

Effects of Elevated Atmospheric CO₂ on a C₃ and a C₄ Invasive Weed

¹G.B. Runion, ¹A.J. Price, ¹S.A. Prior, ¹H.H. Rogers, ¹H.A. Torbert and ²D.H. Gjerstad

¹USDA-ARS, National Soil Dynamics Laboratory, 411 S. Donahue Drive, Auburn, AL 36832, USA

²School of Forestry and Wildlife Sciences, Auburn University, AL 36849, USA

Abstract: Invasive plants are a major threat to the earth's biodiversity and cost U.S. producers \$34 billion annually. Understanding how increased atmospheric CO₂ may alter establishment, spread and control of invasive weeds is crucial to future management strategies. Here we report on the effects of elevated CO₂ on growth of 2 invasive weeds important to Southeastern U.S. agriculture. Sicklepod (*Cassia obtusifolia* L.; C₃ legume) and Johnsongrass (*Sorghum halepense* (L.) Pers.; C₄ grass) were grown at either 375 μmol mol⁻¹ (ambient) or 575 μmol mol⁻¹ (elevated) CO₂ in open top field chambers. Photosynthesis, morphology and biomass were assessed. Growth in elevated CO₂ increased photosynthetic rate and water use efficiency for both species. While both species increased leaf and stem dry weights when grown under elevated CO₂, the sicklepod tended to be more responsive than was Johnsongrass. Both plants tended to partition less total dry weight to reproductive structures when grown under high CO₂. This study suggests that while both weeds are likely to increase in importance, sicklepod may be more of a problem than Johnsongrass in a future CO₂-enriched world; this prediction may change if reproductive success is negatively impacted by elevated CO₂ and this potential deserves further investigation.

Key words: Carbon dioxide, *Cassia obtusifolia*, invasive weeds, johnsongrass, sicklepod, *Sorghum halepense*

INTRODUCTION

Invasive plants have become a serious problem and are now considered to be a major threat to the Earth's biodiversity (Binggeli, 1996). Invasive weeds are estimated to cost U.S. agricultural and forest producers 34 billion dollars each year from decreased productivity and increased costs of production for control (Pimentel, 2002). Johnsongrass (*Sorghum halepense* (L.) Pers.) is native to the Mediterranean region. The exact date and place of its initial introduction into the Southeastern U.S. remains unknown, but probably occurred sometime in the early 19th century (McWhorter, 1971). By the middle of the next century, it had spread over approximately half of the U.S. (Georgia, 1942) and was the second most common weed in Alabama (Harper, 1944). Today, it is known to occur in over 50 countries, being listed as a serious weed in over half of these and is considered the 6th worst weed in the world (Holm *et al.*, 1977). It is currently on the invasive species list for every state in the Southeastern U.S.

In contrast to Johnsongrass, little is known about the introduction of sicklepod. It is thought to be native to the American tropics and was noted as early as 1818 in the Southeastern U.S. (Nuttall, 1818). Harper (1944) listed

the plant as, a tropical weed, fairly common in Alabama, especially in the southern half of the state; however, it was not considered a major problem. By 1960, sicklepod was one of the most common weeds in Alabama and was known throughout the Southern U.S.

Our ability to predict which exotic plant species will become problematic invasive weeds remains ineffective (Binggeli, 1996; Blossey and Kamil, 1996; Williamson, 2001) despite the fact that considerable effort is being spent identifying the characteristics that may confer success following introduction (Rejmanek, 2000). However, little consideration has been given on the potential impacts of climate change on invasive plants. Mooney and Hobbs (2000) noted, Biotic change (species invasion) constantly introduces new players into the landscape that will interact in an unknown manner with the existing biota and a changing climate.

Although, the CO₂ literature contains numerous examples of investigations into effects on weed species (Patterson and Flint, 1990), the response of invasive plants to increasing CO₂ concentration remains a neglected aspect of global change research. Given that elevated CO₂ stimulates photosynthesis, resource use efficiency and carbon allocation to roots (Rogers *et al.*, 1994; Amthor, 1995), it will undoubtedly affect the

physiology and competitiveness of invasive plants (Ketner, 1990; Froud-Williams, 1996). Bright (1998) summarizes, Fast-growing, highly invasive plants may also be able to profit directly from the atmosphere's increased carbon content...any slower-growing natives would tend to lose out to the invaders. Although logical, this idea is currently not supported by sufficient empirical data.

The few examples from available literature on the effects of elevated atmospheric CO₂ on invasive plants have been recently summarized; nearly all species examined showed positive growth responses (Patterson, 1995; Dukes and Mooney, 1999). Work with 2 invasive vines important in the Southeast, kudzu (*Pueraria lobata* Ohwi) and Japanese honeysuckle (*Lonicera japonica* Thumb), suggested that the severity of problems caused by these species is likely to increase as the concentration of CO₂ continues to rise (Sasek and Strain, 1988, 1991).

A limited amount of research has previously been conducted examining the effects of elevated CO₂ on various C₃/C₄ crop/weed combinations (Patterson *et al.*, 1984; Ziska and Bunce, 1997; Ziska, 2000, 2001, 2003). Predictably, results generally showed that C₄ plants tended to show less response to elevated CO₂, regardless of whether they were a crop plant or a weed, than C₃ plants. Further, C₃ weeds tended to have a greater negative effects on growth and yield of both C₃ and C₄ crop plants under high CO₂ than did C₄ weeds. It should be noted that the majority of this prior work was conducted in controlled environmental chambers or glasshouses for short durations, so plants were not exposed to ambient environmental conditions during growth. These studies also often used small containers which may influence the response to elevated atmospheric CO₂ (Arp, 1991). Polley *et al.* (1996), working with invasion of grasslands by woody species such as mesquite (*Prosopis glandulosa* Torr.), Ziska (2002), working with the invasive weed Canada thistle (*Cirsium arvense* L. Scop.), have suggested that rising levels of atmospheric CO₂ seen during the past century may have already had a substantial influence on development and spread of invasive plant species.

Invasive plant pests (via their competitive aggression and absence of natural controls) have the capacity to disrupt terrestrial ecosystems; nowhere is this threat greater than in the Southeastern U.S., with its numerous ports of entry and mild climate. Given that plants will continue to cross our borders, understanding how the rising atmospheric CO₂ concentration may alter establishment, spread and control of invasive weeds will be crucial to future management strategies if production

and profitability of farms and forests are to be maintained. Here we report on the effects of elevated CO₂, in an open top field chamber study using large containers, on growth of 2 invasive weeds (Johnsongrass and sicklepod) of critical importance to agriculture in the Southeastern U.S.

MATERIALS AND METHODS

Three sicklepod (*Cassia obtusifolia* L.), a C₃, N₂-fixing legume and three Johnsongrass (*Sorghum halepense* (L.) Pers.), a C₄ grass, seeds (Azlin Seed Service, P.O. Box 914, Leland, MS 38756) were each planted in a general purpose growing medium (PRO-MIX Bx, Premier Horticulture Inc., Quakertown, PA 18951) in 1.65 L tree-pots (Short One Tree-pot, 10×23 cm, Stuewe and Sons Inc., Corvallis, OR 97333). After establishment, plants were thinned to one plant per pot. Plants were grown in the greenhouse until reaching 4-6 leaf growth stage.

Plants were then transplanted into 10.65 L tree pots (TPOT4 Round Tree-pot, 22×39 cm, Stuewe and Sons Inc., Corvallis, OR 97333) containing the same standard growth medium described above. Sixty containers of each species received transplants; 48 of these were selected for placement in Open Top field Chambers (OTC). The plants in these 48 containers were ranked, according to plant size and placed into four groups of 12 containers each, representing the largest 12 first in declining order down to the smallest 12; one container from each group was randomly assigned to each of the 12 OTCs used in the study (4 containers of each plant species in each chamber). Initial measurements (including height, ground line diameter, number of tillers and number of leaves) were taken on each plant before placement in OTCs.

The study was conducted at the soil bin facilities at the USDA-ARS National Soil Dynamics Laboratory, Auburn, Alabama. The bin used for the experimental setup is 6 m wide and 76 m long and has been modified for container studies; modifications consisted of installing a geomembrane liner (20 mL) and gravel drain system to ensure a good working surface and drainage for container studies. Open top chambers (Rogers *et al.*, 1983), encompassing 7.3 m² of ground surface area, were used to continuously (24 h day⁻¹) deliver target CO₂ concentrations of 375 µmol mol⁻¹ (ambient) or ambient plus 200 µmol mol⁻¹ (elevated) using a delivery and monitoring system described by Mitchell *et al.* (1995). Actual daytime CO₂ concentrations over the measurement period (±SE) were 373.4 (±0.2) and 584.1 (±0.6) for ambient and elevated chambers, respectively (daytime was taken as 7:00 AM to 7:00 PM CST).

The bin was divided into six blocks and each CO₂ treatment was randomly assigned to one open top chamber within each block. The experimental design was a randomized complete block design, with blocks occurring along the length of the soil bin. Plants were placed in the OTCs on 7 June, 2005; CO₂ treatments were initiated on 9 June, 2005. All plants were fertilized with Miracle-Gro® (15:30:15, N:P:K; Scotts Products Inc., Marysville, OH) every other week from placement in the OTCs until harvest. Fertilization was accomplished according to manufacture recommendations by mixing 600 g Miracle-Gro in 130 L deionized water; each plant received 500 mL of this solution. Plants received an iron chelate treatment (1:0:0, N:P:K, plus 1.25% water soluble iron, Ironite Products Co., Scittdale, AZ) on 8 and 14 July, 2005; approximately 20 g of granular Ironite® was added to each pot during each application.

All Johnsongrass containers in each chamber was destructively harvested on July 25, 2005 (47 days of CO₂ exposure); sicklepod containers were destructively harvested on August 8, 2005 (61 days of CO₂ exposure). Immediately before harvest, plant photosynthesis (net C assimilation) was measured on each plant using a Li-Cor 6400 portable gas exchange system (Li-Cor, Inc., Lincoln, NE); conductance and transpiration are concomitantly determined with photosynthesis and instantaneous water use efficiency can then be calculated from these data.

Aboveground portions of all plants in each container were harvested by severing the at the ground-line. Aboveground parameters (e.g., height, diameter, number of nodes, tillers and/or leaves) were assessed using standard practices. Plants were then separated into organ parts (i.e., leaves, stems, roots) and leaf area was determined using a LI-3100 leaf area meter. Roots were separated from the growing medium using the sieve method (Bohm, 1979). Root length was measured using a Comair Root Length Scanner (Hawker de Havilland, Port Melbourne, Australia). Plant organs were then dried (55°C) to a constant weight and dry weights recorded. Dry weights of each organ were considered a measure of photosynthate partitioning; allocation among organ parts was calculated based on these. Data were totaled for each container and the four containers in each open top chamber averaged prior to analysis.

Data analysis was conducted using the mixed model procedures (Proc Mixed) of the Statistical Analysis System (Littell *et al.*, 1996). Error terms appropriate to the randomized block design were used to test the significance of CO₂ concentration. In all cases, differences were considered significant at the $\alpha \leq 0.05$ and trends were recognized at $0.05 \leq \alpha \leq 0.15$.

RESULTS

Photosynthetic rate ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) was increased in both species for plants growing under elevated CO₂ (Table 1). Conductance ($\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$) and transpiration ($\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$) did not differ significantly between CO₂ treatments for Johnsongrass, but tended to be lower for sicklepod plants exposed to elevated CO₂. For both species, instantaneous water use efficiency ($\text{mmol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$) was greater for plants in the elevated CO₂ treatment (Table 1).

Johnsongrass had higher numbers of leaves, leaf area and root length when grown under high CO₂ (Table 2). However, elevated CO₂ only increased height and root length for sicklepod. While, exposure to high CO₂ tended to increase the number of reproductive structures for sicklepod plants, the number of Johnsongrass seed heads tended to be lower under these conditions (Table 2).

Both species increased leaf and stem dry weights when grown under elevated CO₂ conditions; however, effects on reproductive structures were more variable

Table 1: The response of Johnsongrass and sicklepod photosynthesis variables to ambient (375 $\mu\text{mol mol}^{-1}$) and elevated (ambient + 200 $\mu\text{mol mol}^{-1}$) CO₂

Species	Variable	Ambient CO ₂	Elevated CO ₂	Change (%)	p-values
Johnsongrass	Pn	14.55	19.45	33.7	0.0364
	Conductance	0.0795	0.0706	-11.2	0.3138
	Transpiration	3.89	3.60	-7.5	0.3746
	WUE	3.67	5.39	46.9	<0.0001
Sicklepod	Pn	10.66	15.23	42.9	0.0096
	Conductance	0.3835	0.2924	-23.8	0.0769
	Transpiration	5.36	4.68	-12.7	0.0792
	WUE	2.10	3.33	58.6	0.0008

Means with associated separation statistics and percent change (ambient to elevated)

Table 2: The response of Johnsongrass and sicklepod growth variables to ambient (375 $\mu\text{mol mol}^{-1}$) and elevated (ambient + 200 $\mu\text{mol mol}^{-1}$) CO₂

Species	Variable	Ambient CO ₂	Elevated CO ₂	Change (%)	p-values
Johnsongrass	Height (cm)	47.62	49.68	4.3	0.288
	Diameter (mm)	25.65	27.22	6.1	0.317
	No. of tillers	51.5	52.3	1.6	0.830
	No. of leaves	215.6	230.3	6.8	0.018
	No. of seed heads	11.3	9.6	-15.0	0.132
	Leaf area (cm ²)	9844.8	11680.0	18.6	0.014
	Root Length (m)	2594.31	3113.33	20.0	0.046
	Root length (m)	1824.66	2738.33	50.1	0.018
Sicklepod	Height (cm)	110.57	124.65	12.7	0.005
	Diameter (mm)	14.14	14.75	4.3	0.184
	No. of leaflets	999.9	1184.4	18.5	0.170
	No. of branches	8.6	8.4	-2.3	0.657
	No. of pods	176.1	205.3	16.6	0.234
	No. of flowers	19.0	39.8	109.5	0.105
	No. of reproductives	195.1	245.1	25.6	0.166
	Leaf area (cm ²)	5229.9	6298.7	20.4	0.159

Means with associated separation statistics and percent change (ambient to elevated)

Table 3: The response of Johnsongrass and sicklepod plant component part dry weight (g) to ambient (375 $\mu\text{mol mol}^{-1}$) and elevated (ambient +200 $\mu\text{mol mol}^{-1}$) CO_2

Species	Plant part	Ambient CO_2	Elevated CO_2	Change (%)	p-values
Johnsongrass	Leaf	60.82	69.55	14.4	0.019
	Seed head	23.47	19.15	-18.4	0.086
	Stem	148.40	181.18	22.1	0.024
	Total shoot	232.70	269.87	16.0	0.039
	Roots	100.22	104.33	4.1	0.731
Sicklepod	Total plant	332.91	374.20	12.4	0.131
	Leaf	24.89	39.76	59.7	0.013
	Stem	91.31	118.86	30.2	0.013
	Flowers	0.15	0.33	120.0	0.090
	Pods	53.03	44.58	-15.6	0.271
	Total reproductive	53.18	44.91	-15.6	0.279
	Total shoot	169.37	203.53	20.2	0.014
	Root	24.98	34.60	38.5	0.018
	Total plant	194.35	238.13	22.5	0.008

Means with associated separation statistics and percent change (ambient to elevated)

Table 4: The response of Johnsongrass and sicklepod allocation among plant component parts (%) to ambient (375 $\mu\text{mol mol}^{-1}$) and elevated (ambient + 200 $\mu\text{mol mol}^{-1}$) CO_2

Species	Plant part	Ambient CO_2	Elevated CO_2	Change (%)	p-values
Johnsongrass	Leaves	18.350	18.610	1.4	0.755
	Seed heads	7.230	5.270	-27.1	0.013
	Stems	44.600	47.960	7.5	0.007
	Roots	29.820	28.170	-5.5	0.357
	Root to shoot ratio	0.441	0.405	-8.2	0.329
	Total plant	100.000	100.000	0.0	0.000
Sicklepod	Leaves	12.080	16.450	36.2	0.047
	Stems	46.030	49.270	7.0	0.151
	Flowers	0.070	0.140	100.0	0.065
	Pods	29.050	19.020	-34.5	0.091
	Total reproductive	29.120	19.160	-34.2	0.092
	Roots	12.770	15.120	18.4	0.210
Sicklepod	Root to shoot ratio	0.148	0.183	23.6	0.216

Means with associated separation statistics and percent change (ambient to elevated)

(Table 3). Johnsongrass seed head dry weights tended to be lower under high CO_2 , while sicklepod flower dry weight tended to increase; sicklepod pod dry weight was unaffected by atmospheric CO_2 level. These increases in aboveground plant parts resulted in increased shoot dry weight for both species (Table 3). However, while sicklepod plants also increased root dry weight, resulting in significantly greater overall plant dry weight, Johnsongrass roots were unaffected by CO_2 treatment and these plants had only a slight increase in total plant dry weight (Table 3).

Johnsongrass plants grown in elevated CO_2 increased allocation to stems, decreased allocation to seed heads and did not alter allocation to other plant parts (Table 4). In somewhat similar fashion, sicklepod plants increased allocation to leaves and flowers, decreased allocation to pods and did not alter allocation to other plant parts. In both species, root to shoot ratios were not significantly affected by elevated CO_2 exposure (Table 4).

DISCUSSION

Research has shown that elevated atmospheric CO_2 increases growth of most plants due to increased rates of photosynthesis, altered C partitioning and/or increased water and nutrient use efficiencies (Rogers *et al.*, 1994; Amthor, 1995). Summaries have consistently shown that biomass response to atmospheric CO_2 enrichment, for both crops and weeds, varies between plants with a C_3 (33-40% increase) vs. a C_4 (10-15% increase) photosynthetic pathway (Kimball, 1983; Prior *et al.*, 2003).

In a short-term, growth chamber study, Patterson *et al.* (1984) reported that, while both soybean (*Glycine max* (L.) Merr.) and Johnsongrass had a positive response to high CO_2 , the plant relative yield was greater for soybean than for Johnsongrass. Data from our longer-term, open top field chamber study are consistent with this report in that, while both plants increased growth under elevated CO_2 , the response of the C_3 sicklepod (22.5%) was greater than that for the C_4 Johnsongrass (12.4%). Tremmel and Patterson (1993) again working in growth chambers, examined responses of soybean and 5 weed species (including both Johnsongrass and sicklepod) to ambient and elevated CO_2 . They reported that elevated CO_2 increased Johnsongrass leaf area, but did not affect biomass; conversely, high CO_2 increased sicklepod biomass, but did not affect leaf area. They suggested the lack of a CO_2 effect in either biomass or leaf area may make both weeds less competitive when grown with soybean. Again, data from our open top field chamber study are consistent with this previous work; leaf area was increased in Johnsongrass but not sicklepod, while biomass was significantly increased in sicklepod, but only marginally ($p = 0.131$) higher for Johnsongrass.

In a comparison of 4 C_4 crops and 6 C_4 weeds grown for 60 days in a glasshouse, Ziska and Bunce (1997) reported that 8 of the 10 plants (including Johnsongrass) showed a significant increase in photosynthetic response to elevated CO_2 and that the increase for weeds, overall, was almost twice that for crop plants. They added that one of the weeds (*Amaranthus retroflexus* L.) showed a photosynthetic response of +30% to elevated CO_2 , an increase similar to many C_3 plants. Photosynthetic response in our study was also increased for both sicklepod and Johnsongrass; while sicklepod showed a greater response (42.9%), the response for Johnsongrass was similar to that generally observed in C_3 plants (33.7%). Ziska and Bunce (1997) further reported that 4 of the 6 weeds has increased biomass under high CO_2 ; however Johnsongrass, despite increased photosynthesis

showed no effect of CO₂ concentration on biomass. This is, again, similar to our results where Johnsongrass, despite the 33.7% increase in photosynthesis, had only a marginal (12.4%) increase in biomass.

More recently, Ziska (2000, 2001, 2003) has undertaken research examining the effects of elevated CO₂ on various C₃/C₄ crop/weed combinations. Results generally showed that C₄ plants tended to show less response to elevated CO₂, regardless of whether they were a crop plant or a weed, than C₃ plants. Further, C₃ weeds tended to have a greater negative effect on growth and yield of both C₃ and C₄ crop plants under high CO₂ than did C₄ weeds. This would suggest that sicklepod is likely to become a more important exotic weed pest than is Johnsongrass as the atmospheric CO₂ concentration continues to rise.

One aspect, of plant response to elevated CO₂ not generally examined in prior research on weed species is changes in allocation among plant organs. Plants tend to allocate resources to the organ necessary for collecting the resource most limiting to growth; e.g., when plants are grown with adequate soil nutrition, they tend to allocate growth to leaves for the capture of C from the atmosphere; conversely, when plants are grown under elevated CO₂ (especially when soil N or water are limiting), plants tend to partition a higher amount of photosynthate to roots (Rogers *et al.*, 1996). In the present study, in which plants were grown with adequate nutrition, allocation to roots was unaffected by CO₂ treatment; however, sicklepod allocated more of the total dry weight to leaves while Johnsongrass allocated more to stems. Both plants tended to partition less total dry weight to reproductive structures when grown under high CO₂. Both seed head dry weight and allocation were reduced in Johnsongrass in the elevated CO₂ treatment. Similarly, allocation to reproductive structures and total reproductive dry weight in sicklepod were negatively affected by high CO₂. These data suggest that overall reproductive success and possibly spread, of these invasive weeds may decrease in a high CO₂ environment. However, given that sicklepod flower dry weight was increased while pod dry weight was decreased, it may be that high CO₂ was merely delaying reproductive development in this species, which may or may not impact success and spread of sicklepod.

In some of the only recent research specifically aimed at the effects of elevated CO₂ on an important invasive weed species, Ziska (2002) examined Canada thistle (*Cirsium arvense* L. Scop.) at CO₂ concentrations of 285, 382 and 721 µmol mol⁻¹ (approximating the ambient conditions for 1900, 2001 and those projected for 2100).

He reported biomass increases of 126 and 69% for increases from 285-382 and 382-721, respectively. Further, leaf spine number and length also increased as a function of CO₂ concentration. He suggested that rising levels of atmospheric CO₂ may have already had a substantial influence on vegetative development of Canada thistle by stimulation of photosynthesis and growth, as well as possible reductions in leaf herbivory due to altered leaf defenses; this suggestion had been previously made by Polley *et al.* (1996) working with invasion of grasslands by woody species such as mesquite (*Prosopis glandulosa* Torr.). Given that both Johnsongrass and sicklepod have been known to exist in the U.S. for almost 200 years, it is likely that the increase in atmospheric CO₂ concentration during this period has played a role in their spread and enhanced the importance of these invasive species as major exotic weed pests in Southeastern agriculture. The present study, indicating increased photosynthesis, WUE and/or biomass, suggests that, while both weeds are likely to increase in importance, sicklepod (as a C₃ plant having a greater ability to take advantage of this added CO₂) may be more of a problem than Johnsongrass in a future CO₂-enriched world. However, this prediction may change if reproductive success of one or both of these species is negatively impacted by elevated atmospheric CO₂; this potential certainly deserves further investigation.

ACKNOWLEDGEMENT

This research was supported by the Southeast Regional Center of the U.S. Department of Energy's National Institute for Global Environmental Change by Interagency Agreement No. DE-FC02-03-ER63613 and the U.S. Department of Energy's Biological and Environmental Research Program (BER) under Interagency Agreement No. DE-AI02-95ER62088. The authors thank Heidi Finegan, Maria Stoll, Barry Dorman and Jerry Carrington for technical assistance.

REFERENCES

- Amthor, J.S., 1995. Terrestrial higher-plant response to increasing atmospheric (CO₂) in relation to the global carbon cycle. *Global Change Biol.*, 1: 243-274.
- Arp, W.J., 1991. Effects of source-sink relations on photosynthetic acclimation to elevated CO₂. *Plant Cell and Environ.*, 14: 869-75.
- Binggeli, P., 1996. A taxonomic, biogeographical and ecological overview of invasive woody plants. *J. Vegetable Sci.*, 7: 121-124.

- Blossey, B. and J. Kamil, 1996. What determines the increased competitive ability of invasive non-indigenous plants. In: Proceeding of the 9th International Symposium on Biological Control of Weeds. Stellenbosch, South Africa, pp: 3-9.
- Bohm, W., 1979. Methods of studying root systems. Spring-Verlag, New York, 33: 188.
- Bright, C., 1998. Life out of bounds: Bioinvasion in a borderless world. W.W. Norton and Company, New York, pp: 287.
- Dukes, J.S. and H.A. Mooney, 1999. Does global change increase the success of biological invaders? TREE, 14: 135-139.
- Froud-Williams, R.J., 1996. Weeds and climate change: Implications for their ecology and control. Asp. Applied Biol., 45: 187-196.
- Georgia, A.E., 1942. A manual of weeds. Macmillain Co. New York, pp: 593.
- Harper, R.M., 1944. Preliminary report on the weeds of Alabama. Geological Survey of Alabama Bulletin No. 53. Wetumpka Print Co., Wetumpka, AL., pp: 275.
- Holm, L.G., D.L. Plucknett, J.V. Pancho and J.P. Herberger, 1977. The world's worst weeds: Distribution and biology. The University Press of Hawaii, Honolulu, HI., pp: 609.
- Ketner, P., 1990. Will There Be a Weed Problem as a Result of Climate Change? In: Goudriaan, J., H. Van Keulen, H.H. Van Laar (Eds.). Greenhouse effect and primary productivity in European agroecosystems. Centre for Agricultural Publishing and Documentation, Wageningen. The Netherlands, pp: 18-19.
- Kimball, B.A., 1983. Carbon dioxide and agricultural yield: An assemblage and analysis of 770 prior observation. USDA/ARS Water Conservation Laboratory Report Number 14. Phoenix, AZ., pp: 71.
- Littell, R.C., G.A. Milliken, W.W. Stroup and R.D. Wolfinger, 1996. SAS System for Mixed Models. SAS Institute, Inc., Cary, NC, pp: 633.
- McWhorter, C.G., 1971. Introduction and spread of Johnsongrass in the United States. Weed Sci., 19: 496-500.
- Mitchell, R.J., G.B. Runion, S.A. Prior, H.H. Rogers, J.S. Amthor and F.P. Henning, 1995. Effects of nitrogen on *Pinus palustris* foliar respiratory responses to elevated atmospheric CO₂ concentration. J. Exp. Bot., 46: 1561-1567.
- Mooney, H.A. and R.J. Hobbs, 2000. Invasive species in a changing world. Island Press, Washington, D.C., pp: 457.
- Nuttall, T., 1818. The genera of North American plants. Philadelphia, PA., pp: 280.
- Patterson, D.T., 1995. Weeds in a changing climate. Weed Sci., 43: 685-701.
- Patterson, D.T. and E.P. Flint, 1990. Implications of increasing carbon dioxide and climate change for plant communities and competition in natural and managed ecosystems. ASA Spec. Pub. No., 53: 83-110.
- Patterson, D.T., E.P. Flint and J.L. Beyers, 1984. Effects of CO₂ enrichment on competition between a C₄ weed and a C₃ crop. Weed Sci., 32: 101-105.
- Pimentel, D., 2002. Introduction: Non-Native Species in the World. In: Pimentel, D. (Ed.). Biological Invasions: Economic and Environmental Costs of Alien Plant, Animal and Microbe Species. CRC Press, Boca Raton, FL, pp: 3-8.
- Polley, H.W., H.B. Johnson, H.S. Meyeux and C.R. Tischler, 1996. Are Some Recent Changes in Grassland Communities a Response to Rising CO₂ Concentrations? In: Körner, C. and F.A. Bazzaz (Eds.). Carbon Dioxide, Populations and Communities. Academic Press, New York, pp: 177-195.
- Prior, S.A., H.A. Torbert, G.B. Runion and H.H. Rogers, 2003. Implications of elevated CO₂-induced changes in agroecosystem productivity. J. Crop Prod., 8: 217-244.
- Rejmanek, M., 2000. Invasive plants: Approaches and predictions. Aust. Ecol., 25: 497-506.
- Rogers, H.H., W.W. Heck and A.S. Heagle, 1983. A field technique for the study of plant responses to elevated carbon dioxide concentrations. Air Pollut. Control Assn. J., 33: 42-44.
- Rogers, H.H., S.A. Prior, G.B. Runion and R.J. Mitchell, 1996. Root to shoot ratio of crops as influenced by CO₂. Plant Soil, 187: 229-248.
- Rogers, H.H., G.B. Runion and S.V. Krupa, 1994. Plant responses to atmospheric CO₂ enrichment with emphasis on roots and the rhizosphere. Environ. Pollut., 83: 155-189.
- Sasek, T.W. and B.R. Strain, 1988. Effects of carbon dioxide enrichment on growth and morphology of kudzu (*Pueraria lobata*). Weed Sci., 36: 28-36.
- Sasek, T.W. and B.R. Strain, 1991. Effects of CO₂ enrichment on growth and morphology of a native and an introduced honeysuckle vine. Am. J. Bot., 78: 69-75.
- Tremmel, D.C. and D.T. Patterson, 1993. Responses of soybean and five weeds to CO₂ enrichment under two temperature regimes. Can. J. Plant Sci., 73: 1249-1260.
- Williamson, M., 2001. Can the Impacts of Invasive Plants Be Predicted? In: Brundu, G., J. Brock, I. Camarda, L. Child, M. Wade (Eds.). Plant Invasions: Species Ecology and Ecosystem Management. Backhuys Publishers, Leiden, Netherlands, pp: 11-19.
- Ziska, L.H., 2000. The impact of elevated CO₂ on yield loss from a C₃ and C₄ weed in field-grown soybean. Global Change Biol., 6: 899-905.

- Ziska, L.H., 2001. Changes in competitive ability between a C₄ crop and a C₃ weed with elevated carbon dioxide. *Weed Sci.*, 49: 622-627.
- Ziska, L.H., 2002. Influence of rising atmospheric CO₂ since 1900 on early growth and photosynthetic response of a noxious invasive weed, Canada thistle (*Cirsium arvense*). *Funct. Plant Biol.*, 29: 1387-1392.
- Ziska, L.H., 2003. Evaluation of yield loss in field sorghum from a C₃ and a C₄ weed with increasing CO₂. *Weed Sci.*, 51: 914-918.
- Ziska, L.H. and J.A. Bunce, 1997. Influence of increasing carbon dioxide concentration on the photosynthetic and growth stimulation of selected C₄ crops and weeds. *Photosyn. Res.*, 54: 199-208.