

SHRUB INVASION OF GRASSLAND: RECRUITMENT IS CONTINUOUS AND NOT REGULATED BY HERBACEOUS BIOMASS OR DENSITY

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Abstract. Proliferation of woody plants in grasslands and savannas since the 1800s has been widely documented. In the southwestern United States, increased abundance of honey mesquite (*Prosopis glandulosa* var. *glandulosa*) has been attributed to heavy grazing by livestock. Here, we test the hypothesis that *P. glandulosa* invasion of grasslands requires, first, reductions in herbaceous biomass and density such as those that accompany livestock grazing and, second, episodes of high soil moisture availability.

No combination of grass density (nonmanipulated or reduced 50%) or defoliation (none, moderate, heavy) significantly affected *P. glandulosa* seedling emergence within a watering regime (natural and supplemented) at our field site in semiarid southern Texas. Seedling emergence on plots receiving only natural rainfall was high (42%), despite the fact that precipitation was substantially below normal. Supplemental watering, to generate moisture levels approximating years of unusually high annual rainfall, increased emergence to 59%. Seedling survival after 2 yr was high (62–77%) and statistically comparable across the density, defoliation, and watering treatments. Net photosynthesis (A_n) of 1-yr-old seedlings was enhanced by supplemental watering, but reductions in grass density or biomass had little effect on seedling A_n or xylem water potential. Height, aboveground biomass, and leaf area were comparable among 1- and 2-yr-old seedlings across all density, defoliation, and watering combinations.

High seedling emergence and survival on unwatered plots, even during a “drought year,” suggests that *Prosopis* recruitment is not contingent upon unusual or episodic rainfall. Reductions in biomass and density of herbaceous vegetation had no influence on seedling emergence, growth, or survival, suggesting that *Prosopis* invasion is minimally influenced by grass competition. Historic grazing at this site appears to have altered herbaceous composition and reduced above- and belowground biomass production below the threshold level required for competitive exclusion of woody vegetation. Such data suggest that rates and patterns of seed dispersal may be the primary determinants of *P. glandulosa* encroachment on present-day landscapes in semiarid regions. Minimizing livestock dispersal of seed (in the case of leguminous shrubs) and maintenance of an effective fire regime (through production of fine fuels) may be crucial for sustaining herbaceous composition and production in grazed systems prone to invasion by unpalatable woody plants.

Key words: *Chloris cucullata*; competition of invasive woody plants in grasslands; grazing; photosynthesis; *Prosopis glandulosa*; savanna; seedling establishment; tree–grass interactions; woody plant invasion; xylem water potential.

INTRODUCTION

Trends toward increasing woody plant abundance in temperate and tropical grasslands and savannas in recent history have been reported worldwide (Archer 1994, McPherson 1997). Although this phenomenon has been widely recognized (e.g., Grover and Musick 1990) and has significant implications for livestock production systems (Scifres 1980, Scifres et al. 1983), wildlife habitat (Ben-Sharer 1992), and biogeochemistry (Schlesinger et al. 1990), surprisingly little is known of the rates, dynamics, patterns, or successional

processes involved in these vegetation changes. Climatic change and changes in historical atmospheric CO₂ concentrations, fire regimes, rodent populations, and livestock grazing have been suggested as driving forces in this shift in vegetation (Archer et al. 1995, Polley et al. 1996, Brown et al. 1997, Weltzin et al. 1997). While all of these factors have interacted to produce vegetation change, some studies (e.g., Madany and West 1983) have clearly demonstrated that livestock grazing has been a primary factor.

For woody plants with potentially long life-spans and low post-establishment mortality rates, seedling recruitment is probably the most critical stage in the life history (Harper 1977). A variety of direct and indirect effects of livestock grazing may interact to promote woody plant seedling establishment in grass commu-

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nities (Archer 1995a). Reductions in the density and biomass of herbaceous vegetation have been shown to increase the probability of seedling success in old fields and forests (i.e., Goldberg and Werner 1983, Maguire and Forman 1983, McEvoy 1984, De Steven 1991a, b). Changes in species composition and reductions in herbaceous plant basal area, density, and above- and belowground biomass known to accompany chronic livestock grazing (Heitschmidt and Stuth 1991) might therefore create opportunities for tree and shrub seedling establishment in grasslands. Although it is widely assumed that these grazing-induced changes in community structure and function will increase grassland susceptibility to woody plant encroachment, these potential controlling factors have not been adequately quantified.

Experimental studies of woody plant invasion of semiarid grasslands that focus on the critical seedling establishment phase are relatively few and have been primarily controlled environment studies. Such studies predict that reductions in grass competition (achieved via reductions in biomass associated with defoliation) will promote woody plant seedling establishment (van Auken and Bush 1987, 1988, 1989, Polley et al. 1994). Some field studies support this contention (Schultz et al. 1955, McPherson 1993, Bush and van Auken 1995), but others do not (Brown and Archer 1989, Schmidt and Stubbendieck 1993, O'Connor 1995a). Here, we investigated the extent to which changes in herbaceous density and biomass influence woody plant seedling establishment in grasslands under field conditions.

Climatic variability and the unpredictable occurrence of extreme climatic events may interact with grazing to effect rapid shifts in plant recruitment and mortality and change the balance between grasses and woody plants (e.g., Wiegand et al. 1995). Periods of elevated rainfall may trigger episodes of seed production and seedling establishment of woody plants in grasslands (McPherson and Wright 1990, Turner 1990, Harrington 1991, Carter 1994), while drought may promote grass die-off (O'Connor 1993), but have little effect on tree or shrub persistence (Carter 1964, Neilson and Wullstein 1985). It is not clear how rainfall variability might constrain, accentuate, or mitigate grazing influences on woody plant emergence and establishment in grasslands.

In southwestern North America, many temperate, subtropical, and desert grasslands and savannas present at the time of Anglo-European settlement are now shrublands or woodlands dominated by the tree legume, honey mesquite (*Prosopis glandulosa* var. *glandulosa* Torr.) (Archer 1989, 1994). The encroachment of *P. glandulosa* into grasslands and savannas has had significant socioeconomic and environmental impacts on these lands that have been predominantly used for livestock grazing (Fisher 1950, Simpson 1977). An understanding of processes regulating *P. glandulosa* seedling recruitment is, therefore, a critical first step in

developing management strategies to mitigate shrub encroachment. In this study we examined simulated grazing \times soil moisture \times grass competition interactions on *P. glandulosa* seedling emergence and short-term survival. We hypothesized that under conditions of high soil moisture, competition with grasses would be minimal and *P. glandulosa* would successfully germinate and establish regardless of herbaceous biomass and density. This would be the anticipated scenario if seedling establishment were "episodic" and confined to years when rainfall is unusually high. We hypothesized that, conversely, under conditions of low soil moisture ("normal" or below normal rainfall) competition with grasses would be intense and *P. glandulosa* germination and establishment would occur only with a reduction in grass biomass or density, such as that which typically accompanies chronic livestock grazing. To test these hypotheses, we conducted a factorial field experiment, whereby seeds of *P. glandulosa* were planted into plots maintained at two graminoid densities (nonmanipulated and reduced 50%), receiving one of three levels of defoliation (none, moderate, and heavy) and one of two watering regimes (natural and supplemented).

MATERIALS AND METHODS

Study site

Research was conducted on the Texas Agricultural Experiment Station, La Copita Research Area, in Jim Wells County, 15 km SW of Alice, Texas (27°40' N, 98°12' W; elevation 80 m) in the eastern Rio Grande Plains of the Tamaulipan Biotic Province. Contemporary vegetation of the region has been described by Davis and Spicer (1965). Uplands at the study site, which have been grazed by cattle since the late 1800s, are savanna parklands consisting of discrete clusters of woody plants organized beneath *Prosopis glandulosa* (plant nomenclature follows Correll and Johnston 1979). Inter-cluster spaces were dominated by perennial grasses, primarily *Chloris cucullata*. See Archer (1995b) for details on plant community structure and successional patterns. Soils on the study site were fine sandy loams (Runge series) on 1–3% slopes (USDA 1979). Climate is subtropical, with warm winters and hot summers. Mean annual temperature is 22.4°C, with a growing season of 289 d. Mean annual precipitation (720 mm) is highly variable (cv = 35%). When tropical depressions and hurricanes in the Gulf of Mexico spawn inland storms, annual rainfall may exceed 2600 mm. Available weather records for Alice, Texas, indicate there have been five such years between 1912 and 1997 (1919 [3312 mm], 1935, 1941, 1942, and 1971).

Field experiments

In May 1984 livestock were excluded from a 60 \times 60 m area. Seventy-two 2 \times 1 m plots were perma-

nently marked within this enclosure. One-half of the plots (hereafter referred to as "watered" plots) received supplemental water applied every other week (~10 cm each application) from April through October 1984 and 1985 via low pressure irrigation. Our goal was to elevate moisture to levels approximating the highest annual rainfall years in the weather records for this area (2600–3312 mm). The other half of the plots (hereafter referred to as "unwatered") received only natural rainfall. Approximately 10 m separated the watered and unwatered plots. Watered plots were located downslope from unwatered plots to eliminate the possibility of run-on. Herbaceous density and defoliation treatments were randomly assigned to plots within watering treatments.

Density was altered in half of the plots in each watering treatment by placing a gridded 2×1 m frame over each plot and killing 50% of the plants in each 0.25-m^2 block with a nonselective, foliar-active herbicide (glyphosate [N-(phosphonomethyl) glycine]). Plant density was estimated 30 d later using the gridded plot frame to map individual plants, and herbicide was reapplied as necessary. Post-treatment bare ground cover percentages averaged $51 \pm 6\%$ in the control plots vs. $75 \pm 7\%$ in the reduced density plots. The relative composition of species in density-altered plots remained similar to that of the normal-density plots.

Three levels of defoliation (none, moderate [20 cm stubble height], and heavy [5 cm stubble height]) were imposed by clipping monthly throughout the experiment. All clipped biomass was removed from plots. Thus, we imposed a 12-treatment factorial design (three levels of defoliation, two levels of herbaceous density, two levels of watering). Each of the 12 treatments was replicated six times (total = 72 plots).

P. glandulosa emergence, establishment and growth

Prior to the initiation of the experiment, no *P. glandulosa* plants were inside the enclosure. In early July 1984, 30 seeds were planted at a depth of 2 cm in each 2×1 m plot. Laboratory viability trials conducted at 25°C on a random subsample ($N = 1000$ seeds) of the seed lot indicated that 96% were germinable. Seedling emergence was determined 2 wk after planting. Seedling survivorship was noted in October 1984 and again in April and August of 1985. A second cohort of seeds (laboratory germinability = 95%) was planted in late June 1985, and their growth and survival monitored for the remainder of that field season. These planting dates roughly coincide with periods of *P. glandulosa* seed production at this field site.

Seedling performance was estimated for seedlings in four of the 12 treatment combinations: unwatered–normal density–no defoliation (UNN = control), unwatered–low density–heavy defoliation (ULH), watered–normal density–no defoliation (WNN), and watered–low density–heavy defoliation (WLH). For each of these treatments, net photosynthesis (A_n) and xylem

water potential (Ψ) of seedlings were quantified on six dates during 1985. Diurnal measurements of gas exchange (at 0900, 1200, and 1600) on clear days in May, June, July, and August were made on upper/lower leaf surfaces with a portable photosynthesis system (LI-6000, LI-COR, Inc., Lincoln, Nebraska, USA) and a 0.25-L cuvette. At least three *P. glandulosa* seedlings per treatment were followed through each day.

Xylem water potential was determined with a pressure chamber (Scholander et al. 1965). Seedlings were placed in plastic bags containing moistened filter paper after excising to minimize water loss during pressure chamber readings. Seedling Ψ was not checked during June 1985 to ensure that an adequate number of seedlings would be available for measurements during the more stressful period of the growing season. Individual *P. glandulosa* seedlings destructively harvested for Ψ measurements were used to determine aboveground biomass, height, and leaf area.

Soil water content in plots (15 and 30 cm and at 30 cm increments to 1.5 m depth) was estimated (neutron scattering method, van Bavel 1958) in each of the four treatments where plant performance measurements were made (UNN, ULH, WNN, and WLH). Neutron access tubes were read monthly. Soil temperature was estimated on the same plots at 5 and 20 cm depths, using thermocouples ($N = 4$). Aboveground herbaceous biomass was estimated by clipping 0.25-m^2 plots ($N = 10$) in June 1984 and June 1985 at peak standing crop.

Analysis of variance (ANOVA) of arcsine transformed data (Snedecor and Cochran 1980) was used to test for differences in seedling emergence and survival among the 12 treatments. We used a split-plot ANOVA model with water (two levels) as the main treatment, and grass density (two levels) and grass defoliation (three levels) as subplot treatments. Statistical differences in A_n ($P \leq 0.05$) among the four treatments (UNN, ULH, WNN, WLH) were tested with repeated measures analysis of variance (Keppel 1982). Differences in mean Ψ , standing crop biomass, and soil moisture (by depth) among these treatments were tested with standard ANOVA.

RESULTS

Aboveground herbaceous biomass was comparable for all plots when the experiment was initiated in June 1984 (Table 1). Supplemental watering subsequently increased aboveground herbaceous biomass relative to nonsupplemented (unwatered) control plots. However, density reduction and clipping combinations offset watering effects, such that there were no differences on any date between WLH plots and UNN plots. Standing crop biomass on the ULH plots was significantly less than all other treatments. Standing crop on WNN plots was significantly greater than all others during 1985. *P. glandulosa* seedlings were thus exposed to herba-

TABLE 1. Standing crop biomass (g/m^2) on watering, herbaceous density, and clipping treatments in summer 1984 at the start of the experiment and in 1985.

Treatment	Standing crop biomass (g/m^2)	
	1984	1985
ULH	262 ^a (18)	185 ^a (13)
UNN	278 ^a (20)	292 ^b (21)
WLH	255 ^a (21)	263 ^b (19)
WNN	245 ^a (21)	453 ^c (25)

Notes: Values are means of six, 2×1 m plots (1 SE in parentheses). Treatments are: unwatered, low density, heavy defoliation (ULH); unwatered, normal density, no defoliation (UNN); watered, low density, heavy defoliation (WLH); and watered, normal density, no defoliation (WNN). $N = 10$ plots per treatment. Means within a column followed by different letters were statistically different ($P < 0.05$).

ceous aboveground biomass ranging from 185 to 453 g/m^2 .

Annual rainfall for 1984 (506 mm) was well below the long-term average (720 mm); rainfall in 1985 (760 mm) was slightly above normal. Rainfall during the months preceding the 1984 *P. glandulosa* planting was well below normal (35% of long-term mean for January–June), whereas monthly rainfall for the months preceding the 1985 planting was well above normal (Fig. 1).

Supplemental watering increased soil moisture content relative to unwatered controls, and date \times water treatment interactions were significant ($P \leq 0.05$, Fig. 2). Neither plant density nor level of defoliation significantly influenced soil moisture, so data in Fig. 2

were pooled across these treatments. At the time of planting (July 1984), soil water content at 15 cm was significantly greater in the watered plots (37%) than in the unwatered plots (20%).

Analysis of variance indicated no significant differences in soil temperatures within a watering treatment. Soil temperature data were therefore pooled across defoliation–density treatments. Soil temperature date \times watering treatment interactions were significant at each depth ($P < 0.05$). Soil temperature at 5 cm was significantly ($P < 0.05$) reduced on watered plots in 1984 and after 2 July, 1985 (Fig. 3). At the time of planting, soil temperatures at 5 cm were significantly ($P < 0.05$) greater on unwatered plots compared to watered plots. Temperatures at 20 cm followed a similar pattern, although the magnitude of the differences was less. Peak soil temperatures in the upper 5 cm typically exceeded 35–40°C each year during the period of *P. glandulosa* seed germination.

Prosopis seedling emergence and establishment

P. glandulosa seedling emergence in unwatered plots (42% and 44% in 1984 and 1985, respectively) was significantly ($P < 0.01$) less than that which occurred in plots receiving supplemental water (59% and 62%, Table 2). However, watering did not significantly enhance first-year survival of seedlings emerging in 1984 ($P = 0.06$) or 1985 ($P = 0.09$) nor second year survivorship of the 1984 cohort ($P = 0.08$). Density and level of defoliation of herbaceous vegetation affected neither emergence ($P = 0.15$ and 0.24, respectively)

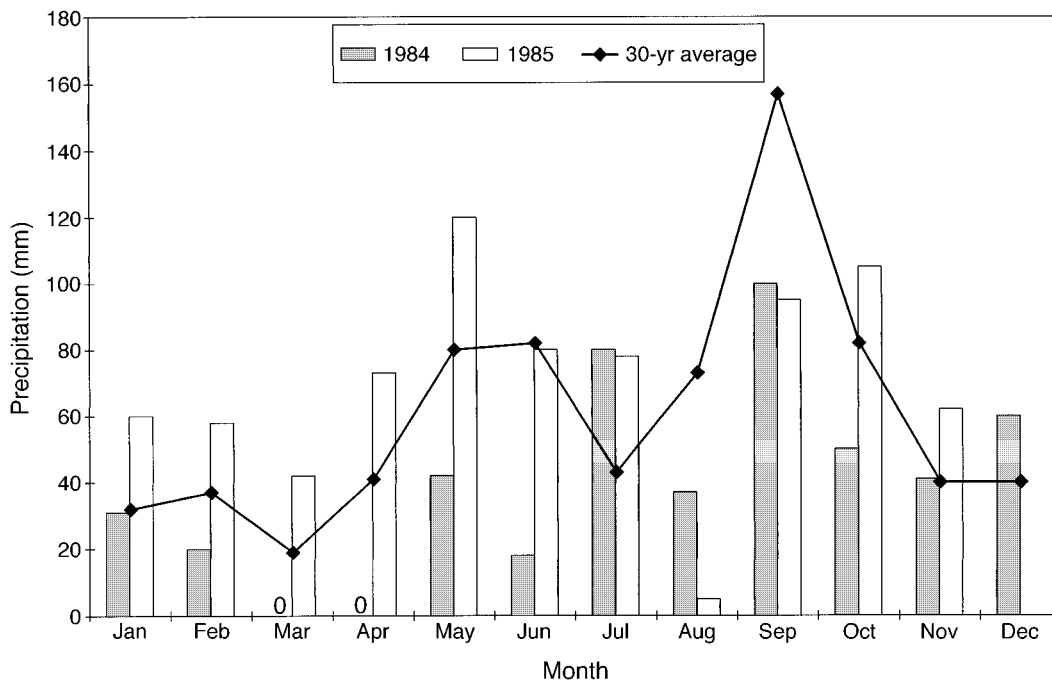


FIG. 1. Monthly precipitation (mm) at Alice, Texas, for 1984 (shaded bars), 1985 (open bars), and the 30-yr average (solid line).

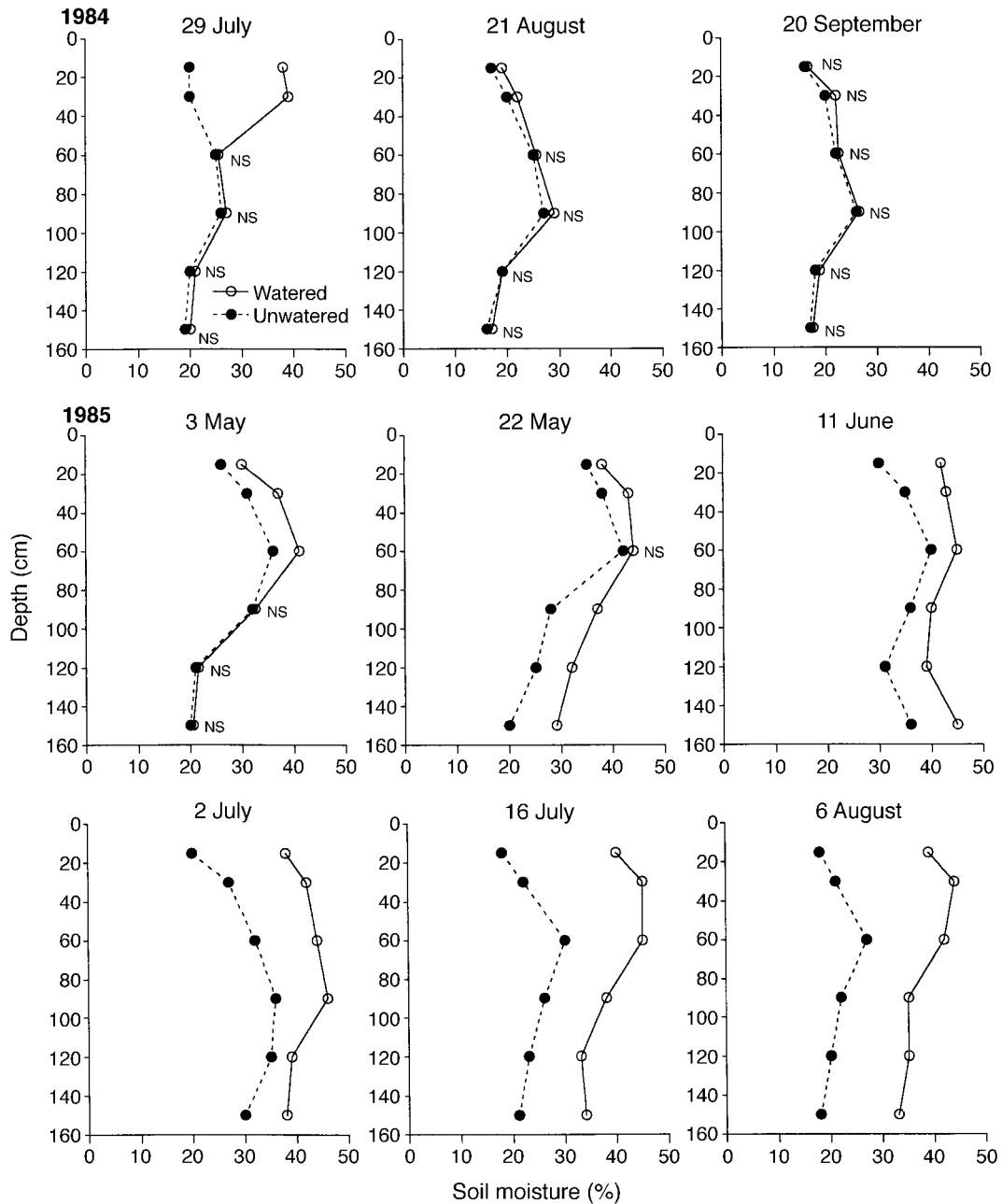


FIG. 2. Soil moisture (percentage) in 1984 and 1985 on plots receiving only natural rainfall (“unwatered”) and on plots receiving supplemental watering (“watered”). For a given depth/date, soil moisture differences between watered and unwatered plots were significant ($P \leq 0.05$), except where noted as NS.

nor survival ($P = 0.28$ and 0.11 , respectively, for first-year survival; $P = 0.65$ and 0.71 , respectively, for second-year survival) of seedlings within a watering regime, even though differences in aboveground biomass among those treatments were significant (Table 1). Interaction terms were nonsignificant, with one exception: water \times density for second-year seedling survival. In this instance, herbaceous density reductions had a slight negative effect on second-year survival among

watered seedlings (85 vs. 82%), whereas among unwatered seedlings, experimental reductions in grass density had a slight positive effect (75 vs. 82%, Table 2).

Seasonal and diurnal patterns of net photosynthesis (A_n) and xylem water potential (Ψ) of 1-yr-old seedlings generally reflected seasonal variation in soil moisture (Tables 3 and 4). There were no statistical differences across watering treatments during May, when soil

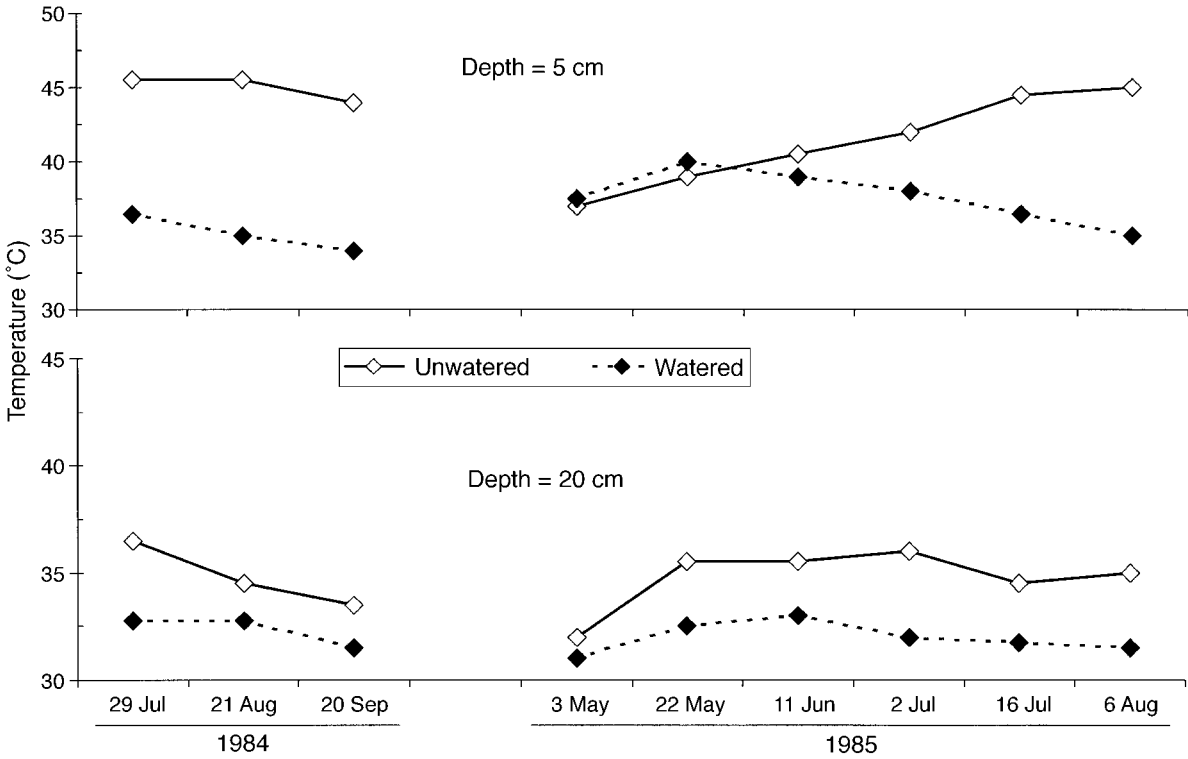


FIG. 3. Mean soil temperature (°C, $N = 4$) at 5- and 20-cm depths on plots receiving only natural rainfall (“unwatered”) and on plots receiving supplemental watering (“watered”).

TABLE 2. Emergence (percentage) of two *P. glandulosa* seedling cohorts (1984 and 1985) and survival (percentage) of the 1984 cohort through 1985 in plots manipulated with respect to soil moisture and the density and level of defoliation of herbaceous plants.

Treatment	Emergence (%)		Survival (%)		
	1984 cohort	1985 cohort	1st year		2nd year
			1984 cohort	1985 cohort	1984 cohort
Watered†	59	62	80	72	84
Normal density†	59	63	82	74	85
No defoliation	58 ^a	60 ^a	82	75	86
Moderate defoliation	56 ^a	65 ^a	80	70	88
Heavy defoliation	62 ^a	63 ^a	85	77	82
Reduced density†	60	62	77	69	82
No defoliation	58 ^a	62 ^a	78	70	88
Moderate defoliation	62 ^a	60 ^a	73	62	80
Heavy defoliation	59 ^a	63 ^a	79	76	78
Unwatered†	42	44	76	66	78
Normal density†	42	46	74	67	75
No defoliation	43 ^b	46 ^b	72	63	78
Moderate defoliation	39 ^b	43 ^b	70	63	75
Heavy defoliation	45 ^b	48 ^b	80	75	75
Reduced density†	41	43	77	65	82
No defoliation	42 ^b	44 ^b	75	67	80
Moderate defoliation	42 ^b	42 ^b	78	66	78
Heavy defoliation	38 ^b	43 ^b	78	62	88
Significance	$P < 0.01$	$P < 0.01$	$P < 0.06$	$P < 0.09$	$P < 0.08$

Notes: For percentage emergence, means within a column followed by different letters were statistically different ($P < 0.05$). There were no significant differences among means within columns for percentage survival. Significance levels for within-cohort full-model ANOVAs are shown at the bottom of each column.

† Pooled means.

TABLE 3. Net photosynthesis (as moles of quanta, $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) of *P. glandulosa* seedlings on six dates in 1985. Seedlings were growing on plots that varied with respect to watering regime, herbaceous plant density, and level of herbaceous defoliation (abbreviations as in Table 1).

Time of day and treatment	Date (1985)					
	3 May	22 May	11 June	2 July	16 July	6 August
0900						
ULH	3.7 ^a (0.8)	9.5 ^a (1.5)	6.2 ^a (1.3)	3.2 ^a (0.5)	3.2 ^a (0.9)	3.5 (0.6)
UNN	8.0 ^b (1.2)	7.2 ^b (0.9)	6.1 ^a (1.0)	4.3 ^a (0.9)	3.5 ^a (0.8)	3.7 (1.1)
WLH	5.0 ^{ab} (0.7)	6.5 ^b (0.5)	14.2 ^b (2.5)	11.7 ^b (2.3)	7.5 ^b (1.5)	3.6 (0.9)
WNN	5.5 ^{ab} (0.9)	6.8 ^b (0.6)	12.1 ^b (2.7)	10.2 ^b (2.6)	8.2 ^b (2.7)	4.8 (1.2)
1200						
ULH	3.5 ^a (0.4)	8.1 ^a (1.8)	5.5 ^a (1.1)	3.3 ^a (1.1)	3.5 ^a (1.1)	1.8 (0.7)
UNN	4.5 ^a (0.6)	7.9 ^a (1.3)	3.3 ^b (0.6)	4.5 ^a (1.6)	4.5 ^a (1.8)	1.7 (0.4)
WLH	7.0 ^b (1.2)	7.4 ^a (1.5)	11.7 ^c (2.6)	9.9 ^b (2.3)	8.1 ^b (2.1)	1.8 (0.5)
WNN	6.5 ^b (1.3)	6.1 ^a (1.4)	10.2 ^c (2.2)	12.3 ^b (3.4)	9.8 ^b (2.8)	0.3 (0.2)
1600						
ULH	0.2 ^a (0.1)	5.4 ^b (1.2)	5.2 ^b (1.3)	0.3 ^a (0.2)	2.8 ^a (0.8)	0.2 (0.0)
UNN	2.1 ^b (0.9)	5.4 ^b (1.6)	2.5 ^a (0.6)	3.2 ^b (1.1)	4.2 ^a (1.3)	0.5 (0.0)
WLH	4.5 ^c (1.4)	8.6 ^a (2.3)	14.6 ^c (3.5)	10.2 ^c (2.7)	7.9 ^b (2.4)	0.1 (0.0)
WNN	4.9 ^c (1.5)	4.4 ^b (1.5)	9.9 ^c (2.6)	13.7 ^c (3.9)	7.8 ^b (2.1)	0.0 (0.0)

Notes: Values are means (± 1 SE) of a minimum of four plants. Within a column, means for a given date-and-time combination followed by the same letter were not significantly different at $P \leq 0.05$; there were no significant differences among means at any time of day on 6 August. ANOVA indicated treatment \times time-of-day interactions were significant ($P \leq 0.05$) at every date; treatment main effects were significant on all but the August date.

moisture levels (Fig. 2) were comparable. However, as water in the soil above 90 cm began to decline through June and July in the unwatered treatments, differences in physiological parameters became significant. Seedlings with supplemental water typically maintained higher levels of A_n (Table 3) and higher Ψ (Table 4), relative to those not receiving supplemental water. Within a watering treatment, density and defoliation of herbaceous vegetation had virtually no influence on A_n or Ψ . By 6 August seedlings on both watered and unwatered plots had begun to shed leaves, even though soil moisture in the watered treatments remained quite high compared to the unwatered plots (Fig. 2). By 20 August, seedlings on both watered and unwatered plots had shed all leaves. Ψ did not differ among treatments until July (Table 4). Predawn Ψ was similar among seedlings regardless of treatment, except on 2 July and 16 July, when soil moisture was at the lowest level in unwatered plots.

Seedling height near the end of the first growing season was statistically comparable between treatments (pooled mean \pm SE for 1984 cohort = 3.6 ± 0.3 cm; 1985 cohort = 3.9 ± 0.4 cm). Aboveground biomass of the 1984 *P. glandulosa* cohort increased 38% between May and August 1985 (Table 5). However, height, leaf area, and aboveground biomass of these seedlings were not significantly different among treatments.

DISCUSSION

The intensity of grass-woody plant interactions should be mediated by resource availability (Scholes

and Archer 1997). However, our field experiments indicated that reductions in grass biomass, achieved by defoliation and density reduction, had minimal influence on *P. glandulosa* emergence, aboveground growth, or survival. In addition, high rates of emergence on unwatered plots occurred even during months and years of substantially below-normal rainfall. Results therefore suggest that emergence and establishment of *P. glandulosa* can potentially occur in most years on this site, regardless of resource availability and livestock grazing pressure on grasses. This experimental evidence is consistent with results of *P. glandulosa* establishment trials in more mesic areas of central Texas, where we observed high rates of emergence (43–60%) and survival (74–97%) in experimental treatments spanning a similar range of aboveground biomass levels (Brown and Archer 1989).

Seedling establishment was not episodic

Discussions of vegetation change in drylands often emphasize event-driven or episodic processes (see Watson et al. 1996). The coefficient of variation of precipitation in the subtropical savannas of southern Texas (35%) is among the highest reported for semiarid regions of the world (Le Houerou and Norwine 1988). Although mean annual rainfall at our study site is 760 mm, tropical depressions and hurricanes in the Gulf of Mexico have generated annual rainfalls as high as 3300 mm. State Climatologist records for Alice, Texas, indicate there have been five years since 1912 when annual rainfall has exceeded 2600 mm (1919, 1935, 1941, 1942, 1971). We therefore hypothesized that establish-

TABLE 4. Xylem water potential (MPa) of *P. glandulosa* seedlings on six dates in 1985. Seedlings occurred on plots varying in their watering regime, herbaceous plant density, and level of defoliation (abbreviations as in Table 1).

Time of day and treatment	Date (1985)				
	3 May	22 May	2 July	16 July	6 August
0600					
ULH	-0.5 (0.1)	-0.5 (0.1)	-1.3 ^a (0.2)	-1.8 ^a (0.4)	-0.3 ^a (0.0)
UNN	-0.5 (0.1)	-0.5 (0.1)	-1.3 ^a (0.3)	-1.4 ^a (0.2)	-0.3 ^a (0.1)
WLH	-0.5 (0.0)	-0.5 (0.1)	-0.3 ^b (0.0)	-0.3 ^b (0.1)	-0.3 ^a (0.1)
WNN	-0.5 (0.1)	-0.5 (0.0)	-0.3 ^b (0.1)	-0.2 ^b (0.0)	-0.3 ^a (0.0)
0900					
ULH	-1.8 (0.2)	-1.3 (0.2)	-4.0 ^a (0.5)	-5.0 ^a (0.6)	-1.0 ^a (0.2)
UNN	-1.7 (0.3)	-1.4 (0.3)	-4.5 ^a (0.4)	-4.1 ^a (0.5)	-2.1 ^b (0.3)
WLH	-1.6 (0.3)	-1.2 (0.2)	-1.4 ^b (0.2)	-1.8 ^b (0.4)	-1.3 ^a (0.3)
WNN	-1.5 (0.2)	-1.3 (0.1)	-1.4 ^b (0.1)	-1.7 ^b (0.3)	-1.2 ^a (0.2)
1200					
ULH	-2.3 (0.3)	-1.8 (0.3)	-4.3 ^a (0.4)	-4.9 ^a (0.5)	-1.6 ^a (0.4)
UNN	-2.4 (0.4)	-1.9 (0.4)	-4.6 ^a (0.5)	-4.1 ^a (0.5)	-2.6 ^b (0.4)
WLH	-1.9 (0.4)	-2.1 (0.4)	-2.8 ^b (0.3)	-2.7 ^b (0.4)	-1.5 ^a (0.3)
WNN	-1.8 (0.3)	-1.9 (0.3)	-2.3 ^b (0.4)	-2.3 ^b (0.3)	-1.6 ^a (0.3)
1600					
ULH	-2.1 (0.3)	-1.6 (0.3)	-4.2 ^a (0.4)	-4.7 ^a (0.4)	-2.2 ^a (0.5)
UNN	-2.0 (0.3)	-1.6 (0.4)	-4.3 ^a (0.3)	-4.1 ^a (0.5)	-2.9 ^a (0.7)
WLH	-1.8 (0.2)	-2.0 (0.4)	-2.4 ^b (0.3)	-2.5 ^b (0.3)	-1.4 ^b (0.5)
WNN	-1.7 (0.4)	-1.9 (0.3)	-2.4 ^b (0.1)	-2.4 ^b (0.2)	-1.3 ^b (0.3)

Notes: Values are means (± 1 SE) of a minimum of three plants. Within a column, means for a given date-and-time combination followed by the same letter are not significantly different ($P \leq 0.05$; there were no significant differences among means at any time of day on 3 May or 22 May). ANOVA indicated significant treatment \times time-of-day interactions on each date; treatment main effects were significant in July and August.

ment of woody plants such as *P. glandulosa* might be confined to such years. However, in our study, rates of *P. glandulosa* emergence on unwatered (natural rainfall only) plots were high (38–48%), even during months and years of substantially below-normal rainfall. This is, perhaps, not surprising, given that *P. glandulosa* is well-adapted to hot desert regions where mean annual rainfall is much lower than that in the central- and southern-Texas portion of its geographic range. In our study, increasing soil moisture enhanced recruitment by increasing seedling emergence rather than seedling survival. Supplemental watering increased emergence by 18%, perhaps by ameliorating soil temperatures. The optimum temperature for *P. glandulosa* germination is 25–30°C (Haas et al. 1973) and soil temperatures in excess of 35°C reduce emergence by retarding imbibition (Scifres and Brock 1969). Temperatures at 5 cm on watered plots were $<32^\circ\text{C}$, whereas temperatures on unwatered plots exceeded 38°C after sowing.

The size and age-class distribution of *P. glandulosa* on this site shows no indication of episodic establishment or mortality (Archer 1989, Boutton et al. 1998) and confirms our experimental assessment that *P. glandulosa* recruitment could have been relatively continuous over the last 100 yr in this bioregion. This contrasts with observations from more arid systems, where establishment of *Prosopis* (Turner 1990; R. E. Miller and L. F. Huenneke, unpublished manuscript) and other woody plants (Harrington 1991, O'Connor 1995a, b, Wiegand et al. 1995) may occur rarely and during years

with unusually high rainfall. Even so, “continuous” recruitment of shrubs in relatively arid systems may be more important than the dogma of “event-driven” or episodic recruitment would suggest (Watson et al. 1997). Management and modeling of grass and woody plant interactions in dryland systems should therefore be cognizant of the need to balance appropriately the effects of infrequent, unpredictable events, as measured at decadal time scales, and the effects of more continuous processes, as measured in time scales of years (Watson et al. 1996). Given the potentially differential effects of increases in atmospheric CO₂ concentration (e.g., Polley et al. 1994, 1996) and changes in rainfall seasonality (Brown et al. 1997) on growth of woody plants and grasses, the reconstruction and extrapolation of woody plant seedling establishment dynamics must be made cautiously.

Herbaceous plants had little effect on Prosopis recruitment

P. glandulosa successfully emerged and established across a broad range (185–453 g/m²) of aboveground herbaceous biomass levels achieved by clipping and by reducing plant density. The fact that *P. glandulosa* seedling gas exchange, water relations, height growth, and survival were minimally influenced by herbaceous manipulation may reflect the ability of *P. glandulosa* quickly to elongate tap roots and access soil moisture beyond the zone effectively exploited by grasses (Brown and Archer 1990). Although seedlings on wa-

TABLE 5. Mean (± 1 SE) height (cm), aboveground biomass (mg), and leaf area (cm²) of *Prosopis* seedlings emerging in July 1984.

Year	Month	Height (cm)	Biomass (mg)	Leaf area (cm ²)
1984	September	3.6 \pm 0.3
1985	May	4.2 \pm 0.7	90.8 \pm 5.7	2.4 \pm 0.2
	August	5.4 \pm 1.1	125.5 \pm 7.8	1.1 \pm 0.4

Notes: There were no significant differences ($P > 0.05$) among density, defoliation, or watering treatments, so data were pooled. Seedlings were not destructively harvested in 1984. Height values represent all seedlings ($N > 400$); biomass and leaf area values taken from plants harvested for gas exchange and water relations data ($N = 50$).

tered plots had higher A_n and Ψ , this did not translate into increased aboveground height, leaf area, or biomass. This may indicate that allocation to root growth is a priority in *P. glandulosa* seedlings over a wide range of resource availabilities. Competition between grasses and *P. glandulosa* seedlings is primarily belowground (van Auken and Bush 1997), so preferential allocation to root development would enable resource partitioning and coexistence of *P. glandulosa* seedlings with grasses early in their life cycle, minimize competitive exclusion, and give seedlings access to deeper, more stable supplies of soil moisture. Similar mechanisms appear to enable successful recruitment of *Pinus radiata* (Sands and Sandian-Nambier 1984) and of oaks (*Quercus* spp.) in semiarid savanna (McPherson 1993, Weltzin and McPherson 1997) and tallgrass prairie (Bragg et al. 1993). Conversely, the inability of woody plant seedlings to extend roots below the depth of grass roots before soil drying can place significant constraints on establishment (Gordon et al. 1989, Williams and Hobbs 1989).

The effects of herbaceous vegetation on woody plant recruitment are variable, and multiple mechanisms can operate in complex ways to influence emergence and establishment (Burton and Bazzaz 1991, De Steven 1991a, b). While grasses may reduce emergence, growth, and survival of woody seedlings (Gordon et al. 1989, Martinez and Fuentes 1993, McPherson 1993), including *P. glandulosa* (Bush and van Auken 1989, 1995, van Auken and Bush 1989, 1997, Polley et al. 1994), the competitive reduction may not be large, and high mortality or complete exclusion may seldom occur. For example, Schmidt and Stubbendieck (1993) found that although survival of evergreen tree (*Juniperus virginiana*) seedlings was highest in grazed pastures (57%), survival of seedlings in pastures that had not been grazed for >50 yr was still 40%. In South African grasslands, *Acacia karroo* seedlings were capable of establishing and surviving within dense grass swards (O'Connor 1995a). In Argentinean grasslands, survival and growth of *P. caldenia* seedlings on sites protected from grazing exceeded that of seedlings on sites subjected to long-term heavy grazing (Distel et

al. 1996). In the Post Oak Savanna of central Texas, *Prosopis* seedling emergence was low (6–8%), but not nil, on plots protected from grazing for 40 yr (Brown and Archer 1989), and only moderate defoliation of grasses was required to produce an eight-fold increase in emergence. Subsequent survival of all seedlings exceeded 80%, implying that thresholds for biotic regulation of *Prosopis* emergence and establishment (Archer 1989, 1995a) are exceeded at low levels of herbaceous disturbance.

Traditional rangeland management practices are predicated on the notion that “proper grazing” can minimize woody plant invasion problems. The implicit assumption is that adjusting stocking rates to maintain grass composition, cover, and biomass will minimize tree and shrub encroachment. The results from numerous grass–shrub seedling competition container experiments cited earlier substantiate this assumption. However, data from this field competition experiment and others (e.g., Brown and Archer 1989, Goerner 1993, Schmidt and Stubbendieck 1993, O'Connor 1995a, Weltzin et al. 1997, Brown and Carter 1998) suggest grazing management strategies to mitigate invasion by unpalatable woody plants should not focus on grass–shrub seedling interference, but instead on minimizing seed dispersal (in the case of leguminous shrubs where livestock may be primary vectors) and on maintaining an effective fire regime.

In summary, the results of our field experiments concur with field observations that indicate woody plant encroachment into grasslands can be high, regardless of grazing pressure or herbaceous composition and biomass (Brown 1950, Paulsen 1950, Humphrey and Mehrhoff 1958, Smith and Schmutz 1975, Bragg and Hulbert 1976, Meyer and Bovey 1982, Hennessy et al. 1983, Towne and Owensby 1984, Smeins and Merrill 1988). Grass utilization by grazing animals may not be a prerequisite for woody plant encroachment, except as described below.

Why has *Prosopis* abundance increased in recent history?

Given the relative ease of establishment and the high survival rates of woody plants such as *P. glandulosa* in grassland and savanna systems, why has their abundance increased only recently? The spread of *P. glandulosa* into Holocene grasslands may have been limited by a lack of effective dispersal agents, a constraint overcome by the introduction of horses, cattle, and sheep into North America (Brown and Archer 1987). Alternatively, *P. glandulosa*, which is capable of vegetative regeneration within 2 wk of germination (Scifres and Hahn 1971), tolerant of repeated top removal during its first growing season (Weltzin et al. 1998), and tolerant of hot fires by its second and third year of growth (Wright et al. 1976), may have always been present in southwestern grassland landscapes as a “seedling bank,” but its dominance suppressed by pe-

riodic fire. Reductions in fire frequency and intensity resulting from reductions in fine fuel mass and continuity associated with heavy, continuous livestock grazing (Baisan and Swetnam 1990, Savage and Swetnam 1990, Covington and Moore 1994) would then have allowed established, but suppressed, woody plants such as *P. glandulosa* to increase in stature, express dominance over the surrounding herbaceous vegetation, and attain seed-bearing size. In the absence of fire, *P. glandulosa*'s expansion into mesic and semiarid grassland with a history of livestock grazing may be regulated more by rates and patterns of seed dispersal and the presence or absence of "seedling predators" (Weltzin et al. 1997) than by abiotic conditions or herbaceous competition.

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