Effects of Elevated CO_2 on Growth Responses of Honey Mesquite Seedlings From Sites Along a Precipitation Gradient

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Abstract: We collected seeds from two honey mesquite (*Prosopis glandulosa* var. *glandulosa)* trees at each of three sites along an east-west precipitation gradient in Texas: Marlin (93.2 cm mean annual precipitation, MAP), Menard (62.0 cm MAP), and Bakersfield (36.6 cm MAP) to test the hypothesis that CO_2 enrichment would differentially affect plant responses along this gradient. However, significant interactions between CO_2 and the site of origin were not observed at either harvest (8- or 16-days postemergence). Growth responses of genotypes of honey mesquite collected from the east-west precipitation gradient were inconsistent with respect to the gradient. Significant growth responses to elevated CO_2 often were of small absolute and relative magnitude, especially at the 16-day harvest. If genetic differences exist among the genotypes used in this investigation, they do not affect growth responses to elevated CO_2 under well-watered conditions. Similar enhancement of seedling plant growth to elevated CO_2 in genotypes of honey mesquite from a wide precipitation gradient suggests that this invasive, woody plant will respond comparably to CO_2 enrichment regardless of precipitation at the site of origin. Whether this genetic potential is displayed in the field, however, is uncertain as existing environmental conditions may constrain responses to CO_2 enrichment. This invasive species likely will continue to be a problem species on rangelands in the future.

Introduction

Honey mesquite (*Prosopis glandulosa* var. *glandulosa*) is an invasive, leguminous shrub that has invaded arid and semiarid rangeland ecosystems and has become dominant on much of the southern mixed-grass and shortgrass prairies in the Great Plains (Ansley and others 2001; Archer 1989, 1990, 1995; Van Auken 2000). 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). Responses of honey mesquite to elevated CO_2 have been primarily conducted in response to soil water conditions (Polley and others 1996, 1999). Because there is genetic variation within species in responses to elevated CO_2 (Andalo and others 2001; Bezemer and others 1998; Curtis and others 1996; Klus and others 2001; Schmid and others 1996; Thomas and Jasienski 1996; Van der Kooij and others 2000), impacts of CO_2 enrichment on honey mesquite plant growth may be genotype-specific (for example, Mulholland and others 1998; Roumet and others 1999). This may be particularly important in the context of increasing shrub encroachment of rangelands, which encompass wide environmental gradients (Polley 1997; Polley and others 1997).

Species like honey mesquite that grow across wide environmental gradients likely differ genetically in ways that may affect growth responses to elevated CO_2. However, this area of research has received little attention. Three potential responses to elevated CO_2 include (1) similar responses to CO_2 by all genotypes from the environmental gradient, (2) greater responses to CO_2 by genotypes from more water-limiting environments because of increased soil water availability associated with elevated CO_2, or (3) greater responses to CO_2 by genotypes from sites with higher precipitation as they are more rapidly growing plants.

An underlying assumption of this study is that honey mesquite differs genetically at different points along an east-west precipitation gradient in western and central Texas. We tested the hypotheses that (1) growth of honey mesquite seedlings grown at ambient CO_2 increases as precipitation at the site of origin increases, and (2) CO_2 enrichment preferentially increases growth in genotypes that already grow most rapidly. Previous investigations have determined that CO_2 enrichment preferentially increased relative growth rate (Poorter 1993) and biomass (Bunce 1997) in species that had high growth rates. We addressed these potential responses in this investigation by growing seedlings of honey mesquite collected from the precipitation gradient in environmentally controlled glasshouses under optimal temperature and soil water conditions.

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Materials and Methods

The CO_2 concentration of air in each of four glasshouse bays (31° 05´N, 97° 20´W) was measured at 4-minute intervals with a Li-Cor Model LI-6262 infrared gas analyzer (Li-Cor, Inc., Lincoln, NE). 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 weekly against a Li-Cor LI-610 dewpoint generator. Air temperature, manually set at 30 °C for both day and night in each bay, was measured in the center of each bay with fine-wire (25 µm diameter) thermocouples. Pure CO_2 gas was injected into appropriate bays as required to maintain the elevated CO_2 concentration. The CO_2 concentration of air in the ambient and elevated CO_2 treatments (two bays per treatment) averaged 366 and 702 µmol mol^{-1}, respectively. Photosynthetic photon flux density (PPFD) was measured on the glasshouse roof with a point quantum sensor (LI-190SB, Li-Cor) and within the bays with 1 m long line quantum sensors (LI-191SA, Li-Cor) mounted about plant height. On average, the daily integral of PPFD inside the bays was 70 percent of that measured above the glasshouse.

Seeds were collected in August 2000 from two individual trees (genotypes) of honey mesquite at each of three sites along a precipitation gradient in Texas: Marlin (93.2 cm mean annual precipitation, MAP), Menard (62.0 cm MAP), and Bakersfield (36.6 cm MAP), resulting in a total of six genotypes. Caution was taken to ensure that these trees were at least 2 km from any major road, and each was visually inspected to determine if the morphology of the trees was typical for the given area.

To prevent confounding influences of seed mass on initial seedling development (Villar and others 1998), seeds of each genotype were weighed prior to planting to ensure similar seed mass within a genotype. Two seeds of each genotype were planted to depth of 2 cm in each of 32, 0.05 m diameter by 1.60 m deep pots on July 20, 2001, for a total of 192 pots. Pots were constructed 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. Pots were filled with a fine sandy loam soil (Pedernales series; fine, mixed, thermic typic Paleustalf; Huckabee and others 1977) with the following properties: pH = 7.1, organic carbon content = 0.57 percent, 76.2 percent sand, 16.2 percent silt, 7.6 percent clay, field capacity = 18 percent on a volumetric basis. Soil in the pots was wetted past field capacity prior to planting by adding one-half strength Hoagland's nutrient solution (Hoagland and Arnon 1950). Following planting, pots with each genotype were randomly assigned to one of four glasshouse bays, two maintained at ambient CO_2 and two at elevated CO_2, with eight pots per genotype in each bay. Full strength Hoagland's solution was added daily to each pot to maintain soil water content near field capacity. Seedlings were randomly thinned to one per pot following emergence.

One-half of the total number of seedlings were harvested at each harvest (8- or 16-days postemergence). Aboveground biomass was separated into stem and leaf components with the area of each leaf blade measured using a LI-3000A portable leaf area meter (Li-Cor, Inc., Lincoln, NE). Soil was manually washed from roots and the depth of deepest root penetration recorded. Roots were digitally scanned at high resolution (600 dpi) using the WinRHIZO software (Regent Instruments, Inc., Quebec, Canada, version 4.1c) and hardware (Hewlett Packard ScanJet 6100C scanner) to determine root length, surface area, and root volume. Roots were not stained prior to analyses, which resulted in underestimations (Bouma and others 2000), but these were minimized by using the WinRHIZO automatic threshold (that is, Lagarde's method) for pale roots with greater sensitivity. Aboveground tissues and roots were dried at 60 ºC for 72 hours prior to weighing.

Data were analyzed using ANOVA by harvest date using a split-split plot design with CO_2 as the split plot and the site of seed origin as the split-split plot in a balanced design (SAS Institute, Inc. 1994). Single degree freedom contrasts were used to compare the two genotypes within each site of seed origin. Means were separated by Duncan's multiple range test at the 0.10 level of significance. When needed to normalize residuals, data were logarithmically transformed before analysis; means and standard errors are reported after back transforming.

Results

Aboveground, but not belowground, variables of honey mesquite seedlings at 8 days postemergence were influenced by both the site of genotype origin and elevated CO_2 (table 1). However, significant interactions between the site of origin and CO_2 were not observed, indicating that growth responses to elevated CO_2 were similar for mesquite seedlings from along the precipitation gradient. Aboveground variables, with the exception of stem mass, were 20 to 110 percent greater for the genotypes from the site with greatest MAP compared to the two lower MAP sites, both of which did not significantly differ for the majority of aboveground responses. Belowground variables did not differ with respect to the site of genotype origin. There were no significant differences for aboveground or belowground growth responses between the two genotypes from each site of collection (data not shown). Elevated CO_2 increased all aboveground variables, but responses were significant for only other leaf area (excluding cotyledon and leaf pair 1) and mass, total leaf mass, and aboveground mass. Total plant mass was similar between CO_2 levels, however, as decreased root mass with elevated CO_2 offset the increased aboveground mass. In contrast to aboveground variables, belowground responses were generally reduced with elevated CO_2, but no significant effects were detected.

In contrast to observed results from the 8-day harvest, both changes in aboveground and belowground variables of honey mesquite seedlings at 16 days postemergence were influenced by the site of genotype origin and elevated CO_2 (table 2). Similar to the 8-day harvest, no significant interactions between CO_2 and the site of genotype origin were observed. Above- and belowground growth responses to the site of genotype origin decreased in magnitude at the 16-day harvest compared to the 8-day harvest. In general, growth responses were greater for genotypes from the wettest than

Table 1—Mean (± 1 SE) aboveground and belowground responses at 8-days postemergence for honey mesquite seedlings of genotypes from along an east-west precipitation gradient in Texas (Marlin [93.2 cm mean annual precipitation, MAP], Menard [62.0 cm MAP] and Bakersfield [36.6 cm MAP]) exposed to ambient and elevated CO_2 concentrations (366 and 702 μmol mol^{-1}, respectively).

Variable	CO_2		MAP at site of genotype origin[a]		
	Ambient	Elevated	93.2	62.0	36.6
			- *cm* -		
Aboveground					
Cotyledon leaf area (cm^2)	2.13 (0.13)	2.27 (0.26)	2.85 (0.26)a	1.89 (0.20)b	1.85 (0.10)b
Cotyledon mass (g)	0.0144 (0.0009)	0.0158 (0.0021)	0.0180 (0.0025)a	0.0149 (0.0014)b	0.0128 (0.0009)b
Leaf pair 1 leaf area (cm^2)	2.27 (0.15)	2.34 (0.34)	2.82 (0.28)a	1.76 (0.33)b	2.19 (0.22)b
Leaf pair 1 mass (g)	0.0080 (0.0015)	0.0091 (0.0014)	0.0101 (0.0015)a	0.0069 (0.0008)c	0.0081 (0.0009)b
Other leaf area (cm^2)	2.28 (0.21)	2.86 (0.22)[b]	3.31 (0.63)a	1.91 (0.27)b	2.27 (0.24)b
Other leaf mass (g)	0.0093 (0.0009)	0.0176 (0.0048)[b]	0.0204 (0.0059)a	0.0081 (0.0013)b	0.0097 (0.0011)b
Stem mass (g)	0.0089 (0.0008)	0.0111 (0.0018)	0.0115 (0.0020)a	0.0094 (0.0022)a	0.0089 (0.0010)a
Total leaf area (cm^2)	6.68 (0.40)	7.48 (1.03)	8.97 (1.07)a	5.56 (0.73)b	6.31 (0.45)b
Total leaf mass (g)	0.0317 (0.0018)	0.0425 (0.0065)[b]	0.0485 (0.0075)a	0.0299 (0.0032)b	0.0305 (0.0019)b
Aboveground mass (g)	0.0406 (0.0022)	0.0537 (0.0077)[b]	0.0599 (0.0089)a	0.0393 (0.0048)b	0.0394 (0.0023)b
Belowground					
Root depth (cm)	51.6 (6.6)	49.6 (4.8)	49.8 (6.4)a	46.4 (10.8)a	53.5 (6.3)a
Root length (cm)	90.1 (12.2)	77.7 (7.8)	92.2 (8.6)a	75.2 (14.4)a	84.0 (14.4)a
Root surface area (cm^2)	17.5 (1.8)	14.8 (1.3)	17.4 (1.4)a	15.3 (2.7)a	16.1 (2.2)a
Root volume (m^3)	0.26 (0.03)	0.21 (0.02)	0.25 (0.02)a	0.23 (0.04)a	0.23 (0.03)a
Root mass (g)	0.0151 (0.0013)	0.0135 (0.0016)	0.0149 (0.0018)a	0.0132 (0.0025)a	0.0147 (0.0014)a
Whole plant					
Total plant mass (g)	0.0557 (0.0027)	0.0672 (0.0086)	0.0749 (0.0097)a	0.0524 (0.0067)b	0.0541 (0.0028)b

[a] Different letters among the MAP levels indicate a significant difference between means.
[b] Significant ($P < 0.10$) difference between ambient and elevated CO_2 means.

Table 2—Mean (± 1 SE) aboveground and belowground responses at 16-days postemergence for honey mesquite seedlings of genotypes from along an east-west precipitation gradient in Texas (Marlin [93.2 cm mean annual precipitation, MAP], Menard [62.0 cm MAP] and Bakersfield [36.6 cm MAP]) exposed to ambient and elevated CO_2 concentrations (366 and 702 μmol mol^{-1}, respectively).

Variable	CO_2		MAP at site of genotype origin[a]		
	Ambient	Elevated	93.2	62.0	36.6
			- *cm* -		
Aboveground					
Cotyledon leaf area (cm^2)	2.39 (0.20)	2.57 (0.15)	2.93 (0.23)a	2.29 (0.20)b	2.08 (0.13)b
Cotyledon mass (g)	1.7553 (0.0011)	1.7585 (0.0010)[b]	1.7594 (0.0012)a	1.7569 (0.0015)b	1.7535 (0.0011)b
Leaf pair 2&3 leaf area (cm^2)	6.02 (0.40)	7.18 (0.39)[b]	7.38 (0.45)a	6.71 (0.55)a	5.44 (0.40)b
Leaf pair 2&3 mass (g)	1.7706 (0.0022)	1.7793 (0.0026)[b]	1.7778 (0.0023)a	1.7779 (0.0044)a	1.7680 (0.0023)b
Other leaf area (cm^2)	9.64 (0.97)	10.18 (1.20)	12.65 (1.52)a	8.70 (0.81)b	7.60 (0.57)b
Other leaf mass (g)	1.7826 (0.0047)	1.7901 (0.0062)	1.7985 (0.0076)a	1.7849 (0.0051)a	1.7723 (0.0025)b
Stem mass (g)	1.7652 (0.0040)	1.7756 (0.0036)	1.7743 (0.0064)a	1.7674 (0.0035)a	1.7666 (0.0027)a
Total leaf area (cm^2)	18.06 (1.48)	19.93 (1.54)	22.96 (2.07)a	17.70 (1.37)b	15.13 (0.72)b
Total leaf mass (g)	5.3085 (0.0074)	5.3280 (0.0086)[b]	5.3358 (0.0103)a	5.3196 (0.0101)a	5.2939 (0.0044)b
Aboveground mass (g)	7.0737 (0.0097)	7.1036 (0.0116)[b]	7.1100 (0.0146)a	7.0870 (0.0130)a	7.0605 (0.0067)b
Belowground					
Root depth (cm)	96.2 (5.7)	101.3 (5.0)	107.2 (6.8)a	93.9 (7.2)b	91.9 (5.3)b
Root length (cm)	201.2 (18.4)	240.3 (20.4)	250.9 (25.2)a	171.5 (17.4)b	218.0 (21.4)ab
Root surface area (cm^2)	32.5 (2.6)	40.1 (2.5)[b]	40.1 (3.4)a	31.5 (3.1)b	34.5 (2.8)ab
Root volume (m^3)	0.44 (0.04)	0.57 (0.04)[b]	0.55 (0.05)a	0.46 (0.06)a	0.45 (0.04)a
Root mass (g)	1.7861 (0.0044)	1.8024 (0.0055)[b]	1.7998 (0.0063)a	1.7955 (0.0085)a	1.7844 (0.0038)a
Whole plant					
Total plant mass (g)	8.8598 (0.0135)	8.9059 (0.0164)[b]	8.9098 (0.0135)a	8.8825 (0.0210)a	8.8449 (0.0102)b

[a] Different letters among the MAP levels indicate a significant difference between means.
[b] Significant ($P < 0.10$) difference between ambient and elevated CO_2 means.

driest site. Consistent with the 8-day harvest, there were no significant differences for aboveground or belowground growth responses between the two genotypes for each site of collection (data not shown). Elevated CO_2 increased all aboveground responses, but significant differences were observed for only leaf area and mass of leaf pairs 2 and 3, total leaf mass, and aboveground mass. The magnitude of these CO_2-induced growth responses was much reduced compared to the 8-day harvest. Belowground responses were greater with elevated CO_2, with significant increases at elevated CO_2 in root surface area, volume, and mass.

Discussion

Growth responses of honey mesquite genotypes collected from the east-west precipitation gradient were inconsistent with respect to the gradient, suggesting that our underlying assumption that honey mesquite differs genetically at different points along an east-west precipitation gradient in western and central Texas was incorrect, at least under well-watered conditions. In addition, this finding does not support our hypothesis that growth of seedlings grown at ambient CO_2 increases as precipitation at the site of origin increases. In general, genotypes from the wettest site (Marlin) had more leaf area, more mass, and greater root growth than genotypes from the driest site (Bakersfield), but growth responses of genotypes from the site with intermediate precipitation (Menard), however, were primarily responsible for the inconsistent growth response along the gradient. Growth responses of seedlings from this site were similar to those of genotypes from the wettest site for some variables and similar to genotypes from the driest site for other variables at the 16-day harvest. This inconsistency merits additional research attention, with a need to investigate additional genotypes from each site.

Elevated CO_2 increased aboveground variable responses at both harvest dates, while belowground variable responses to elevated CO_2 were inconsistent with decreases occurring at the 8-day harvest and increases at the 16-day harvest. Most of these responses, however, were not significant. Significant differences in response to elevated CO_2 often were of small absolute and relative magnitude, especially at the 16-day harvest. Significant interactions between CO_2 and the site of genotype origin were not observed for either the 8-day or 16-day harvest, indicating that observed growth responses to elevated CO_2 were similar for mesquite seedlings regardless of MAP at site of origin. Therefore, our hypothesis that elevated CO_2 would preferentially increase growth of the more rapidly growing plants from the sites with high than low precipitation was not supported for above- or belowground variables at either harvest date. If genetic differences exist among the genotypes used in this investigation, they do not affect growth responses to elevated CO_2 under well-watered conditions.

Inconsistent growth responses of aboveground and belowground variables to elevated CO_2 at the 8- and 16-day harvests are likely attributable to relative sink strengths and carbon allocation patterns of these honey mesquite seedlings. Increased aboveground, but decreased belowground, responses to elevated CO_2 at the 8-day harvest conform to priority of establishing sufficient photosynthetic machinery for seedling survival at the expense of root growth. The reduction in magnitude of aboveground response to elevated CO_2 at the 16-day harvest, and the associated increase in belowground response, indicate that photosynthetic machinery was quickly established and carbon allocation priorities shifted more belowground following the first harvest. Elevated CO_2 did not affect partitioning of dry matter between shoot and root of the grass *Dactylis glomerata* at high nitrogen, but at low nitrogen greater partitioning was observed into the shoot during early stages of growth (Harmens and others 2000). This suggests that in spite of daily additions of full-strength Hoaglands's solution, the inherently low nitrogen status and high leaching potential of the sandy loam soil resulted in low nitrogen availability to honey mesquite seedlings. Under limiting nutrient conditions, plant growth under elevated CO_2 is often negligible (Bernacchi and others 2000; Kimball and others 2002; but see Lloyd and Farquhar 1996).

Similar enhancement of early seedling plant growth in genotypes of honey mesquite from a wide precipitation gradient to elevated CO_2 suggests that this invasive, woody plant will respond comparably to CO_2 enrichment regardless of precipitation at the site of origin. Whether this genetic potential is displayed in the field, however, is uncertain, as existing environmental conditions may constrain responses to CO_2 enrichment. This invasive species likely will continue to be a problem species on rangelands in the future and may even increase competitiveness at the expense of warm-season grasses, which currently dominate the southern mixed-grass and shortgrass prairies, as these grasses are generally not as responsive to elevated CO_2 as is honey mesquite (Polley and others 1994).

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References

Andalo, C.; Goldringer, I.; Godelle, B. 2001. Inter- and intragenotypic competition under elevated carbon dioxide in *Arabidopsis thaliana*. Ecology. 82: 157–164.

Ansley, J. R.; Wu, X. B.; Kramp, B. A. 2001. Observation: long-term increases in mesquite canopy cover in a north Texas savanna. Journal of Range Management. 54: 171–176.

Archer, S. 1989. Have southern Texas savannas been converted to woodlands in recent history? The American Naturalist. 134: 545–561.

Archer, S. 1990. Development and stability of grass/woody mosaics in a subtropical savanna parkland, Texas, U.S.A. Journal of Biogeography. 17: 453–462.

Archer, S. 1995. Tree-grass dynamics in a *Prosopis*-thornscrub savanna parkland: reconstructing the past and predicting the future. Ecoscience. 2: 83–99.

Bernacchi, C. J.; Coleman, J. S.; Bazzaz, F. A.; McConnaughay, K. D. M. 2000. Biomass allocation in old-field annual species grown in elevated CO_2 environments: no evidence for optimal partitioning. Global Change Biology. 6: 855–863.

Bezemer, T. M.; Thompson, L. J.; Jones, T. H. 1998. *Poa annua* shows inter-generational differences in response to elevated CO_2. Global Change Biology. 4: 687–691.

Bond, W. J.; Midgley, G. F. 2000. A proposed CO_2-controlled mechanism of woody plant invasion in grasslands and savannas. Global Change Biology. 6: 865–869.

Bouma, T. J.; Nielsen, K. L.; Koutstall, B. 2000. Sample preparation and scanning protocol for computerized analysis of root length and diameter. Plant and Soil. 218: 185–196.

Bunce, J. A. 1997. Variation in growth stimulation by elevated carbon dioxide in seedlings of some C_3 crop and weeds species. Global Change Biology. 3: 61–66.

Curtis, P. S.; Klus, D. J.; Kalisz, S.; Tonsor, S. J. 1996. Intraspecific variation in CO_2 responses in *Raphanus raphanistrum* and *Plantago lancelata*: assessing the potential for evolutionary change with rising atmospheric CO_2. In: Korner, C.; Bazzaz, F. A., eds. Carbon dioxide, populations, and communities. London: Academic Press: 13–22.

Harmens, H.; Stirling, C. M.; Marshall, C.; Farrar, J. F. 2000. Is partitioning of dry weight and leaf area within *Dactylis glomerata* affected by N and CO_2 enrichment? Annals of Botany. 86: 833–839.

Hoagland, D. R.; Arnon, D. I. 1950. The water-culture method for growing plants without soil. California Agricultural Experiment Station Circular. 347: 1–39.

Huckabee, J. W., Jr.; Thompson, D. R.; Wyrick, J. C.; Paulat, E. G. 1977. Soil survey Bell County Texas. Washington, DC: U.S. Department of Agriculture, Soil Conservation Service.

Kimball, B. A.; Kobayashi, K.; Bindi, M. 2002. Responses of agricultural crops to Free-Air CO_2 Enrichment. Advances in Agronomy. 77: 293–368.

Klus, D. J.; Kalisz, S.; Curtis, P. S.; Terri, J. A.; Tonsor, S. J. 2001. Family- and population-level responses to atmospheric CO_2 concentration: gas exchange and the allocation of C, N, and biomass in *Plantago lanceolata* (Plantaginaceae). American Journal of Botany. 88: 1080–1087.

Lloyd, J.; Farquhar, G. D. 1996. The CO_2 dependence of photosynthesis, plant growth responses to elevated CO_2 concentrations and their interactions with soil nutrient status. I. General principles and forest ecosystems. Functional Ecology. 10: 4–32.

Mulholland, B. J.; Craigon, J.; Black, C. R.; Colls, J. J.; Atherton, J.; Landon, G. 1998. Growth, light interception and yield responses of spring wheat (*Triticum aestivum* L.) grown under elevated CO_2 and O_3 in open-top chambers. Global Change Biology. 4: 121–130.

Polley, H. W. 1997. Invited synthesis paper: implications of rising atmospheric carbon dioxide concentration for rangelands. Journal of Range Management. 50: 562–577.

Polley, H. W.; Johnson, H. B.; Mayeux, H. S. 1994. Increasing CO_2: comparative responses of the C_4 grass *Schizachyrium* and grassland invader *Prosopis*. Ecology. 75: 976–988.

Polley, H. W.; Johnson, H. B.; Mayeux, H. S.; Tischler, C. R.; Brown, D. A. 1996. Carbon dioxide enrichment improves growth, water relations and survival of droughted honey mesquite (*Prosopis glandulosa*) seedlings. Tree Physiology. 16: 817–823.

Polley, H. W.; Mayeux, H. S.; Johnson, H. B.; Tischler, C. R. 1997. Viewpoint: atmospheric CO_2 soil water, and shrub/grass ratios on rangelands. Journal of Range Management. 50: 278–284.

Polley, H. W.; Tischler, C. R.; Johnson, H. B.; Pennington, R. E. 1999. Growth, water relations, and survival of drought-exposed seedlings from six maternal families of honey mesquite (*Prosopis glandulosa*): responses to CO_2 enrichment. Tree Physiology. 19: 359–366

Poorter, H. 1993. Interspecific variation in the growth response of plants to an elevated ambient CO_2 concentration. Vegetatio. 104/105: 77–97.

Roumet, C.; Laurnet, G.; Roy, J. 1999. Leaf structure and chemical composition as affected by elevated CO_2: genotypic responses of two perennial grasses. New Phytologist. 143: 73–81.

SAS Institute, Inc. 1994. SAS/STAT user's guide, release 6.03, 4th ed. Cary, NC: SAS Institute, Inc.

Schmid, B.; Birrer, A.; Lavigne, C. 1996. Genetic variation in the response of plant populations to elevated CO_2 in a nutrient-poor, calcareous grassland. In: Korner, C.; Bazzaz, F. A., eds. Carbon dioxide, populations, and communities. London: Academic Press: 31–50.

Thomas, S. C.; Jasienski, M. 1996. Genetic variability and the nature of microevolutionary responses to elevated CO_2. In: Korner, C.; Bazzaz, F. A., eds. Carbon dioxide, populations, and communities. London: Academic Press: 51–81.

Van Auken, O. W. 2000. Shrub invasions of North American semiarid grasslands. Annual Review of Ecological Systems. 31: 197–215.

Van der Kooij, T. A. W.; De Kok, L. J.; Stulen, I. 2000. Intraspecific variation in the response of *Arabidopsis thaliana* lines to elevated atmospheric CO_2. Phyton-annales Rei Botanicae. 40: 125–132.

Villar, R.; Veneklaas, E. J.; Jordano, P.; Lambers, H. 1998. Relative growth rate and biomass allocation in 20 *Aegilops* (Poaceae) species. New Phytologist. 140: 425–437.