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

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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 CO$_2$ 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 CO$_2$ in open-top field chambers. Although plant height was unaffected by CO$_2$, leaf and flower number tended to increase (approximately 23%) when exposed to elevated CO$_2$. Aboveground plant parts exhibited significant increases in dry weight when exposed to high CO$_2$; 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 CO$_2$. Root dry weight and root length were unaffected by CO$_2$ concentration. Tropical spiderwort allocated more biomass to stems and tended to allocate less to roots when plants were exposed to high CO$_2$. Plant carbon concentration and content tended to be higher in CO$_2$–enriched plants, whereas plant nitrogen concentration tended to be lower; thus, elevated CO$_2$–grown plants had higher C/N ratios. Also, the amount of biomass produced per unit nitrogen was higher for plants exposed to elevated CO$_2$. The growth response of this plant is in the upper range typical for C$_3$ 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 Shely, 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 CO$_2$ concentration in the atmosphere. The concentration of atmospheric CO$_2$ is increasing and is expected to double by the end of this century (Keeling and Whorf, 1994). Given that elevated CO$_2$ 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 CO$_2$ on invasive plants has been recently summarized; nearly all species examined showed positive growth responses to increased CO$_2$ (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...
by these species is likely to increase as the concentration of CO$_2$ continues to rise (Rogers et al., 2008). However, most previous work on the response of invasive weeds to elevated CO$_2$ 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* and the third most troublesome weed in *Arachis hypogaea* 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 CO$_2$ (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 CO$_2$.

**Materials and Methods**

*Commelina benghalensis* seed coats were scarified, and seeds were germinated at ambient CO$_2$ 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 CO$_2$ until plants reached three-leaf growth stage, at which time containers were transferred to open-top CO$_2$ exposure chambers.

The CO$_2$ 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 m$^2$ of ground surface area, were used to continuously (24 h d$^{-1}$) deliver target CO$_2$ 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 CO$_2$ 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 CO$_2$ 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 CO$_2$ 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 [combing 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 sieving 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 Havillard, 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 CO$_2$ 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 \( \text{CO}_2 \) 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 \( \text{CO}_2 \) is due primarily to differences between plants with a \( \text{C}_3 \) (33–40% increase) vs. a \( \text{C}_4 \) (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 \( \text{C}_3 \) plants. Elevated \( \text{CO}_2 \) 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 \( \text{CO}_2 \) continues to rise. Ziska (2001, 2003a) and Ziska and Teasdale (2000), examining the effects of elevated \( \text{CO}_2 \) on \( \text{C}_3/\text{C}_4 \) crop/weed combinations, have shown that \( \text{C}_4 \) plants tended to show less response to elevated \( \text{CO}_2 \), regardless of whether they were a crop plant or a weed, than \( \text{C}_3 \) plants. Furthermore, \( \text{C}_4 \) weeds tended to have a greater negative effect on the growth and yield of \( \text{C}_3 \) and \( \text{C}_4 \) crop plants under high \( \text{CO}_2 \) than did \( \text{C}_3 \) 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 \( \text{CO}_2 \) (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 \( \text{CO}_2 \) on invasive weeds, such as Bromus tectorum L., in the USA, reported that most species exhibited positive growth responses to increased \( \text{CO}_2 \). Ziska (2003b) reported significant \( \text{CO}_2 \)-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 \( \text{CO}_2 \); 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 \( \text{CO}_2 \). Despite the lack of root dry weight response to high \( \text{CO}_2 \), 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 \( \text{CO}_2 \) (Table 3). Plants generally allocate resources to plant organs experiencing the greatest limitation; under high atmospheric \( \text{CO}_2 \), this is generally the root system (Rogers et al., 1996). Given that \( \text{C. benghalensis} \) 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>
<thead>
<tr>
<th>Parameter</th>
<th>Ambient CO(_2)</th>
<th>Elevated CO(_2)</th>
<th>% Change</th>
<th>( P ) values</th>
</tr>
</thead>
<tbody>
<tr>
<td>Inflorescence</td>
<td>3.66</td>
<td>4.75</td>
<td>29.8</td>
<td>0.040</td>
</tr>
<tr>
<td>Leaf</td>
<td>3.45</td>
<td>4.69</td>
<td>35.9</td>
<td>0.012</td>
</tr>
<tr>
<td>Stem</td>
<td>16.34</td>
<td>24.27</td>
<td>48.5</td>
<td>0.045</td>
</tr>
<tr>
<td>Total shoot</td>
<td>23.46</td>
<td>33.71</td>
<td>43.7</td>
<td>0.028</td>
</tr>
<tr>
<td>Root</td>
<td>3.94</td>
<td>4.80</td>
<td>21.8</td>
<td>0.175</td>
</tr>
<tr>
<td>Total plant</td>
<td>27.40</td>
<td>38.52</td>
<td>40.6</td>
<td>0.023</td>
</tr>
</tbody>
</table>

† Mean separation conducted under Proc Mixed of SAS.

<table>
<thead>
<tr>
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<th>Ambient CO(_2)</th>
<th>Elevated CO(_2)</th>
<th>% Change</th>
<th>( P ) values</th>
</tr>
</thead>
<tbody>
<tr>
<td>Height (cm)</td>
<td>95.16</td>
<td>102.45</td>
<td>7.7</td>
<td>0.117</td>
</tr>
<tr>
<td>Leaf number</td>
<td>378.50</td>
<td>464.43</td>
<td>22.7</td>
<td>0.061</td>
</tr>
<tr>
<td>Inflorescence no.</td>
<td>257.13</td>
<td>317.62</td>
<td>23.5</td>
<td>0.072</td>
</tr>
<tr>
<td>Root length (m)</td>
<td>246.51</td>
<td>275.48</td>
<td>11.8</td>
<td>0.541</td>
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</table>

† Mean separation conducted under Proc Mixed of SAS.

<table>
<thead>
<tr>
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<th>% Change</th>
<th>( P ) values</th>
</tr>
</thead>
<tbody>
<tr>
<td>Inflorescence</td>
<td>12.98</td>
<td>13.48</td>
<td>3.9</td>
<td>0.765</td>
</tr>
<tr>
<td>Leaf</td>
<td>13.71</td>
<td>13.28</td>
<td>–3.1</td>
<td>0.711</td>
</tr>
<tr>
<td>Stem</td>
<td>53.83</td>
<td>58.67</td>
<td>9.0</td>
<td>0.016</td>
</tr>
<tr>
<td>Root</td>
<td>19.49</td>
<td>14.57</td>
<td>–25.2</td>
<td>0.147</td>
</tr>
<tr>
<td>Root to shoot ratio</td>
<td>0.17</td>
<td>0.14</td>
<td>–17.6</td>
<td>0.310</td>
</tr>
</tbody>
</table>

† Mean separation conducted under Proc Mixed of SAS.

Shoot C concentration was increased, whereas root C was unaffected, by growth in elevated \( \text{CO}_2 \), resulting in a trend for total plant C concentration to increase (Table 4). As with C, root N concentration was unaffected by \( \text{CO}_2 \) treatment; however, shoot and total plant N concentrations were lower under high \( \text{CO}_2 \). As was seen with C concentration, the C contents of shoots and total plants were increased by exposure to elevated atmospheric \( \text{CO}_2 \); 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 \( \text{CO}_2 \) treatment (Table 5).

Elevated atmospheric \( \text{CO}_2 \) 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 \( \text{C. benghalensis} \) in that N concentrations were lower under elevated \( \text{CO}_2 \); 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 \( \text{CO}_2 \); again, root C/N ratio was not affected (Table 4). Higher C/N ratios of plant tissues produced under high \( \text{CO}_2 \) 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\textsuperscript{−1}) to ambient (375 μmol mol\textsuperscript{−1}) and elevated (ambient + 200 μmol mol\textsuperscript{−1}) CO\textsubscript{2}. Means with associated statistics† and percent change (ambient to elevated) are shown.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Ambient CO\textsubscript{2}</th>
<th>Elevated CO\textsubscript{2}</th>
<th>% Change</th>
<th>P values</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shoot C</td>
<td>8.56</td>
<td>12.41</td>
<td>45.0</td>
<td>0.0277</td>
</tr>
<tr>
<td>Shoot N</td>
<td>0.16</td>
<td>0.18</td>
<td>12.5</td>
<td>0.3703</td>
</tr>
<tr>
<td>Root C</td>
<td>1.66</td>
<td>2.03</td>
<td>22.3</td>
<td>0.1359</td>
</tr>
<tr>
<td>Root N</td>
<td>0.02</td>
<td>0.03</td>
<td>50.0</td>
<td>0.2916</td>
</tr>
<tr>
<td>Total plant C</td>
<td>10.22</td>
<td>14.44</td>
<td>41.3</td>
<td>0.0215</td>
</tr>
<tr>
<td>Total plant N</td>
<td>0.19</td>
<td>0.21</td>
<td>10.5</td>
<td>0.3017</td>
</tr>
<tr>
<td>NUE</td>
<td>148.73</td>
<td>182.50</td>
<td>22.7</td>
<td>0.0002</td>
</tr>
<tr>
<td>NUP</td>
<td>0.86</td>
<td>0.81</td>
<td>0.8</td>
<td>0.6988</td>
</tr>
</tbody>
</table>

† 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\textsubscript{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\textsubscript{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\textsubscript{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 \textit{Gossypium hirsutum} is used in Georgia. Furthermore, herbicide regimes that provide adequate season-long \textit{C. benghalensis} control are costly (Prostko et al., 2004). Recent evidence suggests that elevated CO\textsubscript{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 \textit{C. benghalensis} control may become more serious in Southeastern agronomic systems as atmospheric CO\textsubscript{2} concentration continues to rise. Given that plants will continue to cross geographic borders, understanding how increased atmospheric CO\textsubscript{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 \textit{C. benghalensis} in various cropping systems in ambient and elevated CO\textsubscript{2} environments.

Acknowledgments

The authors thank B.G. Dorman, J.W. Carrington, M.E. Stoll, and H.M. Finegan for technical assistance. This research was supported by the Southeast Regional Center of the U.S. Department of Energy’s National Institute for Global Environmental Change under Cooperative Agreement No. DE-FCO2-03-ER63613 and the U.S. Department of Energy’s Biological and Environmental Research Program (BER) under Interagency Agreement No. DE-AL02-95ER62088.

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