Original Paper Environ. Control Biol., **49** (3), 107–117, 2011

Effects of Elevated Atmospheric CO_2 on Non-native Plants: Comparison of Two Important Southeastern Ornamentals

G. Brett RUNION[1], Heidi M. FINEGAN[2], Stephen A. PRIOR[1], Hugo H. ROGERS[1] and Dean H. GJERSTAD[3]

[1] *USDA-ARS National Soil Dynamics Laboratory, 411 S. Donahue Drive, Auburn, AL 36832, USA*
[2] *Department of Animal Sciences, Auburn University, Auburn University, AL 36849, USA*
[3] *School of Forestry and Wildlife Sciences, Auburn University, Auburn University, AL 36849, USA*

(Received March 31, 2009; Accepted March 19, 2010)

Understanding how ornamentals will respond to the increasing level of CO_2 in the atmosphere will aid future plant selection. In addition, understanding how rising levels of CO_2 affect the potential of introduced ornamentals to become invasive weeds will be crucial to future management. This study was conducted to determine the effects of elevated CO_2 on growth of two non-native plants commonly used as ornamentals in the southeastern U.S. Lantana (*Lantana camara*) and vinca (*Catharanthus roseus*) were grown at either 375 μmol mol^{-1} (ambient) or 575 μmol mol^{-1} (elevated) CO_2 for four months in open top field chambers. Measurements of plant morphology, biomass, and plant tissue nitrogen were made for both species. Lantana growth was more responsive to elevated CO_2 than was vinca. Lantana root and total plant dry weights were increased by 31 and 19%, respectively; in vinca, these values increased by only 9% each. Vinca root length was unaffected by CO_2, however, it was increased by 46% in lantana. Elevated CO_2 had no effect on flower dry weight for either species. This study suggests that rising atmospheric CO_2 will have little impact on vinca as either an ornamental or as a potential invasive weed. Lantana's value as an ornamental may increase due to its abundant growth under elevated CO_2. Lantana's greater root growth may also increase its drought tolerance, adding to its ornamental potential. However, the factors which may make it a more desirable ornamental under future higher CO_2 conditions could also enhance its potential to become a serious invasive weed in the southeastern U.S.

Keywords : global change, CO_2 enrichment, invasive plants, Lantana (*Lantana camara*), vinca (*Catharanthus roseus*)

INTRODUCTION

Carbon dioxide (CO_2) concentrations are commonly raised in ornamental glasshouses to increase productivity (Ottensen and Mentz, 2000). It is known that the concentration of CO_2 in the atmosphere is increasing and may double during this century (Keeling and Whorf, 1994). Understanding how ornamental plants will respond to this increase will aid future selection of plants and varieties best adapted to future conditions. Management, both in the nursery and in the landscape, may also change.

Some plants intentionally introduced to the U.S. for use as either agricultural (e.g., Johnson grass [*Sorghum halepense* (L.) Pers.]) or horticultural (e.g., mimosa [*Albizia julibrissin* Durazz.],

Corresponding author : G. Brett Runion, fax : +1-334-887-8597,
e-mail : brett.runion@ars.usda.gov

Chinese privet [*Ligustrum sinense* Lour.], nandina [*Nandina domestica* Thunb.]) crops have become serious invasive weeds (Holm et al., 1997; Miller, 2003). Invasive weeds have become an increasing problem to the world's agricultural and forestry production over the past few decades and are estimated to cost 34 billion dollars each year from decreased productivity and increased costs of control (Pimentel, 2002). Invasive weeds are now considered to be a major threat to the Earth's biodiversity (Binggeli, 1996; Randall, 2000). Identifying the characteristics of exotic plants that confer success following introduction has become a major research focus (Rejmanek and Richardson, 1996; Williamson and Fitter, 1996) in order to better predict which species will become major threats in the future (Rejmanek, 2000).

Two non-native plants, lantana (*Lantana camara* L.) and vinca [*Catharanthus roseus* (L.) G. Don], were selected for this study due to their ornamental popularity in southeastern U.S. landscapes. These plants also offer a contrast in regard to form (lantana is woody while vinca is herbaceous) and lifecycle (in most of the Southeast, lantana is perennial while vinca is annual).

Lantana is native to tropical regions of North and South America and Africa and has spread to other tropical and subtropical regions of the world (Kohli et al., 2006). This species is valued for its brightly colored flower clusters. In tropical and subtropical climates lantana is a continuous bloomer (Scheper, 1996), but in more temperate regions it blooms only in summer and fall. Lantana grows well in full sun or partial shade and is extremely drought resistant, making it a popular ornamental choice for landscapes in the southeast.

Vinca is native to the island of Madagascar (Wikipedia, 2007). It has been widely cultivated for several hundred years, was introduced into North America in the early 1700's, and can now be found in almost all warm regions of the world. Vinca grows well around old homestead plantings and other disturbed sites. In hot climates, vinca is perennial, while in more temperate climates it is used as an annual in flower beds. Vinca generally flowers all summer into early fall. These plants are popular ornamentals due to their deep green leaves and stems even when no flowers are present.

Despite their use as ornamentals, both species are listed as potential invasive weeds (Global Invasive Species Database, 2007; Royal Botanical Gardens, 2007). Lantana is on the world's top ten most invasive weeds list and is known to occur in over 60 countries and island groups between 35°N and 35°S including Australia, New Guinea, South Africa, and Hawaii (Global Invasive Species Database, 2007). Some lantana species are now considered naturalized into the southeastern United States, especially coastal regions of the Carolinas, Georgia, Florida and the Gulf Coast (Wikipedia, 2007). Vinca is listed as an invasive species for several Pacific Islands, including Hawaii (Royal Botanical Gardens, 2007). Neither species is currently considered a problem weed in the southeastern U.S.

It is well documented that elevated CO_2 increases growth of most plants through stimulating photosynthesis (Long and Drake, 1992), resource use efficiency (Rogers and Dahlman, 1993; Rogers et al., 1994; Amthor, 1995), and/or carbon allocation to belowground plant structure (Rogers et al., 1994). Although it is likely that these effects will result in a CO_2-induced increase in biomass and in the competitiveness of invasive plants, there remains a paucity of data to support this assumption. How non-native plants will respond to the rising level of atmospheric CO_2 is of great importance with respect to their potential as invasive species. Understanding how elevated CO_2 alters the establishment, spread, and control of invasive weeds will be crucial to future management strategies. 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."

The objective of this study was to determine the effects of elevated CO_2 on growth and flowering of lantana and vinca. Effects of elevated CO_2 will be considered in regard to the importance of these species to ornamental horticulture in the southeastern U.S. and in regard to their potential to become invasive weeds in this region.

MATERIALS AND METHODS

Forty-eight plants of each species (vinca cv. "Peppermint"; lantana cv. "Carnival") were purchased from a local nursery and transplanted into 10.65 L tree pots (TPOT4 Round Tree-Pot, 22 cm × 39 cm, Stuewe & Sons Inc., Corvalis, OR 97333) containing a peat based general purpose growing medium (PRO-MIX Bx, Premier Horticulture Inc., Quakertown, PA 18951). All plants of each species were ranked according to size and placed into four groups of twelve plants each; the largest 12 plants were placed into group one and this process was repeated in declining order until the smallest 12 plants were placed into group four. One plant of each species from each group was randomly assigned to open top chambers used in the study (four containers of each plant species in each chamber). Initial measurements (e.g., height, ground line diameter and number of flower heads or buds) were taken for each plant before being placed in the chambers to insure there was no bias in plant size prior to initiation of CO_2 treatments.

This study was conducted at the soil bin facilities at the USDA-ARS National Soil Dynamics Laboratory, Auburn, Alabama. The bin used for this experiment is 6 m wide and 76 m long and has been modified for container studies. Modifications consisted of installing a geomembrane liner (20 mil) and gravel drain system to ensure a good working surface and drainage system for container studies. Open top chambers (Rogers et al., 1983), encompassing 7.3 m^2 of ground surface area, were used to maintain (24 h per day) 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 (μmol mol^{-1}) over the measurement period (±SD) were as follows: ambient daytime = 390.5 (±18.0); elevated daytime = 562.6 (±33.4); ambient nighttime = 425.3 (±28.8); and elevated nighttime = 612.1 (±42.1). Daytime was taken as 7:00 am CDT to 7:00 pm CDT.

The bin was divided into six blocks and each CO_2 treatment was randomly assigned to one open top chamber within each block (total chambers = 12). The experimental design was a randomized complete block design, with blocks occurring along the length of the soil bin. Plants were placed in the chambers on 6 June, 2006 at which time CO_2 treatments were initiated. All plants were fertilized with Miracle-Gro (15:30:15, N: P_2O_5: K; Scotts Products Inc., Marysville, OH) on 30 June, 2006 and 21 August, 2006. Plants were fertilized when visual symptoms of nutrient deficiency indicated a need. Fertilization was accomplished according to fertilizer manufacturer's recommendation (600 g Miracle-Gro was mixed with 130 L deionized water; each plant received 500 ml of this solution). In addition, all plants were given an iron chelate treatment (1:0:0, N: P: K, plus 1.25% water soluble iron, Ironite Products Co., Scottsdale, AZ) on 29 June, 2006 and 30 August, 2006. As with Miracle-Gro, this was conducted according to manufacturer's recommendations (approximately 20 g of granular Ironite was added to each pot during the application). Vinca plants received one additional treatment of Ironite on 21 September, 2006. Plants received deionized water every other day sufficient to achieve leaching.

All plants in each chamber were destructively harvested on 28 September, 2006 after 115 days of CO_2 exposure. Aboveground portions of all plants in each container were harvested by severing the plant at the groundline. Aboveground variables (e.g., height, diameter, and numbers of flowers and leaves) were assessed using standard practices. Diameters were measured at groundline using high precision digital calipers. Plants were then separated into organ parts (i.e., leaves, flowers, stems) and leaf area was determined photometrically using an LI-3100 leaf area meter (Li-Cor, Inc., Lincoln, NE). 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 in a forced air oven at 55°C to a constant weight, and dry weights were recorded. Dry weights of each organ part will be considered a measure of photosynthate partitioning and allocation among organ parts will be calculated based on these weights. Carbon (C) and nitrogen (N) concentrations were determined for each plant part using a LECO CN 2000 (LECO Corporation, St. Joseph, MI). Data were totaled for each container and the four containers in each open top chamber were averaged prior to analysis so that the open top chamber was the experimental unit.

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 treatments. 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

Initial measurements indicated there was no unintended bias in plant size prior to initiation of treatments. In general, lantana tended to respond to elevated CO_2 to a greater extent than did vinca. For example, lantana plants had larger diameters, root lengths, increased specific leaf weight, and tended to be taller when grown under elevated CO_2, while only specific leaf weight was increased for vinca (Table 1). In fact, vinca plants tended to have smaller diameters in the elevated, versus ambient, CO_2 treatment. There was no effect of CO_2 on flower number for vinca while lantana actually had significantly fewer flowers under elevated CO_2 (Table 1).

Lantana also tended to be more responsive to elevated CO_2 than did vinca in regard to dry weight production (Fig. 1). For vinca, only leaf dry weight was significantly increased; however, aboveground, root, and total plant dry weights also tended to be higher under elevated CO_2 (Fig. 1) In contrast, lantana had significantly greater leaf, aboveground, root, and total plant dry weights and also tended to have greater stem dry weight. Further, the increase in total plant dry weight under elevated CO_2 was larger for lantana (19%) than for vinca (9%). While aboveground responses of the two species were similar (12% and 9% for lantana and vinca, respectively), the belowground response to elevated CO_2 was much larger in lantana (31%) than in vinca (9%). The dry weight response of lantana roots to elevated CO_2 was twice that (31%) of any other plant part (5–15%). It is interesting to note that neither species had a change in flower dry weight in response

Table 1 The response of lantana and vinca growth variables to ambient (375 μmol mol^{-1}) and elevated (ambient +200 μmol mol^{-1}) CO_2. Means with associated separation statistics and percent change (ambient to elevated) are shown.

Species	Parameter	Ambient CO_2	Elevated CO_2	% Change	*P*-values
Lantana					
	Height (cm)	56.83	62.45	9.9	0.072
	Diameter (mm)	9.51	10.21	7.4	0.024
	Number of Leaves	809.5	772.3	−4.6	0.611
	Number of Flowers	292.2	272.7	−6.7	0.032
	Leaf Area (cm^2)	1539.5	1578.8	2.6	0.585
	Specific Leaf Weight (g m^{-2})	117.3	131.3	11.9	0.003
	Root Length (m)	498.4	726.6	45.8	0.044
Vinca					
	Height (cm)	54.99	55.84	1.5	0.496
	Diameter (mm)	10.65	10.29	−3.4	0.140
	Number of Leaves	1603.9	1677.0	4.6	0.522
	Number of Flowers	253.7	253.7	0	0.999
	Leaf Area (cm^2)	3941.4	3760.4	−4.6	0.411
	Specific Leaf Weight (g m^{-2})	60.7	72.8	19.9	$<$0.001
	Root Length (m)	127.9	147.7	15.5	0.249

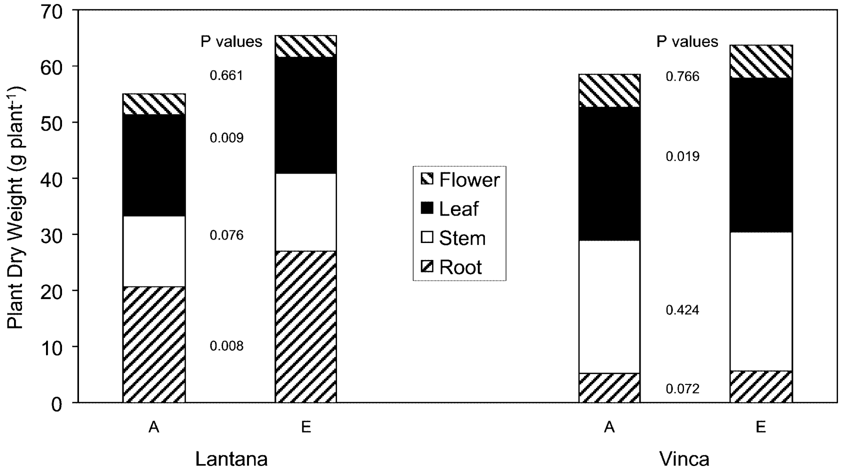

Fig. 1 Plant dry weight (g $plant^{-1}$) of component plant parts (flowers, leaves, stems, and roots) for lantana and vinca when grown under ambient (A=365 μmol mol^{-1}) or elevated (E=ambient plus 200 μmol mol^{-1}) concentrations of atmospheric CO_2. Significance levels (P values) for the difference between CO_2 treatments are given between each set of bars beside their associated plant part. Significance levels for aboveground (flowers+leaves+stems) dry weight were P=0.050 and P=0.066 for lantana and vinca, respectively. Significance levels for total plant dry weight were P=0.016 and P=0.056 for lantana and vinca, respectively.

to elevated CO_2 despite the decrease in flower number for lantana noted above.

Both species exhibited some altered biomass partitioning when exposed to elevated CO_2 (Table 2). Vinca plants allocated more biomass to leaves and tended to allocate less to stems when grown under elevated CO_2. Allocation to roots was unaffected by CO_2 treatment resulting in no change in root to shoot ratio (R:S). In contrast, lantana plants allocated significantly more biomass to roots and less to leaves and stems under elevated CO_2, resulting in a significant increase in R:S (Table 2). Further, lantana allocated a much greater percentage of their biomass to roots (41%) than did vinca (9%).

In contrast to data discussed above, vinca showed a strong response to elevated CO_2 with regard to N concentration (Table 3). All plant component parts had significantly lower N concentra-

Table 2 The response of lantana and vinca allocation among plant component parts (%) to ambient (375 μmol mol^{-1}) and elevated (ambient+200 μmol mol^{-1}) CO_2. Means with associated separation statistics and percent change (ambient to elevated) are shown.

Species	Plant Part	Ambient CO_2	Elevated CO_2	% Change	*P*-values
Lantana					
	Leaves	32.90	31.61	−3.9	0.108
	Flowers	6.70	6.03	−10.0	0.247
	Stems	23.00	21.22	−7.7	0.011
	Roots	37.40	41.14	10.0	0.002
	Root to Shoot Ratio	0.603	0.705	16.9	0.002
Vinca					
	Leaves	40.73	42.93	5.4	0.037
	Flowers	10.10	9.44	−6.5	0.229
	Stems	40.39	38.80	−3.9	0.122
	Roots	8.78	8.83	0.6	0.806
	Root to Shoot Ratio	0.096	0.097	1.0	0.771

tions when grown under elevated CO_2. Lantana also had lower N concentrations under elevated CO_2 for all component parts except stems and roots (Table 3). In comparison with N concentrations, C concentrations were relatively unaffected by CO_2 treatment (generally $<1\%$; data not shown). The lower N concentrations resulted in higher C to N ratios (C:N) for both species under elevated CO_2 (Table 4). C:N increased for all vinca component parts and for all lantana parts except stems and roots.

Lower N concentrations also resulted in lower N content (g plant^{-1}) for vinca grown under elevated CO_2 (Fig. 2). Leaf, flower, aboveground, and total plant N contents were all significantly lower. Lantana exposed to elevated CO_2 also had significantly lower leaf and aboveground N con-

Table 3 The response of plant component part nitrogen (N) concentration (mg g^{-1}) for lantana and vinca plants exposed to ambient (375 μmol mol^{-1}) and elevated (ambient + 200 μmol mol^{-1}) CO_2. Means with associated separation statistics and percent change (ambient to elevated) are shown.

Species	Plant Part	Ambient CO_2	Elevated CO_2	% Change	*P*-values
Lantana					
	Leaf	12.14	8.86	−27.0	0.001
	Flower	16.49	12.42	−24.7	0.006
	Stem	5.10	4.59	−10.0	0.342
	Aboveground	10.01	7.68	−23.3	0.013
	Root	5.82	5.42	−6.9	0.289
	Total Plant	8.44	6.75	−20.0	0.020
Vinca					
	Leaf	18.71	13.92	−25.6	0.001
	Flower	20.20	17.87	−11.5	0.033
	Stem	10.39	9.46	−9.0	0.036
	Aboveground	15.17	12.40	−18.3	0.001
	Root	10.72	9.64	−10.1	0.038
	Total Plant	14.77	12.16	−17.7	0

Table 4 The response of plant component part carbon to nitrogen ratios (C:N), nitrogen use efficiency (g plant biomass produced per g plant N), and nitrogen uptake efficiency (mg plant N per m plant root length) for lantana and vinca plants exposed to ambient (375 μmol mol^{-1}) and elevated (ambient + 200 μmol mol^{-1}) CO_2. Means with associated separation statistics and percent change (ambient to elevated) are shown.

Species	Plant Part	Ambient CO_2	Elevated CO_2	% Change	*P*-values
Lantana					
	Leaf C:N	37.53	49.55	32.0	0.004
	Flower C:N	26.07	33.92	30.1	0.003
	Stem C:N	92.81	98.21	5.8	0.572
	Aboveground C:N	45.23	57.28	26.6	0.007
	Root C:N	74.93	80.45	7.4	0.326
	Total Plant C:N	52.95	64.80	22.4	0.016
	N Use Efficiency	63.96	84.17	31.6	<0.001
	N Uptake Efficiency	1.82	1.15	−36.8	0.024
Vinca					
	Leaf C:N	23.58	30.89	31.0	<0.001
	Flower C:N	21.55	24.30	12.8	0.023
	Stem C:N	42.67	46.91	9.9	0.044
	Aboveground C:N	29.07	35.10	20.7	0.001
	Root C:N	39.10	43.90	12.3	0.019
	Total Plant C:N	29.71	35.70	20.2	0.001
	N Use Efficiency	68.06	82.47	21.2	0.001
	N Uptake Efficiency	6.94	5.46	−21.3	0.097

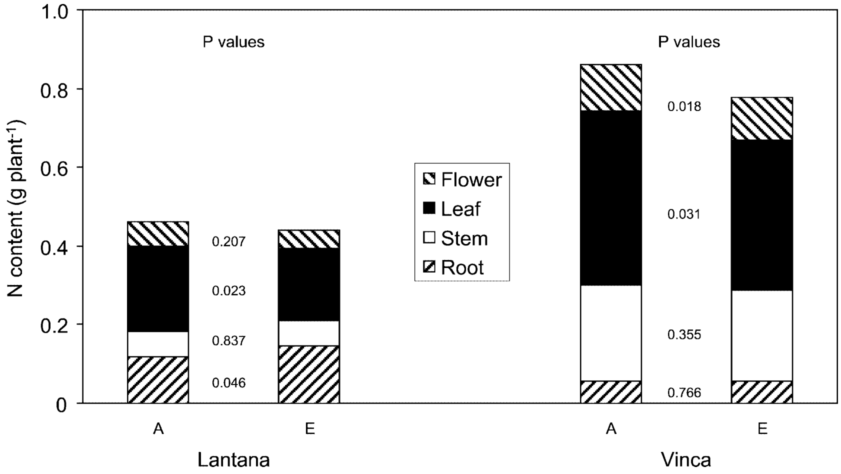

Fig. 2 Plant nitrogen (N) content (g plant^{-1}) of component plant parts (flowers, leaves, stems, and roots) for lantana and vinca when grown under ambient (A = 365 μmol mol^{-1}) or elevated (E = ambient plus 200 μmol mol^{-1}) concentrations of atmospheric CO_2. Significance levels (P values) for the difference between CO_2 treatments are given between each set of bars beside their associated plant part. Significance levels for aboveground (flowers + leaves + stems) N content were P = 0.047 and P = 0.040 for lantana and vinca, respectively. Significance levels for total plant N content were P = 0.487 and P = 0.042 for lantana and vinca, respectively.

tents, however, N content of roots increased for these same plants (Fig. 2). The large increase in lantana root biomass observed for plants in the elevated versus ambient CO_2 treatment (31%) resulted in the increased N content for this plant component part. The more marginal increases in biomass for other lantana (5–19%) and for all vinca (2–15%) plant component parts were, apparently, insufficient to increase total N content of these organs. Given that C concentrations were unaffected by CO_2 treatments, C content of plant organs followed, exactly, the patterns of plant biomass response (data not shown).

Nitrogen use efficiency (g of plant biomass produced per g of plant N) was significantly higher for both lantana and vinca (Table 4). However, nitrogen uptake efficiency (mg of plant N per m of plant root length) was significantly lower for lantana and tended to be lower for vinca (Table 4).

DISCUSSION

One primary purpose of this study was to determine if the ornamental value of the selected plants would change under exposure to atmospheric CO_2 conditions expected to arise during this century. One obvious reason for planting ornamentals is the aesthetics derived from flowers. Atmospheric CO_2 did not influence the number or dry weight of vinca flowers in this study. Similarly, lantana flower dry weight was not altered by elevated CO_2 and flower numbers actually decreased. While this decrease was statistically significant, a reduction of only 20 flowers (from a total per plant of almost 300) is unlikely to have any profound effect on the overall aesthetics of this plant. This suggests that the ornamental value of these two species will not change in a future, higher CO_2 world.

Another attribute of a successful ornamental landscape plant would be its ability to survive and grow under the natural conditions into which it is planted. In fact, ornamental plants can be valued for their size and foliar color, even in the absence of flowers. In our study, as with flowers, growth of vinca was unaffected by CO_2 treatment. Lantana plants exposed to elevated levels of

CO_2 grew larger (height and diameter) than their ambient-CO_2 grown counterparts. Again, as for flowers, while the changes in lantana height (9.9%) and diameter (7.4%) were statistically significant, the overall change in plant size is unlikely to have any major effect on visual impact of these plants as ornamentals as atmospheric CO_2 continues to increase.

Dry weights of both species increased (or tended to increase) under elevated CO_2. Interestingly, this occurred despite non-existent or small changes in measured plant size variables. While this possibly resulted from changes in anatomical characteristics, such as epicuticular waxes (Graham and Nobel, 1996; Prior et al., 1997a) or added layers of leaf palisade cells (Thomas and Harvey, 1983), it was more likely due to increased carbohydrate content. This is supported by the increase in specific leaf weight observed for both species under elevated CO_2. Plants grown under elevated atmospheric CO_2 often exhibit increased levels of non-structural carbohydrates (Yelle et al., 1989; Runion et al., 1999). While higher carbohydrate levels are generally viewed as a positive outcome (implying availability of additional material for subsequent growth and other plant functions), in the absence of a sufficiently strong sink (i.e., a large - particularly woody or tuberous - root system) plants can actually be damaged by excess carbohydrate production resulting from elevated CO_2 (Pritchard et al., 1997). While this possibility was not examined in the present study, it is much more likely to have occurred in vinca (with its fibrous roots) than in lantana, which has a perennial, woody root system.

Plants often exhibit increased root growth following exposure to above-ambient levels of CO_2 (Rogers et al., 1994) as was observed for lantana. The increased partitioning of biomass to roots, as seen for lantana, is also a common response to elevated CO_2 (Rogers et al., 1996). These changes in lantana roots imply an increased ability to gather needed soil resources (Rogers et al., 1992), which suggests not only increased future growth, but also an increase in drought tolerance. Drought resistance is a very desirable characteristic for ornamental plants, particularly in the southeastern U.S. due to the hot climate and frequent droughts typical of summer weather conditions. Both vinca and lantana are currently considered to be relatively drought tolerant species; lantana might become even more so in a future elevated-CO_2 world.

As with increased root growth, a dilution in tissue N (in part due to increased growth) is another commonly observed change for plants grown under elevated CO_2 (Johnson and Lincoln, 1990). This reduction in N leads to increased tissue C:N (Mellilo, 1983; Prior et al., 1997b) as was observed in this study. Since N is a limiting nutrient for insects (Mattson, 1980), CO_2-mediated decreases in N (or increased C:N) could negatively affect herbivore performance (Roth and Lindroth, 1994; Lawler et al., 1997), particularly for early larval instars (Saxon et al., 2004). In addition, excess C from elevated CO_2 exposure may increase production of defensive chemicals which may impact interactions with insects and pathogens (Fajer et al., 1992). To date, effects of elevated CO_2 on plant pests have been variable, with increases (Kobayashi et al., 2006) and decreases (Runion et al., 2010) observed.

This study suggests that rising atmospheric CO_2 will have little impact on the value of vinca as an ornamental species. Lantana, on the other hand, might become a more commonly used landscape plant as CO_2 continues to rise, given its increased growth and its potential to become even more drought resistant due to its larger root system.

The factors which may make lantana a more desirable landscape ornamental under future, higher CO_2 conditions (increased growth, large root response, and altered tissue chemistry) might also increase its ability to become invasive. Lantana seeds are widely dispersed by birds and insects and they germinate rapidly, forming dense thickets that inhibit the growth and sustainability of native plant species (Sharma et al., 2005). The slight decrease in flower production under elevated CO_2 observed in this study might imply a reduction in spread via seed. However, in a summary of 55 wild (non-crop) plant species, Jablonski et al. (2002) noted that carbon allocation to reproductive organs decreased by 14% under elevated CO_2, suggesting that the excess carbon was directed into “structural, defensive, or other non-reproductive tissues”. This may suggest that, for an invasive species, establishment of the plant itself may take precedence over the need for reproduction. Establishing a strong root system (as lantana did in this study) could allow the plant to become more competitive for available soil resources and, therefore, increase success of new invasions. In addition, once established, the roots of lantana produce allelopathic substances which can lead to a competitive advantage over native plants (Jain et al., 1989).

What do these findings mean for invasive plants as atmospheric CO_2 continues to rise? The degree to which plants will become invasive will be species specific. The type of root structure would, in part, determine the extent to which a plant species could invade. In vinca, we observed no significant change in the size of the fibrous root system, while the woody lantana root was significantly increased under elevated CO_2. Findings suggest that vinca will probably not become a problem invasive weed as atmospheric CO_2 increases, while lantana may.

CONCLUSIONS

Currently, neither vinca nor lantana are considered serious invasive weed pests in the southeastern U.S. While vinca is a problem in limited areas (e.g., Pacific Islands), lantana is considered a major invasive weed in large regions of the world (e.g., India, Africa, and Australia). This study suggests that rising atmospheric CO_2 will have little impact on vinca’s ornamental value or its potential to become invasive in the southeastern U.S. Although lantana might become a more desirable ornamental species under higher levels of atmospheric CO_2, its responses (e.g., increased growth, larger root system possibly increasing drought tolerance) may also confer an ability to become a problematic invasive weed in the southeastern U.S. This potential deserves additional research and monitoring in this region.

This work 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 B.G. Dorman and J.W. Carrington for technical assistance.

REFERENCES

Amthor, J. S. 1995. Terrestrial higher-plant response to increasing atmospheric [CO_2] in relation to the global carbon cycle. Global Change Biol. **1**: 243–274.

Binggeli, P. 1996. A taxonomic, biogeographical and ecological overview of invasive woody plants. J. Vegeta. Sci. **7**: 121–124.

Bohm, W. 1979. Methods of Studying Root Systems. Spring-Verlag, New York, NY.

Bright, C. 1998. Life Out of Bounds: Bioinvasion in a Borderless World. W. W. Norton & Company, New York.

Fajer, E. D., Bowers, M. D., Bazzaz, F. A. 1992. The effect of nutrients and enriched CO_2 environments on production of carbon-based allelochemicals in *Plantago*: A test of the carbon/nutrient balance hypothesis. Am. Nat. **140**: 707–723.

Global Invasive Species Database. 2007. Ecology of *Lantana Camara* (shrub) [Online]. Available at http://www.issg.org/database/species/ecology.asp (verified 5 Sept.2007).

Graham, E. A., Nobel, P. S. 1996. Long-term effects of a doubled atmospheric CO_2 concentration on the CAM species *Agave deserti*. J. Exp. Bot. **47**: 61–69.

Holm, L., Doll, J., Holm, E., Pancho, J., Herberger, J. 1997. World Weeds: Natural Histories and Distribution. John Wiley, New York, p. 1129.

Jablonski, L. M., Wang, X., Curtis, P. S. 2002. Plant reproduction under elevated CO_2 conditions: a meta-

analysis of reports on 79 crop and wild species. New Phytol. **156**: 9–26.
Jain, R., Singh, M., Dezman, D. J. 1989. Qualitative and quantitative characterization of phenolic compounds from *Lantana* (*Lantana camara*) leaves. Weed Sci. **37**: 302–307.
Johnson, R. H., Lincoln, D. E. 1990. Sagebrush and grasshopper responses to atmospheric carbon dioxide concentration. Oecologia **84**: 103–110.
Keeling, C. D., Whorf, T. P. 1994. Atmospheric CO_2 records from the sites in the SIO air sampling network. In *Trends '93: A Compendium of Data on Global Change, ORNL/CDIAC-65*, eds. Boden, T. A., Kaiser, D. P., Sepanski, R. J., Stoss, F. W. Oak Ridge, TN: The Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, pp. 16–26.
Kobayashi, T., Ishiguro, K., Nakajima, T., Kim, H. Y., Okada, M., Kobayashi, K. 2006. Effects of elevated atmospheric CO_2 concentration on the infection of rice blast and sheath blight. Phytopathology **96**: 425–431.
Kohli, K., Batish, D. R., Singh, H. P., Dogra, K. S. 2006. Status, invasiveness and environmental threats of three tropical American invasive weeds (*Parthenium hysterophorus* L., *Ageratum conyzoides* L., *Lantana camara* L.) in India. Biol. Invas. **8**: 1501–1510.
Lawler, L. R., Foley, W. J., Woodrow, I. E., Cork, S. J. 1997. The effects of elevated CO_2 atmospheres on the nutritional quality of *Eucalyptus* foliage and its interaction with soil nutrient and light availability. Oecologia **109**: 59–68.
Littell, R. C., Milliken, G. A., Stroup, W. W., Wolfinger, R. D. 1996. SAS System for Mixed Models. SAS Institute, Inc., Cary, NC.
Long, S. P., Drake, B. G. 1992. Photosynthetic CO_2 assimilation and rising atmospheric CO_2 concentrations. In "Crop Photosynthesis: Spatial and Temporal Determinants" (ed. by N. R. Baker and H. Thomas), Elsevier, New York, p. 69–107.
Mattson, W. J. Jr. 1980. Herbivory in relation to plant nitrogen content. Annu. Rev. Ecol. Syst. **11**: 119–161.
Mellilo, J. M. 1983. Will increases in atmospheric CO_2 concentrations affect decay processes? In "Ecosystems Center Annual Report", Marine Biology Laboratory, Woods Hole, MA, pp. 10–11.
Miller, J. H. 2003. Nonnative invasive plants of southern forests: a field guide for identification and control [Online]. Available at http://www.invasive.org/eastern/srs/EV.html (verified 5 Sept. 2007).
Mitchell, R. J., Runion, G. B., Prior, S. A., Rogers, H. H., Amthor, J. S., Henning, F. P. 1995. Effects of nitrogen on *Pinus palustris* foliar respiratory responses to elevated atmospheric CO_2 concentration. J. Exp. Bot. **46**: 1561–1567.
Ottensen, C. O., Mentz, J. 2000. Biomass accumulation and photosynthesis of ornamentals in elevated CO_2 conditions. Gartenbauwissenschaft **65**: 35–39.
Pimentel, D. 2002. Introduction: non-native species in the world. In "Biological Invasions: Economic and Environmental Costs of Alien Plant, Animal, and Microbe Species" (ed. by Pimentel, D.), CRC Press, Boca Raton, FL, pp. 3–8.
Prior, S. A., Pritchard, S. G., Runion, G. B., Rogers, H. H., Mitchell, R. J. 1997a. Influence of atmospheric CO_2 enrichment, soil N, and water stress on needle surface wax formation in *Pinus palustris* (Pinaceae). Am. J. Bot. **84**: 1070–1077.
Prior, S. A., Runion, G. B., Mitchell, R. J., Rogers, H. H., Amthor, J. S. 1997b. Effects of atmospheric CO_2 on longleaf pine: productivity and allocation as influenced by nitrogen and water. Tree Physiol. **17**: 397–405.
Pritchard, S. G., Peterson, C. M., Runion, G. B., Prior, S. A., Rogers, H. H. 1997. Atmospheric CO_2 concentration, N availability, and water status affect patterns of ergastic substance deposition in longleaf pine (*Pinus palustris* Mill.) foliage. Trees **11**: 494–503.
Randall, J. M. 2000. Improving management of nonnative invasive plants in wilderness and other natural areas. In "Proceedings - Rocky Mountain Research Station" (ed. by Cole, D.N., McCool, S. F., Borrie, W. T. O., Loughlin, J.), USDA Forest Service, Publication No. RMRS-P-15 (Vol. 5), p. 64–73.
Rejmanek, M. 2000. Invasive plants: approaches and predictions. Austral Ecol. **25**: 497–506.
Rejmanek, M., Richardson, D. M. 1996. What attributes make some plant species more invasive? Ecology **77**: 1655–1661.
Rogers, H. H., Dahlman, R. C. 1993. Crop responses to CO_2 enrichment. Vegetatio **104/105**: 117–131.
Rogers, H. H., Heck, W. W., Heagle, A. S. 1983. A field technique for the study of plant responses to elevated carbon dioxide concentrations. Air Poll. Control Assn. J. **33**: 42–44.
Rogers, H. H., Peterson, C. M., McCrimmon, J. N., Cure, J. D. 1992. Response of plant roots to elevated

atmospheric carbon dioxide. Plant Cell Environ. **15**: 749–752.

Rogers, H. H., Prior, S. A., Runion, G. B., Mitchell, R. J. 1996. Root to shoot ratio of crops as influenced by CO_2. Plant Soil **187**: 229–248.

Rogers, H. H., Runion, G. B., Krupa, S. V. 1994. Plant responses to atmospheric CO_2 enrichment with emphasis on roots and the rhizosphere. Environ. Pollut. **83**: 155–189.

Roth, S. K., Lindroth, R. L. 1994. Effects of CO_2-mediated changes in paper birch and white pine chemistry on gypsy moth performance. Oecologia **98**: 133–138.

Royal Botanical Gardens. 2007. A Year at Kew: Invasive plants [Online]. Available at http://www.kew.org/plants/islandplants/invasives.html (verified 5 Sept. 2007).

Runion, G. B., Entry, J. A., Prior, S. A., Mitchell, R. J., Rogers, H. H. 1999. Tissue chemistry and carbon allocation in seedlings of *Pinus palustris* subjected to elevated atmospheric CO_2 and water stress. Tree Physiol. **19**: 329–335.

Runion, G. B., Prior, S. A., Rogers, H. H., Mitchell, R. J. 2010. Effects of elevated atmospheric CO_2 on two southern forest diseases. New For. **39**: 275–285.

Saxon, M. E., Davis, M. A., Pritchard, S. G., Runion, G. B., Prior, S. A., Stelzer, H. E., Rogers, H. H., Dute, R. R. 2004. Influence of elevated CO_2, nitrogen, and *Pinus elliottii* genotypes on performance of the redheaded pine sawfly, *Neodiprion lecontei*. Can. J. For. Res. **34**: 1007–1017.

Sharma, G. P., Raghubanshi, A. S., Singh, J. S. 2005. *Lantana* invasion: An overview. Weed Biol. Manage. **5**: 157–165.

Scheper, J. 1996. Floridata [Online]. Available at http://www.floridata.com/ref (verified on 5 Sept. 2007).

Thomas, J. F., Harvey, C. N. 1983. Leaf anatomy of four species grown under continuous CO_2 enrichment. Bot. Gaz. **144**: 303–309.

Wikipedia, the free encyclopedia. 2007. Catharanthus roseus [Online]. Available at http://en.wikipedia.org/wiki/Vinca_rosea (verified 5 Sept. 2007).

Williamson, M. H., Fitter, A. 1996. The characters of successful invaders. Biol. Conserv. **78**: 163–170.

Yelle, S., Beeson, R. C. Jr., Trudel, M. J., Gosselin, A. 1989. Acclimation of two tomato species to high atmospheric CO_2. I. Starch and sugar concentrations. Plant Physiol. **90**: 1465–1472.