

Tropical Spiderwort (*Commelina benghalensis* L.) Increases Growth under Elevated Atmospheric Carbon Dioxide

Andrew J. Price,* G. Brett Runion, Stephen A. Prior, Hugo H. Rogers, and H. Allen Torbert USDA-ARS

Although considerable effort is being spent studying exotic plant pests, little consideration has been given as to how invasive plants might react to the increasing concentration of CO₂ in the atmosphere. Tropical spiderwort (*Commelina benghalensis* L.) is considered one of the world's worst weeds and is becoming more of a problem in agricultural settings of the southeastern USA. Growth responses of tropical spiderwort were evaluated using plants grown in containers with a soilless potting medium under ambient and elevated (ambient + 200 μmol mol⁻¹) levels of CO₂ in open-top field chambers. Although plant height was unaffected by CO₂, leaf and flower number tended to increase (approximately 23%) when exposed to elevated CO₂. Aboveground plant parts exhibited significant increases in dry weight when exposed to high CO₂; leaf, flower, stem, and total shoot dry weights were increased by 36, 30, 48, and 44%, respectively. Total plant dry weight was increased by 41% for plants grown under high CO₂. Root dry weight and root length were unaffected by CO₂ concentration. Tropical spiderwort allocated more biomass to stems and tended to allocate less to roots when plants were exposed to high CO₂. Plant carbon concentration and content tended to be higher in CO₂-enriched plants, whereas plant nitrogen concentration tended to be lower; thus, elevated CO₂-grown plants had higher C/N ratios. Also, the amount of biomass produced per unit nitrogen was higher for plants exposed to elevated CO₂. The growth response of this plant is in the upper range typical for C3 plants.

INVASIVE plants have the capacity to disrupt terrestrial ecosystems; this threat is great in the southeastern USA with its numerous ports of entry and mild climate. Invasive plants have become a serious issue during the past two decades and are considered a major threat to the earth's biodiversity (Binggeli, 1996). Invasive weeds are estimated to cost US agricultural and forest producers 34 billion dollars each year from decreased productivity and increased weed control costs (Pimentel, 2002).

Considerable effort is being spent identifying the characteristics of exotic plants that confer success after introduction and to predict which species will become major threats in the future (Rejmanek, 2000). Our predictive capabilities are weak and ineffective (Binggeli, 1996; Siemann and Rogers, 2001; Williamson, 2001). Several mechanisms might explain the success of invasive plants. These include: escape from natural insect and disease pests, providing a more favorable environment in the introduced range (Klironomos, 2002; Mitchell and Power, 2003); lack of competition from native species on disturbed sites (Masters and Sheley, 2001); novel interactions (e.g., allelopathy) that suppress native vegetation (Callaway and Aschehoug, 2000); and rapid genetic adaptation to new environments (Siemann and Rogers, 2001), resulting in increased photosynthetic capacity and/or resource use efficiency (McDowell, 2002). However, no consideration of how these invasive plants might be affected by a changing climate has been given. Mooney and Hobbs (2000) noted, "Biotic change [species invasion] constantly introduces new biotic players into the landscape that will interact in an unknown manner with the existing biota and a changing climate."

One especially neglected aspect of global change is the consideration of how invasive plants might react to the increasing CO₂ concentration in the atmosphere. The concentration of atmospheric CO₂ is increasing and is expected to double by the end of this century (Keeling and Whorf, 1994). Given that elevated CO₂ stimulates photosynthesis (Long and Drake, 1992), resource use efficiency (Rogers et al., 1994; Amthor, 1995), and carbon allocation to belowground plant structures (Rogers et al., 1994), it will undoubtedly affect the physiology and competitiveness of invasive plants (Ketner, 1990; MacDonald, 1992; Froud-Williams, 1996).

The sparse literature on the effects of elevated atmospheric CO₂ on invasive plants has been recently summarized; nearly all species examined showed positive growth responses to increased CO₂ (Dukes and Mooney, 1999). For example, studies with two invasive species affecting the southeast USA, *Cyperus rotundus* L. and *C. esculentus* L., suggested that the severity of problems caused

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*Corresponding author (andrew.price@ars.usda.gov).

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677 S. Segoe Rd., Madison, WI 53711 USA

USDA-ARS, National Soil Dynamics Lab., 411 S. Donahue Dr., Auburn, AL 36832.

by these species is likely to increase as the concentration of CO₂ continues to rise (Rogers et al., 2008). However, most previous work on the response of invasive weeds to elevated CO₂ has been conducted in indoor growth chambers or glasshouses for short durations (e.g., days to a few weeks).

Commelina benghalensis is native to tropical Asia and Africa (Prostko et al., 2004). It is a monocot and is similar in appearance to sedges. In its native habitat it is a perennial weed but acts as an annual in the more temperate regions of the USA (Prostko et al., 2004). It is unique in that it produces both above- and below-ground flowers. Tropical spiderwort is considered one of the world's worst weeds (Holm et al., 1977) but was not known to occur in the USA until recently. Specifically, this plant is becoming a problem in agricultural settings of the southeastern USA. *Commelina benghalensis* has been reported in Alabama (two locations), Florida (found throughout), Georgia (29 counties), and North Carolina (one location), and its distribution is likely to be much greater than known (Webster et al., 2005). To illustrate the invasive nature of *C. benghalensis*, it was first observed in southern Georgia in 1998 and has since become the most troublesome weed in *Gossypium hirsutum* L. and the third most troublesome weed in *Arachis hypogaea* L. in the areas it inhabits (Webster et al., 2005). Glyphosate (N-[Phosphonomethyl]glycine) applications have little effect on *C. benghalensis*; thus, it has become a major problem on thousands of hectares where glyphosate-resistant cotton is used in Georgia. Herbicide regimes that provide adequate season-long control of *C. benghalensis* are costly. Additionally, *C. benghalensis* hosts many important types of diseases and nematodes (Holm et al., 1977; Prostko et al., 2004).

A paucity of information exists regarding the response of invasive weeds to increased atmospheric CO₂ (i.e., this is the first study examining the response of *C. benghalensis* to these conditions). Such information is critical to predict how invasive weeds will compete with crop plants and affect the management and productivity of agronomic systems. The objective of this research was to evaluate the growth response of *C. benghalensis*, in open-top field chambers, to ambient and elevated concentrations of atmospheric CO₂.

Materials and Methods

Commelina benghalensis seed coats were scarified, and seeds were germinated at ambient CO₂ on moistened paper towels for 48 h. Three seedlings were planted into 11-L plastic containers (TPOT4 Round Treepots, 22 × 39 cm; Stuewe and Sons Inc., Corvallis, OR) filled with a peat-based general purpose growing medium (PRO-MIX Bx; Premier Horticulture Inc., Quakertown, PA). After establishment, plants were thinned to one plant per container. Containers were kept in a glasshouse at ambient CO₂ until plants reached three-leaf growth stage, at which time containers were transferred to open-top CO₂ exposure chambers.

The CO₂ study was conducted in containers at the soil bin facilities of 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 (0.02 mm) 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 d⁻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 CO₂ concentrations over the measurement period (±SE) were as follows: ambient daytime, 384.4 (±0.3); elevated daytime, 579.8 (±0.7); ambient nighttime, 421.0 (±0.6); and elevated nighttime, 629.8 (±0.9). Daytime was defined as 7:00 AM Central Standard Time to 7:00 PM Central Standard Time.

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. Four containers were placed in each open top chamber on 26 Aug. 2005.

Plants were subjected to ambient rainfall but watered (deionized) sparingly as needed to prevent drought-induced plant mortality. All plants were fertilized with Miracle-Gro (5:30:15, N:P:K; Scotts, Marysville, OH) every other week from placement in the open-top chambers until harvest. Fertilization was accomplished by mixing 600 g Miracle-Gro in 130 L deionized water; each plant received 500 mL of this solution.

All plants were destructively harvested on 24 Oct. 2005, corresponding to 60 d of CO₂ exposure. Aboveground portions of all plants in each container were harvested by severing the plant(s) at the ground-line. Aboveground parameters (e.g., height, number of leaves, and inflorescence) were assessed using standard practices. Plants were then separated into aboveground organs (i.e., leaves, stems, and inflorescence [combining immature and mature fruit]), and leaf area was determined using a leaf area meter (LI-3100; Li-Cor, Inc., Lincoln, NE). Roots were separated from the growing media using the sieve method (Bohm, 1979). Cleistogamous flowers were not quantified due to an oversight. Root length was measured using a root length scanner (Comair Root Length Scanner; Hawker de Havilland, Port Melbourne, Australia). Plant organs were dried in a forced-air oven at 55°C to a constant weight, and dry weights were recorded. Dry weights of each organ part are considered a measure of photosynthate partitioning; allocation among organ parts was calculated based on these weights. Data were totaled for each container, and the four containers in each open top chamber were averaged before analysis.

The biomass material was ground (0.2-mm mesh) before carbon (C) and nitrogen (N) analysis using a LECO CN-2000 analyzer (LECO Corp., St. Joseph, MI). Nitrogen and C concentrations and contents were determined for each plant organ and whole plant. Plant N utilization efficiency (unit of biomass produced per unit of N) and N uptake efficiency (unit of N per unit length of fine root) were calculated on a whole-plant basis.

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 concentra-

tion. In all cases, differences were considered significant at the $\alpha \leq 0.05$, and trends were recognized at $0.05 < \alpha \leq 0.15$.

Results and Discussion

Research has shown that elevated atmospheric CO₂ increases the 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). Furthermore, it has been documented that variability in growth response to elevated CO₂ is due primarily to differences between plants with a C₃ (33–40% increase) vs. a C₄ (10–15% increase) photosynthetic pathway (Fuhrer, 2003; Prior et al., 2003). In this study, we found increased dry weights of aboveground plant parts in the upper range of what is typical for C₃ plants. Elevated CO₂ significantly increased the dry weight of leaves (36%), flowers (30%), stems (48%), and total shoot (44%) (Table 1). The increased aboveground growth of tropical spiderwort observed here suggests that it may become more invasive as atmospheric CO₂ continues to rise. Ziska (2001, 2003a) and Ziska and Teasdale (2000), examining the effects of elevated CO₂ on C₃/C₄ crop/weed combinations, have shown 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. Furthermore, C₃ weeds tended to have a greater negative effect on the growth and yield of C₃ and C₄ crop plants under high CO₂ than did C₄ weeds. Whether tropical spiderwort will become more competitive in cropping systems deserves detailed examination of its response when grown with various crop plants.

In addition to dry weight, plant height, leaf number, and flower number also tended to increase (8, 23, and 24%, respectively) when exposed to elevated CO₂ (Table 2). The growth responses observed in this study are consistent with reports of other researchers. Dukes and Mooney (1999), in their summary of the effects of elevated CO₂ on invasive weeds, such as *Bromus tectorum* L. in the USA, reported that most species exhibited positive growth responses to increased CO₂. Ziska (2003b) reported significant CO₂-induced growth stimulation for six invasive weeds.

Although less intensively examined than aboveground growth, plant roots have also been shown to respond positively to elevated CO₂; in fact, roots often exhibit the greatest relative dry weight gain (Rogers et al., 1994). In the present study, however, root dry weight (Table 1) and root length (Table 2) were unaffected by growth in high CO₂. Despite the lack of root dry weight response to high CO₂, total plant weight increased by 41%.

Commelina benghalensis allocated more biomass to stems and tended to allocate less to roots when plants were exposed to high CO₂ (Table 3). Plants generally allocate resources to plant organs experiencing the greatest limitation; under high atmospheric CO₂, this is generally the root system (Rogers et al., 1996). Given that *C. benghalensis* plants received fertilization every other week throughout the study, it is likely that neither water nor nutrients were limiting in this study. Therefore, plants allocated the additional C to aboveground plant parts, accounting for the greater aboveground growth compared with the lack of belowground responses.

Table 1. The response of *Commelina benghalensis* plant component dry weight (g) to ambient (375 $\mu\text{mol mol}^{-1}$) and elevated (ambient + 200 $\mu\text{mol mol}^{-1}$) CO₂. Means with associated statistics† and percent change (ambient to elevated) are shown.

Parameter	Ambient CO ₂	Elevated CO ₂	% Change	P values
Inflorescence	3.66	4.75	29.8	0.040
Leaf	3.45	4.69	35.9	0.012
Stem	16.34	24.27	48.5	0.045
Total shoot	23.46	33.71	43.7	0.028
Root	3.94	4.80	21.8	0.175
Total plant	27.40	38.52	40.6	0.023

† Mean separation conducted under Proc Mixed of SAS.

Table 2. The response of *Commelina benghalensis* growth variables to ambient (375 $\mu\text{mol mol}^{-1}$) and elevated (ambient + 200 $\mu\text{mol mol}^{-1}$) CO₂. Means with associated statistics† and percent change (ambient to elevated) are shown.

Parameter	Ambient CO ₂	Elevated CO ₂	% Change	P values
Height (cm)	95.16	102.45	7.7	0.117
Leaf number	378.50	464.43	22.7	0.061
Inflorescence no.	257.13	317.62	23.5	0.072
Root length (m)	246.51	275.48	11.8	0.541

† Mean separation conducted under Proc Mixed of SAS.

Table 3. *Commelina benghalensis* biomass allocation among plant components (%) when grown under ambient (375 $\mu\text{mol mol}^{-1}$) or elevated (ambient + 200 $\mu\text{mol mol}^{-1}$) CO₂. Means with associated statistics† and percent change (ambient to elevated) are shown.

Parameter	Ambient CO ₂	Elevated CO ₂	% Change	P values
Inflorescence	12.98	13.48	3.9	0.765
Leaf	13.71	13.28	-3.1	0.711
Stem	53.83	58.67	9.0	0.016
Root	19.49	14.57	-25.2	0.147
Root to shoot ratio	0.17	0.14	-17.6	0.310

† Mean separation conducted under Proc Mixed of SAS.

Shoot C concentration was increased, whereas root C was unaffected, by growth in elevated CO₂, resulting in a trend for total plant C concentration to increase (Table 4). As with C, root N concentration was unaffected by CO₂ treatment; however, shoot and total plant N concentrations were lower under high CO₂. As was seen with C concentration, the C contents of shoots and total plants were increased by exposure to elevated atmospheric CO₂; roots, despite no effect on C concentrations, also showed a trend toward increased C content (Table 5) due to a slight increase in root dry weight (Table 1). Nitrogen contents of all plant parts were unaffected by CO₂ treatment (Table 5).

Elevated atmospheric CO₂ generally increases the size of plants and their component parts, resulting in greater total amounts of nutrients taken up; however, as these nutrients are distributed throughout the larger plants, their concentrations per unit weight tend to be diluted (Norby et al., 1986). This dilution effect was noted with *C. benghalensis* in that N concentrations were lower under elevated CO₂; however, the increased dry weights observed may not have been large enough to result in increased N content of plant parts. Higher C, with accompanying lower N, resulted in higher C/N ratios for shoots and total plants exposed to elevated CO₂; again, root C/N ratio was not affected (Table 4). Higher C/N ratios of plant tissues produced under high CO₂ have been commonly reported (Drake et al., 1996; Reich et al., 2006).

Table 4. The response of *Commelina benghalensis* plant carbon (C) and nitrogen (N) concentrations (mg g^{-1}) to ambient ($375 \mu\text{mol mol}^{-1}$) and elevated (ambient + $200 \mu\text{mol mol}^{-1}$) CO_2 . Means with associated statistics† and percent change (ambient to elevated) are shown.

Parameter	Ambient CO_2	Elevated CO_2	% Change	P values
Shoot [C]	364.74	368.12	0.9	0.0257
Shoot [N]	6.98	5.49	-21.3	0.0024
Shoot C/N	53.67	67.90	26.5	0.0001
Root [C]	418.65	423.13	1.1	0.4650
Root [N]	6.11	5.89	-3.6	0.4161
Root C/N	68.89	72.20	4.8	0.2950
Total plant [C]	372.80	374.94	0.6	0.1122
Total plant [N]	6.88	5.54	-19.5	0.0024
Total C/N	55.47	68.42	23.3	0.0002

† Mean separation conducted under Proc Mixed of SAS.

Table 5. The response of *Commelina benghalensis* plant carbon (C) and nitrogen (N) contents (g plant^{-1}) and whole plant N use efficiency† (NUE; $\text{g biomass g}^{-1} \text{N}$) and uptake efficiency (NUP; $\text{g N km}^{-1} \text{root length}$) to ambient ($375 \mu\text{mol mol}^{-1}$) and elevated (ambient + $200 \mu\text{mol mol}^{-1}$) CO_2 . Means with associated statistics‡ and percent change (ambient to elevated) are shown.

Parameter	Ambient CO_2	Elevated CO_2	% Change	P values
Shoot C	8.56	12.41	45.0	0.0277
Shoot N	0.16	0.18	12.5	0.3703
Root C	1.66	2.03	22.3	0.1359
Root N	0.02	0.03	50.0	0.2916
Total plant C	10.22	14.44	41.3	0.0215
Total plant N	0.19	0.21	10.5	0.3017
NUE	148.73	182.50	22.7	0.0002
NUP	0.86	0.81	-5.8	0.6988

† Whole-plant N utilization efficiency defined as unit of biomass produced per unit of N; whole-plant N uptake efficiency defined as unit of N per unit length of root.

‡ Mean separation conducted under Proc Mixed of SAS.

Whole-plant N utilization efficiency (unit of biomass produced per unit of N) was significantly higher for *C. benghalensis* plants grown under elevated CO_2 ; however, N uptake efficiency (unit of N per unit length of fine root) was unaffected (Table 5). Nutrient utilization efficiency generally increases under elevated CO_2 , whereas nutrient uptake efficiency declines in most studies (Rogers et al., 1994); however, this depends greatly on nutrient conditions during the experimental period. Given that plants in the present study received adequate fertilization, it is logical to conclude that uptake efficiency was not affected by atmospheric CO_2 conditions.

Glyphosate applications have little effect on *C. benghalensis* (Prostko et al., 2004); this is a primary reason that it has become a major problem on thousands of hectares where glyphosate-resistant *Gossypium hirsutum* is used in Georgia. Furthermore, herbicide regimes that provide adequate season-long *C. benghalensis* control are costly (Prostko et al., 2004). Recent evidence suggests that elevated CO_2 may increase the tolerance of some weeds to herbicides (Edis et al., 1996; Ziska et al., 1999; Ziska and Teasdale, 2000); thus, the problems associated with *C. benghalensis* control may become more serious in Southeastern agronomic systems as atmospheric CO_2 concentration continues to rise. Given that plants will continue to cross geographic borders, understanding how increased at-

mospheric CO_2 may alter establishment, spread, and control of invasive weeds is crucial to future management strategies if the productivity and profitability of farms and forests are to be maintained. Future research will evaluate growth response of *C. benghalensis* in various cropping systems in ambient and elevated CO_2 environments.

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References

- Amthor, J.S. 1995. Terrestrial higher-plant response to increasing atmospheric [CO_2] in relation to the global carbon cycle. *Glob. Change Biol.* 1:243-274.
- Binggeli, P. 1996. A taxonomic, biogeographical, and ecological overview of invasive woody plants. *J. Veget. Sci.* 7:121-124.
- Bohm, W. 1979. *Methods of studying root systems.* Springer Verlag, New York.
- Callaway, R.M., and E.T. Aschehoug. 2000. Invasive plants versus their old and new neighbors: A mechanism for exotic invasion. *Science* 290:521-523.
- Drake, B.G., M.A. Gonzalez-Meler, and S.P. Long. 1996. More efficient plants: A consequence of rising atmospheric CO_2 . *Annu. Rev. Plant Physiol. Plant Mol. Biol.* 48:609-639.
- Dukes, J.S., and H.A. Mooney. 1999. Does global change increase the success of biological invaders? *Trends Ecol. Evol.* 14:135-139.
- Edis, D., M.R. Hull, A.H. Cobb, and G.E. Sanders-Mill. 1996. A study of herbicide action and resistance at elevated levels of carbon dioxide. *Asp. Appl. Biol.* 45:205-210.
- Froud-Williams, R.J. 1996. Weeds and climate change: Implications for their ecology and control. *Asp. Appl. Biol.* 45:187-196.
- Fuhrer, J. 2003. Agroecosystem responses to combinations of elevated CO_2 , ozone, and global climate change. *Agric. Ecosyst. Environ.* 97:1-20.
- Holm, L.G., D.L. Plucknett, J.V. Pancho, and J.P. Herberger. 1977. *The world's worst weeds: Distribution and biology.* The Univ. Press of Hawaii, Honolulu, HI.
- Keeling, C.D., and T.P. Whorf. 1994. Atmospheric CO_2 records from the sites in the SIO air sampling network. p. 16-26. *In* T.A. Boden et al. (ed.) *Trends '93: A compendium of data on global change, ORNL/CDIAC-65, The Carbon Dioxide Information Analysis Center, Oak Ridge National Lab., Oak Ridge, TN.*
- Ketner, P. 1990. Will there be a weed problem as a result of climate change? p. 18-19. *In* J. Goudriaan et al. (ed.) *Greenhouse effect and primary productivity in European agro-ecosystems.* Centre for Agricultural Publishing and Documentation, Wageningen, the Netherlands.
- Klironomos, J.N. 2002. Feedback with soil biota contributes to plant rarity and invasiveness in communities. *Nature* 417:67-70.
- Littell, R.C., G.A. Milliken, W.W. Stroup, and R.D. Wolfinger. 1996. *SAS System for mixed models.* SAS Institute, Cary, NC.
- Long, S.P., and B.G. Drake. 1992. Photosynthetic CO_2 assimilation and rising atmospheric CO_2 concentrations. p. 69-107. *In* N.R. Baker and H. Thomas (ed.) *Crop photosynthesis: Spatial and temporal determinants.* Elsevier, New York.
- MacDonald, I.A.W. 1992. Global change and alien invasion: Implications for biodiversity and protected area management. p. 197-207. *In* O.T. Solbrig et al. (ed.) *Biodiversity and global change.* International Union of Biological Sciences, Paris, France.
- Masters, R.A., and R.L. Sheley. 2001. Principles and practices for managing rangeland invasive plants. *J. Range Manage.* 54:502-517.
- McDowell, S.C.L. 2002. Photosynthetic characteristics of invasive and

- noninvasive species of *Rubus* (*Rosaceae*). *Am. J. Bot.* 89:1431–1438.
- Mitchell, C.E., and A.G. Power. 2003. Release of invasive plants from fungal and viral pathogens. *Nature* 421:625–627.
- 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, DC.
- Norby, R.J., J. Pastor, and J.M. Melillo. 1986. Carbon-nitrogen interactions in CO₂-enriched white oak: Physiological and long-term perspectives. *Tree Physiol.* 2:233–241.
- Pimentel, D. 2002. *Biological invasions: Economic and environmental costs of alien plant, animal, and microbe species*. CRC Press, Boca Raton, FL.
- 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.
- Prostko, E.P., A.S. Culpepper, T.M. Webster, and J.T. Flanders. 2004. Tropical spiderwort identification and control in Georgia field crops. Georgia Cooperative Extension Publication. Available at <http://www.georgiainvasives.org/pubs/C884.pdf> (verified 5 Dec. 2008).
- Reich, P.B., B.A. Hungate, and Y. Luo. 2006. Carbon-nitrogen interactions in terrestrial ecosystems in response to rising atmospheric carbon dioxide. *Annu. Rev. Ecol. Syst.* 37:611–636.
- 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 Assoc. 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.
- Rogers, H.H., G.B. Runion, S.A. Prior, A.J. Price, H.A. Torbert, and D.H. Gjerstad. 2008. Effects of elevated atmospheric CO₂ on invasive plants: Comparison of purple and yellow nutsedge (*Cyperus rotundus* L. and *C. esculentus* L.). *J. Environ. Qual.* 37:395–400.
- Siemann, E., and W.E. Rogers. 2001. Genetic differences in growth of an invasive tree species. *Ecol. Lett.* 4:514–518.
- Webster, M.W., M.G. Burton, A.S. Culpepper, A.C. York, and E.P. Prostko. 2005. Tropical Spiderwort (*Commelina benghalensis*): A tropical invader threatens agroecosystems of the southern United States. *Weed Technol.* 19:501–508.
- Williamson, M. 2001. Can the impacts of invasive plants be predicted? p. 11–19. *In* G. Brundu et al. (ed.) *Plant invasions: Species ecology and ecosystem management*. Backhuys Publishers, Leiden, the Netherlands.
- 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. 2003a. 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. 2003b. Evaluation of the growth response of six invasive species to past, present and future atmospheric carbon dioxide. *J. Exp. Bot.* 54:395–404.
- Ziska, L.H., and J.R. Teasdale. 2000. Sustained growth and increased tolerance to glyphosate observed in a C₃ perennial weed, quackgrass (*Elytrigia repens*), grown at elevated carbon dioxide. *Aust. J. Plant Physiol.* 27:159–166.
- Ziska, L.H., J.R. Teasdale, and J.A. Bunce. 1999. Future atmospheric carbon dioxide may increase tolerance to glyphosate. *Weed Sci.* 47:608–615.