

Respiration and C₂H₄ Production in Various Harvested Crops Held in CO₂-enriched Atmospheres

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Abstract. The respiration rate (O₂ uptake) and the rate of C₂H₄ production were measured before, during, and after 24 hours of treatment with 60% CO₂ (20% O₂) in 18 kinds of fruits and vegetables by use of an automated system connected to a microcomputer. High CO₂ decreased respiration only in climacteric fruit and broccoli, which were producing C₂H₄. Ethylene production decreased with CO₂ treatment of peaches, tomatoes, and broccoli, but that of bananas increased. In five nonclimacteric fruits (three citrus species, grapes, and Japanese pears) and several vegetables (carrots, onions, cauliflower, and cabbage), in which C₂H₄ production was not detected, high CO₂ affected respiration little, if at all. When eggplants, cucumbers, podded peas, spinach, and lettuce were treated with high CO₂, C₂H₄ production began and respiration increased. These results indicate that the respiratory responses of harvested horticultural crops to high CO₂ might be mediated by the effects of CO₂ on the action and/or synthesis of C₂H₄.

There have been many studies of the storage of fruit and vegetables since the report of Kidd and West (1927) concerning the beneficial effects of high CO₂/low O₂ storage (controlled atmosphere, CA). Since CO₂ is a product of respiration, it would be expected that respiration rate would decrease as CO₂ concentration in the atmosphere increases (Hewer, 1987). Succinic acid accumulates and the activities of enzymes involved in its metabolism decrease in several fruits stored in high CO₂, which is indirect evidence for this possibility (Biale, 1960; Kader, 1986).

Carbon dioxide inhibits C₂H₄ action competitively and helps regulate C₂H₄ biosynthesis (Burg and Burg, 1967). Therefore, some of the benefits of storage in a high-CO₂ atmosphere arise when C₂H₄ production or C₂H₄-mediated reaction is inhibited (Herner, 1987). It is not well-known how high CO₂ affects respiration and C₂H₄ synthesis; these two may be related (Sisler and Wood, 1988).

The manner in which horticultural commodities respond to CO₂ depends on the nature of the commodity and on the concentration and length of exposure to the gas (Herner, 1987). Although CO₂ concentrations > 5% to 10% should be avoided in long-term storage, short-term exposure to very high CO₂ (20% to 100%) has beneficial effects on the storage life of some harvested commodities (Herner, 1987; Higashio et al., 1980).

Using an automated microcomputer system for the measurement of O₂ uptake, we determined that respiratory responses to high CO₂ differed among horticultural crops and among developmental stages (Kubo et al., 1989a, 1989b). In these studies, however, the effects of high CO₂ levels on C₂H₄ production were not measured.

The present study was designed to examine the effects of 60% CO₂ in the presence of 20% O₂ on the respiratory activity and C₂H₄ production in various horticultural crops.

Materials and Methods

Eighteen kinds of horticultural crops (Table 1) were used for the high-CO₂ treatments. All plant material was obtained from a commercial market in Okayama, Japan.

Treatment conditions. Plant material weighing =1 kg was placed in a respiration chamber (5.5 liter). Air was passed through the chamber for 12 hr, followed by a gas mixture of 60% CO₂ ± 0.001%, 20% O₂ ± 0.001%, and 20% N₂ ± 0.001% for 24 hr, and by air for another 24 hr. The gas flow rate was 100 ml·min⁻¹ and the chamber was at 25 ± 1°C.

Measurement of respiration and C₂H₄ production. Both O₂ uptake and C₂H₄ production were measured using an automated system connected to a microcomputer. The details of this system were described previously (Inaba et al., 1989). Briefly, the system consisted of a gas flow system, three gas chromatography (GC), a microcomputer, and interface. Two GCS, equipped with a thermal conductivity detector and molecular sieve 5A and Porapak Q column, were used for measurement of O₂, CO₂, and N₂. N₂ was used as an internal standard to improve the accuracy of measurement of O₂. Another GC, with a flame ionization detector and activated alumina column, was used for measurement of C₂H₄. All operations, including gas sample injection, were regulated by the microcomputer. The measurement of O₂ and C₂H₄ could be reproduced with an accuracy of 0.01% and 0.1 ppm, respectively. Uptake and production were measured every 3 hr during the experimental period. All measurements were repeated at least three times per treatment.

Results

Three modes of response to 60% CO₂, in terms of O₂ uptake and C₂H₄ production, were observed among the crops examined (Table 1). Typical responses of O₂ uptake—decrease, no change, or increase—are shown in Figs. 1, 2, and 3, respectively. Suppression of O₂ uptake by 60% CO₂ was observed in the climacteric fruits and in broccoli, which were producing C₂H₄ before the CO₂ treatment. The rate of O₂ uptake in peaches decreased to 55% of the control while C₂H₄ production decreased to trace levels during the CO₂ exposure. Both respiration and C₂H₄ production returned to levels close to those of the control when the samples were transferred back to air (Fig. 1).

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Table 1. Effects of exposure to 60% CO₂ plus O₂ and 20% N₂ at 25C on the rates of O₂ uptake and C₂H₄ production in various fruits and vegetables.²

Respiratory response	Species	O ₂ uptake (ml·kg ⁻¹ ·hr ⁻¹) ^y		O ₂ uptake in (B) as percent of (A)	C ₂ H ₄ production (μl·kg ⁻¹ ·hr ⁻¹) ^x	
		Control (A)	CO ₂ -treated (B)		Control	CO ₂ -treated
Decrease	Peach (<i>Prunus persica</i> Batsch)	39.2 ± 1.7	21.5 ± 0.6	55	14.2 ± 3.8	Trace
	Tomato (<i>Lycopersicon esculentum</i> Mill.)	17.8 ± 1.2	13.2 ± 2.3	74	10.1 ± 0.3	2.3 ± 0.9
	Banana (<i>Musa sapientum</i> L.)	66.8 ± 2.5	49.2 ± 3.3	74	0.8 ± 0.6	8.2 ± 0.3
No change	Broccoli (<i>Brassica oleracea</i> L., italica)	312 ± 18	112 ± 15	35	2.6 ± 0.8	0.5 ± 0.3
	Satsuma mandarin (<i>Citrus unshiu</i> Marc.)	11.0 ± 0.5	12.5 ± 1.9	114	Trace	Trace
	Iyokan (<i>Citrus iyo</i> Hort. ex Tanaka)	17.4 ± 0.9	19.1 ± 0.8	110	Trace	Trace
	Lemon (<i>Citrus limon</i> Burm. f.)	10.6 ± 0.6	11.5 ± 1.2	108	Trace	Trace
	Grape (<i>Vitis labrusca</i> L. × <i>Vitis vinifera</i> L.)	9.0 ± 0.3	9.5 ± 0.4	106	Trace	Trace
	Japanese pear (<i>Pyrus serotina</i> Rehd.)	6.0 ± 0.4	6.9 ± 0.8	115	Trace	Trace
	Carrot (<i>Daucus carota</i> L.)	15.5 ± 1.1	15.9 ± 0.9	103	Trace	Trace
	Onion, dry (<i>Allium cepa</i> L.)	14.0 ± 1.0	14.7 ± 0.8	105	Trace	Trace
	Cauliflower (<i>Brassica oleracea</i> L., botrytis)	71.7 ± 4.9	66.7 ± 3.1	93	Trace	Trace
	Cabbage (<i>Brassica oleracea</i> L., capitata)	15.5 ± 0.3	15.1 ± 0.9	97	Trace	Trace
Increase	Eggplant (<i>Solanum melongena</i> L.)	30.0 ± 0.8	49.6 ± 0.7	165	Trace	0.4 ± 0.2
	Cucumber (<i>Cucumis sativum</i> L.)	21.4 ± 1.3	49.2 ± 5.6	230	Trace	2.1 ± 0.6
	Podded pea (<i>Pisum sativum</i> L.)	93.0 ± 5.1	120 ± 7.3	129	Trace	2.6 ± 0.3
	Spinach (<i>Spinacia oleracea</i> L.)	116 ± 5.1	142 ± 7.4	122	Trace	0.3 ± 0.1
	Lettuce, crisphead type (<i>Lactuca sativa</i> L.)	26.8 ± 0.7	75.2 ± 1.2	281	Trace	1.2 ± 0.2

¹Crops were exposed to 60% CO₂ for 24 hr at 25C.

²Rates of O₂ uptake just before the end of CO₂ treatment. Means ± SE. n = 3.

³Rates of C₂H₄ production just before the end of CO₂ treatment. Means ± SE. n = 3.

Responses in tomatoes and broccoli were similar to those observed for peaches. The rates of O₂ uptake in ripening bananas exposed to 60% CO₂ decreased to 74% of those of the control after 24 hr, and C₂H₄ production increased =10-fold.

Oxygen uptake changed little in five of the nonclimacteric fruits (three species of citrus, grapes, and Japanese pears) and in several vegetables (carrots, onions, cauliflower, and cabbage; Table 1, Fig. 2) exposed to high CO₂. Upon transfer back to air O₂ uptake increased slightly in Japanese pears (Fig. 2) and onions (data not shown), whereas that of the seven other non-climacteric fruits and vegetables remained at the same levels as those of the controls. Ethylene production by crops classified as "no change" types was not detected during or after exposure to 60% CO₂ (Table 1).

The presence of 60% CO₂ increased O₂ uptake (Table 1, Fig. 3) and slightly stimulated C₂H₄ production (Table 1) in eggplant and spinach. After return to air, both O₂ uptake and C₂H₄ production increased in these two crops. The response of cucumber to high CO₂ was similar to that of eggplant (Table 1). Oxygen uptake and C₂H₄ production by lettuce increased during CO₂ treatment (Table 1), with O₂ uptake increasing to almost three times that of the control at the end of the CO₂ treatment. After return to air, both rates increased further (Fig. 3). Oxygen uptake and C₂H₄ production of peas increased during the 60% CO₂ treatment. After return to air, O₂ uptake increased further and C₂H₄ production remained high (Fig. 3).

Discussion

The beneficial effects of high CO₂ in the CA storage of horticultural crops are generally thought to arise through a suppression of respiration (Kader, 1986). Our results showed that O₂ uptake was reduced by high CO₂ only in ripening climacteric fruits and in broccoli, all of which were producing C₂H₄.

Kerbel et al. (1988) reported that 'Bartlett' pears maintained in a mixture of air plus 10% CO₂ exhibited reduced respiration

and C₂H₄ production. Similar observations have been reported for strawberries (Li and Kader, 1989) and apples (Chaves and Tomas, 1984). Inhibition of C₂H₄ production in high CO₂ environments has been reported for tomatoes (Buescher, 1979) and sweet peppers (Wang, 1977).

Treatment of avocados with 5% to 10% CO₂ does not affect the respiration rate at the preclimacteric stage but delays the onset of the climacteric and reduces the respiration rate at the climacteric peak (Young et al., 1962). Similarly, tomatoes and bananas exhibited reduced respiration with high CO₂ levels at the climacteric stage, but CO₂ had little effect at the preclimacteric stage (Kubo et al., 1989b).

The results reported here show that high CO₂ affected the respiration rate little if at all in the fruits (nonclimacteric) and vegetables that were not producing measurable levels of C₂H₄. High CO₂ levels inhibit the action of C₂H₄ (Biale, 1960). The presence of 10% CO₂ abolishes the biological activity of 1 ppm C₂H₄ (Burg and Burg, 1967). Therefore, suppression of respiration by high CO₂ in crops producing C₂H₄ might occur mainly because of inhibition of the action and/or synthesis of C₂H₄. If so, high CO₂ levels would not suppress respiration that is not accelerated by endogenous C₂H₄.

Other evidence of the suppression of respiration by high CO₂ levels is the inhibition of certain enzymes (e.g., succinic dehydrogenase, cytochrome oxidase, and phosphofructokinase) and disturbed organic acid metabolism, for example, the accumulation of succinic acid (Biale, 1960; Kader, 1986; Kerbel et al., 1988). These phenomena have been found in ripening pears (Frenkel and Patterson, 1973; Kerbel et al., 1988) and apples (Monning, 1983; Shipway and Bramlage, 1973). Further investigation of these enzymes and metabolic intermediates in nonclimacteric fruits is needed.

Our findings show that respiration and/or C₂H₄ production in some vegetables were enhanced during high CO₂ treatment. In some cases, further increases occurred after the treatment ended.

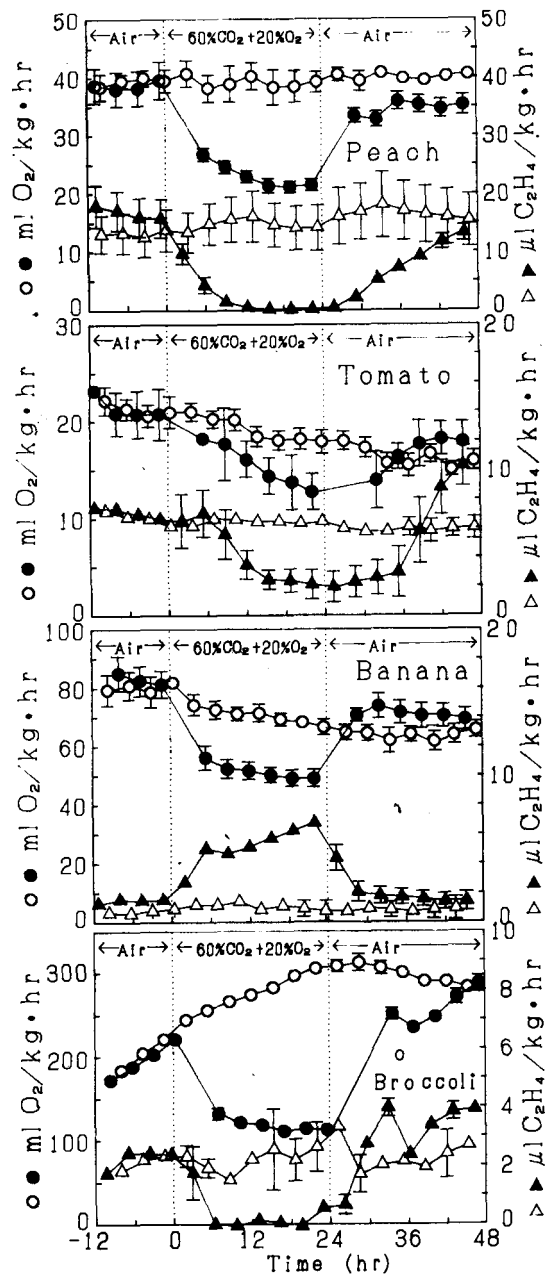


Fig. 1. Effects of exposure to 60% CO₂ plus 20% O₂ and 20% N₂ on the rates of O₂ uptake (●, ○) and C₂H₄ production (▲, △) at 25 ± 1°C in three species of climacteric fruits and in broccoli (●, ▲ CO₂-treated, ○, △ control). Vertical bars are the standard error. n = 3.

This suggests that CO₂ might act simultaneously as an inducer and suppressor of C₂H₄ synthesis or action in some vegetables. Enhanced respiration during CO₂ exposure has been reported for lemons (Young et al., 1962) and potatoes (Perez-Trejo, 1981). Siriphanich and Kader (1985) found that high CO₂ levels promoted respiration and C₂H₄ production in lettuce. These increases in respiration and C₂H₄ production by exposure to excess CO₂ maybe related to physiological injury (Kader, 1986). We observed the development of brown stain, a CO₂ disorder, on lettuce after the CO₂ treatment. No signs of CO₂-induced disorders were seen in the other crops. Further investigation is needed to determine the mechanism by which high CO₂ influences C₂H₄ production in fruit and vegetable crops.

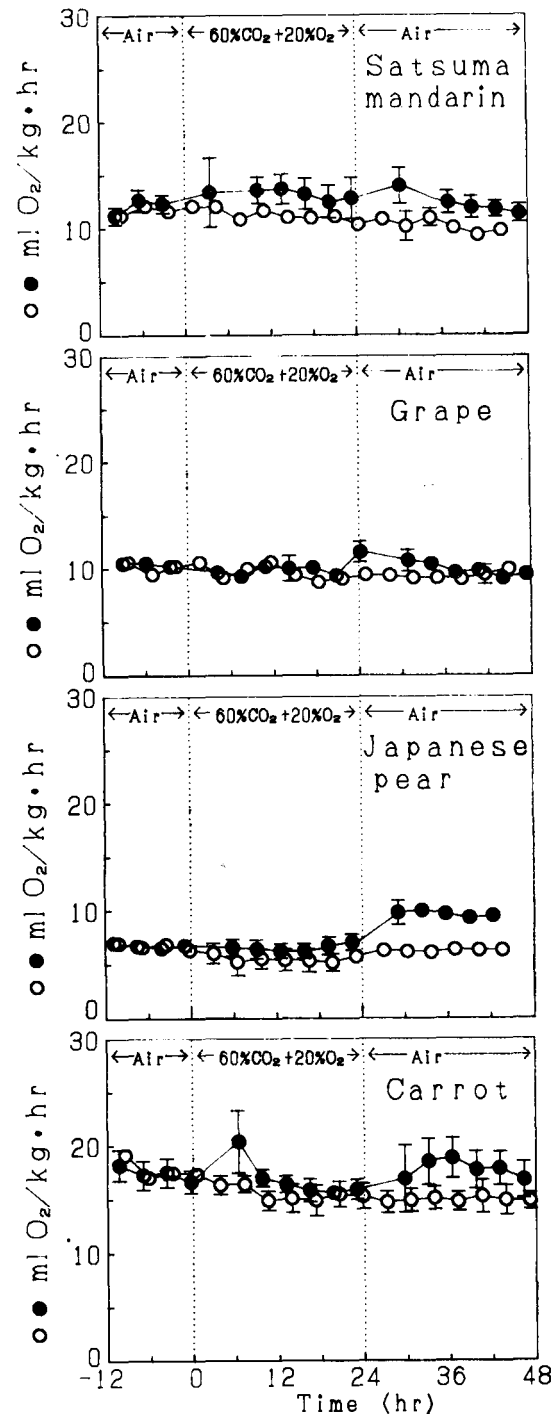


Fig. 2. Effects of exposure to 60% CO₂ plus 20% O₂ and 20% N₂ on the O₂ uptake rate at 25 ± 1°C in three nonclimacteric fruits and in carrot (● CO₂-treated, ○ control). Vertical bars are the standard error. n = 3.

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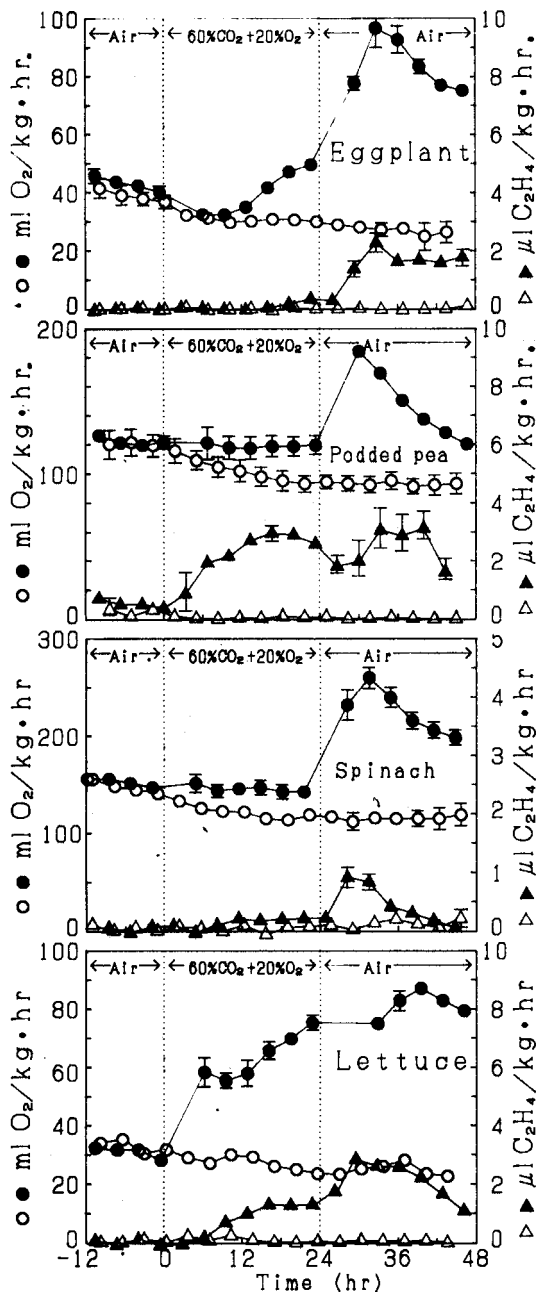


Fig. 3. Effects of exposure to 60% CO₂ plus 20% O₂ and 20% N₂ on the rates of O₂ uptake (●, ○) and C₂H₄ production (▲, △) at 25 ± 1C in four species of vegetables (●, ▲ CO₂-treated, ○, △ control). Vertical bars are the standard error. n = 4.

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