

Growth rate and survivorship of drought: CO₂ effects on the presumed tradeoff in seedlings of five woody legumes

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Summary Traits that promote rapid growth and seedling recruitment when water is plentiful may become a liability when seedlings encounter drought. We tested the hypothesis that CO₂ enrichment reinforces any tradeoff between growth rate and drought tolerance by exaggerating interspecific differences in maximum relative growth rate (RGR) and survivorship of drought among seedlings of five woody legumes. We studied invasive species of grasslands that differ in distribution along a rainfall gradient.

Survivorship of drought at ambient CO₂ concentration ([CO₂]) was negatively related to RGR in well-watered seedlings in one of two experiments, but the relationship was weak because interspecific differences in RGR were small. Contrary to our hypothesis, there was no significant relationship among well-watered seedlings between RGR at ambient [CO₂] and either the relative or absolute increase in RGR at elevated [CO₂]. As predicted, however, CO₂ enrichment reinforced interspecific differences in survivorship of seedlings exposed to similar rates of soil water depletion. Doubling [CO₂] improved seedling survivorship of the most drought-tolerant species throughout the period of soil water depletion, but did not consistently affect survivorship of more drought-sensitive species. Midday xylem pressure potentials of drought-treated seedlings were less negative at elevated [CO₂] than at ambient [CO₂], but no other measured trait was consistently correlated with improved survivorship at high [CO₂]. Carbon dioxide enrichment may not reinforce species differences in RGR, but could exaggerate interspecific differences in drought tolerance. To the extent that seedling persistence in grasslands correlates with drought survivorship, our results indicate a positive effect of CO₂ enrichment on recruitment of woody legumes that are currently tolerant of drought.

Keywords: invasive plants, leaf gas exchange, osmotic potential, xylem pressure potential.

Introduction

The association between photosynthesis and transpiration is thought to impose physiological and morphological constraints

on plants that prevent genotypes from dominating under conditions of both high and low water availability. This presumed tradeoff between tolerance of water shortage and growth under well-watered conditions (Orians and Solbrig 1977, Smith and Huston 1989) is one example of the general tradeoff that is thought to exist between plant tolerance of low resources and plant growth when resources are abundant (Chapin 1980, Tilman 1988). With respect to water availability, the tradeoff implies a negative correlation between maximum relative growth rate (RGR) and either growth or survivorship under water limitation. Rapidly growing plants invest heavily in leaves (Tilman 1988, Poorter and Remkes 1990), exhibit high specific leaf area (SLA; Poorter and Remkes 1990, Cornelissen et al. 1999), and may have high rates of photosynthesis and transpiration per unit of leaf dry mass (Orians and Solbrig 1977, Poorter et al. 1990), traits that are presumably incompatible with continued growth and survival under drought conditions.

Recent studies indicate that atmospheric CO₂ enrichment often exaggerates species (or genotypic) differences in both RGR and drought tolerance, and thus may reinforce existing trends in vegetation by favoring plants under the conditions in which they already prosper (Groninger et al. 1995, Bunce 1997, Arp et al. 1998, Catovsky and Bazzaz 1999, Polley et al. 1999). Catovsky and Bazzaz (1999), for example, found that atmospheric CO₂ enrichment increased growth more in tree seedlings typical of xeric than of mesic habitats when soils were dry, but that the reverse was true when water was plentiful. Others have shown that atmospheric CO₂ enrichment preferentially increases RGR (Poorter 1993) or biomass (Bunce 1997) in species that already have high growth rates. Bunce (1997) found that stimulation of RGR correlated positively with the increase in net assimilation rate (NAR) at elevated CO₂ concentration ([CO₂]). Mechanisms underlying interspecific differences in the response of drought tolerance to CO₂ enrichment, however, are poorly defined.

We predicted that CO₂ enrichment would exaggerate interspecific differences in RGR and drought survival among woody seedlings by increasing RGR more in well-watered

seedlings of rapidly growing species than of slowly growing species and by preferentially increasing survivorship in the most drought-tolerant species. We evaluated effects of atmospheric CO₂ enrichment on RGR and survivorship of drought in seedlings of five woody legumes, *Acacia farnesiana* (L.) Willd. (huisache), *Gleditsia triacanthos* L. (honey locust), *Leucaena leucocephala* (Lam.) de Wit. (leadtree), *Parkinsonia aculeata* L. (retama) and *Prosopis glandulosa* Torr. var. *glandulosa* (honey mesquite). All species occur in the state of Texas, USA and are potential invaders of grasslands, and all except *Gleditsia* are regarded as weeds outside the USA (Holm et al. 1979). To our knowledge, there is no published comparison of drought responses among these potentially invasive species even though interspecific differences in their geographic distributions indicate that they differ in response to water deficit. *Gleditsia* and *Acacia* occur most frequently in relatively mesic ecosystems in eastern or southern Texas with annual rainfall exceeding 800 mm, whereas *Prosopis* dominates grazing lands with as little as 200 mm of annual precipitation.

We measured RGR of well-watered seedlings and quantified seedling mortality during an extended period without irrigation at ambient and elevated [CO₂]. The soil water content experienced by seedlings in mature vegetation likely depends more on how rapidly established plants deplete soil water than on rates of seedling transpiration. To minimize feedbacks of seedling transpiration on soil water content in this experiment, we exposed all drought-treated seedlings to similar rates of soil water depletion. Traits that might contribute to species differences in RGR and in response to drought were measured to provide insight into mechanisms controlling interspecific variation and its response to [CO₂].

Materials and methods

Experimental design and measurements

We conducted two experiments in environmentally controlled greenhouses with seedlings of *Acacia farnesiana*, *Gleditsia triacanthos*, *Leucaena leucocephala*, *Parkinsonia aculeata* and *Prosopis glandulosa* (hereafter all species are referred to by generic name only). Each experiment included three treatments: [CO₂] (ambient, elevated); species; and watering regime (wet, dry). *Acacia*, *Parkinsonia* and *Prosopis* were studied in 1997. *Gleditsia* and *Leucaena* and a second maternal family of *Prosopis* were studied in 1998. Inclusion of *Prosopis* in each experiment provided a reference for comparing results of the two experiments. *Leucaena* seeds were collected from several trees near the city of Beeville in southern Texas, USA. Seeds of the remaining species and of each of the two maternal families of *Prosopis* were collected from one tree per species near the city of Temple in central Texas. Seeds were collected the year before the start of the experiments.

Seedlings were grown in a sandy loam soil in 0.05-m diameter by 0.60-m deep pots. The pot size was chosen to facilitate control and monitoring of soil water content, while permitting largely unrestricted development of taproots. Pots were made

from polyvinyl chloride pipe that was cut in half longitudinally. The two lengths 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. Three samples of the soil used to fill pots were oven-dried at 100 °C for 72 h and weighed. The mass of soil added to each pot was calculated based on the mean ratio of the oven-dried mass to air-dried mass of these samples. Two days before planting, soil in each pot was wetted to drip by adding 100 ml of Hoagland's nutrient solution (Hoagland and Arnon 1950) and about 200 ml of water. Pots were weighed after drainage stopped, and were randomly assigned to wet and dry treatments. Water was added as necessary to maintain soil water content in pots assigned to the wet treatment near drip level. No additional water was added to pots assigned to the dry treatment. These pots were weighed every 2 to 4 days after seedlings emerged. Soil relative water content (RWC) per pot assigned to the dry treatment 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).

Two scarified seeds of a given species were planted in each pot. Seeds of *Acacia*, *Parkinsonia*, and one maternal family of *Prosopis* each were planted in 48 pots assigned to the wet treatment and in 90 pots assigned to the dry treatment on June 23, 1997. Seeds of the remaining species and of a second family of *Prosopis* each were planted in 48 pots assigned to the wet treatment and in 120 pots assigned to the dry treatment on July 31, 1998. At planting in 1997, pots with each species and water treatment were randomly divided between greenhouse bays maintained at nominal CO₂ concentrations of 390 and 700 µmol mol⁻¹. To minimize any effect of bay on plant performance, plants and the appropriate CO₂ treatment were switched between bays every 2 weeks. In 1998, the two CO₂ treatments were replicated across two blocks (two pairs of greenhouse bays). Pots with each species and water treatment were randomly divided among the greenhouse bays. At emergence (Day 0), one seedling per pot was randomly designated as the target or experimental plant. Remaining seedlings were removed.

Our objective in the dry treatment was to minimize feedbacks of seedling transpiration on soil water content by exposing seedlings across species and CO₂ treatments to similar rates of soil water depletion. To accomplish this, we manipulated the leaf area of two additional seedlings of *Prosopis* that were grown in every pot assigned to the dry treatment. Imbibed seeds from a third family of *Prosopis* were planted in these pots following emergence of target seedlings. Leaves of the additional seedlings were clipped as necessary to equalize the rate at which soil water content declined among dry pots during each experiment.

Well-watered plants were harvested near midday (1200–1400 h CST) on Days 14, 17, 21 and 28 of the 1997 experiment ($n = 4$ per species and CO₂ treatment, with a double harvest of $n = 8$ on Days 14 and 28) and on Days 14, 17, 24 and 28 of the 1998 experiment ($n = 3$ per species and CO₂ treatment in each

block). Drought-treated plants were harvested on Days 17 and 21 of the 1997 experiment ($n = 8$ per species and CO₂ treatment) and on Days 17 and 24 of the 1998 experiment ($n = 3$ per species, CO₂ treatment and block) for measurements of biomass and plant water relations. Xylem pressure potential (Ψ_x) was measured on excised shoots with a pressure chamber (Model 3005, Soil Moisture Equipment, Golita, CA). During 1997, Ψ_x was measured at predawn and midday on excised shoots of four plants per species from the Day 17 and 21 harvests of drought-treated plants and from the Day 21 harvest of well-watered plants. Midday Ψ_x was measured on drought-treated plants harvested on Days 17 and 24 and on well-watered plants harvested on Day 24 of the 1998 experiment. At all harvests, roots were washed free of soil. All plant material was weighed after oven drying at 60 °C for 72 h.

Stems of some plants collected at midday on Day 21 of the 1997 experiment ($n = 3$ plants per species, CO₂ treatment and water treatment) and on Day 24 of the 1998 experiment ($n = 2$ plants per species, CO₂ treatment and water treatment) were recut under water, enclosed in plastic bags and rehydrated overnight in a refrigerator with the stem base immersed in water. The following day, Ψ_x and fresh weights were measured as shoots dried in the laboratory to determine pressure–volume relationships. Values of osmotic potential at full hydration (π_{100}) and at turgor loss point (π_0) and tissue RWC at turgor loss (R_0) were derived from these data by standard methods (Schulte and Hinckley 1985, Koide et al. 1989). The π_{100} was derived from the linear regression of $1/\Psi_x$ on RWC of the plant. The turgor loss point was estimated as described by Schulte and Hinckley (1985). The method uses deviation of measured values from the regression of $1/\Psi_x$ on RWC and from points fitted by the regression to estimate π_0 .

Net photosynthesis and stomatal conductance to water were measured on recently expanded leaves of plants of each treatment with a portable gas exchange system (LI-6200, Li-Cor, Lincoln, NE). Gas exchange was measured on mostly clear days (Days 21–23 of each experiment: July 14–15, 1997 and August 22–23, 1998) near the [CO₂] at which plants were grown. Air temperature and humidity during measurements also approximated the growing conditions. Gas exchange parameters were calculated based on one-sided leaf area (von Caemmerer and Farquhar 1981). During the 1998 experiment, a portable lighting system (Q Beam 3200A console, Q Beam 1205 lamp, Quantum Devices, Barneveld, WI) supplied light at a constant 1700 $\mu\text{mol m}^{-2} \text{s}^{-1}$ during gas exchange measurements.

Drought-treated plants that were not harvested were followed until death. The date of death was taken as the day on which leaves and stems lost all green color. Plants recorded as dead were rewatered. None were found to be alive. We excluded pots in which seedlings did not emerge or in which rates of soil water depletion differed greatly from those of the majority of pots. Emergence was especially low in *Leucaena* during the 1998 experiment.

For each experiment and CO₂ treatment, mean values per species of net assimilation rate (NAR), leaf area ratio (LAR)

and RGR were calculated for the 14–28 day interval based on formulae from classical growth analysis (Radford 1967, Hunt 1982). Relationships between leaf area and total plant biomass and between time and the ratio of leaf area to plant biomass were assessed to determine formulae appropriate for calculating NAR and LAR (Radford 1967).

Carbon dioxide control and environmental conditions

The [CO₂] and dew point temperature of air in each greenhouse bay were measured at 4-min intervals with a Li-Cor Model LI-6262 infrared gas analyzer. The [CO₂] readings were corrected for atmospheric pressure measured with a Druck model DPI 260 pressure indicator (Druck, New Fairfield, CT). The infrared analyzer was calibrated daily against four CO₂ gas standards and monthly against a dew point 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 silicon photodiode (LI-190SB, Li-Cor) and above plants in each bay with silicon detectors along a 1-m-long sensing surface (LI-191SA, Li-Cor).

Pure CO₂ gas was injected into the appropriate bay as required to maintain the elevated [CO₂]. Air temperature within the air-conditioned bays was maintained near that outdoors by manually adjusting thermostatic controls. The [CO₂] of air in ambient and elevated treatments averaged 387 and 702 $\mu\text{mol mol}^{-1}$, respectively, during 1997 and 390 and 737 $\mu\text{mol mol}^{-1}$, respectively, during the 1998 experiment. Standard deviations of [CO₂] were calculated daily. During the two experiments, the average of these values ranged from 3.7 $\mu\text{mol mol}^{-1}$ in the elevated [CO₂] treatment to 15.5 $\mu\text{mol mol}^{-1}$ in the ambient [CO₂] treatment, where concentration was not directly controlled. Daytime mean temperatures peaked at 29 °C during July 1997, and decreased linearly with time thereafter to 26 °C in mid-October. Daytime temperatures varied little during the 1998 experiment and averaged 27 °C. Daytime vapor pressure deficit averaged 1.5 kPa. The daily integral of PPFD inside the bays averaged 92 and 93% of that measured above the greenhouse during 1997 and 1998, respectively.

Statistics

Data collected from drought-treated plants harvested on Days 17–24 were analyzed with a three-way analysis of variance (ANOVA) that included CO₂ treatment, species identity, harvest date, and appropriate interaction terms (Sokal and Rohlf 1981). Effects of [CO₂], species identity and watering treatment on leaf gas exchange and plant biomass on Days 17–24 of each of the two experiments were analyzed with a three-way ANOVA. Significant differences among three or more means were assessed with Student-Newman-Keuls multiple range test. Data were transformed before analysis when required to satisfy assumptions of ANOVA.

Effects of [CO₂] on relationships between the proportion of drought-treated seedlings surviving and the number of days into drought (survivorship curves) were analyzed with non-

parametric tests that are based on ranks, the log-rank and Wilcoxon tests. Repeated-measures analysis of variance was used to test for treatment effects on the number of days of drought on which various percentages of seedlings were alive.

Results

Soil RWC

Seedlings of five woody legumes were grown with ample water or were exposed to an extended period without irrigation in current ambient and elevated $[\text{CO}_2]$. In pots from which water was withheld, soil RWC declined to about 0.15 during the first 25–30 days of the two experiments, then decreased slowly thereafter (Figure 1). Across species, soil RWC was significantly ($P < 0.005$) lower in the ambient $[\text{CO}_2]$ treatment than in the elevated $[\text{CO}_2]$ treatment through Day 21 in 1997. Thereafter, RWC did not differ between CO_2 treatments ($P > 0.21$). In 1998, differences in soil RWC between CO_2 treatments varied with species. Across dates, soil RWC was greater

in pots containing *Gleditsia* at ambient $[\text{CO}_2]$ than in pots containing any species at elevated $[\text{CO}_2]$ ($P < 0.042$) and was lowest in pots containing *Prosopis* in the elevated $[\text{CO}_2]$ treatment ($P < 0.028$).

Growth rates

Interspecific differences in RGR of well-watered seedlings were small, but RGR at ambient $[\text{CO}_2]$ was lowest in *Prosopis* in both experiments (Table 1). Across experiments at ambient $[\text{CO}_2]$, there was no relationship between RGR and either mean NAR ($P = 0.56$) or LAR ($P = 0.40$). *Leucaena* biomass was unaffected by CO_2 treatment, but final biomass of the other species increased by factors of 1.11 to 1.43 in response to elevated $[\text{CO}_2]$. Effects of CO_2 enrichment on RGR were inconsistent, with RGR ranging between 0.79 and 1.49 of that at ambient $[\text{CO}_2]$. These inconsistencies partly reflect the transient nature of the CO_2 effects on RGR. In 1998, for example, atmospheric CO_2 enrichment increased RGR of *Prosopis* seedlings during the first 2 weeks of growth and then reduced RGR between Days 14 and 28, resulting in an 11% increase in final biomass of the seedlings.

There was no significant relationship between RGR at ambient $[\text{CO}_2]$ and either the relative ($P = 0.29$) or absolute increase in RGR at elevated $[\text{CO}_2]$ ($P = 0.65$) or between RGR at ambient $[\text{CO}_2]$ and the relative stimulation of plant biomass by atmospheric CO_2 enrichment ($P = 0.18$). Across species, the increase in RGR at elevated $[\text{CO}_2]$ was positively correlated with the relative increase in NAR (Figure 2), but it was not significantly related to relative changes in LAR ($P = 0.44$).

Biomass and water relations

Total biomass did not differ between well-watered and drought-treated seedlings on Day 17 in either 1997 ($P = 0.60$) or 1998 ($P = 0.19$). However, drought reduced seedling biomass on Day 21 of the 1997 experiment (from 0.272 to 0.226 g; $P = 0.0001$, $n = 24$ and 48 for wet and dry treatments, respectively) and on Day 24 of the 1998 experiment (from 0.243 to 0.218 g; $P = 0.05$, $n = 36$).

In both experiments, atmospheric CO_2 enrichment increased leaf, root, stem and total biomass of drought-treated seedlings harvested on Days 17–24, with mean increases ranging between 23 and 42% (Figure 3). Effects of elevated $[\text{CO}_2]$ on root and total biomass in 1997 were significant only on the second of the two harvest dates. Effects of elevated $[\text{CO}_2]$ on stem biomass in 1997 and on root biomass in 1998 differed among species. Drought-treated *Parkinsonia* seedlings were about twice the size of *Acacia* and *Prosopis* seedlings during 1997 and had greater leaf, stem and root biomass. *Leucaena* seedlings were smaller than those of other species studied during 1998 because of low root and stem biomass.

Predawn Ψ_x did not differ among drought-treated seedlings of *Acacia*, *Parkinsonia* and *Prosopis* ($P = 0.13$) or between CO_2 treatments ($P = 0.10$) during 1997, but declined from Day 17 to Day 21 (-0.54 and -1.82 MPa, respectively; $P = 0.0001$, $n = 23$). Across harvest dates, midday Ψ_x was significantly higher in *Prosopis* (-1.39 MPa) than in *Acacia* (-1.81 MPa)

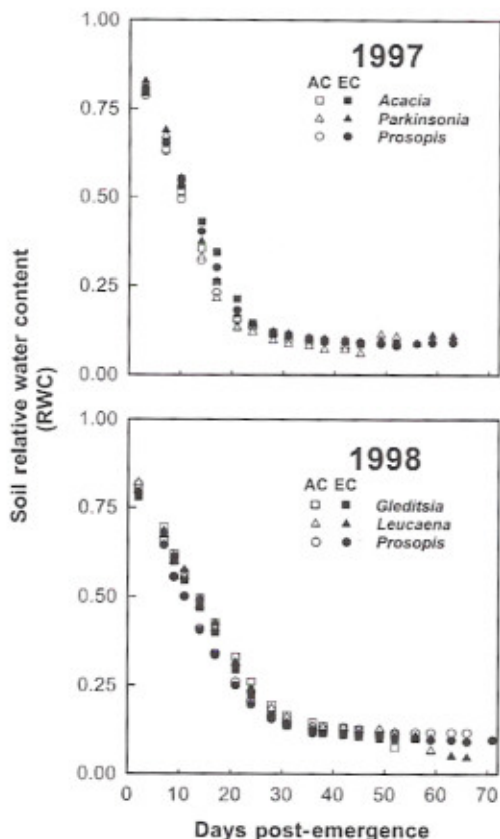


Figure 1. Mean soil relative water content (RWC) at two CO_2 concentrations ($[\text{CO}_2]$) (AC = ambient $[\text{CO}_2]$, EC = elevated $[\text{CO}_2]$) in pots containing living seedlings of three woody species each in 1997 and 1998. Watering was discontinued in each year after wetting soil to drip shortly before seedling emergence on Day 0. Because soil RWC was followed only until seedlings died or were harvested, the sample size of each mean declined from a maximum of 40 in 1997 and 60 in 1998.

Table 1. Final biomass (Day 28) and mean values of relative growth rate (RGR), net assimilation rate (NAR) and leaf area ratio (LAR) calculated over Days 14–28 for well-watered seedlings of woody legumes grown at ambient CO₂ concentration, and the stimulation of final biomass and RGR by atmospheric CO₂ enrichment.

Year/species	Biomass (g)	RGR (day ⁻¹)	NAR (g m ⁻² day ⁻¹)	LAR (m ² g ⁻¹)	Biomass (Elevated/Ambient)	RGR (Elevated/Ambient)
1997						
<i>Acacia</i>	0.293	0.037	6.92	0.005	1.25	1.49
<i>Parkinsonia</i>	0.526	0.040	12.72	0.003	1.43	1.10
<i>Prosopis</i>	0.275	0.032	6.24	0.005	1.37	1.34
1998						
<i>Gleditsia</i>	0.317	0.058	11.35	0.006	1.19	1.19
<i>Leucaena</i>	0.198	0.049	4.84	0.010	1.00	0.96
<i>Prosopis</i>	0.279	0.048	9.02	0.006	1.11	0.79

and *Parkinsonia* (−1.95 MPa) during 1997 and was higher in *Leucaena* (−1.32 MPa) than in *Gleditsia* (−1.70 MPa) during 1998 (midday Ψ_x for *Prosopis* = −1.54 MPa). Across species and harvest dates during 1998, atmospheric CO₂ enrichment increased midday Ψ_x of drought-treated plants from −1.66 to −1.38 MPa ($P = 0.014$, $n = 36$). Elevated [CO₂] increased midday Ψ_x of drought-treated seedlings from −3.10 to −1.46 MPa ($P < 0.05$, $n = 12$) on the second of two harvest dates during 1997.

Atmospheric CO₂ enrichment did not affect π_0 during 1997, but decreased π_{100} in *Acacia* from −0.83 to −1.24 MPa ($n = 6$) and lowered the RWC at turgor loss (R_0) for drought-treated plants from 0.77 to 0.64 ($n = 9$). Only in *Parkinsonia* was there evidence of osmotic adjustment in response to drought, with π_{100} decreasing from −0.98 MPa among well-watered seedlings to −1.40 MPa among drought-treated seedlings ($n = 6$). The π_0 was significantly lower in *Prosopis* and *Parkinsonia* (−1.98 and −2.04 MPa, respectively) than in *Acacia* (−1.56 MPa). Drought-treated seedlings from 1998 harvests were cooled excessively during rehydration and could not be used for pressure–volume measurements. However, π_{100} , π_0 and R_0 of well-watered seedlings did not differ among species or between CO₂ treatments in 1998 (not shown).

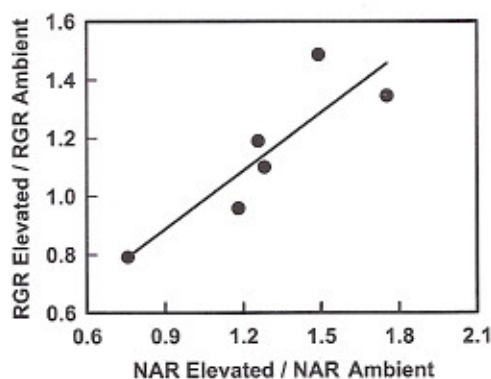


Figure 2. Relationship between the proportional stimulation of relative growth rate (RGR) at elevated [CO₂] and the relative increase in net assimilation rate (NAR) at elevated [CO₂] over Days 14–28 following emergence for well-watered seedlings of woody legumes across experiments in 1997 and 1998 ($r^2 = 0.77$, $P = 0.02$).

Leaf gas exchange

Leaf photosynthetic rates did not differ among the three species studied during 1997 ($P = 0.52$), but increased by 52% at high [CO₂] and decreased by 49% in response to drought (Fig-

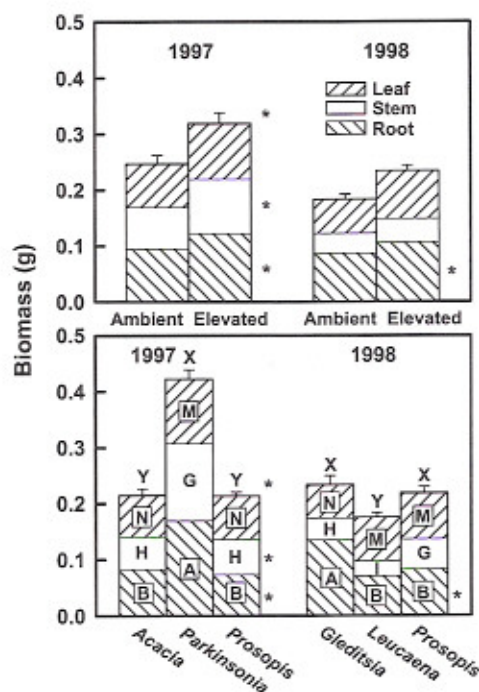


Figure 3. Total biomass and its allocation among tissues of drought-exposed seedlings grown during two experiments (1997: *Acacia*, *Parkinsonia*, *Prosopis*; 1998: *Gleditsia*, *Leucaena*, *Prosopis*) at ambient and elevated CO₂ concentrations. Seedlings were harvested on Days 17–24 of soil water depletion from fully hydrated conditions. Error bars indicate 1 SE for total biomass. Biomass of each tissue type and of whole plants was greater at elevated [CO₂] than at ambient [CO₂] (upper panel) in both 1997 ($P < 0.0001$, $n = 45$) and 1998 ($P < 0.02$, $n = 36$). Within each year, means for total biomass and for each yield component do not differ significantly between species (lower panel) if labeled with the same letter ($n = 30$ –31 and 24 for 1997 and 1998, respectively). An asterisk indicates that the CO₂ effect (upper panel) or species effect (lower panel) differed with harvest date or other treatments.

ure 4). The effects on net photosynthesis (A) of high $[\text{CO}_2]$ and drought, measured on Days 21 and 22 of soil water depletion, were significant across other treatments. Stomatal conductance (g) did not differ significantly among the three species in 1997 ($P = 0.06$), but drought reduced g from 0.18 to 0.07 $\text{mol m}^{-2} \text{s}^{-1}$ across species ($P = 0.0001$, $n = 26-43$). There was a marginally significant ($P = 0.10$) tendency for g of drought-treated seedlings to decline more at ambient $[\text{CO}_2]$ than at elevated $[\text{CO}_2]$ (Figure 5). Across species in 1997, g of drought-treated plants declined linearly with decreasing RWC at both ambient ($P = 0.07$, $r^2 = 0.25$) and elevated $[\text{CO}_2]$ ($P = 0.02$, $r^2 = 0.42$). During 1998, CO_2 enrichment increased A in *Prosopis* alone (from 12.4 to 22.2 $\mu\text{mol m}^{-2} \text{s}^{-1}$; $n = 11$) and reduced g in all species except *Prosopis* (not shown), with the largest decrease in *Gleditsia* (from 0.18 to 0.08 $\text{mol m}^{-2} \text{s}^{-1}$; $n = 13$). Drought did not significantly ($P = 0.08$) affect A in 1998 (Figure 4), but reduced g at ambient $[\text{CO}_2]$ (Figure 5). Stomatal conductance of drought-treated plants was not significantly related to soil RWC ($P = 0.25$), which differed little among pots during the gas exchange measurements.

Survivorship of drought

Elevated $[\text{CO}_2]$ increased survivorship of *Prosopis* and *Par-*

kinsonia seedlings during 1997 (Figure 6) and of *Prosopis* seedlings during 1998 (Figure 7), as indicated by significant effects of $[\text{CO}_2]$ on the time trends of survivorship of each species (*Prosopis*: $P = 0.014$ log-rank test, $P = 0.008$ Wilcoxon test during 1997; $P = 0.06$ log-rank test, $P = 0.10$ Wilcoxon test during 1998 and *Parkinsonia*: $P = 0.08$ log-rank test, $P = 0.07$ Wilcoxon test). However, survivorship curves of *Acacia* seedlings from 1997 and of *Gleditsia* and *Leucaena* seedlings from 1998 did not differ consistently between CO_2 treatments ($P > 0.20$). Small differences between CO_2 treatments on certain dates apparently rendered the entire CO_2 effect non-significant for these species.

Across species in 1997, atmospheric CO_2 enrichment increased the length of the drought period required to reach 50% survivorship by 4 days (from 37.7 to 42.0 days; $P = 0.05$), and increased the maximum period of drought survival by a mean of 11 days (from 53.7 to 64.7 days; $P = 0.10$). Similar results were obtained in 1998. Atmospheric CO_2 enrichment increased the length of drought required to reduce survivorship to 50% by 4 days (from 48.7 to 53.3 days; $P = 0.02$) and prolonged the onset of death of the final surviving seedling by an average of 10 days (from 61.0 to 71.0 days; $P = 0.02$). Across CO_2 treatments, species did not differ in these measures of drought survivorship in 1997 ($P > 0.45$), but atmospheric CO_2 enrichment prolonged survival by the greatest period in species that were the most drought-tolerant at ambient $[\text{CO}_2]$

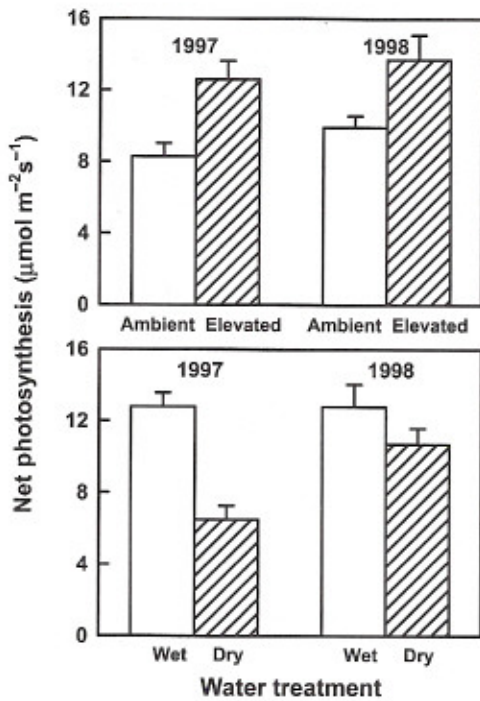


Figure 4. Photosynthetic rates of woody seedlings grown during 1997 and 1998 under well-watered conditions (Wet) or exposed to similar rates of soil water depletion (Dry) at both ambient $[\text{CO}_2]$ and elevated $[\text{CO}_2]$. Net photosynthesis was measured 21–23 days following emergence at the $[\text{CO}_2]$ at which plants were grown ($n = 34-35$ for CO_2 treatments and 43 and 26 under wet and dry conditions during 1997; $n = 35$ for each treatment during 1998). Error bars indicate 1 SE. Photosynthesis increased in elevated $[\text{CO}_2]$ and decreased under dry conditions in 1997 ($P < 0.0006$). In 1998, there was no effect of water treatment, and the CO_2 effect differed among species.

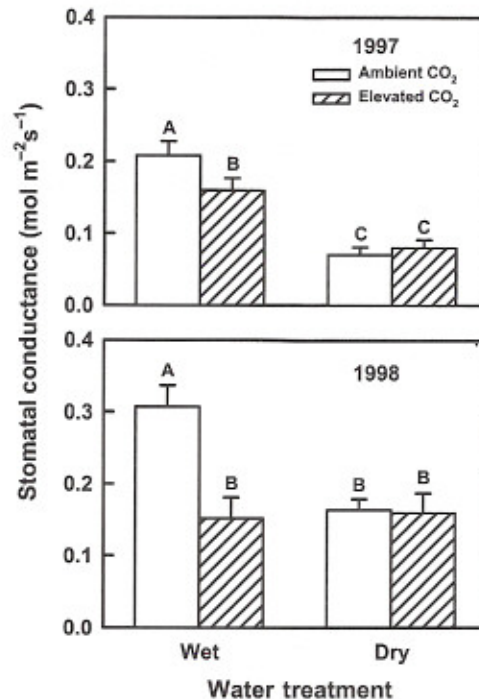


Figure 5. Stomatal conductance of woody seedlings grown under well-watered conditions (Wet) or exposed to similar rates of soil water depletion (Dry) at both ambient and elevated CO_2 concentrations. Stomatal conductance was measured 21–23 days following emergence at the $[\text{CO}_2]$ at which plants were grown ($n = 12-22$ during 1997; $n = 17-18$ during 1998). Error bars indicate 1 SE.

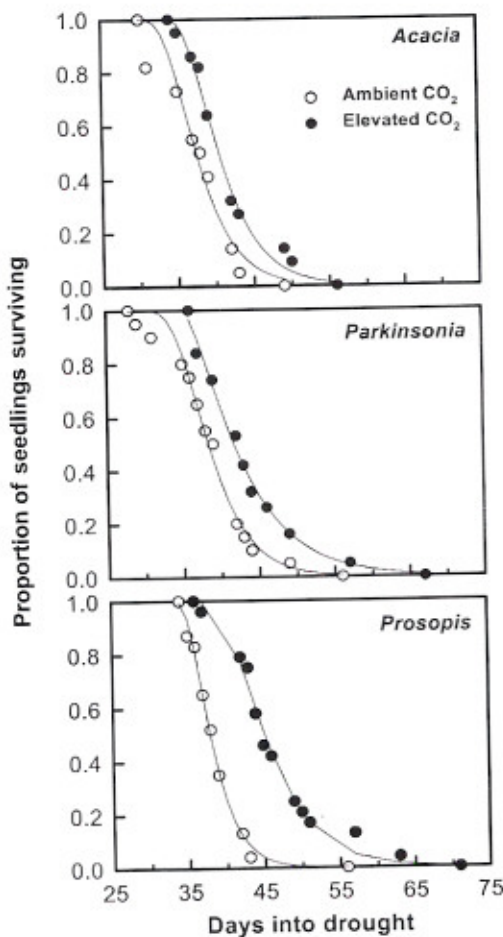


Figure 6. Relationship between seedling survivorship and days into soil water depletion from fully hydrated conditions for woody legumes grown during 1997 at ambient and elevated CO₂ concentrations ($n = 19-24$). Solid lines are fits of sigmoid curves to data.

(*Prosopis*, *Parkinsonia*; Table 2). In 1998, species differed in the period of drought required to reduce survivorship to 50 and 0% ($P < 0.006$). *Gleditsia* was the least drought-tolerant of the three species studied in 1998 (Figure 7). Across CO₂ treatments, *Prosopis* survived for about 2 weeks longer than the other species. In 1998, as in 1997, the greatest increase in the maximum period of drought survival at elevated [CO₂] occurred in the most drought-tolerant species, *Prosopis* (Table 2).

There was some evidence of a negative relationship between RGR and survivorship of drought at ambient [CO₂], but the relationship was weak because interspecific differences in RGR were small (Table 2). In 1998, the ranking of species by RGR was the inverse of species rankings by each of two indices of survivorship, the maximum period of drought survival (days to 0% survival) and the drought period required to reduce survivorship to 50%. In 1997, however, the fastest and the slowest growing species at ambient [CO₂] (*Parkinsonia* and *Prosopis*, respectively) did not differ in either index of drought survivorship. There was no relationship between survivorship

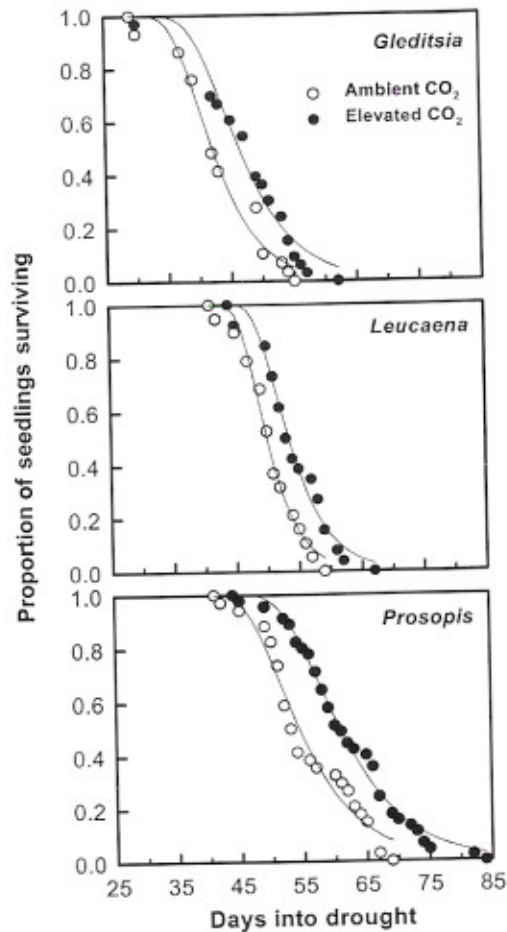


Figure 7. Relationship between seedling survivorship and days into soil water depletion from fully hydrated conditions for woody legumes grown during 1998 at ambient and elevated CO₂ concentrations ($n = 19-45$). Solid lines are fits of sigmoid curves to data.

and either NAR or LAR at ambient [CO₂] in either year (data not shown).

Discussion

We tested the prediction that atmospheric CO₂ enrichment exaggerates interspecific differences in maximum growth rate and drought tolerance among seedlings of woody species that differ in distribution along a rainfall gradient. If an interspecific tradeoff exists between drought tolerance and plant growth capacity, as is generally thought (Orians and Solbrig 1977, Smith and Huston 1989), atmospheric CO₂ enrichment could reinforce trends in seedling establishment that contribute to species patterns along water gradients.

Interspecific differences in drought tolerance were relatively small among the five woody legumes studied, but the differences were usually consistent with our prediction that atmospheric CO₂ enrichment increases survivorship more in drought-tolerant species than in drought-sensitive species. In 1997, for example, atmospheric CO₂ enrichment improved

Table 2. Number of days into drought during two experiments (1997, 1998) when survivorship of woody seedlings grown at ambient and elevated CO₂ concentrations ([CO₂]) reached 50 and 0%. Columns headed Δ indicate the number of days by which atmospheric CO₂ enrichment prolonged survival. Values in parenthesis are mean relative growth rates (RGR) of well-watered seedlings grown at ambient [CO₂].

Year/species (RGR)	Days to 50% survival			Days to 0% survival		
	Ambient [CO ₂]	Elevated [CO ₂]	Δ	Ambient [CO ₂]	Elevated [CO ₂]	Δ
1997						
<i>Prosopis</i> (0.032)	38	45	7	56	71	15
<i>Parkinsonia</i> (0.040)	38	41	3	56	67	11
<i>Acacia</i> (0.037)	37	40	3	49	56	7
1998						
<i>Prosopis</i> (0.048)	54	61	7	69	84	15
<i>Leucaena</i> (0.049)	50	53	3	59	67	8
<i>Gleditsia</i> (0.058)	42	46	4	55	62	7

survivorship of both *Prosopis* and *Parkinsonia* throughout the period of seedling mortality, but did not consistently affect survivorship of the more drought-sensitive species *Acacia*. In 1998, atmospheric CO₂ enrichment increased survivorship of the most drought-tolerant species, *Prosopis*, but did not significantly affect survivorship curves of *Gleditsia* or *Leucaena*. In both 1997 and 1998, atmospheric CO₂ enrichment prolonged survival by the greatest period in species that were most drought-tolerant at ambient [CO₂] (*Prosopis*, *Parkinsonia*).

Percentage survival of drought-sensitive species did not differ at all times between CO₂ treatments. However, doubling [CO₂] increased the maximum period of drought survival by a mean of 10–11 days and increased the mean duration of drought required to reduce survivorship to 50% by 4 days across the species studied. This benefit of high [CO₂] on drought-treated plants apparently derived from changes that improved seedling water status. Midday Ψ_x of drought-treated seedlings was less negative at elevated [CO₂] than at ambient [CO₂], despite an increase in seedling size and leaf weight at high [CO₂] and despite the absence of a CO₂ effect on predawn Ψ_x . Elevated [CO₂] may have prolonged survival by reducing transpiration rates or by improving seedling tolerance of low water potentials, (cf. Miao et al. 1992, Morse et al. 1993, Polley et al. 1999). None of these CO₂ effects was consistently demonstrated, however. High [CO₂] apparently reduced transpiration per unit leaf area by reducing stomatal conductance, at least during the early stages of soil water depletion. By Days 21–23 of each drought period, this CO₂ effect had disappeared. Studies with other woody species have yielded similar results (Heath 1998, Centritto et al. 1999). Plants grown at elevated [CO₂] may have maintained positive turgor pressures at lower water potentials, a trend suggested by the decrease in plant RWC at turgor loss that occurred during 1997 at high [CO₂]; however, as in other studies with woody plants, CO₂ effects on this measure of drought tolerance were inconsistent (Morse et al. 1993, Tschaplinski et al. 1993, 1995, Polley et al. 1996, 1999, Centritto et al. 1999). Several mechanisms apparently contributed to improved drought tolerance at elevated [CO₂], but no single mechanism predominated.

Effects of atmospheric CO₂ enrichment on RGR also differed among species, but did not follow the pattern usually reported. Atmospheric CO₂ enrichment has been shown to preferentially increase RGR (Poorter 1993) or biomass (Bunce 1997) in species that grow most rapidly at ambient [CO₂]. Neither trend was evident in our data. There was no relationship between RGR at ambient [CO₂] and either the relative or the absolute increase in RGR at elevated [CO₂] or between RGR at ambient [CO₂] and the relative stimulation of plant biomass by atmospheric CO₂ enrichment. These results are surprising because both the proportional increase in biomass and the absolute increase in RGR at high [CO₂] will be greater in species that grow most rapidly at ambient [CO₂] if CO₂ enrichment stimulates RGR by about the same percentage among species (Bunce 1997). That this pattern was not observed implies that RGR was stimulated proportionally less at high [CO₂] in rapidly growing species than in slowly growing species, consistent with the trend measured by Tischler et al. (2000) on seedlings of five epigeal species. Interspecific differences in the response of RGR to [CO₂] were highly correlated with CO₂ effects on NAR, as reported by Bunce (1997) and Tischler et al. (2000). This correlation implies that interspecific differences in the photosynthetic response to [CO₂] largely accounted for the differences in stimulation of RGR among species.

Our results provide some support for the presumed negative correlation (tradeoff) between growth potential and survivorship of drought. As predicted by the tradeoff model, the most slowly growing species at ambient [CO₂] (*Prosopis*) was also the most drought-tolerant of the species studied. In 1998, there was an inverse relationship between the ranking of species by RGR and the ranking of species by each of two indices of drought survivorship. Because interspecific differences in both RGR and drought survivorship were small, however, this test of the tradeoff model is not definitive. In a study with eight C₄ grasses, Fernández and Reynolds (2000) found no correlation between growth rate and reduction in biomass production in response to drought, and concluded that rapidly growing perennial species are rare in xeric systems because they deplete soil water quickly, not because they are less drought-tolerant than slowly growing species.

Our results indicate that atmospheric CO₂ enrichment may not exaggerate species differences in RGR, but may reinforce interspecific differences in drought tolerance. Low water availability can be a significant barrier to woody plant establishment in grasslands (Harrington 1991, O'Connor 1995, Davis et al. 1998). Because mortality rates of woody plants typically are highest among seedlings, factors that reduce seedling mortality could alter rates or patterns of woody recruitment. Benefits of atmospheric CO₂ enrichment to woody invaders may be direct, as in the positive effect of atmospheric CO₂ enrichment on seedling survivorship reported here, but could also be indirect, as when high [CO₂] benefits woody seedlings by reducing grass depletion of soil water (Polley et al. 1997). To the extent that seedling persistence in grasslands is positively correlated with drought survivorship, our results indicate that atmospheric CO₂ enrichment will increase recruitment of the five woody legumes, with greatest benefit to *Parkinsonia* and *Prosopis*.

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