

## Effects of Elevated Atmospheric CO<sub>2</sub> on Invasive Plants: Comparison of Purple and Yellow Nutsedge (*Cyperus rotundus* L. and *C. esculentus* L.)

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The rise in atmospheric CO<sub>2</sub> concentration coupled with its direct, often positive, effect on the growth of plants raises the question of the response of invasive plants to elevated atmospheric CO<sub>2</sub> levels. Response of two invasive weeds [purple nutsedge (*Cyperus rotundus* L.) and yellow nutsedge (*Cyperus esculentus* L.)] to CO<sub>2</sub> enrichment was tested. Plants were exposed to ambient (375 μmol mol<sup>-1</sup>) or elevated CO<sub>2</sub> (ambient + 200 μmol mol<sup>-1</sup>) for 71 d in open top chambers. Photosynthetic rate did not differ between CO<sub>2</sub> treatments for either species. Conductance was lower in purple nutsedge and tended to be lower in yellow nutsedge. Purple nutsedge had higher instantaneous water use efficiency; a similar trend was noted for yellow nutsedge. Purple nutsedge had greater leaf area, root length and numbers of tubers and tended to have more tillers under high CO<sub>2</sub>. In yellow nutsedge, only tuber number increased under CO<sub>2</sub> enrichment. Leaf dry weight was greater for both species when grown under elevated CO<sub>2</sub>. Only purple nutsedge made seed heads; CO<sub>2</sub> level did not change seed head dry weight. Root dry weight increased under the high CO<sub>2</sub> treatment for purple nutsedge only, but tuber dry weight increased for both. Total dry weight of both species increased at elevated CO<sub>2</sub>. Purple nutsedge (under elevated CO<sub>2</sub>) tended to increase allocation belowground, which led to greater root-to-shoot ratio (R:S); R:S of yellow nutsedge was unaffected by CO<sub>2</sub> enrichment. Findings suggest both species, purple more than yellow nutsedge, may be more invasive in a future high-CO<sub>2</sub> world.

INVASIVE plant species are considered to have the capacity to disrupt Earth's biodiversity (Binggeli, 1996; Randall, 2000). These plants cost US agriculture and forestry 34 billion dollars each year from decreased productivity and increased costs of control (Pimentel, 2002). Considerable effort is being spent identifying the characteristics of exotic plants that confer success after introduction (Rejmanek and Richardson, 1996; Williamson and Fitter, 1996) and to predict which species will become major threats in the future (Rejmanek, 2000).

How invasive weeds will respond to the well documented rise in atmospheric CO<sub>2</sub> concentration (Keeling and Whorf, 2005) is of much importance with respect to invasiveness and control. Bright (1998) has stated that, "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."

Two of the world's most troublesome invasive weeds are purple nutsedge (*Cyperus rotundus* L.) and yellow nutsedge (*C. esculentus* L.); both are perennial herbaceous sedges and have the C<sub>4</sub> photosynthetic pathway (Santos et al., 1997). The biology and life cycle of purple and yellow nutsedge are well documented (Stoller and Sweet, 1987; Wills, 1987). Briefly, both species appear grass like, but their stems are triangular in cross-section. Both have fibrous roots that branch prolifically, rhizomes, tubers, bulbs, and inflorescences that consist of irregular compound umbels. Their leaves are mostly basal and linear in shape with a prominent mid-rib. Yellow nutsedge grows 0.3 to 0.8 m in height with yellowish-brown flowers; purple nutsedge grows 0.3 to 0.6 m with purple to brown flowers (Ministry of Agriculture and Lands of British Columbia, 2007). Purple nutsedge reproduction is mainly by chains of tubers produced at the ends of its many rhizomes; seed production seems to be a minor contributor to reproduction and spread (Thullen and Keeley, 1979). Yellow nutsedge reproduces by tubers occurring singly at the ends of rhizomes and by seeds (Wills, 1987). Tubers are the most significant means of propagation in most cultivated areas (Stoller and Sweet, 1987) due mainly to inadequate vigor of seedlings. In the first year of growth, a single yellow nutsedge clone produced 17,681 tubers in Zimbabwe (Lapham, 1985). Tuberation is far more photoperiod sensitive in yellow than purple nutsedge (Stoller and Sweet, 1987).

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**Abbreviations:** OTC, open-top chamber; WUE, water use efficiency.

Worldwide distribution of purple and yellow nutsedge has been thoroughly investigated (Bendixen and Nandihalli, 1987; Holm et al., 1991a,b). Purple nutsedge, which is native to Eurasia (USDA-ARS, 1970), is a highly aggressive weed and infests 52 crops in 92 countries (Holm et al., 1991b). It is likely the most noxious member of its genus and has been ranked the “world’s worst weed” (Holm et al., 1991a,b). Yellow nutsedge is native to the Eastern Mediterranean (Zeven and de Wet, 1982; Negbi, 1992; Steckel, 2007). This invasive weed is found on every continent of the world except Antarctica and is adapted to conditions ranging from tropical to subarctic. It has been ranked as the 16th worst weed in the world (Holm et al., 1991a,b). It is found in over 21 crops in more than 30 countries (Holm et al., 1991b). Yellow nutsedge is more cold tolerant than purple nutsedge (Bendixen and Nandihalli, 1987); this allows the tubers to survive low air and soil temperatures, so it has disseminated widely (Stoller and Sweet, 1987). Yellow nutsedge grows in crop field canopies, although growth and reproduction are reduced at lower light levels (Santos et al., 1997; Jordan-Molero and Stoller, 1978). Purple nutsedge is less shade tolerant (Santos et al., 1997). In a review of the interference and interaction of purple and yellow nutsedge with crops, Keeley (1987) found that both species can significantly reduce crop yields and that early emergence of these weeds was a primary factor influencing the extent of this loss.

Because elevated CO<sub>2</sub> stimulates photosynthesis (Long and Drake, 1992), resource use efficiency (Rogers and Dahlman, 1993; Rogers et al., 1994; Amthor, 1995), and carbon allocation to belowground plant structures (Rogers et al., 1994), it is likely to affect the growth and competition of invasive plants (Ketner, 1990; MacDonald, 1992; Froud-Williams, 1996; Patterson, 1995). Dukes and Mooney (1999) report a few examples of invasive species (individually and in monoculture) responding positively to elevated CO<sub>2</sub> levels. Studies with two invasive vines, kudzu [*Pueraria lobata* (Willd.) Ohwi] and Japanese honeysuckle (*Lonicera japonica* Thunb.), suggested that high CO<sub>2</sub> could worsen problems with both species (Sasek and Strain, 1988, 1989, 1991). Work with shrubs that invade rangelands indicated that increased water use efficiency under elevated CO<sub>2</sub> could enhance their competitive ability over native plants (Polley et al., 1994, 1996, 1997). In more recent work, Ziska (2002, 2003) suggests that CO<sub>2</sub> enrichment may already have played a substantial role in weed invasion in the USA. Ziska further found that CO<sub>2</sub> response by six invasives was about three times that for any species previously tested. Ziska and Bunce (1997) report increasing photosynthetic and growth stimulation in C<sub>4</sub> crops and weeds by high CO<sub>2</sub>.

The purpose of this experiment was to address the response of purple nutsedge and yellow nutsedge to elevated atmospheric CO<sub>2</sub> concentration. These aggressive C<sub>4</sub> perennials are two of the most noxious invasive weeds; to our knowledge, no previous attempts have been made to conduct detailed studies on the effects of elevated CO<sub>2</sub> on these invasives.

## Materials and Methods

Three yellow nutsedge and three purple nutsedge tubers (Azlin Seed Service, Leland, MS) were planted in a peat-based gen-

eral purpose growing medium (PRO-MIX Bx; Premier Horticulture Inc., Quakertown, PA) in 1.65-L tree-pots (Short One Tree-pot, 10 × 23 cm; Stuewe and Sons Inc., Corvallis, OR). After establishment, plants were thinned to one plant per pot. Plants were grown in the greenhouse until reaching the 4- to 6-leaf growth stage and were transplanted into 10.65 L tree pots (TPOT4 Round Tree-pot, 22 cm × 39 cm; Stuewe and Sons Inc.) containing the same standard growth medium described above and transferred to open top chambers (OTCs).

Forty-eight containers of each species were selected for placement in OTCs. 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 (four containers of each plant species in each OTC). Initial measurements (including height, ground line diameter, number of tillers, leaves, and seed heads) were taken on each plant before placement in OTCs to ensure there was no unintended bias in plant size among OTCs before initiation of CO<sub>2</sub> treatment.

The study was conducted at the soil bin facilities at the USDA-ARS National Soil Dynamics Laboratory, Auburn, Alabama. The bin used for the experiment is 6 m wide and 76 m long and has been modified by installing a geomembrane liner (20 mil) and gravel drain system to ensure a good working surface and drainage for container studies. Open top chambers (Rogers et al., 1983a), encompassing 7.3 m<sup>2</sup> of ground surface area, were used to continuously (24 h d<sup>-1</sup>) deliver target CO<sub>2</sub> concentrations of 375 μmol mol<sup>-1</sup> (ambient) or ambient plus 200 μmol mol<sup>-1</sup> (elevated) using a previously described delivery and monitoring system (Mitchell et al., 1995). Actual CO<sub>2</sub> concentrations over the measurement period (±SE) were as follows: ambient daytime, 374.6 (±0.2); elevated daytime, 586.5 (±0.5); ambient nighttime, 420.0 (±0.4); and elevated nighttime, 646.9 (±0.6) μmol mol<sup>-1</sup> (daytime was taken as 0700 CST to 1900 CST).

The bin was divided into six blocks, and each CO<sub>2</sub> treatment was randomly assigned to one OTC within each block. The experiment was conducted as a randomized complete block, with blocks occurring along the length of the soil bin. At one end of the bin is a building that at certain times of the day casts a shadow over the first block. At the opposite end of the bin is a road where automobiles and nighttime lighting might affect the last block. A blocked design was used to statistically account for any potential influence of these conditions on treatment response.

Unchambered control plots were not included in the study; therefore, chamber effects are not accounted for in discussing the results of this study. However, the OTCs used in this study are truly open topped; they do not contain a frustum, or any other type of constriction at the top, which may result in a large differential between chambered and open plots. Furthermore, the OTCs used in this study are set up to exchange three full chamber volumes of air every minute; previous studies with these OTCs have shown that this rapid exchange greatly reduces the environmental effects of the chambers. Last, given that all plots (elevated and ambient) had chambers, the chamber effect should have been the same or similar for all plants in this study.

Plants were placed in the OTCs on 14 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. Six hundred grams of Miracle-Gro was mixed in 130 L deionized water, and each plant received 500 mL of solution. In addition, plants received an iron chelate treatment (1:0:0, N:P:K plus 1.25% water soluble iron; Ironite Products Co., Scottsdale, AZ) on 8 and 14 July 2005; 20 g of granular Ironite was added to each pot during each application.

All plants were destructively harvested beginning 24 Aug. 2005, corresponding to 71 d of CO<sub>2</sub> 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), with which conductance and transpiration are concomitantly determined with photosynthesis, and instantaneous water use efficiency can be calculated from these data. Each measured leaf was detached, and leaf area in the Li-Cor cuvette was determined photometrically using a LI-3100 leaf area meter for subsequent calculation of net photosynthetic rate.

Aboveground portions of all plants in each container were harvested by severing the plant(s) at the ground line. Aboveground parameters (e.g., number of tillers, leaves, and seed heads) were assessed. Plants were separated into organ parts (i.e., leaves and seed heads), and leaf area was determined photometrically 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 dried in a forced-air oven at 55°C to a constant weight, and dry weights were recorded. The dry weight of each organ part was 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.

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<sub>2</sub> concentration. In all cases, differences were considered significant at the  $\alpha \leq 0.05$ , and trends were recognized at  $0.05 < \alpha \leq 0.10$ .

## Results and Discussion

There was a relatively high degree of variability in plant size at initiation of the experiment (e.g., initial height and diameter of the largest plants was at least twice that of the smallest plants for both species). Use of the ranking scheme provided an ability to distribute this variability among the OTCs in a manner that provided no pretreatment bias in plant size between the two CO<sub>2</sub> treatments; initial plant size measurements confirmed this fact. Nonetheless, statistical analyses were attempted using initial plant size or grouping number as covariates; in neither case did this use of covariates change the analysis. Statistical analyses revealed no block effect for any variable measured for either species.

Table 1. The response of purple nutsedge and yellow nutsedge gas exchange variables to ambient (375  $\mu\text{mol mol}^{-1}$ ) and elevated (ambient + 200  $\mu\text{mol mol}^{-1}$ ) CO<sub>2</sub>. Means with associated separation statistics and percent change (ambient to elevated) are shown.

| Species         | Variable       | Ambient CO <sub>2</sub> | Elevated CO <sub>2</sub> | % Change | P value |
|-----------------|----------------|-------------------------|--------------------------|----------|---------|
| Purple nutsedge | Pn†            | 9.06                    | 9.44                     | 4.2      | 0.799   |
|                 | conductance‡   | 0.063                   | 0.046                    | -27.0    | 0.021   |
|                 | transpiration§ | 2.17                    | 1.70                     | -21.7    | 0.084   |
|                 | WUE¶           | 4.26                    | 5.83                     | 36.9     | 0.043   |
| Yellow nutsedge | Pn             | 11.37                   | 9.37                     | -17.6    | 0.136   |
|                 | conductance    | 0.094                   | 0.061                    | -35.1    | 0.087   |
|                 | transpiration  | 3.74                    | 2.27                     | -39.3    | 0.066   |
|                 | WUE            | 3.32                    | 4.56                     | 37.3     | 0.097   |

† Photosynthesis in  $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ .

‡ Conductance in  $\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$ .

§ Transpiration in  $\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$ .

¶ Water use efficiency in  $\text{mmol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$ .

Photosynthetic rate ( $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ) did not differ among CO<sub>2</sub> treatments for purple or yellow nutsedge (Table 1). This was not unexpected because C<sub>4</sub> species (such as these nutsedges), having a CO<sub>2</sub>-concentrating mechanism at the site of rubisco, often show limited response to elevated CO<sub>2</sub> (Amthor, 1995). Although some C<sub>4</sub> plants show increases in photosynthesis when grown under CO<sub>2</sub> enrichment, these increases tend to be lower than those observed for C<sub>3</sub> plants. However, some C<sub>4</sub> weeds have shown increases in photosynthesis similar to those generally observed for C<sub>3</sub> species (Ziska and Bunce, 1997). It is possible that differences in photosynthesis might have existed between CO<sub>2</sub> treatments for these two weeds at other times during their growth; having collected gas exchange measurements only before harvest, this cannot be determined.

Purple nutsedge had lower conductance ( $\text{mol H}_2\text{O m}^{-2} \text{ s}^{-1}$ ) when grown under CO<sub>2</sub>-enriched conditions, which resulted in a trend for a lower transpiration rate ( $\text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$ ) (Table 1). These responses resulted in significantly higher instantaneous water use efficiency (WUE) ( $\text{mmol CO}_2 \text{ mol}^{-1} \text{ H}_2\text{O}$ ) for purple nutsedge. It has been shown that increased WUE for C<sub>4</sub> species derives mainly from reduced transpiration (Rogers and Dahlman, 1993). Improved plant/water relations under CO<sub>2</sub> enrichment due to decreased stomatal conductance and increased WUE confer an ability to withstand drought conditions (Rogers et al., 1983b), which may cause this invasive weed to become even more of a problem due to an improved ability to compete for resources in a future high-CO<sub>2</sub> world (Ziska and Bunce, 1997). Similarly, Polley et al. (1994, 1996, 1997) found that greater WUE gave invasive shrubs a competitive edge over native species in western rangelands. In our study, similar trends for decreased transpiration and conductance and increased WUE were also noted for yellow nutsedge (Table 1). The observed increased WUE for purple and yellow nutsedge suggests that both invasive weeds will likely become worse agronomic problems under high CO<sub>2</sub>.

Purple nutsedge had greater leaf area, root length, and numbers of tubers and tended to have greater numbers of tillers when grown under high CO<sub>2</sub> (Table 2). As with our previous results, yellow nutsedge was less responsive to elevated CO<sub>2</sub>, and only

**Table 2.** The response of purple nutsedge and yellow nutsedge growth variables to ambient (375  $\mu\text{mol mol}^{-1}$ ) and elevated (ambient + 200  $\mu\text{mol mol}^{-1}$ )  $\text{CO}_2$ . Means with associated separation statistics and percent change (ambient to elevated) are shown.

| Species         | Parameter                   | Ambient $\text{CO}_2$ | Elevated $\text{CO}_2$ | % Change | P value |
|-----------------|-----------------------------|-----------------------|------------------------|----------|---------|
| Purple nutsedge | no. of tillers              | 92.5                  | 100.0                  | 8.1      | 0.090   |
|                 | no. of leaves               | 900.0                 | 935.8                  | 4.0      | 0.287   |
|                 | no. of seed heads           | 5.7                   | 4.5                    | -21.1    | 0.249   |
|                 | leaf area ( $\text{cm}^2$ ) | 8660.5                | 11,354.4               | 31.1     | 0.006   |
|                 | root length (m)             | 3303.1                | 3965.2                 | 20.0     | 0.012   |
|                 | no. of tubers               | 368.4                 | 435.5                  | 18.2     | 0.001   |
| Yellow nutsedge | no. of tillers              | 199.2                 | 184.2                  | -7.5     | 0.053   |
|                 | no. of leaves               | 1364.2                | 1252.2                 | -8.2     | 0.117   |
|                 | leaf area ( $\text{cm}^2$ ) | 16,324.1              | 16,633.7               | 1.9      | 0.672   |
|                 | root length (m)             | 3114.8                | 3078.3                 | -1.2     | 0.880   |
|                 | no. of tubers               | 504.7                 | 580.4                  | 15.0     | 0.030   |

the number of tubers significantly increased. Because tubers are a main mode of reproduction and dispersal, the stimulation of tuber number by high  $\text{CO}_2$  suggests greater establishment and spread of both nutsedge species. However, purple nutsedge has greater vigor and is more competitive than the yellow species when conditions are optimum (Bendixen, 1973). Given that nutrients and water were well supplied in our study, it is logical to conclude that purple nutsedge was more responsive than yellow nutsedge under these growth conditions. Because nutrients (and sometimes water) are often supplied in agronomic settings, it is likely that purple nutsedge will become a greater problem for farmers as the atmospheric  $\text{CO}_2$  concentration continues to rise.

Both species increased leaf dry weight when grown under elevated  $\text{CO}_2$  conditions (Table 3); however, the increase for purple nutsedge was much larger than that observed for yellow nutsedge (20.3% vs. 5.2%, for purple and yellow, respectively). Purple nutsedge produced seed heads during the course of the experiment, whereas yellow nutsedge did not; however,  $\text{CO}_2$  concentration did not affect dry weight of seed heads. Because purple nutsedge flowers earlier than yellow nutsedge (Williams, 1982)

**Table 3.** The response of purple nutsedge and yellow nutsedge plant component part dry weight (g) to ambient (375  $\mu\text{mol mol}^{-1}$ ) and elevated (ambient +200  $\mu\text{mol mol}^{-1}$ )  $\text{CO}_2$ . Means with associated separation statistics and percent change (ambient to elevated) are shown.

| Species         | Plant part        | Ambient $\text{CO}_2$ | Elevated $\text{CO}_2$ | % Change | P value |
|-----------------|-------------------|-----------------------|------------------------|----------|---------|
| Purple nutsedge | leaf              | 89.19                 | 107.30                 | 20.3     | 0.007   |
|                 | seed head         | 7.00                  | 6.58                   | -4.6     | 0.822   |
|                 | total shoot       | 96.20                 | 113.98                 | 18.5     | 0.002   |
|                 | roots             | 80.93                 | 104.45                 | 29.1     | 0.002   |
|                 | tubers            | 121.86                | 155.80                 | 27.9     | <0.001  |
|                 | total belowground | 202.78                | 260.25                 | 28.3     | <0.001  |
|                 | total plant       | 298.98                | 374.23                 | 25.2     | <0.001  |
| Yellow nutsedge | leaf              | 145.26                | 152.84                 | 5.2      | 0.032   |
|                 | roots             | 86.63                 | 85.74                  | -1.0     | 0.922   |
|                 | tubers            | 92.97                 | 121.05                 | 30.2     | 0.001   |
|                 | total belowground | 179.60                | 206.79                 | 15.1     | 0.059   |
|                 | total plant       | 324.86                | 359.63                 | 10.7     | 0.023   |

and seed heads are not present in some populations (Stoller and Sweet, 1987), the observed absence of seed heads for yellow nutsedge was not unexpected. Further, because purple nutsedge rarely reproduces by seed (Thullen and Keeley, 1979), the lack of response to  $\text{CO}_2$  enrichment may be relatively inconsequential.

The increase in tuber dry weight was similar for purple and yellow nutsedge under high  $\text{CO}_2$ , resulting in greater belowground dry weight for both species (Table 3). However, root dry weight was greater under high  $\text{CO}_2$  only for purple nutsedge, suggesting the potential for greater belowground competition and indicating that problems resulting from this species are likely to be greater. Although both nutsedge species exhibited increased total plant dry weight when exposed to elevated  $\text{CO}_2$ , the response was larger for purple (25.2%) than yellow (10.7%) nutsedge (Table 3). The response for yellow nutsedge biomass to elevated  $\text{CO}_2$  was similar to increases (10–15%) generally reported in the literature for  $\text{C}_4$  plants (Kimball 1983; Prior et al., 2003); however, the response of purple nutsedge approached that commonly found in  $\text{C}_3$  plants (33–40%). Research has shown that increased plant growth under elevated atmospheric  $\text{CO}_2$  generally results from increased rates of photosynthesis, altered C partitioning, and/or increased water and nutrient use efficiencies (Pritchard et al., 1999; Urban 2003). Given that neither photosynthesis (see Table 1) nor C partitioning (Table 4) tended to be affected by  $\text{CO}_2$  concentration in either species, the most likely explanation for the observed biomass increases is the increased water use efficiencies noted for both species (Table 1). However, because photosynthesis was measured only before harvest, it is possible that differences in photosynthesis might have existed between  $\text{CO}_2$  treatments for these two weeds at other times during their growth; this might be particularly true for purple nutsedge given its large biomass response to elevated  $\text{CO}_2$ . Furthermore, given that the actual WUE response to elevated  $\text{CO}_2$  was similar for the two species (Table 1), it is unlikely that WUE alone can explain the differential biomass response between species observed in this study.

Although purple and yellow nutsedge increased above- and belowground dry weights under high  $\text{CO}_2$ , the response was larger for belowground structures for both species (Table 3). Greater root growth, compared with shoot growth, has been observed in many plant species when grown under high  $\text{CO}_2$  (Hunt et al., 1991; Rogers et al., 1996). This indicates an ability to accumulate more resources, suggesting greater competition with crops (i.e., weediness) and more difficulty in control. Ziska et al. (2004) suggested that perennial weeds that reproduce from belowground structures may be more difficult to control under high  $\text{CO}_2$  conditions in the future. This could be true of the two nutsedges we studied because tuber number and dry weight increased. Tubers are the primary means of reproduction and spread of nutsedges and are a main deterrent to control. To further exacerbate the problem of controlling invasive species, recent evidence suggests that elevated  $\text{CO}_2$  may increase the tolerance of some weeds to herbicides (Ziska et al., 1999; Ziska and Teasdale, 2000). This finding will be particularly relevant for future nutsedge control in agronomic settings given the belowground responses reported here and the fact that nutsedges are relatively unresponsive to common herbicides, such as glyphosate.

Table 4. The response of purple nutsedge and yellow nutsedge allocation among plant component parts (%) to ambient (375  $\mu\text{mol mol}^{-1}$ ) and elevated (ambient + 200  $\mu\text{mol mol}^{-1}$ )  $\text{CO}_2$ . Means with associated separation statistics and percent change (ambient to elevated) are shown.

| Species         | Plant part          | Ambient $\text{CO}_2$ | Elevated $\text{CO}_2$ | % Change | P value |
|-----------------|---------------------|-----------------------|------------------------|----------|---------|
| Purple nutsedge | leaves              | 30.11                 | 29.16                  | -3.2     | 0.239   |
|                 | seed heads          | 2.36                  | 1.87                   | -20.8    | 0.290   |
|                 | total aboveground   | 32.48                 | 31.03                  | -4.5     | 0.121   |
|                 | roots               | 26.85                 | 27.47                  | 2.3      | 0.462   |
|                 | tubers              | 40.67                 | 41.50                  | 2.0      | 0.390   |
|                 | total belowground   | 67.52                 | 68.97                  | 2.1      | 0.121   |
|                 | root to shoot ratio | 2.124                 | 2.297                  | 8.1      | 0.056   |
| Yellow nutsedge | leaves              | 45.42                 | 42.98                  | -5.4     | 0.159   |
|                 | roots               | 26.33                 | 23.55                  | -10.6    | 0.158   |
|                 | tubers              | 28.26                 | 33.47                  | 18.4     | 0.001   |
|                 | total belowground   | 54.58                 | 57.02                  | 4.5      | 0.159   |
|                 | root to shoot ratio | 1.241                 | 1.355                  | 9.2      | 0.238   |

Plants tend to allocate resources to the organ necessary for collecting the resource most limiting to growth (Rogers et al., 1996). In the present study, where plants were grown under optimal soil resource conditions, allocation among plant organs tended to be unresponsive to  $\text{CO}_2$  treatment (Table 4). One exception to this was an increased allocation to tubers observed only for yellow nutsedge. This increased allocation to reproductive structures suggests that yellow nutsedge tuber sprouts might be more vigorous under future, higher  $\text{CO}_2$  conditions. However, this increased allocation to tubers did not alter root to shoot ratio of yellow nutsedge due to a slight decrease in allocation to roots for this species. Purple nutsedge allocated numerically (although not statistically) more biomass to roots and tubers, which resulted in a larger root to shoot ratio for these plants (Table 4). Larger root to shoot ratios could impart resistance to soil resource stress.

This study found that both nutsedges benefitted from elevated atmospheric  $\text{CO}_2$  and that, overall, purple nutsedge was more responsive to  $\text{CO}_2$  enrichment than was yellow nutsedge. These findings suggest that although both invasive weeds may become larger problems for farmers, purple nutsedge could be even more troublesome in a future high  $\text{CO}_2$  world. However, because these invasive weeds were not grown under competition with crop plants, the exact manner in which they will respond to increasing atmospheric  $\text{CO}_2$  enrichment under actual field conditions is not known. Mooney and Hobbs (2000) have pointed out that, "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."

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