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Woody invasion of grasslands: evidence that CO_2 enrichment indirectly promotes establishment of *Prosopis glandulosa*

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Abstract

Grasslands worldwide have been invaded by woody species during the last 200 years. Atmospheric CO_2 enrichment may indirectly have facilitated invasion by reducing soil water depletion by grasses. We used a two-step correlative approach to test this hypothesis with the invasive and native shrub honey mesquite (*Prosopis glandulosa* Torr. var. *glandulosa*). 1) Water content to 0.15 m depth was measured in grassland exposed to a CO_2 gradient from 200 to 550 μmol/mol to evaluate the prediction that CO_2 enrichment lessens soil water depletion by grasses. 2) Soil water content and emergence and survival of mesquite seedlings were measured in adjacent grassland plots from which grass roots were excluded to 0.15 m depth to reduce water depletion or that were irrigated to increase soil water levels. With these measurements, we tested the hypothesis that mesquite establishment is limited by water. Excluding grass roots doubled emergence of mesquite and almost tripled the fraction of emergent seedlings that survived for 12 weeks following the first of two plantings. Seedlings were taller, heavier, and had greater leaf area when grown without grass roots. Root exclusion did not measurably affect soil water during the 3-week period of seedling emergence, but soil water content over the 12 weeks that seedling survival was studied was higher in plots from which grass roots were excluded and following an April than May planting. Survivorship of mesquite seedlings correlated positively with soil water content. Percentage survival of seedlings increased from 1.5% to 15% and 28% at the soil water content measured in grassland exposed to CO_2 concentrations of 270 (preindustrial), 360 (current), and 550 μmol/mol (future), respectively. We infer that recent and projected increases in atmospheric CO_2 concentration may be large enough to increase establishment of invading mesquite seedlings in grasslands that are severely water-limited.

Introduction

Invasion of the world's grasslands by woody species is among the dominant ecological changes of the last two centuries (reviews by Mayeux et al. (1991); Archer (1994)). Consequences range from a decrease in livestock production to changes in processes affecting carbon sequestration (McPherson et al. 1993), nutrient accumulation and cycling (Stock et al. 1995) and regional climate (Schlesinger et al. 1990). Woody invasion has been attributed to land use changes, including the introduction of large numbers of domestic livestock (Harrington 1991; Bahre and Shelton 1993; Archer 1994), fire suppression (Johnston 1963; Burkhardt and Tisdale 1976), and elimination of native herbivores (Belsky 1984; Weltzin et al. 1997), acting alone or in combination with atmospheric CO_2 enrichment (Mayeux et al. 1991; Polley et al. 1996a; Bond and Midgley 2000) and climatic change (Neilson 1986; Brown et al. 1997). Although diverse, these factors could contribute to woody ingress via only three general mechanisms. Changes could 1) facilitate dispersal of woody seed (livestock), 2) lessen the frequency or intensity of disturbances that kill woody

seedlings (fire suppression, eradication of native herbivores), or 3) improve woody establishment and growth by reducing resource depletion (interference) by grasses or by lessening effects of interference or of environmental constraints on woody performance (overgrazing, CO_2 enrichment, climatic change).

Debate over primary causes of woody ingress continues (Bahre and Shelton 1993; Archer et al. 1995), partly because of uncertainty as to whether existing vegetation is a significant deterent to invasion. If grasses usually pose only a minor barrier to invasion, grazing and other factors that reduce grass biomass cannot be a primary cause of woody ingress. If, on the other hand, woody establishment is resource- or interference-limited, CO_2 enrichment and other factors that modify the extent to which grasses deplete essential resources will affect vegetation dynamics independent of dispersal rates.

Honey mesquite (*Prosopis glandulosa* Torr. var. *glandulosa*) is an aggressive native invader of grasslands in the southwestern United States and northern Mexico that has increased greatly in abundance and visibility in these regions during the last two centuries (Johnston 1963; Archer 1989). The leguminous shrub now is the dominant woody plant on about 45 million ha of grazing lands that vary in annual rainfall from less than 200 mm to about 1000 mm (Johnson and Mayeux 1990; McPherson 1997).

Mesquite can establish in ungrazed grassland, but emergence, survival, and early growth of seedlings usually is low (Meyer and Bovey 1982; Brown and Archer 1989; Bush and Van Auken 1990; Van Auken and Bush 1997) because of inference from grasses for both light (Brown and Archer 1989; Bush and Van Auken 1990) and soil resources (Van Auken and Bush 1997). Depletion of soil water may be a particularly important mechanism by which grasses limit establishment of mesquite (Ueckert et al. 1979), although this has not been widely tested (but see, Brown and Archer (1999)). There is evidence, however, that other woody seedlings encounter severe interference from grasses for water (Harrington 1991). Woody establishment in arid environments is correlated with rainfall and with soil water availability (O'Connor 1995; Jeltsch et al. 1997) and occurs in pulses following large precipitation events (Williams and Hobbs 1989; Turner 1990). Carbon dioxide enrichment and other factors that reduce transpiration rates and soil water depletion on grasslands (Field et al. 1997; Owensby et al. 1997; Morgan et al. 1998; Niklaus et al. 1998) could, therefore, lessen water limitation to

establishing seedlings and indirectly improve woody establishment (Polley et al. 1997).

We tested the hypothesis that CO_2 enrichment indirectly promotes woody establishment in grassland by reducing water depletion by herbaceous vegetation. To minimize disruptive treatment applications in a long-term CO_2 experiment, we used a two-step, correlative approach to test the hypothesis. 1) We tested the prediction that CO_2 enrichment reduces soil water depletion by herbaceous plants by measuring mean volumetric water content over 0–0.15 m depth in grassland exposed to a gradient in CO_2 concentration from 200–550 μmol/mol. 2) We tested the prediction that increasing water availability increases mesquite establishment by simultaneously measuring soil water content and emergence and survival of mesquite seedlings in adjacent grassland plots from which roots of grasses were excluded to 0.15 m to reduce water depletion or that were irrigated to increase soil water. Strong limitation by light generally is believed to minimize plant response to changes in soil resources, so we studied seedling performance in both undisturbed grassland and in plots in which uppercanopy leaves of grasses were removed to increase light penetration to the soil surface. The initial hypothesis, that CO_2 enrichment could facilitate woody recruitment by reducing soil water depletion on grassland, would find correlative support if woody establishment was limited by water and CO_2 enrichment reduced water depletion by grasses. Mesquite plants apparently are most vulnerable to drought and other factors as young seedlings (Brown and Archer 1989), so we restricted our study to the three months following seed dissemination.

Methods

Site characteristics

This study was conducted during 1998 in a grassland in Bell County, Texas, USA (31°05′ N, 97°20′ W) from which cattle had been excluded for 5 years. Soils at the study site are classified as fine-silty, carbonatic, thermic Udorthentic Haplustolls. The surface 0.4 m of soil is composed mostly (55%) of clay. Vegetation is dominated by the perennial C_4 grass *Bothriochloa ischaemum* (L.) Keng, var. *songarica* (Rupr.). This variety of *B. ischaemum*, introduced to the USA from China in 1917, and the more wintertolerant variety *ischaemum* have been extensively

planted to reclaim marginal farmland and to increase forage production in the southern Plains of the United States (Sims and Dewald 1982). An estimated 2 million ha in Oklahoma and Texas, USA have been planted to these Old World bluestems (Berg and Sims 1995).

An average of 45% of mean annual precipitation at the site (879 mm, 85 year record) falls during the 5-month period included in this study (April through August). Precipitation during this period in 1998 (38.6, 22.6, 13.2, 32.3, and 57.9 mm for the months of April, May, June, July, and August, respectively) was 42% of the 85-year mean. Monthly mean temperature increased from 18.9 to 30.8 °C from April to July 1998. Mean temperatures for the months of May, June, and July (25.7, 29.2, and 30.8 °C) were 2.0–2.5 °C higher than the 85-year mean.

Experimental design

Nine blocks (each 1.2 m × 2.7 m) were established in grassland that was a near monoculture (ca. 90%) of *B. ischaemum* during March 1998. Blocks were separated by 1 m walkways, and were arranged in a 3 by 3 grid with the long axis of each block oriented along a north-south trajectory. Three treatments were assigned to each block in a split-split plot design (Figure 1). Treatments applied to the 6 blocks on the east of the 3 by 3 grid of blocks included 2 light levels at the soil surface (low, high), 2 planting dates (April, May), and 2 root exclusion treatments (none, roots of grasses excluded to 0.15 m depth with 0.15 m diameter pipe). Light and planting date treatments described above were applied to the remaining 3 blocks, but root exclusion treatments were replaced in these blocks by 2 irrigation regimes (0, 500 ml applied weekly to 0.15 m diameter plots). It was anticipated that soil water content would differ more consistently between irrigation than root exclusion treatments, necessitating fewer replications of irrigation treatments to establish statistical significance.

In split-split plot designs as used here, areas to which a treatment are applied are divided into units to which additional treatments are applied. Light treatments in this study were divided into planting date treatments which were divided in turn into root exclusion or irrigation treatments. Each block was divided into two 1.2 m × 1.35 m areas to which the 2 light treatments were randomly applied. Photosynthetic photon flux density (light) at the soil surface and above the plant canopy in each 1.2 m × 1.35 m
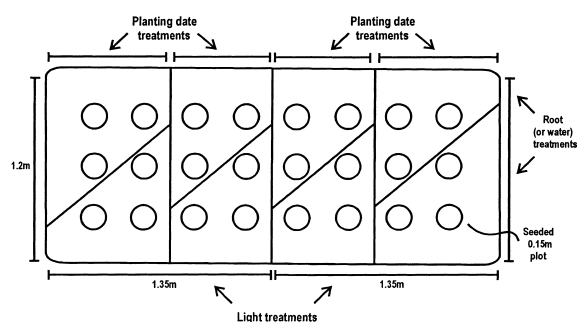

Figure 1. Diagram illustrating the spatial application of light, planting date, and root exclusion or irrigation treatments in 1 of 9 experimental blocks in *Bothriochloa ischaemum* grassland. Circles denote 0.15-m diameter plots in which 5 mechanically-scarified seeds of *Prosopis glandulosa* (honey mesquite) were planted.

area was measured at mid-day on clear days in April and June 1998 by placing a 1 m long probe containing silicon photodiodes (SunScan, Delta-T Devices, Ltd.) diagonally across each area. Light at the soil surface in undisturbed vegetation, the low light treatment, averaged 6.0 ± 0.4 (SE) % ($\bar{x}$ = 109 μmol(photon) m^{-2} s^{-1}) and 8.3 ± 1.9% ($\bar{x}$ = 171 μmol m^{-2} s^{-1}) of that measured above the canopy in April and June ($\bar{x}$ = 1820 and 2055 μmol m^{-2} s^{-1}), respectively. Standing dead and green leaves were clipped from upper plant canopies in areas assigned to the high-light treatment to increase light at the soil surface to a mean of 18.9 ± 0.8% ($\bar{x}$ = 344 μmol m^{-2} s^{-1}) and 15.0 ± 1.1% ($\bar{x}$ = 309 μmol m^{-2} s^{-1}) of that above the canopy in April and June, respectively. Areas assigned to each light treatment were split into two 1.2 m × 0.68 m units, and were randomly assigned to mid-April or mid-May planting dates to assess possible temporal effects on mesquite establishment. Areas assigned to planting date treatments were divided diagonally, and were randomly assigned to root exclusion treatments (6 blocks) or to irrigation treatments (remaining 3 blocks).

Three circular plots (0.15 m diameter) were marked in areas assigned to each root exclusion or irrigation treatment (Figure 1), yielding a total of 6 circular plots per planting date treatment, 12 plots per light treatment, and 24 plots per block (8 plots in each of 3 rows). Centers of adjacent circular plots were separated by 0.3 m. Plot centers were 0.3 m from block edges. Lengths of 0.15 m diameter polyvinylchloride pipe were driven 0.15 m into soil to exclude roots of neighboring grasses. Grasses that remained within these 0.15 m plots were killed with herbicide

(glyphosate [N-(phoshonomethyl) glycine]). Pipe was inserted 2 weeks before the April planting to minimize changes in nutrient availability that result from decay of severed roots over longer periods. Other circular plots were marked with short (10 mm long) pieces of 15 cm diameter pipe on the soil surface.

Volumetric soil water content over 0–0.15 m depth was measured weekly using time domain reflectometry (TDR). Single-diode probes with two stainless steel wave guides spaced 10 mm apart were installed vertically into soil. A single probe was placed in 1 circular plot exposed to each combination of treatments in each of 6 of the total of 9 blocks studied (4 blocks with root exclusion treatments and 2 blocks with irrigation treatments). Propagation time of electromagnetic waves through these permanently installed probes was measured with a MoisturePoint MP-917 instrument (Environmental Sensors Inc., Victoria, Canada). An empirical equation from Topp et al. (1980) was used to calculate volumetric water content of soil from these measurements. Calculations from the TDR technique were corrected to volumetric water content determined gravimetrically using a linear regression developed from measurements in soil adjacent to experimental blocks ($r^2 = 0.66$, n = 32).

Honey mesquite seeds (n = 5), collected the previous year from an isolated *P. glandulosa* tree, were mechanically-scarified and placed just below the soil surface (approximately 5 mm depth) in each 0.15 m diameter circular plot assigned to early planting on April 15, 1998 and in each circular plot assigned to late planting on May 13, 1998. Emergence from a subsample of 50 scarified seeds planted in moist soil in a greenhouse was 98%. Plots were surveyed 1 week after planting, then twice weekly thereafter. Emergent seedlings were marked with plastic picks, and the number of surviving seedlings per plot was recorded. Percentage emergence of mesquite seedlings equaled the percentage of seeds disseminated that emerged. Seedling survival was calculated for each sampling date as a percentage of the number of emergent seedlings. Surviving seedlings were destructively harvested 12 weeks after planting by clipping at ground level. Stem height from the cotyledonary node and leaf area per seedling were then measured.

Following the final harvest of mesquite seedlings, aboveground tissues of *B. ischaemum* were clipped at ground level from the 1.2 m × 0.68 m areas of each block in the late planting treatment. To estimate belowground biomass of *B. ischaemum*, soil cores (0.055 m diameter × 0.3 m deep) were taken from each of 2 circular plots that had been seeded with mesquite in each root exclusion × light treatment per block (total of 6 blocks). Cores were divided into two 0.15 m lengths. Roots were then separated from soil by hand. All plant material was weighed after oven drying at 60 °C for 72 h.

Soil water along a CO_2 gradient

To determine effects of CO_2 enrichment on soil water, we measured volumetric water content over 0–0.15 m depth in *B. ischaemum*-dominated grassland located 20 m to the east of seed-addition plots. As part of a long-term experiment, this grassland was exposed during daylight to a uniform gradient in CO_2 concentration from 550-200 μmol/mol in 2 tunnel-shaped chambers aligned parallel to each other along a north to south axis. The 2 chambers each are 1 m wide and tall, and are composed of ten 5-m long compartments in which aerial growth of vegetation is enclosed in a transparent polyethylene cover (Johnson et al. 2000). During daylight, photosynthesis of enclosed vegetation depletes the CO_2 concentration of air as it is moved by blowers from the air intake to the outlet of each chamber. The desired CO_2 gradient is maintained by automatically adjusting the rate of air flow through each chamber in response to changes in light and net CO_2 uptake by vegetation. A continuous gradient in CO_2 concentration from 550 to 350 μmol/mol is maintained in one chamber. A CO_2 gradient from 360 to 200 μmol/mol is maintained in the other chamber. The direction of air flow in each chamber is reversed at night, and night-time CO_2 concentrations are regulated at 150 μmol/mol above daytime values along each chamber. The CO_2 concentration in each 5-m compartment along chambers is measured every 20 min. Mean values of daytime CO_2 concentration for each of the ten 5-m long compartments in each chamber were calculated from these measurements. *Bothriochloa ischaemum* comprised 43% and 58% of total aboveground biomass in superambient and subambient chambers, respectively, at the end of the previous growing season.

Five-m compartments in chambers are separated by ducts with chilled-water cooling coils that are used to reset air temperature and dew point to values measured outside chambers. Soil in each of the 20 compartments is isolated to a depth of 0.9 m from surrounding soil with a rubber-coated fabric. Water was

added through a surface irrigation system to match precipitation.

Two or three multiple-diode TDR probes (type K, Environmental Sensors Inc., Victoria, Canada) are installed vertically into soil to 0.6 m depth in each 5-m compartment. By incorporating multiple diodes, probes provide for measurements of volumetric soil water content averaged over 0.15-m increments over the 0.6-m length. Propagation time of electromagnetic waves through probes was measured with a Moisture-Point MP-917 instrument (Environmental Sensors Inc., Victoria, Canada). Here, we analyze soil water content in the surface 0.15 m of soil in each of the 15 compartments along the CO_2 gradient in which *B. ischaemum* contributed >40% of total aboveground biomass at season's end in 1997.

Statistical analyses

Light, planting date, and root exclusion treatments were applied to seeded areas in a split-split plot design. Planting date treatments (2) were nested within light treatments (2). Root exclusion treatments (2) were nested within planting dates. We tested for treatment main effects and interactions on average soil water content (0–0. 15 m) over 3 and 12 week-periods following planting and on seedling characteristics and root biomass of grass with an analysis of variance (ANOVA) that accommodated the split-split plot design. A repeated-measures ANOVA was used to analyze treatment effects on soil water content over different periods to account for the correlation between successive water measurements. The effect of manipulations employed to impose light treatments on aboveground biomass of the grass *B. ischaemum* was analyzed with a univariate ANOVA. Treatment main effects and interactive effects on seedling emergence and survival were tested with a categorical ANOVA (Agresti 1996). Tests of hypotheses were evaluated using a generalized linear model similar to that used in ANOVA of continuous variables. A single value of percentage emergence and percentage survival was calculated for each set of three 0.15-m diameter plots in each root exclusion or irrigation treatment for use in this analysis. Soil water content over the first 3 weeks and full 12 weeks of measurements following each planting date was used in correlations with emergence and survival, respectively.

Table 1. Root biomass (grass + mesquite) and characteristics of 12-week-old mesquite seedlings from the April (early) planting in plots from which living grass roots were excluded to 0.15 m depth or present (n = 12 plots). Statistical significance of differences between root exclusion treatments is indicated by the P-value.

Parameter	Grass roots		
	Present	Excluded	P value
	Root biomass		
0–0.15 m depth (g/m²)	99.2	49.5	0.03
0.15–0.30 m depth (g/m²)	22.0	37.0	0.12
	Mesquite seedlings		
Height from cotyledons(cm)	4.9	7.0	0.03
Leaves/plant	5.5	7.2	0.06
Leaf area (cm²)	4.0	6.6	0.05
Aboveground biomass (g)	0.033	0.058	0.01

Results

Biomass of the dominant grass

Aboveground biomass of *B. ischaemum* was 15% greater in treatments with low light at the soil surface than in those with high light at the soil surface (866 and 754 g/m²). Root biomass in the surface 0.15 m of soil was greater in undisturbed soil than in plots from which grass roots were excluded with pipe (Table 1). Root biomass over 0.15–0.30 m depth, however, did not differ between root exclusion or light treatments.

Seedling emergence and survival

Of the treatments applied, manipulation of light least affected seedling performance. Light levels beneath the closed grass canopy were within the range of values reported to greatly reduce mesquite establishment (6–8% of sunlight), but the small differences in light produced by our treatment had minimal effect on seedlings. There were no significant interactions among light, planting date, and root exclusion or irrigation treatments for parameters measured.

Ninety-two percent of seedlings emerged within 3 weeks of planting. Emergence was higher by more than a factor of 3 following the April than May planting (P < 0.0001), and was more than doubled by excluding grass roots (P < 0.0001; Figure 2). Interactions among treatments were not significant. Excluding grass roots almost tripled the fraction of emergent seedlings that survived the April planting (53% vs. 19%; P = 0.01). So few seedlings emerged from plots
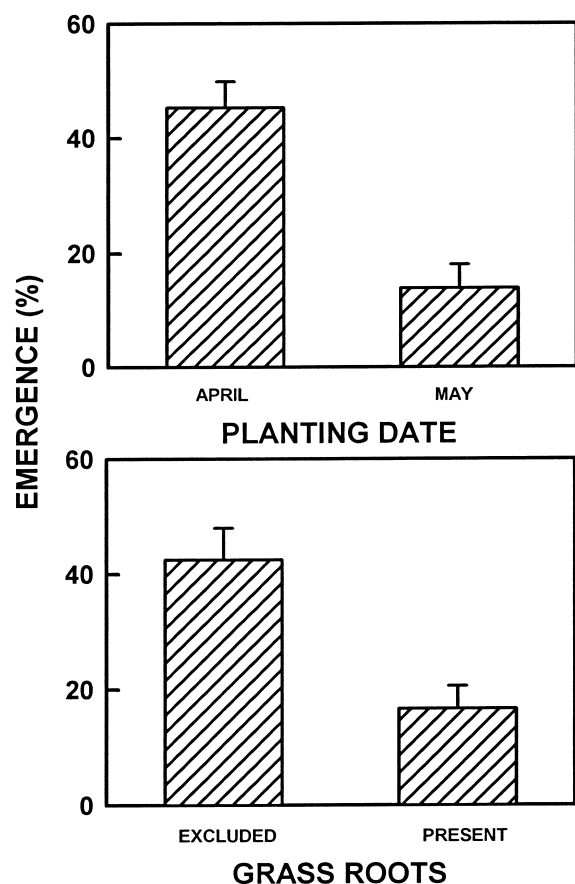
Figure 2. Emergence of mesquite seedlings by planting date (upper panel) and in plots from which grass roots were excluded to 0.15 m depth or present (lower panel). Error bars indicate 1 SEM, n = 24.

with neighbor roots at the May planting (seedlings emerged from only 2 of 180 seed) that it was not meaningful to compare survival between root treatments. Percentage survival was slightly higher among seedlings that emerged after the April than May planting (41% and 34%, respectively), but this difference was not significant (P = 0.14). As a result of both greater emergence and higher survival, the number of surviving seedlings from the April planting was higher by a factor of 5 in plots from which roots were excluded than in those in which grass roots were present (56 and 11 seedlings, respectively). Excluding grass roots increased the number of seedlings from the May planting by a factor of 7.5 (15 and 2 seedlings, respectively).

Excluding grass roots also increased the size of surviving seedlings (Table 1). Seedlings harvested 12 weeks after the April planting were taller, heavier, and had more leaves and greater total leaf area when grown without grass roots. Light treatment had no significant effect on seedling size. Few seedlings survived the May planting, so treatment effects on size could not be analyzed meaningfully.

Effects of planting date and root exclusion on soil water

Treatments did not affect water content of the upper 0.15 m of soil during the 3 weeks following either planting, the period of seedling emergence (treatment means varied between 27.4% and 28.4% volumetric water content, n = 16). Soil water content averaged over the 12 weeks that seedling survival was studied was slightly, but significantly, higher following the April than May planting (P = 0.02) and in plots from which roots were excluded than in those in which grass roots were present (P = 0.006; 25.3% and 23.9% volumetric water content for both comparisons, n = 16). Effects of root exclusion treatments on soil water content differed marginally between the time periods considered (P = 0.07). Across planting dates, volumetric water content was lower when averaged over 12 weeks than over the 3 weeks following planting. The decrease in mean water content over time was greater in plots in which grass roots were present (from 28.3% to 23.9%, n = 16) than in those from which roots were excluded (from 27.4% to 25.3%, n = 16). Percentage survival was positively correlated with the 12-week average of soil water content across planting dates and root exclusion treatments in plots in which 4 or more seedlings emerged (Figure 3).

Effects of irrigation on seedlings and soil water

Irrigation did not affect emergence at the April planting, but tripled emergence following the May planting (irrigation × planting date interaction, P = 0.008; Figure 4). Survival following the April planting was not affected by irrigation (P = 0.33), but survival was higher (P = 0.03) by a factor of 2 at high than low light (33.3% and 14.8% survival, respectively). None of the 32 seedlings that emerged from the May planting survived for 12 weeks. Plots to which water was added tended to be slightly wetter, especially during the 3-week period of seedling emergence (25.5% vs. 24.5% volumetric water content for irrigated and control plots, respectively), but differences in soil water content were not significant (P = 0.55).
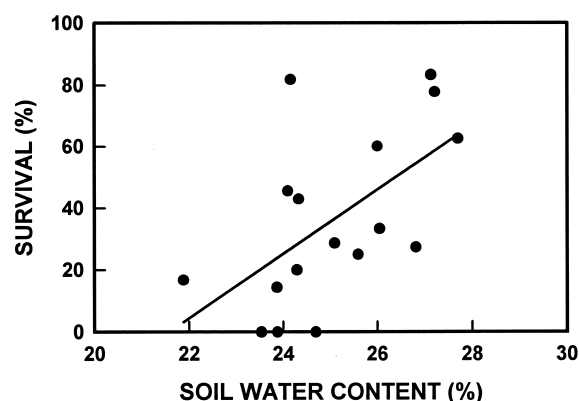
Figure 3. Relationship of percentage survival of emergent mesquite seedlings to mean soil water content (0–0.15 m depth) over 12 weeks following planting. Included are data from the two planting date and root exclusion treatments in which 4 or more seedlings emerged. The line is a linear regression fit to data (% survival = −224.61 + 10.41 * % soil water, r^2 = 0.34, P = 0.01, n = 17).
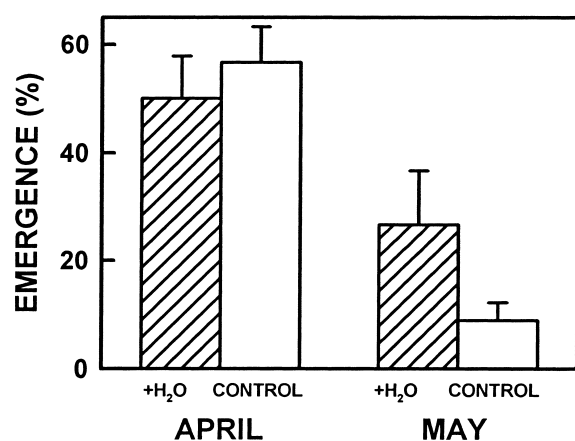

Figure 4. Emergence of mesquite seedlings by planting date in 0.018 m^2 plots to which 0 ml (control) or 500 ml of water was added weekly (+H_2O). Error bars indicate 1 SEM, n = 6.

Effects of CO_2 enrichment on soil water

Mean soil water content over the 3-month period beginning May 14, 1998 was calculated for the 15 five-m compartments along the CO_2 gradient in which *B. ischaemum* dominated, as it did in plots to which mesquite seeds were added. The relationship of soil water content to CO_2 concentration was best described with a hyperbola (r^2 = 0.56, P = 0.006; (Figure 5)). Greatest increase in volumetric water content occurred over subambient CO_2 concentrations. Indeed, the 1.3% increase in soil water content over preindustrial to current CO_2 concentrations (270–360 μmol/mol) matched the increase from 360 to 550
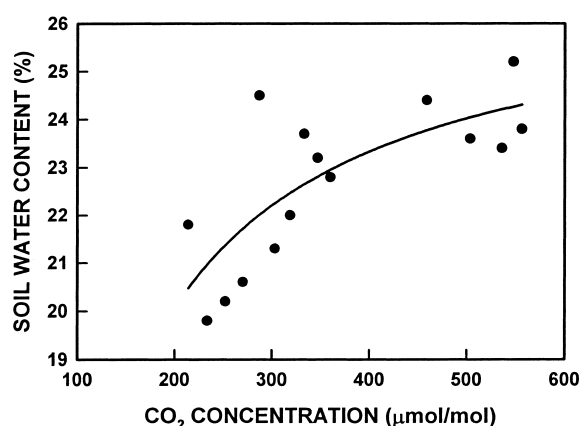

Figure 5. Relationship between mean volumetric water content (0–0.15 m depth) over a 3-month period (May–August) in 1998 and atmospheric CO_2 concentration in *Bothriochloa ischaemum* grassland. The line is a hyperbolic fit to data (% soil water = ((−56.11 + 1.496 * CO_2)/(1 + 0.0556* CO_2)), r^2 = 0.56, P = 0.006, n = 15 means). Each point is the average of 2–3 independent measurements on each of 13 dates.

μmol/mol CO_2. As calculated from regression (Figure 5), soil water content in grassland exposed in elongated chambers to the current CO_2 concentration was 23.0%. This value was similar to that measured in the plots with *B. ischaemum* roots present to which mesquite seeds were added (23.9%).

Discussion

Grasslands have experienced numerous changes during the last two centuries, but invasion by woody plants is among the most obvious and, perhaps, most important (Mayeux et al. 1991; Archer 1994). Debate over the role of rising CO_2 concentration and, indeed, of other factors in woody ingress continues (Archer et al. 1995), partly because of uncertainty as to whether existing vegetation poses a significant barrier to invasion (Brown et al. 1998).

We hypothesized that CO_2 enrichment could indirectly promote woody establishment by slowing soil water depletion by herbaceous vegetation. Implicit in this hypothesis is the assumption that water depletion by grasses is a significant deterent to woody recruitment in our relatively-mesic grassland, as it is in other systems (Knoop and Walker 1985; Harrington 1991; O'Connor 1995; Polley et al. 1997; Davis et al. 1998). Grass reduced mesquite establishment, but did not exclude the shrub, even during the very dry year of this study. Interference in the upper 0.15 m of soil

from *B. ischaemum* roots decreased seedling establishment by about 80% and reduced aboveground biomass of surviving seedlings by 40%. Grasses did not have the hypothesized effect on soil water during the initial 3-week period of mesquite emergence, but reduced average soil water content during the 12 weeks that seedling survival was followed. That soil water was not affected by grasses during mesquite emergence was surprising, for surface soils usually were moister to the touch in plots from which grass roots were excluded. Perhaps, measurements integrated over 0–0.15 m depth underestimated changes in water content at the soil surface. Consistent with this possibility is the observation that irrigation greatly improved emergence at the May planting, but had no measurable effect on soil water content. For the full period studied, however, both soil water content and seedling establishment were higher in plots from which grass roots were excluded than in those with roots present. Across planting date and root exclusion treatments, survival of mesquite seedlings correlated positively with soil water content.

Correlative support for our initial hypothesis that CO_2 enrichment indirectly facilitates woody recruitment also requires evidence that higher CO_2 concentrations increase soil water content sufficiently to improve seedling establishment. Over both subambient and superambient CO_2 concentrations, soil water content over 0–0.15 m depth increased through values that altered seedling survival. Soil water content at the current CO_2 concentration averaged 23.0%. At this water content, we calculate from the linear regression of seedling survival on soil water (Figure 3) that only 15% of emergent mesquite seedlings survived. Soil water content at the preindustrial CO_2 concentration of 270 μmol/mol averaged 21.7%, a level at which fewer than 1.5% of seedlings in adjacent plots survived. Survivorship increased to 28% at the soil water content (24.3%) measured in grassland exposed to 550 μmol/mol. During the dry period of this study, recent plus projected increases in atmospheric CO_2 concentration increased soil water content sufficiently to improve survivorship of mesquite seedlings. To our knowledge, this is the first field evidence, albeit correlative evidence, that CO_2 enrichment could indirectly promote woody establishment. Care should be taken not to extrapolate results too greatly, however, because we considered only one aspect of population demography for only a short period. We do not know, for example, if CO_2 enrichment will influence growth rates or fecundity of es-

tablished mesquite, either directly or indirectly via changes in woody-grass competition. The extent to which CO_2 enrichment affects soil water content also may vary. In tallgrass prairie, for example, higher leaf temperatures (Kirkham et al. 1991) and greater leaf area (Owensby et al. 1993) sometimes negated expected savings in soil water at elevated CO_2.

Whether relatively small and early increases in seedling survivorship accelerate woody invasion also depends on whether seedling mortality rates remain high following the initial 3-month period of establishment. Seedlings may have died of water stress or grasses may have competitively displaced mesquite had our experiment continued beyond 3 months, but available evidence suggests that this is not likely. Mortality usually is greatest during initial establishment. Only 3 to 48% of mesquite seedlings survived for 4 months during a dry year in western Texas, USA, whereas survivorship of initial seedlings after 2 years ranged from 0 to 17% (Ueckert et al. 1979). Because mesquite seedlings can grow rapidly (Tischler et al. 1996), survival of larger seedlings may become mostly uncoupled from effects of resource depletion by grasses (Brown and Archer 1989, 1990). Measurements of predawn water potentials on seedlings may aid in defining the period over which mesquite is most sensitive to manipulation of root interference from grasses and other treatments that affect soil water content.

Our experiment was conducted during a very dry year when volumetric water content approached the minimum to which plants deplete water in the heavy clay soil studied (about 20% volumetric content) and at which mesquite seedlings survive. During most years, soil water content probably exceeds the minimum required for mesquite establishment. Our results thus concur with those of Brown and Archer (1989, 1999) in indicating that establishment of honey mesquite may ultimately be dispersal-limited in this mesic portion of the shrubs' range. Unless eliminated by fire or herbivores, honey mesquite apparently could spread rapidly in *B. ischaemum*-dominated grasslands when limitations on dispersal are overcome. Because water limitation is more frequent in drier parts of mesquite's range, woody establishment should be more sensitive to CO_2 concentration and other factors that influence how quickly grasses use soil water in these drier areas.

Although grasses did not exclude honey mesquite, interference from grasses significantly slowed growth of surviving mesquite seedlings. Grasses may, there-

fore, prolong the period during which woody seedlings are most vulnerable to herbivores and fire (see also, Van Auken and Bush (1997); Weltzin et al. (1998)). It has been predicted that the intensity of belowground interference should decline as aboveground biomass and competition for light increase (e.g., Wilson and Tilman (1995)). Light at the soil surface approached values reported to reduce establishment of mesquite (Brown and Archer 1989). Under these conditions, at least, belowground interference remained a significant control on mesquite establishment.

The correlative approach taken in this study of woody recruitment provides insight into a possible indirect effect of CO_2 enrichment, but obviously does not fully address the role of atmospheric CO_2 concentration in woody plant establishment. Direct tests of CO_2 effects on recruitment and other aspects of woody plant dynamics clearly are preferable for this latter objective, but must be limited in long-term CO_2 studies to minimize disruptive treatment applications. Correlative studies do not, for example, account for direct positive effects of CO_2 enrichment on seedling survivorship. Doubling CO_2 concentration doubled percentage survival of mesquite seedlings that were exposed to similar rates of soil water depletion in glasshouse studies (Polley et al. 1996b, 1999). It is possible, therefore, that CO_2 enrichment could benefit water-limited mesquite more than suggested here.

Effects of grasses on woody establishment vary through time and in space, and operate through a variety of mechanisms (Scholes and Archer 1997). By reducing water limitation to establishing seedlings, the continuing rise in atmospheric CO_2 concentration could facilitate mesquite establishment on dry grasslands and reinforce overgrazing, seed dispersal, and fire suppression in promoting mesquite invasion. This indirect benefit of CO_2 to water-limited seedlings likely is small in mesic grasslands in most years, but could be more important in dry grasslands and shrublands.

Acknowledgements

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