INTERACTION OF CO_2 AND ENVIRONMENTAL FACTORS ON CROP RESPONSES

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Summary

Significant yield increases for most plant species are observed with CO_2 enrichment. Greatest response to CO_2 appears to occur when irradiance levels are high. Higher photosynthetic rates result when temperature and CO_2 concentration are increased with increasing irradiance. While total dry matter accumulation increases under these conditions, horticultural quality or yield does not necessarily increase.

1. Introduction

Growing plants in greenhouses allows for greater control of the factors influencing plant growth than under field conditions. Temperature, water, and nutrients are more readily controlled in greenhouses than are irradiance and gases (O_2 and CO_2). Research starting in the late 1950's led to commercial CO_2 enrichment in greenhouses (Wittwer and Robb, 1964). However, control of CO_2 concentration in greenhouses has not been precise. CO_2 often is injected at a constant rate into the greenhouse irrespective of irradiance, crop photosynthetic rate or air infiltration. Precise control of CO_2 concentration is possible with the development of computers for greenhouse environmental control. Computers can maintain constant CO_2 concentration or vary CO_2 concentration based on irradiance and stage of crop development to optimize plant growth. Currently, little information is available for development of such strategies.

This paper reviews selected physiological and yield responses of plants to CO_2 enrichment. Potentially undesirable plant responses due to elevated temperatures necessary for photosynthetic maximization will also be discussed.

2. Response to CO_2 enrichment

2.1. Yield

Many plant responses to CO_2 enrichment are quantified easily, e.g. greater dry weight and earlier flowering. However, the economic value of CO_2 enrichment is difficult to quantify for many crops. For example, is "early" yield of tomatoes more important than total yield? Does a 20% increase in dry weight of a pot chrysanthemum result in greater economic yield? Questions like these can be answered only by the grower, based on the grower's production and marketing situation. Therefore, in this paper, biological responses to CO_2 enrichment are presented without any judgment of the horticultural or economic benefits.

Some previously reported crop responses to CO_2 enrichment are summarized in Table 1. Both within crop and among crop responses are reported. Typically, yield increases were in the range of 20-30% in response to a 1000 ppm CO_2 enrichment, although exceptions exist with much greater responses being reported (e.g. Lindstrom, 1965; Kimball and Mitchell, 1979). Enrichment normally resulted in accelerated development, earlier flower (Goldsberry, 1961; Calvert, 1972) and/or earlier fruit maturation (Calvert, 1972; Hand and Soffe, 1971).

Responses to CO_2 vary with duration of enrichment and the level of other environmental factors. Tomato yields were proportional to enrichment time. Yield was lower when the start of enrichment was delayed in the morning compared to early termination in the afternoon (Calvert and Slack, 1976). Hand and Soffe (1971) found 32 to 72% higher tomato yields after 6 weeks of picking when plants were grown in 1200 ppm CO_2 at a temperature regime modulated by irradiance level, compared with plants grown at 600 ppm CO_2 at a constant temperature. However, final yields after 22 weeks of harvest were only 11 to 25% greater. Increasing CO_2 concentration from 600 to 1200 ppm alone without modulation increased yield 0 to 7% depending on the cultivar. Kimball and Mitchell (1979) found that using a direct contact heat exchanger at the start of cooling (26.5^o) in combination with delayed ventilation (29.5^o), resulted in tomato yield increases up to 64% compared with plants growing in a conventionally ventilated greenhouse which was vented at 26.5^o. Daytime CO_2 concentrations averaged 856 and 1094 ppm for the conventionally and the delayed ventilated greenhouses, respectively. At 1000 ppm CO_2, tomato response to an irradiance-dependent day temperature regime was greater with above average irradiance conditions than with below average irradiance conditions (Rudd-Jones, et al., 1978). Yields were enhanced with higher temperatures whether the increased temperature was achieved with irradiance-dependent or steady state temperature control.

Ito (1978) found cucumber yield to be greater during the first 45 days of harvest when temperatures were allowed to increase to 33^o prior to ventilation instead of 28^o. Total yield over 90 days, however, was lower in the higher temperature treatment because yield was significantly lower during the second 45 days. Mortensen and Moe (1983) found a significant interaction between irradiance and CO_2 concentration as they affect dry weight accumulation of chrysanthemum.

2.1.2. Photosynthesis

The basis for CO_2 enrichment in the greenhouse is photosynthetic enhancement and, therefore, total yield enhancement. Normally net photosynthesis (Pn) increases with increasing CO_2 concentrations up to a point of saturation where further increases in CO_2 do not increase Pn. As CO_2 concentration or irradiance increases, the optimum temperature for maximum Pn also increases (Gaastra, 1959; Enoch and Hurd, 1977). Wittwer and Robb (1964) recommended that greenhouse daytime temperature be elevated 3 to 5.5^oC during CO_2 enrichment. Enoch and Hurd (1977) further predicted the optimum temperature (T_{opt}) for maximum Pn in spray carnation to be:

$$T_{opt} = -6.47 + 2.336 \ln C + 0.03195 \quad I \qquad (1)$$

where T_{opt} is expressed in ^{o}C, C in ppm CO_2, and I in Wm^{-2} PAR. Heins, et al. (1984) determined the optimum temperature (T_{opt}) for maximum Pn at a particular CO_2 concentration in chrysanthemum to be:

$$T_{opt} = -30.2 + 4.27 \ln C + 4.153 \ln I \qquad (2)$$

where T_{opt} is expressed in ^{o}C, C in ppm CO_2 and I in $\mu mol\ s^{-1}m^{-2}$ PAR. The optimum temperature for maximum photosynthesis at 500 $\mu mol\ s^{-1}m^{-2}$ PAR is predicted to increase 2.7^{o} and 4.8^{o} for carnation and chrysanthemum, respectively when CO_2 is increased from 300 to 1000 ppm. These values are very similar to those suggested by Wittwer and Robb (1974). Heins, et al. (1984) further determined that an optimum CO_2 concentration for maximum Pn in chrysanthemum could be predicted by:

$$C_{opt} = 3.65\ I^{.9129} \qquad (3)$$

where C_{opt} is expressed in ppm CO_2 and I in $\mu mol\ s^{-1}m^{-2}$ PAR. Substituting the value of C from equation 3 into equation 2 allows prediction of optimum temperature and optimum CO_2 concentration at a particular irradiance for Pn maximization. At 500 $\mu mol\ s^{-1}m^{-2}$, the optimum CO_2 concentration and temperature are predicted to be ca. 1050 ppm and $25^{o}C$.

The increase in Pn with CO_2 enrichment is most likely due, in part, to reduced photorespiration. Ehleringer and Bjorkman (1977) found the quantum yield (mol CO_2 assimilated/mol of photons absorbed) to increase at 21% O_2 from 0.02 to 0.075 as intercellular CO_2 concentration increased from 100 to 1000 ppm. Over this range of CO_2 concentrations, and at 2% O_2, the quantum yield remained 0.08. Ku et al. (1977) found that photosynthesis in potato decreased as the O_2 concentration increased from 2 to 21%. This decrease was nearly compensated for by a 2-fold increase in CO_2 concentration. Mortensen and Moe (1983) reported Pn to increase 51% when O_2 was decreased from 21% to 2% at 330 ppm CO_2 but the increase was only 9% at 1500 ppm CO_2.

2.1.3. Transpiration

Stomata gradually closed (Enoch and Hurd, 1977; 1979) and transpiration decreased as CO_2 concentration increased. This decrease in transpiration can be significant. Enoch and Hurd (1979) found transpiration in carnation to decrease ca. 0.04% per ppm in the range 330 to 1500 ppm CO_2. This translated to a 28% reduction in transpiration as CO_2 concentration increased from 300 to 1000 ppm. Due to the expected increase in global CO_2 concentration over the next 50 years, they further predicted a 40-50% increase in water use efficiency (defined as the ratio between net photosynthesis rate and transpiration rate.

2.2. Plant responses to temperature

Increasing plant dry weight by increased Pn does not necessarily increase yield or quality. The pattern of dry weight distribution in the plant is the critical factor. For example, increasing dry weight of a plant by partitioning the added dry weight to the roots does little to improve quality of a potted chrysanthemum or to increase yield of a tomato crop, but if this increased dry weight is partitioned to the stems and flowers in chrysanthemum or to the fruit in tomato, it is of greater horticultural significance.

To achieve maximum Pn with increasing CO_2 concentration, an increase in day temperature (DT) is required (Enoch and Hurd, 1977; Heins, et al., 1984). However, the higher DT may not produce a higher quality plant. Karlsson and Heins (1984a) showed stem length in chrysanthemum increased linearly with DT. Also, with increase DT the dry weight partitioned to the flowers decreased while partitioning to the stem increased (Karlsson and Heins, 1984b). These responses to high DT were also observed when pot chrysanthemum were grown in a Pn maximization environment with CO_2 concentrations and temperature optimized based on irradiance (Heins, et al., 1984). Compared to plants grown under traditional day temperatures, total plant dry weight increased 28% and stem length increased 20% on the plants in the optimized environment. The increase in total dry weight and stem length was accompanied by a decrease in the percent dry weight partitioned to the flowers, and an increase in the percent partitioned to the stems. The plants in the optimized environment were horticulturally less desirable even though flower size remained the same. Adequate height control was later achieved in the optimized environment by increasing diaminozide application.

The stem elongation response to DT is a factor that must be taken into account when considering Pn maximization strategies with other floricultural crops, as the response is not limited to chrysanthemum. A similar response of increasing stem length with increasing DT has been observed recently in *Lilium longiflorum* (unpublished data). Both in *Lilium* and chrysanthemum, a further increase in stem length occurred at comparable DT when plants were exposed to low night temperatures (NT). These data suggest that attempts to maximize Pn by increasing day temperatures at elevated CO_2 concentrations will result in increased plant height on some species. In addition, if lower NT are then used to conserve energy, further increases in stem length are likely. Other cultural procedures to control stem length, such as increased growth retardant applications, may be necessary for pot plant production when these types of control strategy are used. However, this increase in stem length may be desirable for cut flower production.

3. Concluding remarks

Significant yield increases for most plant species are observed with CO_2 enrichment. Greatest response to CO_2 appears to occur when irradiance levels are high. As temperature and CO_2 concentration are increased with increasing irradiance, higher Pn rates result. Total dry matter accumulation does increase under these conditions, but the horticultural quality or yield does not necessarily increase. Research in the future, addressing Pn maximization, should be concerned not only with dry matter production, but also with the factors controlling dry matter partitioning.

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* References to be continued on page 28

Table 1. Influence of enriched carbon dioxide atmosphere on plant growth and yield. This table is representative of the CO_2 literature and is not intended to be a complete listing of all references.

Crop	Effect	Response	CO_2 conc.	Reference
African violet	Dry weight	+ 20%	500 ppm	Shaw and Rodgers (1964)
Carnation	Yield	+ 37%	200 vs 500 ppm	Goldsberry (1961)
		+ 7%	350 vs 500 ppm	
	Earlier flowering	2 weeks	550 ppm	
	Yield	+ 9%	Not stated	Holley and Juengling (1946)
	Number of "Fancy" grade flowers	+ 20%		
	Cutting production	270 more cuttings/m^2	550 ppm	Goldsberry (1966)
Cucumber	Yield	+10-25%	Variable, up to 9000 ppm	Owen and Small (1926)
	Yield	+27-38%	1300 ppm	Ito (1978)
Geranium	Branching	+ 14%	1100 ppm	Shaw and Rodgers (1964)
	Flower number	+ 72%		
	Shorter mature time	1 month		
	Improved cutting production	12-40%	Not stated (probably 1000 ppm)	Malmburg (1966)

Table 1 (Con't)

Crop	Effect	Response	CO_2 conc.	Reference
Chrysanthemum	Stem length Weight	+19-37% + 0-47%	1200-1500 ppm	Koths and Adzima (1965)
	Fresh weight Stem length	+33-48% +26-28%	1000 ppm 1000 ppm	Shaw and Rodgers (1964)
	Cutting production	+29%	1109-1800 ppm	Kobel (1965)
	Dry weight	+27-60%	1600 ppm	Mortensen and Moe (1983)
Rose	Yield	+31%	1100 ppm	Shaw and Rodgers (1964)
	Yield	+60%	1200-2000 ppm	Lindstrom (1965)
	Yield	+14-22%	2000 ppm	Mattson and Widmer (1971)
	Yield	+23%	1000 ppm	Hand and Cockshull (1975)
Snapdragon	Fresh weight Dry weight	+57%-86% +67-90%	1200-2000 1200-2000	Lindstrom (1964)
Sweet Pepper	Yield	+33%	1000 ppm	Vijverberg and Uffelen (1977)
Tomato	Early yield Total yield	+26% 9%	1200 ppm + temp modulation	Hand and Soffe (1971)
	Early yield Total yield	+84-95% +30%	900 ppm	Calvert (1972)
	Total yield	+40%	1000 ppm	Madsen (1976)
	Yield	+63%	1000 ppm + delayed ventilation	Kimball and Mitchell (1979)

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