Responses of Seedlings of Five Woody Species to Carbon Dioxide Enrichment

Charles R. Tischler
Justin D. Derner
H. Wayne Polley
Hyrum B. Johnson

Abstract: Encroachment of woody species into formerly productive rangeland is an immense problem in the Southwest. Effects of predicted global change scenarios on seedlings of such species are largely unstudied. Seedlings of five invasive woody legume species (honey mesquite [*Prosopis glandulosa*], huisache [*Acacia farnesiana*], honey locust [*Gleditsia triacanthos*], Eve's necklace [*Sophora affinis*], and Paloverde [*Parkinsonia aculeata*]) were grown for 23 days in glasshouses in Temple, TX, at ambient and twice ambient levels of atmospheric carbon dioxide. Plants were kept well watered and fertilized. Seedlings of all species responded positively to CO_2 enrichment, with significant differences in seedling mass observed 1 week after emergence. Mesquite and huisache responded most strongly to elevated CO_2. Other work from our laboratory suggests that at least for honey mesquite and huisache, seedling mortality is near zero beyond 3 weeks postemergence, even under water stress conditions. Thus, these invasive species will likely become even more problematic in the future as atmospheric CO_2 increases.

Introduction

It is now widely accepted that atmospheric CO_2 concentration has increased in the recent past and will continue to increase (Trabalka and others 1986). An environment enriched in CO_2 has direct stimulatory effects on plants with C_3 photosynthetic carbon metabolism (Bunce 1997), although moderate effects, as well as indirect effects, are noted in C_4 plants (Owensby and others 1993). Because most of the grasslands in the Southwestern United States consist of C_4 species that have been or are currently being invaded by C_3 woody species (Polley and others 1996), effects of this atmospheric change on growth and development of brush species merits study.

For most invasive species, success in the seedling stage is a critical factor influencing eventual success of that species. One reason for this is that woody species tend to be long-lived perennials that are avoided by livestock, and relatively resistant to environmental extremes, insects and pathogens, and other common causes of mortality. It has been proposed that elevated CO_2 may have a significant positive effect on woody plant species and that this is manifest in invasion by woody plants and subsequent thickening in grass-dominated ecosystems (Bond and Midgley 2000).

We studied effects of a twice ambient CO_2 atmosphere on the growth and development of five invasive woody legumes for the first 23 days after emergence in these experiments. These species differ markedly in invasive potential, and we hypothesize that positive effects of CO_2 would be most pronounced on the most invasive species. Mesquite (*Prosopis glandulosa*) and huisache (*Acacia farnesiana*) are found in almost pure stands on millions of acres of rangeland in Texas, with mesquite being cosmopolitan but more prevalent in the western portion of south-central and southwestern Texas, and huisache being more prevalent in south-central Texas and the eastern portion of the Rio Grande Plains, but not extending north beyond central Texas. Paloverde (*Parkinsonia aculeata*), honey locust (*Gleditsia triacanthos*), and Eve's necklace (*Sophora affinis*) are rare to common across the eastern half of Texas, generally never existing in pure stands, but being minor components of mixed woodlands. Occasionally Eve's necklace and Paloverde are used as ornamentals.

Materials and Methods

Seed of the five species used in this experimentation were harvested and scarified during the summer of 1996. Individual seed were weighed so that a narrow range of seed masses could be selected for each species, thus insuring relatively consistent cotyledonary leaf area for each species. The range of seed masses used for each species were Eve's Necklace 0.010 to 0.0800 g; Honey locust 0.0801 to 0.0900 g; Paloverde 0.1110 to 0.1160 g; mesquite 0.0451 to 0.0500 g; and huisache: 0.0651 to 0.0700 g. Planting dates were staggered to synchronize seedling emergence among species. Eve's necklace seed were planted on August 19, Honey Locust on August 26, and Paloverde, Mesquite, and Huisache were planted on August 27, with emergence for all species occurring on August 30 and 31, 1996.

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Charles R. Tischler, H. Wayne Polley, and Hyrum B. Johnson are Plant Physiologist, Research Leader and Ecologist, respectively, USDA-ARS Grassland, Soil & Water Research Laboratory, 808 E. Blackland Road, Temple, TX 76502, U.S.A.; FAX: (254) 770-6561; e-mail: ctischler@spa.ars.usda.gov. Justin D. Derner is a Range Scientist, USDA-ARS, High Plains Grasslands Research Station, 8408 Hildreth Road, Cheyenne, WY 82009, U.S.A.

Seed were planted at a depth of 1.5 cm in commercial potting mix in tapered plastic cones 25 cm deep and 6.25 cm in diameter. Total cone volume was 425 cm^3. Cones were watered at planting and weekly with full strength Hoagland's solution, and with tap water as necessary. As seedlings emerged, cones were transferred to interlocking racks, each with a capacity of 20 cones. Species were randomized within a rack, with four individuals of each species in a rack.

Two adjacent glasshouse bays at the Grassland, Soil, and Water Research Laboratory (Temple, TX) were utilized; CO_2 concentrations were 365 and 700 ppm. Air within each bay was sampled each 4 minutes with a Li-Cor Model LI-622262 infrared gas analyzer to determine CO_2 concentration. Pure CO_2 was injected into the 700 ppm glasshouse bay as needed to maintain the desired concentration, while in the 365 ppm bay, outside air was circulated through the glasshouse to maintain ambient conditions. Air temperature was maintained near that of outdoor temperature. The late summer of 1996 was dry with few clouds, and thus the seedlings received saturating levels of light most of the time.

Destructive harvests were made on days 3, 8, 13, 18, and 23. Root and shoot dry mass, and cotyledonary and true leaf dry mass and area were determined for seven plants of each species at each harvest. Data was analyzed by standard ANOVA techniques, with comparisons made only within a species and harvest date.

Results

Cotyledonary Mass

On days 8 and 13, some significant effects of elevated CO_2 on cotyledonary mass were observed (table 1). These effects were not observed later in development, probably because of the slow progression of the cotyledonary leaves to senescence, and the weight loss experienced by cotyledonary leaves before they abscise. With the exception of Paloverde, cotyledonary mass of all other species was at near maximum at day 3. This is because Paloverde is the only species that has significant expansion of cotyledonary leaves (6.13 cm^2 at day 13, compared to 2.6 cm^2 for mesquite at day 13, the next greatest area—both values for ambient atmosphere). Because of different developmental strategies between the woody species and differences in rates of development, detailed comparisons between the species are not meaningful.

Cotyledonary Leaf Area and True Leaf Mass and Area

When statistical differences were noted, cotyledonary leaf area and true leaf mass and area were greater for species in elevated versus ambient CO_2 atmospheres (data not presented). Because elevated CO_2 modifies plant phenology, we did not attempt to make comparisons of specific leaf weights, because these comparisons are not instructive.

Root Mass

By day 23, root mass for all species was numerically higher at elevated CO_2 (table 2). None of these differences reached statistical significance because of the great deal of variation in root mass from plant to plant. Larger sample sizes would be required to establish statistical significance.

Total Biomass

At day 23, total biomass was greater in every case for plants in enriched CO_2, although this difference was significant only for mesquite (table 3). However, we observed significant differences for Paloverde at days 8, 13, and 18; for Locust at days 8 and 18; for Mesquite additionally at days 3, 8, 13, and 18; for Huisache at days 8, 13, and 18, and for Eve's Necklace at day 13. These data suggest an overall significant effect of CO_2 on biomass accumulation, but point out a complicating factor often overlooked by investigators. This is the effect of "rests" or temporary lapses in growth (often concomitant with increases in complexity) as described by Stebbins (1976) and Vogel (1980). Comparisons between species become meaningless if one species is in a "rest" stage while a second is actively growing, as Stebbins (1976) demonstrated.

Table 1—Cotyledonary masses of five woody species at five sampling dates.

Entry	Cotyledon mass[a]				
	Day 3	Day 8	Day 13	Day 18	Day 23
	mg				
Paloverde 350	0.028a	0.041b	0.050a	0.044b	0.043a
Paloverde 700	.026a	.057a	.057a	.053a	.051a
Locust 350	.016a	.012b	.010b	.010a	.010a
Locust 700	.016a	.015a	.011a	.009a	.010a
Mesquite 350	.018a	.023b	.021b	.017b	.018a
Mesquite 700	.018a	.031a	.038a	.033a	.027a
Huisache 350	.013a	.010b	.008a	.006a	.003a
Huisache 700	.014a	.014b	.008a	.005a	.004a
Eve's necklace 350	.015a		.012a		.015a
Eve's necklace 700	.016a		.015a		.018a

[a]Values for a species in a column followed by a different letter are significantly different ($P \leq 0.05$), Duncan's Multiple Range Test.

Table 2—Root dry mass of five woody species at five sampling dates.

Entry	Root mass[a]				
	Day 3	Day 8	Day 13	Day 18	Day 23
	mg				
Paloverde 350	0.017a	0.036a	0.043a	0.062a	0.081a
Paloverde 700	.016a	.034a	.050a	.067a	.087a
Locust 350	.016a	.016b	.029a	.049a	.067a
Locust 700	.015a	.020a	.034a	.054a	.075a
Mesquite 350	.010b	.015a	.017b	.033b	.047a
Mesquite 700	.012a	.016a	.023a	.046a	.070a
Huisache 350	.012a	.013a	.017a	.029b	.040b
Huisache 700	.012a	.249a	.023a	.039b	.058a
Eve's necklace 350	.013a		.017a		.041a
Eve's necklace 700	.013a		.023a		.045a

[a]Values for a species in a column followed by a different letter are significantly different ($P \leq 0.05$), Duncan's Multiple Range Test.

Table 3—Total dry mass of five woody species at five sampling dates.

Species	CO_2	Total mass[a] Day 3	Day 8	Day 13	Day 18	Day 23
		mg				
Paloverde	350	0.051b	0.077b	0.134b	0.166b	0.240a
Paloverde	700	.048a	.111a	.168a	.230a	.267a
Locust	350	.039a	.049b	.079a	.118b	.167a
Locust	700	.039a	.070a	.093a	.139b	.189a
Mesquite	350	.031b	.049b	.070b	.123b	.167b
Mesquite	700	.035a	.062a	.096a	.173a	.295a
Huisache	350	.028a	.042b	.059b	.091B	.125a
Huisache	700	.031a	.053a	.088a	.129a	.188a
Eve's necklace	350	.033a		.058b		.153a
Eve's necklace	700	.035a		.089a		.199a

[a]Values for a species in a column followed by a different letter are significantly different ($P \leq 0.05$), Duncan's Multiple Range Test.

Conclusions

Our data for five woody species vividly illustrate positive growth effects of elevated CO_2 early in the development of species. However, our glasshouse results probably grossly underestimate the effects of CO_2 in field or range situations. By increasing water use efficiency of all species in an ecosystem, elevated CO_2 alters water balance of the system, thus favoring seedling establishment. Although no data exists on this topic, it would also be logical to expect a positive influence of elevated CO_2 on reproductive output of shrub and brush species, thus enriching the seedbank of these invaders.

Obviously, cumulative effects of increasing CO_2 on rangeland ecosystems is an experiment in progress, whose result will not be completely chronicled for centuries. However, the data we present suggests that increasing CO_2 will favor shrub and brush invasion at the expense of grass communities.

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