Carbon dioxide enrichment improves growth, water relations and survival of droughted honey mesquite(*Prosopis glandulosa*) seedlings

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Summary   Low water availability reduces the establishment of the invasive shrub *Prosopis* on some grasslands. Water deficit survival and traits that may contribute to the postponement or tolerance of plant dehydration were measured on seedlings of *P. glandulosa* Torr. var. *glandulosa* (honey mesquite) grown at CO_2 concentrations of 370 (ambient), 710, and 1050 µmol mol^{-1}. Because elevated CO_2 decreases stomatal conductance, the number of seedlings per container in the elevated CO_2 treatments was increased to ensure that soil water content was depleted at similar rates in all treatments. Seedlings grown at elevated CO_2 had a greater root biomass and a higher ratio of lateral root to total root biomass than those grown at ambient CO_2 concentration; however, these seedlings also shed more leaves and retained smaller leaves. These changes, together with a reduced transpiration/leaf area ratio at elevated CO_2, may have contributed to a slight increase in xylem pressure potentials of seedlings in the 1050 µmol mol^{-1} CO_2 treatment during the first 37 days of growth (0.26 to 0.40 MPa). Osmotic potential was not affected by CO_2 treatment. Increasing the CO_2 concentration to 710 and 1050 µmol mol^{-1} more than doubled the percentage survival of seedlings from which water was withheld for 65 days. Carbon dioxide enrichment significantly increased survival from 0% to about 40% among seedlings that experienced the lowest soil water content. By increasing seedling survival of drought, rising atmospheric CO_2 concentration may increase abundance of *P. glandulosa* on grasslands where low water availability limits its establishment.

Keywords: atmospheric CO₂, leaf shedding, osmotic potential, root biomass, water deficit, xylem pressure potential.

Introduction

Seedling establishment is critical to the persistence and spread of many plant species; however, plants are most vulnerable to biotic and abiotic stresses at the seedling stage. Dehydration is among the most frequent causes of seedling mortality (Cook 1979). Low soil water availability contributes to the high mortality of seedlings of the invasive shrub *Prosopis* (mesquite; *P. glandulosa* Torr. *var. glandulosa*, *P. glandulosa* var. *torreyana* (L. Benson) M.C. Johnst., *P. velutina* Woot.) on some grasslands in the southwestern United States (Paulsen 1950, Parker and Martin 1952) and limits the establishment of woody species on other grasslands (Harrington 1991, O'Connor 1995). For example, more *Prosopis* seedlings die from desiccation on vegetated plots than on bare plots in desert grassland because grasses deplete surficial water (Glendening and Paulsen 1955). Conversely, highly successful establishment of *Prosopis* may follow heavy rainfall (Turner 1990) or changes in the seasonality of precipitation (Neilson 1986).

Abundance and density of *Prosopis* have increased substantially on grasslands in the southwestern USA during the last 125 years (Glendening 1952, Johnston 1963, Buffington and Herbel 1965), partly coincident with the nearly 30% increase in atmospheric CO_2 concentration resulting from industrialization (Neftel et al. 1985, Raynaud and Barnola 1985). Despite demonstrations that CO_2 concentration may impact plant water relations (Morison 1993), little attention has been given to the possibility that rising CO_2 may contribute to shrub invasion or to vegetation change by enhancing seedling survival of water deficit (e.g., Marks and Strain 1989).

Increased CO_2 concentration may, for example, increase root growth (Polley et al. 1994, Tischler et al. 1996), and thereby increase access of woody seedlings to soil water both within and below the rooting zone of neighboring plants (Polley et al. 1996). Additional carbohydrates produced by more rapidly photosynthesizing plants may serve as osmoticum, which helps maintain positive turgor pressures longer under water deficit (Sionit et al. 1981, Morse et al. 1993; but see, Tschaplinski et al. 1993, 1995). Perhaps the best documented and most consistent effect of increased CO_2 concentration is a decrease in stomatal conductance and transpiration/leaf area ratio (Morison 1985). Where the reduction in conductance is not offset by an increase in leaf area, establishing plants may delay dehydration by depleting soil water more slowly (Paez et al. 1983, Rogers et al. 1984, Tolley and Strain 1985, Wray and Strain 1986).

Slower depletion of soil water may benefit individually grown plants or species monocultures of defined density. It is not obvious, however, that seedlings in highly competitive environments will benefit by using water more conservatively. Water saved by more slowly transpiring seedlings may be used by neighboring plants or lost to evaporation (Cohen 1970).

Little is known about the effects of CO_2 concentration on seedling survival when soil water is depleted at a near constant rate, as may occur in competitive environments.

We evaluated plant survival of soil water depletion and measured several traits of *Prosopis glandulosa* seedlings grown at current and elevated CO_2 concentrations at similar rates of soil water depletion. The traits included root growth and tissue osmotic potential, which may contribute to the postponement or tolerance of plant dehydration. Because increased CO_2 concentration appears to benefit droughted plants primarily by reducing transpiration and soil water depletion, we predicted that survival of *P. glandulosa* seedlings would not differ significantly among CO_2 treatments when soil water content declined at similar rates.

Materials and methods

Experimental design

Prosopis glandulosa seedlings were grown in a sandy loam soil in 0.05 m diameter and 0.60 m deep pots. Pots were fashioned from polyvinyl chloride pipe cut longitudinally into two pieces of equal size to facilitate recovery of intact root systems. The two halves of each pot were taped together and secured at the base with a perforated cap. Each pot was weighed when empty and after it had been filled with air-dried soil. Two samples of air-dried soil were oven-dried at 100 °C for 72 h and weighed. The mean ratio of oven-dried to air-dried soil mass was used to calculate the mass of soil added to each pot. Soil in each pot was wetted to drip by adding 100 ml of Hoagland's nutrient solution (Hoagland and Arnon 1950) and approximately 200 ml of water.

Three scarified seeds, collected the previous year from an isolated *P. glandulosa* tree, were planted in each of 150 pots on June 2, 1995. Fifty pots were randomly assigned to each of three air-conditioned greenhouse bays maintained at nominal CO_2 concentrations of 370 (ambient), 700, and 1050 μmol mol^{-1}. Soil in each pot was watered to drip daily until seedlings emerged on June 5, 1995 (Day 0). One pot per CO_2 treatment was discarded because no seedlings emerged. Watering was then discontinued, and pots were weighed after drainage stopped. Subsequently, pots were weighed every two to four days to determine rates of soil water depletion. Soil relative water content (RWC) per pot was calculated by dividing the amount of water in the soil on each date (mass of soil plus water on each date minus mass of oven-dried soil) by the amount of water retained in soil after drainage ceased (mass of fully wet soil minus that of oven-dried soil). For each CO_2 treatment, evaporation was estimated as water loss from two unplanted pots.

One seedling that emerged on Day 0 in each pot was randomly designated as the "target" or experimental plant. Remaining plants at the ambient CO_2 concentration were removed one week after emergence. Leaves of the two additional plants per pot in the elevated CO_2 treatments were removed as needed to achieve rates of soil water depletion similar to those measured in the ambient CO_2 treatment. Shoots of additional plants in the elevated CO_2 treatments were

completely removed 35 days after emergence (Day 35). Xylem pressure potential (ψ_x) was measured near midday (1200–1400 h CST) with a pressure chamber (Model 3005, Soil Moisture Equipment, Golita, CA) on excised shoots of five randomly selected target plants from each CO_2 treatment on Days 10, 15, 21, 25, 30, and 37. Leaf area of plants harvested on Days 10 through 25 was measured immediately thereafter with a photoelectric meter (LI-3000A, Li-Cor, Inc., Lincoln, NE). For each CO_2 treatment, stems were collected on Days 30 and 37 ($n = 5$ and $n = 3$, respectively) and recut under water. Shoots were rehydrated in distilled water in a dark, humid chamber in the laboratory. Xylem pressure potentials and fresh weights were measured as shoots dried in the laboratory. Values of osmotic potential at full hydration (π_{100}) and at the turgor loss point (π_0) were derived from these data by standard methods (Koide et al. 1989).

At all harvests, soil was washed from roots which were then separated into lateral roots and taproots. All plant material was weighed after drying at 60 °C for 72 h. Leaves that were shed as soil RWC declined were not recovered. Residual leaf and plant biomass at each harvest included only the leaves that plants retained. Leaf area of plants (on which pressure–volume relationships were measured) was estimated by multiplying measured leaf mass by the mean specific leaf area of plants harvested from the appropriate CO_2 treatment on Days 20 and 25.

The total number of leaves per target plant (excluding cotyledons) that had been produced and the number of leaves that had been lost or shed on Days 25, 30, 35, 39, 45, 50, and 56 were recorded. A doubly pinnate leaf was considered to have been shed when 50% of leaflets had been lost. The area of each leaf present on Day 42 was estimated from a linear relationship between the logarithm of the sum of the rachises' lengths of the leaf and leaf area ($r^2 = 0.85$, $P < 0.0001$, $n = 11$).

After harvests, 19 planted pots per CO_2 treatment remained and were rewatered to drip on Day 65. Survival was assessed 2 weeks later.

Carbon dioxide control and environmental conditions

The CO_2 concentration and dewpoint temperature of air in each greenhouse bay were measured at 4-min intervals with a Li-Cor Model LI-6262 infrared gas analyzer. The CO_2 readings were corrected for atmospheric pressure measured with a Druck model DPI 260 pressure indicator (Druck, Inc., New Fairfield, CT). The infrared analyzer was calibrated daily against four CO_2 gas standards and monthly against a dewpoint generator (LI-610, Li-Cor). Air temperature was measured in the center of each bay and outside the greenhouse with fine-wire (25 μm diameter) thermocouples. Photosynthetic photon flux density (PPFD) was measured on the greenhouse roof with a quantum sensor (LI-190SB, Li-Cor) and within the greenhouse bays with 1-m long line quantum sensors (LI-191SA, Li-Cor) mounted above plant height.

Pure CO_2 gas was injected into the greenhouse bays as required to maintain desired concentrations. Air temperature within air-conditioned bays was maintained near outdoor temperature by manually adjusting thermostatic controls.

The CO$_2$ concentration of air averaged 370 (ambient), 710, and 1050 μmol mol^{-1} for the three CO$_2$ treatments. Standard deviations of CO$_2$ concentration were calculated daily: the average deviation ranged from 11.4 μmol mol^{-1} at the mid-level CO$_2$ concentration to 19.9 μmol mol^{-1} at the lowest CO$_2$ concentration. Daytime temperatures averaged 28.2 °C during the first 6 weeks of the experiment and 29.6 °C during the final 5 weeks. The vapor pressure deficit of air during daylight averaged 1.8 kPa. On average, the daily integral of PPFD inside the greenhouse was 69% of that measured above the greenhouse.

Statistics

Analysis of variance (ANOVA) with repeated measures (Potvin et al. 1990) was used to discern effects of CO$_2$ concentration and time since emergence (day) on leaf production and shedding. Data collected at harvests on Days 10 through 37 were analyzed with a two-way ANOVA that included CO$_2$ treatment, date, and a CO$_2$ × date interaction (Sokal and Rohlf 1981). Student-Newman-Keuls multiple range test was used to determine significant differences among three or more means. Bonferroni-adjusted significance levels were used in single degree of freedom comparisons within harvest date. Data were transformed logarithmically before analysis when required to satisfy assumptions of ANOVA. Standard errors for transformed data were omitted in presentation of results using the original scale of measurement. Effects of CO$_2$ concentration on seedling survival were analyzed with a chi-square test of independence. The chi-square analysis was also used to test whether survival varied with soil RWC across CO$_2$ treatments. Seedlings were divided into two classes based on the soil RWC to which they were exposed on Day 59: RWC 0.06 to 0.13 and RWC 0.13 to 0.20.

Results

Soil water declined at similar rates in the three CO$_2$ treatments (Figure 1). Soil RWC declined from about 0.75 to 0.25 during the first 25 days, but decreased more slowly thereafter. Early in the experiment, transpiration/leaf area ratio was apparently lower in seedlings in the elevated CO$_2$ treatment than in the ambient CO$_2$ treatment because additional plants per pot were required in the elevated CO$_2$ treatments to deplete soil water at the same rate as the single plant per pot in the 370 μmol mol^{-1} treatment. Only after shoots of the two additional plants per pot in the elevated CO$_2$ treatments were removed (Day 35) did average soil RWC in pots in the 370 μmol mol^{-1} treatment consistently fall below that in the elevated CO$_2$ treatments.

Across harvests from Days 10 through 37, ψ_x was slightly, but significantly, higher (less negative) in seedlings in the 1050 μmol mol^{-1} CO$_2$ treatment than in the lower CO$_2$ treatments (0.26 to 0.40 MPa, $P = 0.01$) (Figure 2). Xylem potentials remained high through the first 25 days of the experiment and then declined sharply when soil RWC fell below approximately 0.25 (Figure 1).
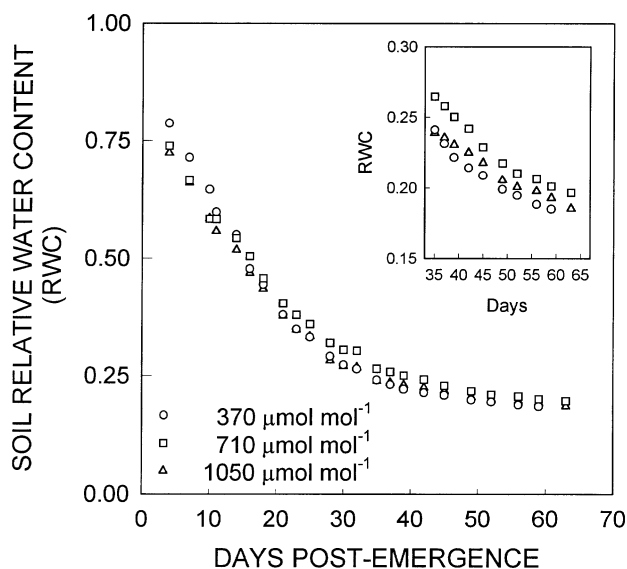

Figure 1. Mean soil relative water content (RWC) at each of three CO$_2$ concentrations following emergence of *P. glandulosa* seedlings (Day 0). Watering was discontinued after soil was wetted to drip on Day 0. Because plants were harvested from each CO$_2$ treatment on Days 10 through 37, the sample size of each mean declined from 49 on Day 4 to 19 on Day 39. Inset: Vertically expanded graph of changes in soil RWC over Days 35 to 63 post-emergence.
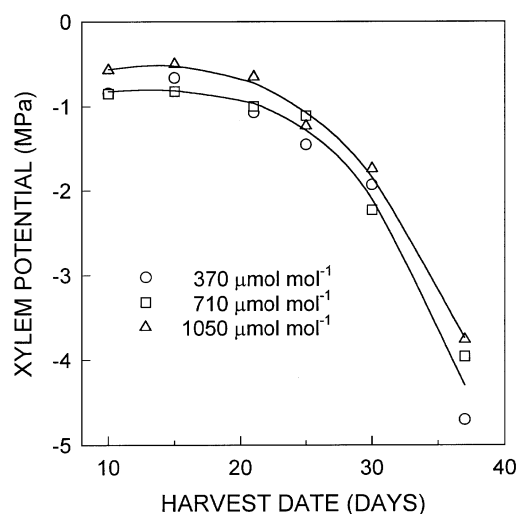

Figure 2. Mean xylem pressure potential (ψ_x) of seedlings of *P. glandulosa* harvested from each of three CO$_2$ treatments on Days 10 through 37 after emergence. Lines are cubic polynomial regressions, computed with log transformed values of ψ_x, for plants grown at 1050 μmol mol^{-1} ($r^2 = 0.86$, $P < 0.0001$, $n = 30$) and at lower (370 and 710 μmol mol^{-1}) CO$_2$ concentrations ($r^2 = 0.65$, $P < 0.0001$, $n = 60$).

Neither osmotic potential at full hydration (π_{100}) nor potential at the turgor loss point (π_0) was affected by CO$_2$ treatment (Table 1). On Day 37, midday values of ψ_x (Figure 2) were below those at which tissues lost turgor (Table 1).

In all CO$_2$ treatments, root biomass increased until the final harvest on Day 37 (Figure 3). Across harvest dates, however,

root biomass was significantly greater at elevated CO_2 concentrations than at ambient concentration. Slopes of linear relationships between the logarithm of biomass of lateral roots as

Table 1. Tissue osmotic potential at full hydration (π_{100}) and at the turgor loss point (π_0) for seedlings of *P. glandulosa* harvested 30 and 37 days after emergence in each of three CO_2 treatments ($n = 8$). Parameters did not differ significantly between harvest dates.

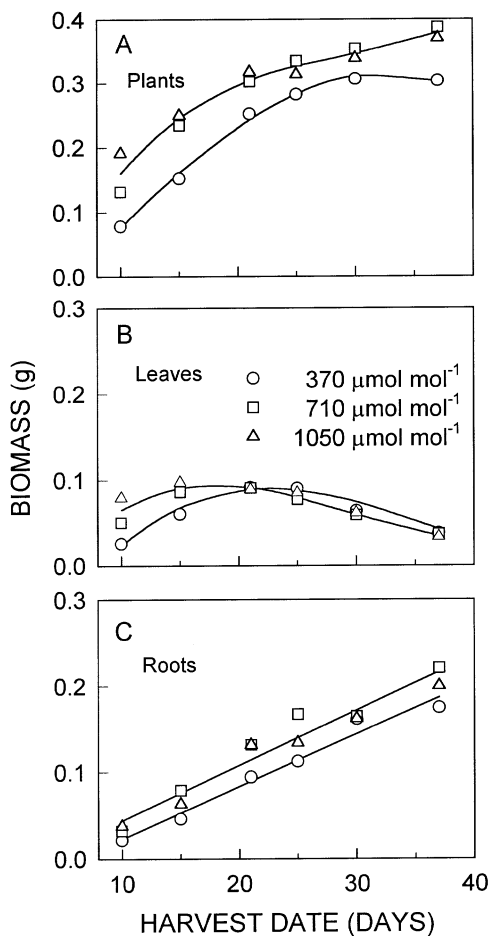| Parameter	Growth CO_2 concentration ($\mu mol\ mol^{-1}$)		
	370	710	1050
π_{100}	−1.74	−1.72	−1.68
π_0	−2.14	−2.19	−2.14

Figure 3. (A) Plant, (B) leaf and (C) root biomass of seedlings of *P. glandulosa* harvested from each of three CO_2 treatments on Days 10 through 37 after emergence. Leaves that were shed were not included in calculating plant or leaf biomasses. Lines are polynomial regressions through data for plants grown at 370 $\mu mol\ mol^{-1}$ (plant biomass, $r^2 = 0.83$, $P < 0.0001$; leaf biomass, $r^2 = 0.65$, $P < 0.0001$; root biomass, $r^2 = 0.82$, $P < 0.0001$, $n = 30$) and at elevated (710 and 1050 $\mu mol\ mol^{-1}$) CO_2 concentrations (plant biomass, $r^2 = 0.67$, $P < 0.0001$; leaf biomass, $r^2 = 0.52$, $P < 0.0001$; root biomass, $r^2 = 0.77$, $P < 0.0001$, $n = 60$). Arithmetic means are shown, but statistical analysis of plant biomass data was performed following logarithmic transformation. Note the difference in scale of the *y*-axis in A.

the dependent variable and the logarithm of total root biomass as the independent variable did not differ among CO_2 treatments ($P > 0.05$; not shown). Across CO_2 treatments, however, the slope of this allometric relationship was slightly greater than unity (1.18), indicating that the contribution of lateral roots to total root biomass increased as plants grew. The ratios of lateral root biomass to total root biomass and of lateral root biomass to leaf area were significantly greater in the 710 μmol mol^{-1} treatment than in the other CO_2 treatments (Table 2), partly because roots grew faster at elevated CO_2.

Despite the increase in root biomass at elevated CO_2, residual plant biomass (total biomass less that of shed leaves) did not differ significantly ($P > 0.008$, Bonferroni inequality) among CO_2 treatments after Day 21 (Figure 3). This partly reflects the effects of leaf shedding, which began in the highest CO_2 treatment near Day 15. Leaf biomass in the 710 and 1050 $\mu mol\ mol^{-1}$ treatments was double and triple that in the ambient CO_2 treatment on Day 10, but did not differ significantly among plants harvested from the three CO_2 treatments from Days 15 to 37. Cotyledons and then older leaves at the bases of plants were shed first. Shedding proceeded to progressively younger leaves. Leaf loss began in the highest CO_2 treatment when ψ_x was above −1.0 MPa, but accelerated between Days 25 and 30 as ψ_x declined to between −1.5 and −2.0 MPa.

Trends in leaf loss were also evident in nondestructive measurements taken on plants that were used to assess survival (Figure 4). The number of leaves produced did not vary with CO_2 treatment from Days 25 to 57. Plants grown at elevated CO_2, however, retained fewer leaves as soil dried than plants grown at ambient CO_2 concentration. By Day 45, plants grown at 710 and 1050 $\mu mol\ mol^{-1}$ had, on average, only 69 and 56%, respectively, the number of leaves present on plants grown at 370 $\mu mol\ mol^{-1}$. Also, the young leaves retained near the tops of seedlings were smaller in the elevated CO_2 treatment than in the ambient CO_2 treatment. On average, area/leaf ratio at elevated CO_2 was about 67% of that at ambient CO_2 concentration (mean = 157, 104, and 107 mm^2/leaf at 370, 710, and 1050 $\mu mol\ mol^{-1}$, respectively). As a result, leaf area/plant at 710 and 1050 $\mu mol\ mol^{-1}$ was on average 56% (280 cm^2) and 34% (173 cm^2) of that at ambient concentration on Day 42 (504 cm^2).

Table 2. Contribution of lateral roots to total root biomass and the ratio of lateral root biomass to leaf area for *P. glandulosa* seedlings harvested on Days 10 through 37 after emergence from each of three CO_2 treatments ($n = 30$). Values within a row followed by the same letter did not differ significantly (Student-Newman-Keuls test). Arithmetic means for lateral root biomass/leaf area are shown, but statistical analysis was performed after logarithmic transformation.

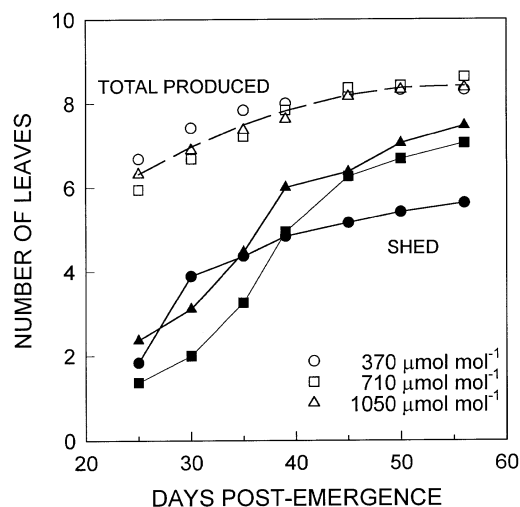| Parameter	Growth CO_2 concentration ($\mu mol\ mol^{-1}$)		
	370	710	1050
Lateral root biomass/ Total root biomass	0.33 b	0.39 a	0.33 b
Lateral root biomass/ Leaf area (g m^{-2})	44.3 b	72.3 a	66.5 b

Figure 4. Total number of leaves produced (open symbols) and number of leaves lost or shed (closed symbols) by seedlings of *P. glandulosa* as soil water content declined at each of three CO$_2$ concentrations ($n = 19$). The dashed line is a polynomial regression through data on leaf production at all CO$_2$ concentrations ($r = 0.23$, $P < 0.0001$, $n = 399$). Separate solid lines were drawn through data on leaf loss at each CO$_2$ concentration.
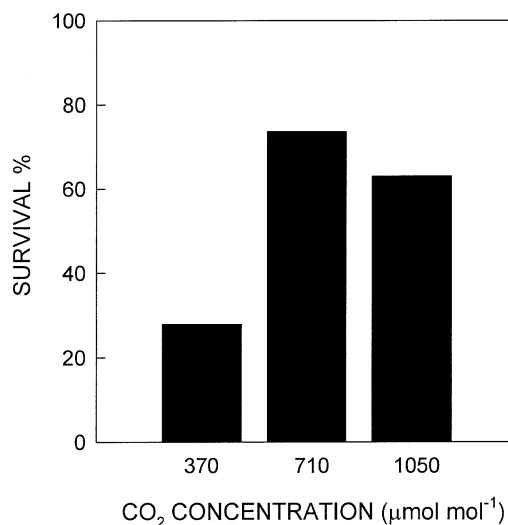

Figure 5. Percentage survival of *P. glandulosa* seedlings grown at three CO$_2$ concentrations following 65 days without added water ($n = 19$). Soil was wetted to drip at seedling emergence.

Despite greater leaf retention at the ambient atmospheric CO$_2$ concentration, water loss from pots with single plants did not differ significantly among CO$_2$ treatments ($P = 0.09$) between Days 35 and 59. Mean water loss per pot over the period was lower at 370 than at 710 μmol mol^{-1} (mean = 18.3 and 20.9 ml respectively) and was only slightly greater at 370 than at 1050 μmol mol^{-1} (mean = 18.3 versus 17.1 ml), implying that lower transpiration/area ratio largely offset the effect of greater leaf area on transpiration at ambient CO$_2$ concentration. Most water loss between Days 35 and 59 may have been due to evaporation, rather than to transpiration. Water loss from unplanted pots that were last wetted on Day 0 averaged 16.7 ml ($n = 6$) over the same period.

Percentage survival of seedlings from which water was withheld for 65 days was more than doubled at elevated CO$_2$ concentrations compared with that at ambient CO$_2$ concentration (Figure 5). Because survival was lower in pots with lowest soil RWC on Day 59 (survival was correlated with soil RWC; $P < 0.0001$, chi-square test of independence), reduced survival among plants grown at 370 μmol mol^{-1} partly reflected the lower mean soil RWC to which these plants were exposed after Day 35 (Figure 1). However, a positive effect of CO$_2$ on survival was also evident when soil RWC was similar among the treatments. Among pots with soil RWC between 0.06 and 0.13 on Day 59, for example, percentage survival was 38% ($n = 8$), 40% ($n = 5$), and 0% ($n = 10$) at 1050, 710, and 370 μmol mol^{-1}, respectively. Percentage survival at higher soil RWC was also increased by CO$_2$ enrichment. Survival at soil RWCs between 0.13 and 0.20 was 82% ($n = 11$), 86% ($n = 14$), and 63% ($n = 8$) at 1050, 710, and 370 μmol mol^{-1}, respectively.

Discussion

Low soil water availability is a frequent contributor to seedling mortality in *Prosopis* and is an important constraint on grassland invasion by this (Paulsen 1950, Glendening and Paulsen 1955) and other woody species (Harrington 1991, O'Connor 1995). There are several ways in which increased CO$_2$ concentration could improve a plant's capacity both to tolerate dehydration and to postpone desiccation. There is limited evidence that rising CO$_2$ will increase osmotic adjustment (Sionit et al. 1981, Morse et al. 1993, Eamus et al. 1995) and thereby increase the tolerance of some plants to dehydration. Mature individuals of *P. glandulosa* adjust osmotic potentials diurnally and seasonally (Nilsen et al. 1983), but neither osmotic potential at full hydration nor that at the point of turgor loss was affected by CO$_2$ in this study.

Perhaps the most consistent and important benefits of higher CO$_2$ concentration to water-stressed plants result from changes in plant growth and transpiration that slow the development of water stress. Elevated CO$_2$ concentration may increase plant access to water by increasing root growth (Polley et al. 1994), improve plant water balance by increasing the fraction of plant biomass invested in roots (Tolley and Strain 1985, Miao et al. 1992, Polley et al. 1994), and delay the onset of water stress by reducing transpiration/leaf area ratio and the rate at which soil water is depleted (Paez et al. 1983, Rogers et al. 1984, Wray and Strain 1986). Each of these responses occurred in seedlings of *P. glandulosa*. Because of the difficulty of experimentally controlling soil water depletion, it has been difficult to determine whether effects of CO$_2$ on factors other than the rate of water depletion contributed to increased drought tolerance.

By including additional plants per pot in the elevated CO$_2$ treatments, we attempted to minimize the benefit that experimental seedlings could derive by "conserving" soil water and

thus to simulate patterns of soil water depletion that establishing seedlings might experience in nature. Because of the limited volume and depth of pots used in this experiment, we also restricted the larger root systems that developed at elevated CO_2 (Figure 3) from exploring a greater volume of soil or deeper soil layers. Establishing *P. glandulosa* seedlings develop vigorous taproots that in 1 month can reach depths of 1.25 m or more (Tischler et al. 1996). By accessing water at this depth, *P. glandulosa* seedlings rapidly become uncoupled from more shallowly rooting grasses in the use of soil water (Brown and Archer 1989). Elevated CO_2 concentration increased root biomass of *P. glandulosa* seedlings by a mean of 20 to 30% during the initial 37 days of growth (Figure 3). Tischler et al. (1996) observed similar relative effects of CO_2 on rooting depth of seedlings of this shrub. Raising CO_2 to near 700 and 1000 μmol mol^{-1} increased maximum depth of *P. glandulosa* taproots after 1 month's growth by an average of 23% (from 1.10 m to 1.35 m). Root biomass of periodically droughted *P. glandulosa* was also stimulated by increasing CO_2 from 220 to 340 μmol mol^{-1} (Polley et al. 1994).

Despite limitations to their capacity to both explore a larger soil volume and "conserve" soil water, *Prosopis* seedlings survived soil water depletion better in the elevated CO_2 treatments than in the ambient CO_2 treatment (Figure 5). Part of the increase in survival reflected the slightly higher soil water content in the enriched CO_2 treatments than in the ambient CO_2 treatment following Day 35 (Figure 1); however, elevated CO_2 also increased survival of seedlings exposed to very similar soil water contents. Thus, among plants that developed both the highest and lowest soil water contents before rewatering, survival was higher at elevated CO_2 concentrations than at ambient concentration. Particularly important was the finding that CO_2 enrichment increased survival from 0 to 40% among the subset of plants exposed to the lowest soil RWCs.

How elevated CO_2 increased survival of droughted *P. glandulosa* seedlings cannot be established from these data. Elevating CO_2 may have lowered the ψ_x at which death occurred or delayed the onset of lethal water potentials by promoting less negative ψ_x at a given soil RWC. The latter explanation seems the more plausible. Before differences in leaf loss among treatments were pronounced, ψ_x was higher at 1050 μmol mol^{-1} than at lower CO_2 concentrations, presumably because higher CO_2 slowed water loss per unit leaf area and increased potential water uptake per unit leaf area by slightly increasing the ratio of lateral root mass to leaf area. Leaf area subsequently declined more rapidly and the ratio of lateral root mass to leaf area likely increased more rapidly at elevated CO_2 concentrations than at ambient CO_2 concentration. This may further have improved plant water balance at elevated CO_2, although any resulting benefit may have been at least partially offset by greater water loss/area when soil RWC declined below about 0.25.

Plants of *P. glandulosa*, like those of many other species, are most vulnerable during the seedling stage. Because *P. glandulosa* can grow rapidly, surviving seedlings may quickly become tolerant of fire (Glendening and Paulsen 1955, Wright et al. 1976) and defoliation (Glendening and Paulsen 1955), and

can survive depletion of surface water by accessing deeply placed soil water (Paulsen 1950, Brown and Archer 1989). By increasing seedling survival of drought, rising CO_2 concentration may increase the abundance of *P. glandulosa* on grasslands where low water availability currently limits its establishment.

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