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Response of Seedlings of Two Hypogeal Brush Species to CO₂ Enrichment

Charles R. Tischler¹
Justin D. Derner²
H. Wayne Polley³
Hyrum B. Johnson⁴

Abstract: Previous work has demonstrated that epigeal woody invasive plants (with expanding, photosynthetic cotyledons), such as honey mesquite (*Prosopis glandulosa* L.), respond positively to elevated atmospheric CO₂ concentrations in as little as 3 days after emergence. No research has addressed the behavior of larger seeded, hypogeal invasive plants (common in south Texas) exposed to elevated CO₂. We studied two such species, guajillo (*Acacia berlandieri* Benth.) and cat claw acacia (*Acacia greggii* Gray var. *wrightii* (G. Bentham) D. Isely), to quantify growth stimulation at a doubled concentration of CO₂. Seedlings were grown in glasshouses in 1.5 m tubes at Temple, TX, in the late summer of 2000. Only seeds within a narrow range of masses were selected for each species, to reduce effects of seed mass on seedling size. Plants were harvested 15 days after emergence. Leaf area, shoot weight, leaf weight, root weight, and depth of root penetration were determined for each plant. Both species exhibited marked root length at sampling, with mean values of about 75 and 90 cm for guajillo and cat claw acacia, respectively. For both species, all parameters demonstrated a positive numerical response to elevated CO₂, although no differences were statistically significant. The lack of statistical verification of the observed differences was likely caused by the great deal of variability observed within both species. For example, values for specific parameters varied by as much as a factor of six within a species and CO₂ treatment. These results suggest that seedling growth responses to elevated CO₂ may be smaller in hypogeal than in co-occurring epigeal species.

Introduction

Several studies have demonstrated that seedlings of C₃ species demonstrate significant positive growth responses to elevated CO₂ concentrations relatively soon after emergence. For example, Tischler and others (2000) found that for five herbaceous species, significant responses to doubled ambient CO₂ concentration were observed by 3 days after emergence. In another study utilizing woody species, significant responses were observed by one week after emergence (Tischler and others 2003). All species utilized in these studies were epigeal—that is, the cotyledons were elevated above soil level by elongation of the hypocotyl. Furthermore, in all species utilized in these studies, the cotyledons expanded and quickly became photosynthetically active.

Another grouping of dicots is termed “hypogeal.” In these species, the cotyledons remain at planting depth (or often, in nature, on the soil surface), as the epicotyl elongates to elevate the growing point above the soil surface. In this grouping of plants, the cotyledons serve only a storage function and do not contribute to the photosynthetic activity of the plant. Numerous surveys indicate that hypogeal species have a considerably greater seed mass than epigeal species (for example, see Ng 1985; Bazzaz and Pickett 1980).

Total reproductive output represents a balance between seed size and seed number (Smith and Fretwell 1974). For a species to allocate a larger proportion of resources to a smaller number of seeds, hypogeal germination morphology (and

greater seed mass) must confer an advantage to the seedling. One advantage is resistance to clipping. Adventitious buds in the axles of the cotyledons are at or below soil level in hypogeal seedlings, so these seedlings readily survive clipping at soil level. In epigeal species, clipping at soil level severs the hypocotyl and cotyledons, and thus removes meristematic tissue. Another advantage of hypogeal germination (and the concomitant abundance of seed reserves) is an innate ability to survive stresses, such as low light levels, in the seedling stage (Ganade and Westoby 1999). A tradeoff of hypogeal germination morphology may be depressed seedling relative growth rate (Maranon and Grubb 1993; Stebbins 1976a, b). Indeed, the literature indicates that seedling growth rates are slower in hypogeal than epigeal species. This fact prompted us to question if the rapid growth response to elevated CO₂ observed in epigeal species might be delayed or less dramatic in hypogeal species. If so, CO₂ enrichment might actually be a disadvantage for hypogeal species in competitive situations where growth rate is important, and thus results from one functional type could not be extrapolated to the other type when assessing potential effects of increasing atmospheric CO₂ concentrations on ecosystem dynamics. The two hypogeal species we chose to study were guajillo (*Acacia berlandieri* Benth) and cat claw acacia (*Acacia greggii* Gray var. *wrightii* [G. Bentham] D. Isely). Guajillo is a significant brush species in south Texas, from west of Corpus Christi to Uvalde. Guajillo thrives on chalky limestone (caliche) outcroppings, where it is the predominant species, as well as on deeper soils where it is

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one component of a mixed brush community. Cat claw (called Wright acacia in the older literature) is also one component of mixed brush stands in south Texas.

Materials and Methods

Seeds of guajillo were harvested from shrubs near Beeville, TX, in June of 1999. Cat Claw Acacia seeds were harvested from trees near Pearsall, TX, in 1998. Both groups of seeds were stored in a seed vault. Because there is considerable variability in seed mass in these species, we weighed individual seeds and selected those within a relatively narrow band of seed masses. For guajillo, this was from 0.42 to 0.58 g, whereas values for cat claw acacia ranged from 0.16 to 0.24 g. Obtaining uniform guajillo seed is especially difficult because as seed mature, they are rapidly parasitized by weevils of the genus *Bruchid*. Seeds which appear normal often already have damage to the embryo, which becomes obvious only after the seedling emerges.

Seeds were planted at a 2 cm depth in 1.5 m pvc tubes (5-cm diameter) containing Pedernales Fine Sandy loam soil wetted with tenth strength Hoagland's solution. Two seeds were planted per tube. In cases when both seed germinated, the weaker of the two seedlings was destroyed. Seeds were planted on August 1, 2001. Four groups of tubes of each species were assigned to four separate greenhouses, two maintained at ambient CO₂ concentration and two maintained at 700 ppm CO₂. Periodic monitoring of light levels indicated that irradiance was very similar among greenhouses. As is common in August in central Texas, days were sunny with only occasional scattered clouds, analogous to conditions encountered by Tischler and others (2003) in a prior experiment with woody epigeal seedlings. Plants were monitored for insect infestation, but none was observed. However, several guajillo plants were attacked by fungus. These plants were discarded.

Seedlings were watered as needed to maintain soil near drip capacity with one-tenth strength Hoagland's solution for the duration of the experiment. At 15 days after emergence, the culture tubes were removed from the greenhouse and carefully split so that roots could be washed from the soil media. Leaf area was determined with a photoelectric leaf area meter, and root lengths were measured with a meter stick and recorded. Plants were divided into leaves, root, and stem (remnants of the seedcoat and hypogeal cotyledons were discarded), dried at 70 C for 24 hours, and weighed.

The growth period of 15 days was selected based on earlier experimentation, which indicated that no responses to elevated CO₂ were observed in these species at earlier harvest dates.

Results

Data presented in tables 1 and 2 indicate no significant effect of elevated CO₂ by day 15 on any plant parameter for either species, although values were numerically higher in elevated CO₂ for all parameters except root length for guajillo. These results, although not unexpected, are in stark contrast

Table 1—Plant parameters of 15-day-old Guajillo seedlings.

Parameter	CO ₂ Concentration (ppm)		
	365 (n = 8)	700 (n = 12)	P
Leaf area (cm ²)	37.6	43.7	0.4777
Rooting depth (cm)	77.9	75.9	0.4760
Stem wt (mg)	32.9	43.7	0.0814
Root wt (mg)*	151.2	173.7	0.3498
Leaf wt (mg)	178.2	246.7	0.2290
Total biomass (mg)	362.3	464.2	0.1978

*Remnants of seed coat and hypogeal cotyledons not included in mass.

Table 2—Plant parameters of 15-day-old Cat Claw Acacia seedlings grown at two CO₂ concentrations.

Parameter	CO ₂ Concentration (ppm)		
	360 (n = 13)	700 (n = 14)	P
Leaf area (cm ²)	22.1	26.1	0.3498
Rooting depth (cm)	90.2	92.2	0.7322
Stem wt (mg)	27.4	33.1	0.1805
Root wt (mg)*	98.7	117.39	0.0954
Leaf wt (mg)	122.9	156.0	0.1789
Total biomass (mg)	249.0	306.5	0.1172

*Remnants of seed coat and hypogeal cotyledons not included in mass.

with data we previously presented for epigeal herbaceous and woody species (Tischler and others 2000, 2003), where significant positive effects of CO₂ were observed between 1 and 3 days after emergence.

The root lengths of the two species were somewhat greater than would have been expected, based on behavior of mesquite (*Prosopis glandulosa* L.) in other experiments. The fact that root lengths were greater for the smaller-seeded catclaw was also unexpected.

Discussion

Several features of these data sets merit further consideration. First, total biomass of the guajillo seedlings, 362 and 464 mg, respectively, for ambient and elevated CO₂, was still less than the 420 to 580 mg range of the seed used in the experiment. Of course, a portion of the seed mass was contributed by the inert seed coat, but at very best, at 15 days the seedlings were barely more massive than the starting seed. The same general trends were true for cat claw acacia (249 and 307 mg for seedlings at ambient and elevated CO₂, with an initial seed mass of 160 to 240 mg). A second significant feature of the data sets is the somewhat amazing root length of the seedlings (approximately 75 cm for guajillo; greater than 90 cm for cat claw acacia).

In work with epigeal woody species at ambient and elevated CO₂, Tischler and others (2003) observed significant effects of elevated CO₂ on total biomass for mesquite at day

3, and for parkinsonia (*Parkinsonia aculeata* L.), honey locust (*Gleditsia triacanthos* L.), and huisache (*Acacia farnesiana* (L.) Willd.) at day 8. These experiments were conducted in an earlier year (1996) in the same greenhouse, with all aspects of plant culture being the same, except for the fact that seed were planted about August 26, as compared to August 1 in this study. Thus, seedlings in this study experienced slightly longer day length than those in the 1996 study. Obviously, it is hazardous to compare seedlings grown in two separate experiments, but given the similarity of the experimental system, it is clear that the hypogeal species' response was much less than would have been expected from woody epigeal species.

Another interesting observation relates to root lengths. Admittedly, the root lengths we measured were longer than would be expected in a shallow soil or caliche outcropping. However, the fact that roots penetrated $\frac{3}{4}$ to almost one meter with no major increase in seedling dry weight suggests that these two hypogeal species may reach a developmental stage that could be described as "established" with only minimal carbon input from photosynthetic activity. This observation argues against any significant role for elevated CO₂ in improving seedling establishment or seedling competitive ability of guajillo and cat claw acacia, in stark contrast to observations of corresponding epigeal species. Thus, blanket predictions about effects of elevated CO₂ on ecosystem processes, especially seedling recruitment, must be tempered with an understanding of how seedling morphology can modify these responses.

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The Authors

- ¹ Plant Physiologist, USDA-ARS Grassland, Soil & Water Research Laboratory, Temple, TX. ctischler@spa.ars.usda.gov
- ² Research Leader, USDA-ARS Grassland, Soil & Water Research Laboratory, Temple, TX.
- ³ Ecologist, USDA-ARS Grassland, Soil & Water Research Laboratory, Temple, TX.
- ⁴ Range Scientist, USDA-ARS, High Plains Grasslands Research Station, Cheyenne, WY.

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