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# Woody plant invasion of grasslands: establishment of honey mesquite (*Prosopis glandulosa* var. *glandulosa*) on sites differing in herbaceous biomass and grazing history

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**Summary.** Emergence and survival of honey mesquite (*Prosopis glandulosa* var. *glandulosa* Torr.) seedlings was quantified on sites with contrasting grazing histories: long-term continuous grazing (LTG) and long-term protection (LTP) from grazing by cattle. On each site, different levels of herbaceous defoliation were imposed at monthly intervals (no defoliation = ND, moderate = MD and heavy = HD). The two weeks following seed dissemination appeared to be the most critical to *Prosopis* establishment on LTP-ND plots. Openings in the herbaceous layer created by moderate defoliation of grasses on the LTP site increased germination and/or survival 7- to 8-fold during this period. However, increasing the degree of defoliation from moderate to heavy did not stimulate additional emergence on either the LTP or LTG site. Emergence from scarified seed placed in cattle dung (17 to 30%) was lower than that of bare seed placements in various microhabitats (43–60%). However, deposition of scarified *Prosopis* seed in dung in conjunction with graminoid defoliation may be the most likely combination of events when livestock are present. Emergence from seeds transported into grasslands by other fauna likely would be low, unless seeds were deposited in areas where grasses had been defoliated. *Prosopis* survival was comparably high in dung and bare seed placements after one growing season. Survival of seedlings present two weeks after seed dissemination ranged from 74 to 97% at the end of the second growing season. Seedling survival and shoot development (biomass, leaf area and height) were similar on LTP and LTG sites, regardless of the level of herbaceous defoliation or seed placement. In addition, the magnitude and patterns of net photosynthesis, stomatal conductance and xylem water potential were comparable among one-year-old seedlings on ND, MD and HD plots, even though differences in herbaceous species composition and above- and below-ground biomass between these treatments were substantial. Such data suggest competition for soil resources between grasses and *Prosopis* may be minimal early in the life cycle of *Prosopis*. High rates of *Prosopis* emergence and establishment on LTP-MD plots are counter to the widespread assumption that long-term and/or heavy grazing is requisite for *Prosopis* encroachment into grasslands. Results are discussed with regard to factors contributing to the recent, widespread invasion of this woody legume into grasslands of southwestern North America.

**Key words:** Competition – Conductance – Dispersal – *Paspalum plicatulum* – *Schizachyrium scoparium* – Xylem water potential

Mesquite (*Prosopis* spp.) has been in North America since the Pliocene (Axelrod 1937) and wood of *Prosopis* dated 3300 yr BP has been recovered from archaeological sites in southern Texas (Hester 1980). However, the density of *Prosopis* within its historic range appears to have increased at the expense of grasslands in southwestern North America since the introduction of domestic livestock (Bogusch 1952; Humphrey 1958; Buffington and Herbel 1965; Johnston 1963; Lehman 1969; Archer 1989).

Climatic change, overgrazing, and reductions in fire frequency have been proposed as causes for the recent invasion of grasslands by woody plants (Hastings and Turner 1965; Neilson 1986). While each of these factors may facilitate encroachment, Rummel (1951) and Madany and West (1983) found that savannas protected from livestock persisted, despite low frequency of fire. In contrast, grazed savannas had substantially higher densities of woody plants which appeared after the introduction of livestock. The close proximity of the edaphically similar sites ruled out climatic change as a causal agent.

Although numerous studies have cited the importance of the relationship between grazing, graminoid biomass and woody plant invasion, little quantification has been provided. In their model of savanna stability Walker et al. (1981) identified graminoid biomass as the key factor limiting woody plant encroachment. Factors which decrease grass biomass or the capacity of grasses to exploit moisture in upper layers of soil and limit recharge in the lower profile enhance woody plant growth (Sariano and Sala 1983;

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*Abbreviations:* LTG, long-term grazed; LTP, long-term protected from grazing; ND, non-defoliated; MD, moderate defoliation; HD, heavy defoliation

Knoop and Walker 1985) and should also promote woody plant seedling establishment. Grazing of grasses should decrease their transpiration and root initiation, extension, and biomass accrual (e.g., Carmen and Briske 1982; Archer and Tieszen 1983) thus reducing their ability to pre-empt resources (Caldwell et al. 1987) and exclude invading woody plants. Changes in herbaceous composition which accompany grazing (e.g. Launchbaugh 1955; Humphrey 1958) may also increase site susceptibility to woody plant invasion if species of heavily grazed sites are less effective in interfering with woody seedlings than are species characteristic of more lightly grazed sites (e.g. Eissenstat and Caldwell 1988). However, field observations suggest herbaceous standing crop or grazing history may have little influence on *Prosopis* establishment (Brown 1950; Humphrey and Mehrhoff 1958; Meyer and Bovey 1982; Smith and Schmutz 1975).

To determine the role of herbaceous defoliation and grazing history on *P. glandulosa* var. *glandulosa* Torr. establishment in grasslands we tested the following hypotheses: (1) A positive correlation exists between level of graminoid defoliation and *Prosopis* seedling emergence and survival; (2) at a given level of graminoid defoliation the probability of *Prosopis* seedling establishment will be greatest on sites with a history of heavy grazing; and (3) the probability of *Prosopis* seedling establishment will be greatest when seeds germinate between grass tussocks. Because of the importance of livestock in *Prosopis* seed dissemination (Mooney et al. 1977, Brown and Archer 1987) we also hypothesized (4) *P. glandulosa* establishment would be significantly enhanced when germination occurred in cattle dung.

### *Site description*

Research was conducted at the Texas A&M Native Plant and Animal Conservancy in east-central Texas near College Station (30°35′ N; 96°21′ W) on a Post Oak (*Quercus stellata*) savanna site (plant nomenclature follows Correll and Johnston 1979). Mean annual rainfall is 990 mm with peaks in April and September. Mean monthly temperatures range from a low of 11° C in January to a high of 29° C in July. The frost-free period averages 270 days and extends from March through November. Soils on the study sites were clay loams with an A horizon extending to a depth of 25 cm and underlain by a $B_{tg}$ horizon.

Two spatially distinct sites were selected for the studies. One site, denoted LTG (long-term grazed), had been subjected to 30 yr of continuous heavy grazing by cattle. The other site, denoted LTP (long-term protected), had been excluded from livestock grazing since 1945. The LTP and LTG sites were within 200 m of each other on similar soils. When the study began, cattle were removed from the LTG site. Ocular estimates of canopy cover by species (Daubenmire 1959) were made at the initiation of the study in 20 plots (1 × 1 m) placed at 2 m intervals along two parallel 10 m transects on each site. Species richness and diversity were calculated as exp ($H'$), where $H' = -\sum p_i \ln p_i$ and $p_i$ was the relative cover of species i (Peet 1974).

## Methods

### *Treatments*

In April, 1984 eighty plots (1 × 1 m) were randomly selected on both the LTG and LTP sites for the *Prosopis* seedling establishment experiment. On each site, 40 of these plots received moderate defoliation (MD, i.e., herbaceous vegetation clipped at height of 25 cm) and 40 plots received heavy defoliation (HD, i.e., clipping at height of 10 cm). Defoliations were imposed monthly during the 1984 and 1985 growing season, and biomass removed was exported from the site. An additional twenty plots (1 × 0.25 m) were also selected for moderate and heavy monthly defoliation on each site and reserved for quantifying herbaceous standing crop. *Prosopis* seeds were not sown in these plots, which were treated similarly to plots used in the *Prosopis* seedling establishment trials, except that they were clipped to 10 cm in June and September 1984 and May 1986 for standing crop estimates. Forty non-defoliated plots (ND) on the LTP site were also randomly selected to serve as controls. Because of the heavy grazing by cattle, there were no non-defoliated plots designated on the LTG site.

Herbaceous standing crop on each grazing history × defoliation treatment was estimated in June and September of 1984 and again in May 1986 by weighing biomass removed on clipped auxiliary plots (30 days regrowth) and by clipping 10 randomly selected plots (1.0 × 0.25 m) from the control area to 10 cm height. Aboveground biomass was partitioned into two categories: standing (live and current years' dead) and litter (previous years' dead, which formed an amorphous mat on the soil surface). Belowground biomass was determined by extracting 20 soil cores per treatment to a depth of 25 cm in August 1985. Ten cores were taken from directly beneath bunchgrasses and ten from open spaces between grasses. Preliminary sampling indicated 75% of the herbaceous root biomass occurred in the upper 25 cm of soil.

### *Prosopis seedling establishment*

*P. glandulosa* is a hard-seeded legume and scarification of the seed coat greatly enhances its germination (Mooney et al. 1977). Ungulates consuming pods of *Prosopis* typically disperse scarified, germinable seed (see Brown and Archer 1987 and references therein). Consequently, we used mechanically scarified seeds in our field establishment trials. Germinability of a subsample of 1000 scarified seeds in a controlled environment at 30° C was 96%.

*P. glandulosa* seeds were placed in each of the forty 1 × 1 m plots in each grazing history/defoliation combination: long-term grazed, moderately defoliated (LTG-MD); long-term grazed, heavily defoliated (LTG-HD); long-term protected, non-defoliated (LTP-ND); long-term protected, moderately defoliated (LTP-MD); and long-term protected, heavily defoliated (LTP-HD). Five seeds were placed in each of five locations within each plot in May, 1984: 1) open spaces between bunchgrasses; 2) on tussocks of brownseed paspalum (*Paspalum plicatulum*) $> 1$ dm$^2$ basal area; 3) in dessication cracks; 4) in dung pats between bunchgrasses; and 5) in dung pats on bunchgrasses. Dung pats, which weighed approximately 750 g (fw) and covered about 1 dm$^2$ when placed on the ground, were formed from fresh dung collected from cattle not having access to *Prosopis* seeds. *Prosopis* seedling emergence (number of seedlings/number of seeds disseminated), was quantified two weeks after dissemination. Survival of seedlings, expressed as a percentage of the number of seedlings emerging, was noted at monthly intervals along with height and leaf number through 1985. Emergence was again quantified in 1985 by placing five seeds per plot in open spaces between bunchgrasses in each defoliation x grazing history treatment combination.

Net photosynthesis (*Pn*) and stomatal conductance (*g*) of seedlings emerging in 1984 from open spaces between bunchgrasses on LTP-HD, LTP-MD, and LTP-ND treatments was measured in May, June, and July, 1985 ($n=3$; one seedling from three different plots in each treatment). Diurnal measurements (0900, 1200 and 1600 h) of gas exchange on both leaf surfaces were made with a 0.25 l cuvette and a closed-flow portable photosynthesis system (LI-6000, LI-COR, Inc., Lincoln, NE) on clear days. The same plants were followed on each day. Xylem water potential (*XWP*) of seedlings on LTP-HD and LTP-MD plots ($n=3$/treatment) were determined with a pressure chamber (Scholander et a. 1965) at predawn and 0900, 1200, and 1600 h. Measurements of water potential required destructive sampling, thus, *XWP* was not determined for seedlings on control (LTP-ND) plots because of low rates of seedling emergence. Attenuation of photosynthetically active radiation (*PAR*) in the canopy was measured on each date with a quantum sensor (LI-190S-1, LI-COR, Inc., Lincoln, NE) at 50 cm, 25 cm, 10 cm and ground level on five plots per treatment. Gravimetric soil moisture to 20 cm was estimated bimonthly between bunchgrasses. Soil temperature was monitored with copper-constantan thermocouples at depths of 5 and 20 cm between bunchgrasses in four plots per treatment.

Chi-square analysis was used to test for differences in seedling emergence and survival among grazing history, defoliation and seed placement treatments. Differences in cover, above- and belowground standing crop and seedling morphometric parameters were determined by analysis of variance (AOV). Repeated measures AOV was used to test for differences in *Pn* and *g* (Keppel 1982). Standard AOV and Duncan's Multiple Range test were used to test for differences in *XWP*, *PAR* and soil moisture and temperature. All differences at $P<0.05$ were accepted as significant.

## Results

### *Site characteristics*

The LTP site was co-dominated by the perennial bunchgrasses little bluestem (*Schizachyrium scoparium*) and brownseed paspalum (*Paspalum plicatulum*) (Table 1). Diversity on the LTG site was higher and the contribution of little bluestem and brownseed paspalum toward community composition was lower compared to the LTP site. Two grasses, oldfield threeawn (*Aristida longiseta*) and Scribner's dicanthelium (*Dicanthelium oligosanthes*) contributed substantially to foliar cover on the LTG site but did not occur in samples from the LTP site. Litter cover was lowest and forb and bare ground cover greatest on the LTG site.

Periodic clipping reduced aboveground standing crop below that in ND plots. However, standing biomass after 30 days regrowth on moderately defoliated (MD) plots on the LTP and LTG sites was comparable to that in LTP-ND plots, even after two seasons of clipping (Table 2). Differences between LTP-ND and moderately defoliated plots were mainly in litter accumulation. Regrowth 30 days after clipping was least on heavily defoliated (HD) plots and did not differ between sites with different grazing histories. Belowground biomass was greatest beneath *Paspalum* tus-

**Table 1.** Mean (±SE) foliar cover (%) and diversity [exp ($H'$)] on a long-term protected (LTP) and long-term grazed (LTG) site near College Station, TX in 1984 ($N=20$). Within a site, cover of plant categories was comparable on moderately and heavily defoliated plots, so these data were pooled. Cover of each species or plant category shown differed significantly between LTP and LTG sites

| | LTP | LTG |
|---|---|---|
| Grasses | | |
| *Schizachyrium scoparium* | 30±1.5 | 11±1.3 |
| *Paspalum plicatulum* | 39±2.7 | 19±2.1 |
| *Aristida longiseta* | 0±0.0 | 17±1.6 |
| *Dicanthelium oligosanthes* | 0±0.0 | 15±0.8 |
| Others | 3±0.1 | 9±3.1 |
| Forbs | 2±0.5 | 10±1.8 |
| Litter | 22±3.8 | 10±2.2 |
| Bare Ground | 4±0.7 | 8±1.1 |
| Diversity | 0.49 | 0.89 |

**Table 2.** Mean (±SE) herbaceous biomass on sites with different grazing histories (LTP = long-term protection from cattle grazing; LTG = long-term heavy grazing by cattle) and monthly defoliation regimes (ND = non-defoliated; MD = moderate defoliation [clipped to 25 cm]; HD = heavy defoliation [clipped to 10 cm]). Means for each date within a given biomass category (standing vs litter) followed by the same letter were not significantly different

| Date | Defoliation Regime | Biomass (g/m$^2$) | | | |
|---|---|---|---|---|---|
| | | Standing | | Litter | |
| | | LTP | LTG | LTP | LTG |
| May 1984 | ND | 386±32a | – | 167±13a | – |
| | MD | 323±25a | 340±30a | 52± 6b | 63±5b |
| | HD | 177±12b | 191±16b | 26± 3c | 34±5c |
| Sept. 1984 | ND | 407±27a | – | 187±19a | – |
| | MD | 360±22a | 380±28a | 65± 5b | 78±5b |
| | HD | 187±16b | 201±18b | 34± 3c | 40±2c |
| May 1986 | ND | 392±23a | – | 195±16a | – |
| | MD | 342±24a | 375±27a | 68± 3b | 72±4b |
| | HD | 178±12b | 195±15b | 39± 2c | 43±3c |

**Table 3.** Mean (±SE) root biomass (g/m$^3$) beneath *Paspalum plicatulum* tussocks and in interspaces between tussocks on plots with different grazing histories (LTP = long-term protection from cattle grazing; LTG = long-term grazing by cattle) and defoliation treatments (ND = non-defoliated; MD = moderate defoliation; HD = heavy defoliation). Means followed by the same letter were not significantly different

| Grazing History | Microsite | Belowground Biomass (g/m$^3$) | | |
|---|---|---|---|---|
| | | ND | MD | HD |
| LTP | Bunchgrass | 2350±290a | 1270±110b | 1120±140b |
| | Interspace | 1430±410b | 630±190c | 580±130c |
| LTG | Bunchgrass | – | 560± 95c | 490± 49c |
| | Interspace | – | 300± 82d | 230± 62d |

**Table 4.** Mean (±SE) reduction (%) in photosynthetically active radiation (*PAR*) on 27 July 1985 at different heights above the ground in three defoliation treatments ($N = 10$). For a given defoliation treatment the main effect of grazing history was not significant so data were pooled across sites. *PAR* was read mid-way between monthly defoliation events. Height, level of defoliation and their interaction were significant. Patterns were similar in May and June (data not shown)

| Level of Defoliation | Height above ground (cm) | | | | |
|---|---|---|---|---|---|
| | 50 | 25 | 15 | 10 | 0 |
| None | 0±0a* | 7±1a | 27±5a | 42±6a | 86±13a |
| Moderate | 0±0a | 0±0b | 15±2b | 23±8b | 27±10b |
| Heavy | 0±0a | 0±0b | 0±0c | 0±0c | 7± 1c |

* Means within a column followed by different letters differed significantly ($P < 0.05$)

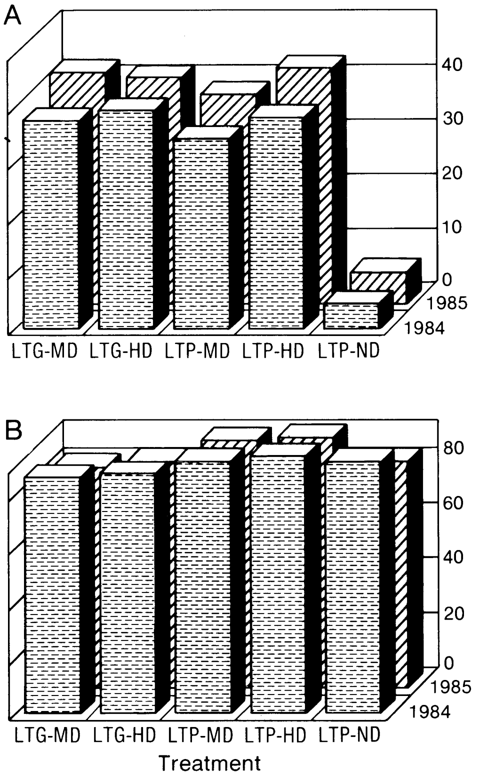

**Fig. 1. A** Mean emergence (%) of scarified *P. glandulosa* seeds disseminated in spring of 1984 and 1985. **B** End of season survival (%) of mesquite seedlings germinating in 1984. Site-treatment codes are as follows: *LTP* long-term protection from livestock grazing; *LTG* long-term heavy livestock grazing; *ND* no defoliation; *MD* moderate defoliation; *HD* heavy defoliation

socks on LTP-ND plots and least in interspaces of defoliated plots (Table 3). Within microsites, root biomass was greater on LTP plots relative to LTG plots. Differences between MD and HD plots were not significant on either site.

*PAR* at ground level in non-defoliated plots was substantially reduced relative to clipped plots (Table 4). There was little attenuation in the heavily defoliated plots. Soil temperatures did not differ on LTP and LTG sites within

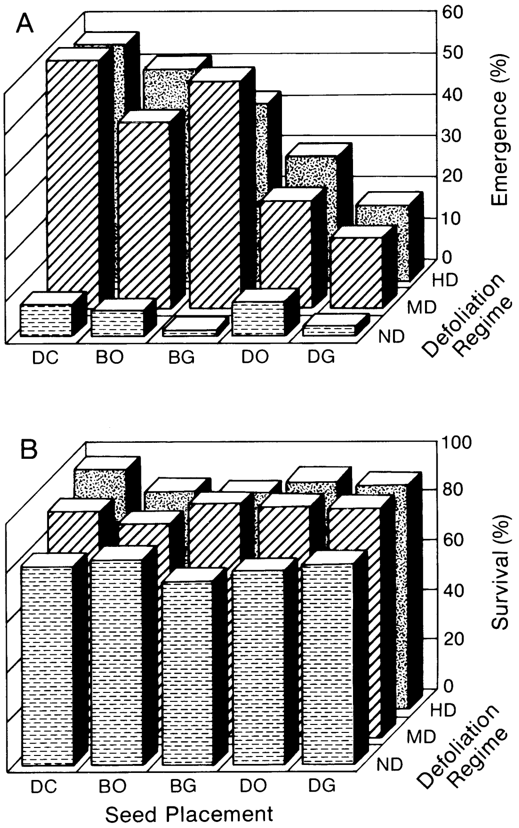

**Fig. 2 A, B.** Mean percent emergence **A** and survival **B** of *P. glandulosa* seedlings in plots receiving various levels of herbaceous defoliation at 30 d intervals (*ND* no defoliation; *MD* moderate defoliation; *HD* heavy defoliation) as a function of seed placement (*DC* dessication crack; *BO* bare seeds between bunchgrasses; *BG* bare seeds on *Paspalum* tussocks; *DO* seeds in dung pats between bunchgrasses; *DG* seeds in dung pats on grass tussocks). Survival data reflect the percentage of seedlings emerging in May 1984 alive at the end of 1985. There were no differences between sites with different grazing histories (LTP vs LTG) for a given seed placement, so sites were pooled

defoliation treatments. In May, soil temperature at 5 cm was comparable on ND, MD and HD plots. However, in June–October, soil temperatures averaged 4 to 9° C and 7 to 14° C greater on MD and HD plots, respectively, compared to ND plots ($P < 0.05$). No differences in soil temperature were evident at 20 cm. Soil moisture in the upper 25 cm decreased from 16% in May to 4% in August, but did not differ significantly between sites or treatments.

### *Seedling emergence and survival*

No significant interactions between grazing history and level of defoliation were obtained for either seedling emergence or survival, thus each factor will be discussed independently. All seedling emergence observed occurred within two weeks of seed placement. Relative to LTP-ND plots, *Prosopis* seedling emergence was 7- to 8-fold greater with defoliation of herbaceous vegetation in both 1984 and 1985, regardless of grazing history (Fig. 1A). However, differences in emergence between MD and HD plots and sites were not significant in either year. The percentage of seedlings surviving after two growing seasons was not affected

**Table 5.** Mean (±SE) height, number of leaves, aboveground biomass, and leaf area for *P. glandulosa* seedlings emerging in May 1984. No significant differences occurred between grazing history or defoliation treatments so data were pooled. No destructive harvests were made in 1984. Estimates of height and leaf number were made from the entire population ($n = \geq 700$). Estimates of biomass and leaf area were from seedlings destructively harvested for *XWP* estimates ($n = 12$)

| Year | Month | Height (cm) | Leaf Number | Aboveground Biomass (mg) | Leaf Area (cm$^2$) |
|---|---|---|---|---|---|
| 1984 | May | 3.9±0.6 | – | – | – |
| | July | 5.2±1.0 | 3.8±0.7 | – | – |
| | September | 5.5±0.8 | 5.9±1.2 | – | – |
| 1985 | May | 5.8±1.1 | 4.5±1.0 | 112.4± 7.5 | 10.5±1.4 |
| | June | 6.5±1.2 | 6.2±1.6 | 157.7± 8.8 | 12.7±1.8 |
| | September | 7.0±1.1 | 6.1±1.4 | 169.2±12.3 | 11.9±1.7 |

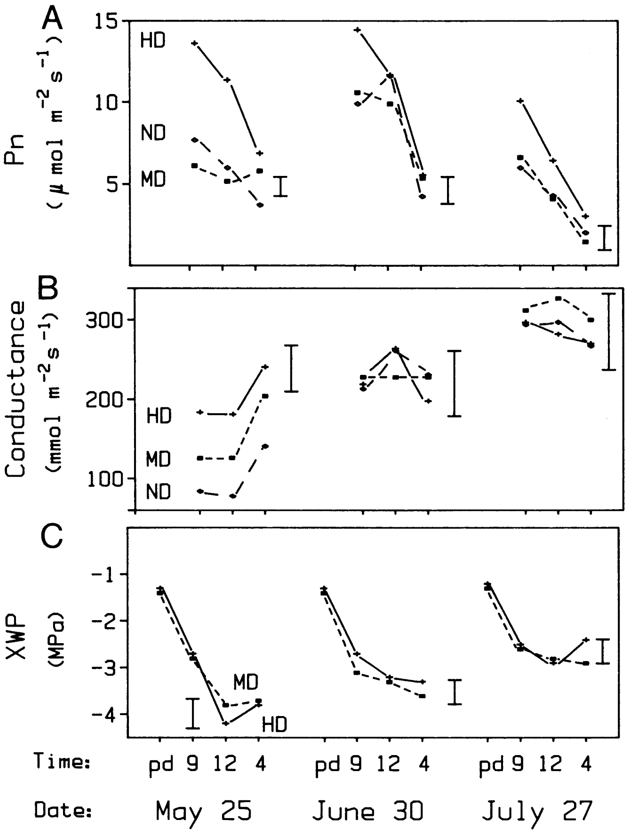

**Fig. 3A–C.** Diurnal trends (PD = pre-dawn) in **A** net photosynthesis (*Pn*), **B** conductance (*g*) and **C** xylem water potential (*XWP*) for *P. glandulosa* seedlings on LTP plots receiving different levels of herbaceous defoliation (HD = heavy; MD = moderate; ND = none). See Table 6 for summary of AOV analysis. Maximum standard errors (SE) observed on each date are shown. SE's were, on average, within 15, 20 and 10% of the means, for *Pn*, *g* and *XWP*, respectively. *XWP* for seedlings on ND treatments was not measured because of low numbers of plants on these plots

**Table 6.** AOV results for measurements of net photosynthesis (*Pn*), conductance (*g*) and xylem water potential (*XWP*) on one year old *P. glandulosa* seedlings on three dates in 1985. Results for main effects (TRT = level of herbaceous defoliation; TOD = time of day) and their interaction (T × T) are shown

| Parameter | Variable | 25 May | 30 June | 27 July |
|---|---|---|---|---|
| *Pn* | TRT | ** | NS | NS |
| | TOD | ** | * | * |
| | T × T | * | ** | * |
| *g* | TRT | * | NS | NS |
| | TOD | ** | * | NS |
| | T × T | * | ** | * |
| *XWP* | TRT | NS | NS | NS |
| | TOD | ** | ** | ** |
| | T × T | ** | ** | * |

NS = $P > 0.05$; * = $0.01 < P < 0.05$; ** = $P < 0.01$

by grazing history or level of herbaceous defoliation (Fig. 1 B).

Among seed placement treatments on defoliated plots, grazing history (LTP vs LTG) had no significant effect on either emergence or survival, so data were pooled. On defoliated plots, seedling emergence was lowest in dung (17 to 30%) and higher (40 to 60%) among other locations (Fig. 2 A). Seedling emergence was ≤8% on LTP-ND plots, regardless of seed placement. Survivorship of seedlings emerging in 1984 exceeded 74% at the end of 1985 and was not significantly affected by seed placement (Fig. 2 B). Aboveground seedling development was not affected by grazing history or level of herbaceous defoliation. Seasonal trends in seedling height, leaves/plant, leaf area and biomass, pooled across sites and defoliation treatments, have been summarized in Table 5.

### *Seedling gas exchange and water relations*

A significant treatment by time of day interaction for *Pn* was the result of higher *Pn* among seedlings on HD plots relative to MD and ND plots at 0900 h (Fig. 3 A, Table 6). At this time of day, when sun angles were low, denser herbaceous foliage on MD and ND plots may have limited *PAR* reaching seedlings (Table 4), which were typically <7 cm in height (Table 5). There were no differences in *Pn* among seedlings on MD and ND plots on any sample date.

Conductance (*g*) was significantly greater among seedlings on HD plots compared to those in ND plots in May, but neither of these differed from seedlings on the MD plots (Fig. 3 B). Diurnal patterns of *g* among seedlings in different treatments were inconsistent in July and August and treatment effects were not significant. Levels of tissue *XWP* were comparable among seedlings on MD and HD plots on each date (Fig. 3 C).

## Discussion

### *Seedling emergence*

Field surveys in southern Texas indicate *Prosopis* seedling emergence occurs in fall and spring, coincident with peaks in bimodal rainfall (Brown and Archer 1987). On this central Texas site where annual precipitation is also bimodal, seeds were placed in plots in May, a time when temperatures optimal for germination (Scifres and Brock 1969) typically coincide with moisture availability. Autumn germination would also be expected on this site and the patterns of emergence and survival noted in our spring experiment might differ for seedlings emerging in the fall.

The two weeks following seed dissemination appeared to be the most critical to *Prosopis* establishment on LTP-ND plots (Fig. 1). This was true in both 1984 and 1985. Openings in the herbaceous layer created by defoliation of grasses on the LTP site increased germination and/or survival markedly during this period. However, increasing the degree of defoliation from moderate to heavy did not stimulate additional emergence on either site. Survival of *Prosopis* seedlings present two weeks after seed dissemination was comparably high, regardless of site grazing history or level of herbaceous defoliation (Fig. 1 B).

Low rates of emergence in LTP-ND plots relative to MD and HD plots appeared to reflect high mortality of developing seedlings rather than reduced germination. When plots were first checked two weeks after seed dispersal, shriveled hypocotyls and cotyledons were frequently observed in ND plots, indicating germination had occurred. High mortality of seedlings within two weeks of germination on ND plots may have resulted from low *PAR* at ground level (Table 4). *Prosopis* seeds do not require light to germinate, but seedling establishment can be reduced 50% at *PAR* levels 5% that of full sun (Scifres et al. 1973). Litter, which comprised >30% of the aboveground biomass on LTP-ND plots and formed a dense, continuous mat, would have contributed substantially to the attenuation of *PAR*, in addition to reducing convective cooling at ground level (Knapp and Seastedt 1986). Reductions in litter accumulation and continuity on MD and HD plots (Table 2) may have contributed substantially to the higher rates of seedling emergence on these plots (e.g. Golberg and Werner 1983).

Although seedling emergence from dung was lower than that of bare seed placements (Fig. 2 A), deposition of *Prosopis* seed in dung in conjunction with graminoid defoliation is perhaps the most likely combination of events when livestock are present (Brown and Archer 1987). Cattle, horses and sheep consume large quantities of *Prosopis* pods and a high proportion of the seeds escape mastication and are scarified in the digestive tract, improving their germinability two- to three-fold relative to non-ingested seed (Mooney et al. 1977). The fact that emergence of scarified seed from dung increased markedly when dung occurred in plots where grasses were defoliated suggests that effective agents of *Prosopis* dispersal are those which transport large numbers of germinable seeds and deposit them in areas where grasses have been grazed (Figs. 1 A and 2 A). Reduced emergence in dung relative to bare seed placements may reflect predation by rodents attracted to dung (Janzen 1982) or the rapid dehydration and subsequent "mummification" of pats. The latter resulted in dung pats persisting well into the second growing season. Localized nutrient enrichment presumed to accompany dung deposition (Weeda 1967) did not enhance aboveground growth or survival of *Prosopis* relative to bare seed placements. However, the proportion surviving in all locations was high (74 to 97%; Fig. 2 B).

### *Seedling survival*

*Prosopis* seedling survival was high and weather (temperature, precipitation, etc.) for 1984 and 1985 was typical with respect to the long-term norms (Griffiths 1981). Thus, with respect to climatic variables, we have no basis for presuming to have observed an unusual episode of seedling establishment. Our results were similar to those of Meyer and Bovey (1982) with respect to uniformly high levels of *Prosopis* establishment in grass-dominated stands receiving varying levels of defoliation. Long-term patterns of *Prosopis* seedling growth and survival under the various grazing history/defoliation regimes await documentation.

*Prosopis* establishment in grasslands has often been described as a consequence of shifts in herbaceous composition and production resulting from grazing. The assumption implicit in inferences derived from observing *Prosopis* encroachment in grazed grasslands is that plants of retrogressed sites cannot pre-empt resources sufficiently to exclude invading woody plants. Our data from sites with contrasting grazing histories do not support this assumption. Differences in herbaceous composition, diversity and above- and belowground biomass were marked on the LTP and LTG sites, yet the probability of *Prosopis* seedling establishment was comparably high (Fig. 1). In controlled environment studies where rooting volumes are restricted, competition between grasses and *Prosopis* seedlings can be intense (Van Auken and Bush 1987, 1988). In the field, however, survival of seedlings on tussocks was comparable to that of seedlings establishing in unvegetated interspaces, even though root biomass beneath the tussocks was 1.6 to 2.1 times greater than that of interspaces (Table 3). In addition, survival (Fig. 1 B), shoot development (Table 5) and physiological activity (Fig. 3) of seedlings was comparable on defoliated and non-defoliated plots, suggesting competition for soil resources between grasses and *Prosopis* may be minimal early in the life cycle of *Prosopis* (e.g. Eissenstat and Mitchell 1983; Sands and Sandian-Nambier 1984).

Maintenance of *Pn* throughout the growing season (Fig. 3 A) coupled with slow aboveground growth (Table 5) suggests seedlings were preferentially allocating carbon belowground. Three weeks after emergence, *Prosopis* seedlings in Arizona grasslands had tap roots 33 cm long; by the end of the second growing season their roots had penetrated to 68 cm (Glendening and Paulsen 1955). In southern Texas we observed seedling tap roots extending >40 cm within 4 months of germination (unpublished work). The fact that *g* and *XWP* of *Prosopis* seedlings increased from late spring through summer (Fig. 3 B and C) while moisture in the upper 25 cm of soil decreased form 16% in May to 4% in August, suggests their roots were developing and effectively accessing soil water at deeper depths. Rapid root development in *Prosopis* seedlings would facilitate partitioning of belowground resources and reduce competition with perennial grasses whose roots were largely (75%) concentrated in the upper 25 cm of soil on our site.

### *Why has mesquite invaded grasslands only recently?*

Prosopis can germinate and establish over a range of soil types (Ueckert et al. 1979), moisture (Scifres and Brock 1969, Scifres and Brock 1971) and light regimes (Scifres et al. 1973). The results of our two year experiment further suggest grasses are ineffective in excluding *P. glandulosa* from certain sites, except perhaps when there are large accumulations of litter. However, even on LTP-ND plots emergence ranged from 1 to 8% and subsequent survival from 74 to 83%, depending on seed placement (Fig. 2). Thus, density of mesquite plants could have increased, albeit perhaps rather slowly, in grasslands throughout the Holocene. Why then has *Prosopis* invasion apparently occurred only recently on many sites (Johnston 1963, Buffington and Herbal 1965, Archer 1989)?

Historical reports suggest the spread of *Prosopis* has been lateral, from drainages and riparian zones into upland prairies within its historic range (see Johnston 1963; Archer et al. 1988). Thus, seed sources may have been available throughout the Holocene. Our data on seedling establishment and that of Smith and Schmutz (1975) and Meyer and Bovey (1982) provide evidence in support of the hypothesis that prior to the introduction of domestic livestock, limited seed dispersal may have been a primary constraint to *Prosopis* invasion of grasslands (see Brown and Archer 1987, Archer et al. 1988 for elaboration). Although recurring fire may have kept *Prosopis* low in stature, the species is tolerant of fire (Glendening and Paulsen 1955) and survival of 2- and 3-yr old seedlings can exceed 60 and 90%, respectively, following hot burns (Wright et al. 1976). Thus, only short fire-free intervals would be required for establishment.

*Prosopis* is thought to have evolved with megafauna in the New World (Mooney et al. 1977), many of which were extinct by the end of the Pleistocene (Martin 1967). The loss of North American megafauna potentially utilizing *Prosopis* and it's fruit (pods) may have subsequently restricted it's spread into grasslands until the introduction of livestock (e.g. Janzen 1986). That *Prosopis* has expressed itself only in recent history on many sites suggests other native herbivores were either disseminating few seeds or that the seeds dispersed were not germinable or capable of establishing. Relative to native Holocene fauna known to consume *Prosopis* pods and seeds, domestic livestock are much more effective agents of dispersal in that they transplant large numbers of germinable seeds away from parent plants harboring host-specific seed predators and deposit them in grazed habitats (Brown and Archer 1987) where emergence and survival could be high (Fig. 1).

Alternatively, *Prosopis* may have always been present in grasslands, but recurring fires kept plants from developing in stature and producing seed. With the introduction of large numbers and high concentrations of domestic livestock into North America, dispersal of germinable *Prosopis* seed into grassland would have increased greatly (Brown and Archer 1987) and even moderate grazing would have caused a many-fold increase in emergence (Fig. 1 a and 2 a). As herbaceous biomass was reduced by continued grazing, probabilities of *Prosopis* seedling survival would not have necessarily increased (Fig. 1 b). However, frequency and intensity of fire would have decreased, thus allowing more plants to grow to reproductive maturity and increase the availability of seed for additional dispersal.

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