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Impact of increased CO₂ level on Horticultural crops

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Abstract

Elevated atmospheric CO₂ enhances not only the yield of horticultural crop but could also affect their nutritional quality. Plant growth can be stimulated by elevation of CO₂; photosynthesis increases and economic yield is often enhanced. The application of more CO₂ can increase plant water use efficiency and result in less water use. After reviewing the available CO₂ 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 CO₂ and other trace gases (i.e., nitrous oxide from fertilizer application and methane under anaerobic conditions) to the atmosphere; and 4) determining how CO₂-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.

Keywords: CO₂, Horticultural crops, photosynthesis increases and economic yield

Introduction

Cultural management of fruit trees under plastic house or glasshouse conditions to improve the fruit quality and to obtain maturation of earlier fruit has become a common practice. Under such cultural conditions, environmental factors including CO₂ concentration, temperature, water status in soil, etc. may affect vegetative and fruit growth as well as fruit quality. Although numerous researchers have studied the effect of CO₂ enrichment on fruit production, the effect on fruit quality is not well documented. CO₂ enrichment enhances photosynthesis and leads to a higher biomass production and economic yield in C3 plants (Kimball 1983; Bowes 1993) [22, 4]. The response of the photosynthetic activity to CO₂ enrichment differs between herbaceous plants and tree species. In the former, initial stimulation of photosynthesis by short-term CO₂ enrichment decreases or disappears during long-term CO₂ enrichment (Masuda *et al.* 1989; Idso and Kimball 1991; Bowes 1993; Makino 1994) [28, 15, 17, 4, 27]. However, no such effect on the regulation of photosynthesis has been observed in trees (Idso *et al.* 1991; Idso and Kimball 1992) [16, 15, 17]. Besides photosynthesis, mineral supply, and sink activity are assumed to be involved in the differential response to long-term CO₂ enrichment among plant species (Arp 1991; Idso *et al.* 1991; Fisher *et al.* 1997) [2, 15, 17, 8].

Elevated CO₂ has frequently been demonstrated to increase the yield of various crops, including vegetables (Kimball, 1983; Long *et al.*, 2004) [22, 26]. Elevated CO₂ (from 355 to 800-900 μmol mol⁻¹) increased the yield of lettuce, carrot, and parsley by 18%, 19%, and 17%, respectively. The level of CO₂ 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) [23, 33]. 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) [14]. This rise, along with other trace gases, is widely thought to be a primary factor driving global climate change (IPCC, 2007) [19]. Aside from the debate on anthropogenic-driven climate change, vegetation will be directly impacted and research has shown that plants respond positively to elevated CO₂ (Amthor, 1995) [1]. Most of this 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. We will attempt to discuss the effects of the rise in atmospheric CO₂ concentration on plant growth and water relations with a focus toward implications for horticultural production systems with suggestions for future research areas.

Effect of CO₂ enrichment on vegetative and fruit growth

It has been reported that photosynthesis is enhanced by elevated CO₂ concentration in the atmosphere depending on the growth conditions such as pot size and nutrient supply (Sage 1994)^[35]. The trees which are grown in containers with an adequate size and since a sufficient amount of fertilizer are applied, it appears that root growth and nutrient supply did not affect the response to CO₂ enrichment.

It was observed that CO₂ enrichment stimulated the growth of both vegetative parts and fruits which proceeded simultaneously after blooming, particularly in the former. ¹³C tracer experiments revealed that when the sink activity in fruit increased with maturation, fruit predominantly imported photo assimilates. These results together with the fact that elevated CO₂ enhanced the photosynthetic activity (Kimball 1983; Bowes 1993; Makino 1994)^[22, 4, 27], suggest that at ambient CO₂ concentration, vegetative growth is more severely suppressed due to the insufficient supply of photosynthates. This fact implies that fruit has a higher activity as sink for photo assimilates than vegetative parts at the maturation stage of fruits.

It was observed that although elevated CO₂ concentration had no significant effect on bud formation, it promoted the formation and development of flower buds (data not shown) and also increased mature fruit weight. Similar phenomena were observed in tomato: CO₂ enrichment had no significant effect on the number or development of flowers, while it increased significantly both fruit number and fruit weight (Knecht and O'Leary 1974)^[24]. These results suggest that CO₂ enrichment is more effective in stimulating fruit growth than development including the formation of buds and flowers. This may imply that CO₂ enrichment contributes to plant biomass production mainly through the enhancement of photosynthesis and photo assimilate translocation rather than through the formation of reproductive organs by stimulating the functions of plant growth regulators.

Sugar metabolism and CO₂ enrichment

It was observed that although long-term CO₂ enrichment increased the average fruit size, it had no significant effect on fruit quality including TSC, acidity, and hardness, whereas, short-term CO₂ enrichment during maturation of fruit increased the fruit sugar concentration. Our results suggest that the effect of CO₂ enrichment on fruit production and quality differs depending upon the stages of fruit growth: CO₂ enrichment during the initiation and fruitlet stages increases fruit size, while the same treatment during maturation of fruit increases the fruit sugar concentration. It has been reported that the effect of CO₂ enrichment on plant growth is markedly dependent on the plant age (Neales and Nicholls 1978; Ingvarlsen and Veierskov 1994)^[32, 18]. However, the reason why the total sugar concentration in fruit increases by the elevation of the CO₂ concentration during the maturation of fruit is not thoroughly understood. Nevertheless, based on our results, the increase in the sugar concentration in fruit by CO₂ enrichment appears to be due to extended maturation and enhancement of the sugar metabolism. It is generally recognized that sorbitol, a major translocation form of photo assimilates, is converted to mainly fructose, and glucose, then finally to sucrose in Japanese pear (Yamaki and Moriguchi 1989)^[37]. Furthermore, sorbitol translocated into fruit has been reported to be converted to fructose and glucose by the N AD⁺-dependent sorbitol dehydrogenase and sorbitol

oxidase enzymes, respectively and then from these sugars sucrose is synthesized by the sucrose-metabolizing enzymes such as sucrose synthase and sucrose-phosphate synthase (Moriguchi *et al.* 1992)^[29].

Impact of CO₂ on Vegetable Crop

Generally, eCO₂ (700-1000 μmol mol⁻¹) can promote the yield of vegetables (Gruda and Tanny, 2014)^[10]. The sources of CO₂ have changed from traditional straw bales and organic soils to relatively pure CO₂ from industrial waste or CO₂ generators (Gruda, 2005)^[12]. Elevated CO₂ has frequently been demonstrated to increase the yield of various crops, including vegetables (Kimball, 1983; Long *et al.*, 2004)^[22, 26]. Elevated CO₂ (from 355 to 800-900 μmol mol⁻¹) increased the yield of lettuce, carrot, and parsley by 18%, 19%, and 17%, respectively. Optimizing other environmental factors with eCO₂ further increased plant productivity and yield (Kirschbaum, 2011)^[25]. Elevated CO₂ (900 μmol mol⁻¹) with additional light (ambient + 100 μmol m⁻² s⁻¹ photosynthetically active radiation or PAR) increased the early yield of tomato and pepper by 15% and 11%, respectively (Fierro *et al.*, 1994)^[9]. Elevated CO₂ (600-700 μmol mol⁻¹) increased the average root dry mass of sugar beet by 26% in high N availability (10 mM NO₃⁻) and by 12% in 1 mM NO₃⁻ (Demmers-Derks *et al.*, 1998)^[5]. More examples of yield benefits for other vegetable crops are reviewed by Gruda (2005)^[12].

There is less information on the effect of CO₂ concentration on the nutritional quality of vegetables (Gruda, 2005; Moretti *et al.*, 2010)^[12]. Elevated CO₂ promotes soluble sugar accumulation in the edible parts of vegetables. The increased CO₂ fixation under eCO₂ promotes the synthesis of triose phosphate in leaves (Long *et al.*, 2004)^[26], which can be further transformed into other carbohydrates, e.g., glucose, fructose, and sucrose.

The meta-analysis showed that eCO₂ increased the concentrations of glucose by 13.2%, fructose by 14.2%, sucrose by 3.7% (at *p* = 0.07), and total soluble sugar by 17.5% in terms of all vegetables (Jinlong Dong *et al.* 2018)^[6]. The increment of total soluble sugar in leaf (an organ for carbohydrate synthesis) under eCO₂ was the greatest (36.2%) among all the classes of vegetables. The increment can reach 38-188% in the leaves of Chinese cabbage and 16-53% in the leaves of oily sowthistle (Jin *et al.*, 2009)^[20]. Compared to leafy vegetables, the increments of total soluble sugar were less in fruit and root vegetables, and were 8.5% and 16.3%, respectively. This indicates that the synthesized carbohydrates in leaves cannot be fully translocated to fruits as well as to roots, although one needs to be cautious regarding the species variation. For example, eCO₂ (950 μmol mol⁻¹) increased total soluble sugar in strawberry fruits by 20% relative to 350 μmol mol⁻¹ (Wang and Bunce, 2004). Similarly, the total soluble sugar was increased by 13% in radish and 20% in turnip under 1,000 μmol mol⁻¹ CO₂ compared to 400 μmol mol⁻¹ control (Azam *et al.*, 2013)^[3].

The leafy vegetables generally contain a greater concentration of nitrate, eCO₂ may promote N assimilation in leaves (Stitt and Krapp, 1999)^[36]. For example, eCO₂ increased the N concentration in the inner leaves of lettuce cv. "Batavia Rubia Munguía" noninoculated with arbuscular mycorrhizal fungi to a greater extent than the outer leaves. Moreover, eCO₂ limits the uptake of nitrogen and the synthesis of nitrogenous compounds of vegetables to a lesser extent than that of other

crops (mainly grain crops) (9.5% vs. 10-15%), probably because N deficiency is more common for grain crop cultivation in soils compared to vegetable cultivation.

Higher CO₂ results in greater photosynthetic rates initially but often photosynthetic acclimation, i.e., down regulation of net photosynthetic rates in the long term (Long *et al.*, 2004; Kirschbaum, 2011)^[26, 25], which indicates that increases in CO₂ concentration can substantially affect vegetable quality. Elevated CO₂ had increased the sucrose concentration of tomato fruits to a greater extent at the early fruiting stage than that at the later fruiting stage. The same pattern was noticed in terms of the concentrations of soluble sugars and organic acids in grapes. Plants grown in moderate vs. low light can generate more ATP and NADPH for carbon fixation, whereas high vs. moderate light may cause photoinhibition resulting from excessive light intensity that produces greater amounts of reactive oxygen species. Elevated CO₂ can improve vegetable quality under certain light intensities.

Conclusion

At an elevated CO₂ concentration, the photosynthetic activity and translocation of photo assimilates are accelerated. In general, elevated CO₂ increases plant growth (both above- and belowground) and improve 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 CO₂, 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. eCO₂ can promote the accumulation of soluble sugar including glucose and fructose, and the accumulation of antioxidants including ascorbic acid, total phenols, and total flavonoids, but reduce the levels of protein, nitrate, Mg, Fe, and Zn in products. 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 CO₂ and other trace gases (through irrigation and fertilization) is of critical importance. How CO₂-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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