilsen, E. T., Sharifi, M. R. & Rundel, P. W. 1983. Estimates of N_2-fixation from variations in the natural abundance of I5N in Sonora Desert ecosystems. Oecologia 56: 367–373.

Smith, D. A. & Schmutz, E. M. 1975. Vegetative changes on protected versus grazed desert grassland ranges in Arizona. J. Range Manage. 28: 453–457.

Tharp, B. C. 1926. Structure of Texas vegetation east of the 98th meridian. University of Texas Bulletin 2606.

Ueckert, D. N., Smith, L. L. & Allen, B. L. 1979. Emergence and survival of honey mesquite seedlings on several soils in west Texas. J. Range Manage. 32: 284–287.

Weeda, W. C. 1967. The effects of cattle dung patches on pasture growth, botanical composition, and pasture utilization. N.Z. J. Agr. Res. 10: 150–159.

Webb, S. L. & Wilson, M. F. 1985. Spatial heterogeneity in postdispersal predation on *Prunus* and *Uvularia* seeds. Oecologia 67: 150–153.

Welch, D. 1985. Studies in the grazing of heather moorland in northeast Scotland. IV. Seed dispersal and plant establishment in dung. J. Appl. Ecol. 22: 461–472.

Wright, H. A., Bunting, S. C. & Neuenschwander, L. F. 1976. Effect of fire on honey mesquite. J. Range Manage. 29: 467–471.