A Review of Elevated Atmospheric CO_2 Effects on Plant Growth and Water Relations: Implications for Horticulture

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***Abstract*. Empirical records provide incontestable evidence for the global rise in carbon dioxide (CO_2) concentration in the earth's atmosphere. Plant growth can be stimulated by elevation of CO_2; photosynthesis increases and economic yield is often enhanced. The application of more CO_2 can increase plant water use efficiency and result in less water use. After reviewing the available CO_2 literature, we offer a series of priority targets for future research, including: 1) a need to breed or screen varieties and species of horticultural plants for increased drought tolerance; 2) determining the amount of carbon sequestered in soil from horticulture production practices for improved soil water-holding capacity and to aid in mitigating projected global climate change; 3) determining the contribution of the horticulture industry to these projected changes through flux of CO_2 and other trace gases (i.e., nitrous oxide from fertilizer application and methane under anaerobic conditions) to the atmosphere; and 4) determining how CO_2-induced changes in plant growth and water relations will impact the complex interactions with pests (weeds, insects, and diseases). Such data are required to develop best management strategies for the horticulture industry to adapt to future environmental conditions.**

The level of CO_2 in the atmosphere is rising at an unprecedented rate, has increased from ≈280 ppm at the beginning of the industrial revolution (≈1750) to ≈380 ppm today, and is expected to double preindustrial levels sometime during this century (Keeling and Whorf, 2001; Neftel et al., 1985). This global rise can be primarily attributed to fossil fuel burning and land use change associated with industrial and/or population expansion (Houghton et al., 1990). This rise, along with other trace gases, is widely thought to be a primary factor driving global climate change (IPCC, 2007). Aside from the debate on anthropogenic-driven climate change, vegetation will be directly impacted and research has shown that plants respond positively to elevated CO_2 (Amthor, 1995). Most of this research has focused on agricultural and forest species with limited work on specialty crops associated with horticulture. Horticulture is a diverse industry (encompassing many small businesses) that impacts the landscape of both rural and urban environments and has an economic impact of $148 billion annually in the United States (Hall et al., 2005). We will attempt to discuss the effects of the rise in atmospheric CO_2 concentration on plant growth and water relations with a focus toward implications for horticultural production systems with suggestions for future research areas.

PLANT GROWTH

Carbon dioxide links the atmosphere to the biosphere and is an essential substrate for photosynthesis. Elevated CO_2 stimulates photosynthesis leading to increased carbon (C) uptake and assimilation, thereby increasing plant growth. However, as a result of differences in CO_2 use during photosynthesis, plants with a C_3 photosynthetic pathway often exhibit greater growth response relative to those with a C_4 pathway (Amthor, 1995; Amthor and Loomis, 1996; Bowes, 1993; Poorter, 1993; Rogers et al., 1997). The CO_2-concentrating mechanism used by C_4 species limits the response to CO_2 enrichment (Amthor and Loomis, 1996). For C_3 plants, positive responses are mainly attributed to competitive inhibition of photorespiration by CO_2 and the internal CO_2 concentrations of C_3 leaves (at current CO_2 levels) being less than the Michaelis-Menton constant of ribulose bisphosphate carboxylase/oxygenase (Amthor and Loomis, 1996). Although increased photosynthesis under elevated CO_2 enhances growth for most plants, summaries have consistently shown that this increase varies for plants with a C_3 (33% to 40% increase) versus a C_4 (10% to 15% increase) photosynthetic pathway (Kimball, 1983; Prior et al., 2003).

Given that most horticulture species have a C_3 pathway, it is expected that they will show similar responses to elevated CO_2. Early work (Cummings and Jones, 1918) demonstrated that both vegetable and flower crops benefited from above ambient concentrations of CO_2; both cyclamens and nasturtiums showed increased dry weight and greater flower yield when exposed to elevated CO_2. Since this early work, others have shown that ornamental species respond positively to elevated levels of CO_2 (Davis and Potter, 1983; Gislerød and Nelson, 1989; Mattson and Widmer, 1971; Mortensen, 1987, 1991; Mortensen and Gislerød, 1989; Mortensen and Moe, 1992; Mortensen and Ulsaker, 1985). In fact, increasing the concentration of CO_2 in glasshouses is an economically efficient

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method of enhancing growth of ornamental and vegetable crops (Mastalerz, 1977; Mortensen, 1987).

In addition to stimulating photosynthesis and aboveground growth, elevated CO_2 can alter C partitioning/allocation. Increased C supply from elevated atmospheric CO_2 can preferentially induce the distribution of photosynthate belowground (Ceulemans and Mousseau, 1994; Lekkerkerk et al., 1990; Prior et al., 1997; Rogers et al., 1994). In many cases, the largest proportion of the extra biomass produced under elevated CO_2 is found belowground (Rogers et al., 1994; Wittwer, 1995), often resulting in increased root-to-shoot ratio (Rogers et al., 1996). This is not surprising in that plants tend to allocate photosynthate to tissues needed to acquire the most limiting resource (Chapin et al., 1987); when CO_2 is elevated, the most limiting resource becomes water or nutrients.

Although less studied than aboveground response, plants often show increased rooting under CO_2 enrichment (Chaudhuri et al., 1986, 1990; Del Castillo et al., 1989; Rogers et al., 1992). In addition to this early work with plants in containers, increased rooting has also been observed in the field using both open-top field chambers (OTC) and free-air CO_2 enrichment systems (FACE). Elevated CO_2 increased dry weight of root systems for both soybean (44%) and sorghum (38%) growing in OTC (Prior et al., 2003). Prior et al. (1994) also found increases in cotton fine roots (dry weight and length) under FACE and that these plants had proportionately more of their roots allocated away from the row center. Furthermore, Prior et al. (1995) reported that these FACE cotton plants had larger taproots and increases in the number and size of lateral roots. The development of more robust root systems in CO_2-enriched environments may allow for greater carbohydrate storage and infers greater exploration of the soil for resources such as water and nutrients to meet plant growth needs during periods of peak demand such as boll development and filling.

In addition to increases in rooting, colonization of roots with mycorrhizae (the symbiotic association of plant roots with fungi) has been shown to increase under elevated CO_2 (Norby et al., 1987; O'Neill et al., 1987; Runion et al., 1997). Mycorrhizae increase nutrient uptake by their host plants (Abbott and Robson, 1984), provide additional water to plants through hyphal proliferation in soil (Luxmoore, 1981), and protect roots from pathogenic microorganisms (Marx, 1973).

Because horticultural plants are generally grown in containers without resource limitations (i.e., water and nutrients), increased root growth or mycorrhizal colonization may not become critical for survival and growth until after outplanting into the landscape. However, as a result of limited rooting space, growth in containers has been shown to dampen the response to CO_2 enrichment (Arp, 1991). For plants to use a higher level of atmospheric CO_2, they must have a means of storing the additional carbohydrates produced. We have shown that plants with a tuberous or woody root system tend to respond to CO_2 enrichment to a greater degree than plants with smaller or more fibrous root systems (Rogers et al., 1994; Runion et al., 2010). The limited rooting volume experienced by plants growing in containers may help explain the fact that increased growth of horticultural species under elevated CO_2 is sometimes slightly lower than that generally observed for other C_3 plants, falling in the range of 15% to 25% (Mortensen, 1991, 1994). Nonetheless, the increased biomass production under high CO_2 should be advantageous for horticultural plants in that they should attain a marketable size more rapidly.

PLANT WATER RELATIONS

In addition to the effects of CO_2 on photosynthesis and C allocation mentioned, elevated CO_2 can impact growth through improved plant water relations (Rogers and Dahlman, 1993). In fact, most plants (both C_3 and C_4 species) exhibit improved plant water relations. Elevated CO_2 slows transpiration by inducing the partial closure of leaf stomatal guard cells (Jones and Mansfield, 1970). Studies in growth chambers and glasshouses have shown that elevated CO_2 reduces transpiration for both C_3 (Allen et al., 1994; Jones et al., 1984, 1985; Pallas, 1965; Prior et al., 1991; Valle et al., 1985) and C_4 (Chaudhuri et al., 1986; Pallas, 1965; Van Bavel, 1974) plants. Dugas et al. (1997), using stem flow gauges under actual field conditions, also showed that whole-plant transpiration was reduced under elevated CO_2 for both a soybean (C_3) and a sorghum (C_4) crop.

This reduction in transpiration, coupled with increased photosynthesis, can contribute to increased water use efficiency (WUE = the ratio of carbon fixed to water transpired), which has often been reported (Baker et al., 1990; Morison, 1985; Sionit et al., 1984). In fact, Kimball and Idso (1983) cited 46 observations that cumulatively showed that transpiration would be lowered by an average of 34%, which, coupled with an economic yield enhancement of 33% (over 500 observations), suggested a doubling of WUE for a doubling of CO_2 level. From a physiological standpoint, increased WUE may represent one of the most significant plant responses to elevated CO_2 (Rogers et al., 1994).

Plants with a C_4 photosynthetic pathway show a smaller response to elevated CO_2 than plants with a C_3 pathway. However, both C_3 and C_4 plants show reduced transpiration under elevated CO_2. Therefore, WUE should be primarily controlled by transpiration in C_4 plants, whereas both are important in C_3 plants. This was demonstrated by Acock and Allen (1985) using data from Valle et al. (1985) and Wong (1980). In a more recent long-term field study, similar calculations showed contributions of 74% and 26% (for photosynthesis and transpiration, respectively) in soybean compared with respective contributions of 42% and 58% in sorghum (Prior et al., 2010a). Although photosynthesis still dominated WUE increase in C_3 soybean, relative contributions of the two processes were more similar for C_4 sorghum than that reported by Acock and Allen (1985).

Given the fact that elevated CO_2 can reduce transpiration, it has been suggested that this might partially ameliorate the effects of drought (Bazzaz, 1990) and allow plants to maintain increased photosynthesis. This has frequently been observed (Acock and Allen, 1985; Gifford, 1979; Goudriaan and Bijlsma, 1987; Nijs et al., 1989; Rogers et al., 1984; Sionit et al., 1981; Wong, 1980); however, it should be noted that much of this work was conducted in growth chambers and glasshouses using plants growing in containers. Working with container-grown soybean in field OTC, Prior et al. (1991) reported that, at elevated levels of CO_2, xylem pressure potential of water-stressed plants was equivalent to that of adequately watered plants, indicating amelioration of drought stress.

It has been suggested that in more natural environments, although instantaneous WUE is increased, whole-plant water use may be differentially affected as a result of increased plant size. Allen (1994) reported that larger plant size [higher leaf area index (LAI)] counterbalanced the reduction in water use, offsetting enhanced WUE. Jones et al. (1985) showed that, although elevated CO_2 increased WUE for plants with both a high and a low LAI, this increase was greater for plants with a lower LAI. Working with longleaf pine growing in large (45 L) containers, we found that nitrogen (N) availability was also an important factor affecting the interaction of WUE and plant water stress (Runion et al., 1999). Longleaf pine seedlings grown with adequate N grew larger under elevated CO_2, resulting in increased whole-plant water use and increased water stress despite increased WUE. Seedlings grown with limited N did not exhibit a growth response to elevated CO_2, so the increased WUE resulted in decreased whole-plant water use and reduced stress.

In addition to improved plant water relations, elevated CO_2 can also affect water movement through the landscape. Water infiltration can be increased and sediment loss through runoff can be decreased in high CO_2 environments (Prior et al., 2010b). These improvements can result from increased plant rooting (as noted previously) and from changes in soil physical properties. Elevated CO_2 can increase soil C, aggregate stability, and hydraulic conductivity and decrease soil bulk density (Prior et al., 2004). These improvements in soil/water relations will be particularly important for horticultural plants in the landscape.

Water is also a crucial resource in many horticultural production facilities and its conservation is becoming an increasingly important issue. The fact that elevated CO_2 can increase plant WUE (Rogers et al., 1994) may indicate that plants could be watered less frequently as CO_2 levels continue to rise. However, because these plants are generally grown with optimal nutrients, elevated CO_2 may increase plant size to a point where watering frequency will need to be maintained at current levels or even increased. This interaction of elevated CO_2 and resource availability will also be of critical importance for horticultural species after outplanting to the landscape where periodic droughts could be relatively frequent. The landscape's response may not be adequately reflected by studies of small numbers of plants grown in containers; obviously, more work is needed within this important industry to maximize plant growth, health, and efficient use of resources.

PRIORITY TARGETS FOR FUTURE RESEARCH

Although much is known regarding the effects of elevated CO_2 on plants, horticultural species have received much less attention than agronomic and forest species. Although it is likely that most horticultural species will benefit (through increased growth) from rising CO_2, research to support this contention is lacking. Horticulture comprises diverse species in terms of growth forms (e.g., annuals, perennials, trees, shrubs, forbs, grasses, vegetables, floriculture crops, C_3, C_4) and the conditions in which they are grown (e.g., container versus in-ground, indoor versus outdoor). Knowledge of how these diverse plant types will respond to elevated CO_2 under current growing conditions would be valuable in terms of adapting management strategies to future environmental conditions. For example, although container-grown plants are known to respond positively to elevated CO_2 in terms of increased growth, it is also known that root restriction can dampen this CO_2 response; therefore, it is important to determine optimal container sizes for producing marketable plants on timely schedules.

As noted previously, positive growth responses to elevated CO_2 result not only from increased uptake and assimilation of CO_2, but also from decreased transpiration, which improves plant water relations and WUE. Water conservation is a critical issue for crop production, particularly in certain regions of the United States. Within the horticulture industry, adjustments to watering frequency may become a crucial management decision. Knowledge of the effects of rising CO_2 on whole-plant water use will aid managers in optimizing irrigation schedules and amounts.

In addition to understanding the effects of rising CO_2 on water use of currently grown horticultural species, it is important for the industry to breed or screen for varieties and species with higher degrees of drought tolerance. It will also be important that these efforts be conducted at current and future levels of atmospheric CO_2 to select plants that show large responses to elevated levels of CO_2. One predicted outcome of global climate change is alterations in precipitation patterns with more extreme weather events, including droughts (IPCC, 2007). It is crucial to the industry that plants survive after outplanting in residential and commercial landscape environments.

One means of improving survivability is through use of mulch to conserve soil water. In an agronomic setting, cover crops used in no-tillage management systems can act as mulch (Balkcom et al., 2007). We have shown that these cover crops increase soil C (Prior et al., 2005) and aid in the improvement of soil physical properties (Prior et al., 2004), which also improves soil water relations (Prior et al., 2010b). Mulch (commonly pine bark, pine straw, or wood chips in the southeastern United States) contains high concentrations of plant organic C and, when used in landscape settings, can contribute to soil C sequestration. However, the extent of this contribution is not currently known, locally, regionally, or nationally. Furthermore, depending on the fate of these materials (e.g., left on site, burned on site, or used as a fuel source at forest products mills), the potential net increase in soil C from using these materials in landscape settings is also largely unknown.

In addition to mulch, the horticulture industry adds to soil C content through burial of container media at the time of outplanting. In container-grown plant production of nursery crops, plants are grown in a predominantly pine bark-based substrate. Pine bark is composed almost entirely of organic C, having a C content greater than 60% (Simmons and Derr, 2007). When these plants are outplanted to the landscape, this represents a very large amount of C possibly being sequestered in soil. Carbon can also be sequestered in plant biomass through positive growth responses to rising CO_2. However, to date, little is known concerning the C sequestration potential of the horticulture industry as a whole; this is critical to assess its potential contribution to mitigating potential climate change.

The C sequestration potential of the horticulture industry will be affected by the C:N ratio of inputs from biomass, mulch, and container media. The C:N ratio of these inputs can be high, suggesting slow decomposition and, therefore, slow release of CO_2 back to the atmosphere, aiding mitigation of global climate change. At present, the amount of C added to soil through outplanting container-grown horticultural plants is largely unknown. There is also little knowledge of the residence time of these materials in soil and of the rate of soil CO_2 flux back to the atmosphere. This knowledge will be crucial to determining the C sequestration potential of the horticulture industry and its contribution to potential global climate change through flux of CO_2 from soil to air.

There is also little information on the flux of other trace gases (nitrous oxide and methane) in these systems. Horticulture production facilities often use large amounts of water in irrigation as well as large amounts of fertilizers; this combination of resources could result in substantial fluxes of other gases. Like with CO_2 flux, this information is critical to determining the industry's potential contribution to climate change. It is also necessary to develop best management strategies that minimize trace gas flux, maximize resource use efficiency, and optimize growth and economic gain.

Another largely unknown but important consideration of rising CO_2 will be management of pests (weeds, insects, and diseases) in these systems. Weeds often show greater growth responses to elevated CO_2 than do crop plants, which may be the result of weeds having greater genetic diversity and physiological plasticity than managed plants (Ziska and Runion, 2007). How rising CO_2 will impact weed management strategies in horticultural systems is unknown. The interactions of plants with both insects and diseases are complex and vary according to the host–pest system of interest; however, these interactions have received very little attention (Ziska and Runion, 2007). More knowledge in this area is required to develop best management strategies to deal with these potentially serious threats to productivity and profitability not only in horticulture, but for agriculture and forestry as well.

CONCLUSIONS

In general, elevated CO_2 increases plant growth (both above- and belowground) and improves plant water relations (reduces transpiration and increases WUE). It is likely these benefits will also occur for horticultural plants, but data to support this are lacking relative to crop and forest species. In addition to basic research on the response of diverse horticultural species to future levels of atmospheric CO_2, it may become crucial to breed or screen varieties and species of horticultural plants for increased drought tolerance as a result of predicted changes in precipitation patterns. It is also important to determine the amount of C sequestered in soil from horticulture production practices not only for improvement of soil water-holding capacity, but also to aid in mitigation of projected global climate change. Furthermore, determining the contribution of the horticulture industry to these projected changes through flux of CO_2 and other trace gases (through irrigation and fertilization) is of critical importance. How CO_2-induced changes in plant growth and water relations will impact the complex interactions with pests (weeds, insects, and diseases) is a deficient area of research not only for horticulture, but for plants in general. All this information is needed to develop best management strategies for the horticulture industry to successfully adapt to future environmental change.

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