Suppression of Postharvest Plant Pathogenic Fungi by Carbon Monoxide

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ABSTRACT

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The effect on postharvest plant pathogens of controlled atmospheres (CA) enriched with carbon monoxide (CO) (9%) were studied in vitro and in vivo at 5.5 and 12.5 C. Test fungi differed greatly in response to CO. The mean percent growth in air + CO ranged from 20 to 100% of that in air alone. Generally the effect of CO was much greater if the atmosphere was low in O_2. An atmosphere of CO + 2.3% O_2 resulted in a mean percent growth 4.8 to 89.5% of that in air. Suppression sometimes was increased by CO_2 (5 or 18%) added to the low O_2 + CO atmosphere. The test fungi most sensitive to CO were *Monilinia fructicola, Penicillium expansum, P. italicum, P. digitatum,* and *Whetzelinia sclerotiorum* and the diseases they cause were similarly suppressed. Compared to similar fruit incubated in air, those exposed to CO in a CA (2.3% O_2 + 5% CO_2) showed 80–90% reduction in the rate of rot development caused in strawberries by *Botrytis cinerea,* in apples by *P. expansum,* in lemons by *W. sclerotiorum,* and in oranges by *P. italicum* and *P. digitatum* after inoculation and incubation for 11–23 days at 5.5 or 12.5 C. No phytotoxicity of CO was observed. Occasional off-flavors were associated more closely with O_2 and CO_2 modification than with CO addition.

Postharvest losses caused in some perishable fruits and vegetables by rot-causing fungi can be reduced during transit and storage by using controlled atmospheres (CA) with lowered oxygen (O_2) content and elevated carbon dioxide (CO_2) (6–11,13–16,18,20, 26,27,30–32). Suppression of fungal growth commonly has been slight, however, except at CO_2 levels phytotoxic to many commodities (ie, > 10–20%). Occasionally, in vitro fungal growth or in vivo disease development is even more extensive in CA than in air (2,3, 21,22,28,29,35–38). At least in part disease suppression in CA may result from delayed senescence and an extension of the natural resistance of the commodity to decay. Thus, disease suppression sometimes may be an expression of the physiological state of the commodity, not the fungistatic effects of the CA (5,32).

Recently carbon monoxide (CO) has been used in CA storage primarily for its beneficial effects on the commodity, but disease suppression sometimes has been reported. Discoloration has been inhibited in lettuce during transit (4,23,25,33,34). Boarini and Buonocore (4) reported that 1% CO added to CA (2–3% CO_2 + 2–3% O_2) storage of endive at O C for periods up to 39 days reduced bacterial activity, wilting, and growth of the flower stem. Kader et al (25) observed less decay (pathogens not specified) in CO-treated tomato and pepper fruits than in those held in air. Woodruff (39) reported that CO (5–20%) effectively controlled unspecified decays of several fruits and vegetables, but presented no data.

Kader et al (24) found that CO (5–10%) + 4% O_2 atmospheres retarded the in vitro growth of *Botrytis cinerea* and reduced rot incidence and severity in tomatoes. The suppression was less if CO was added to air rather than to a low -O_2 CA.

A fungistatic gas in CA might suppress postharvest pathogens during storage and transit. This study was done to test whether CO might be a beneficial component in CA. Effects of CO on mycelial growth of common fruit rot-causing fungi were investigated in air, in a low concentration of oxygen, in high concentrations of carbon dioxide, and in combinations of low oxygen and high carbon dioxide concentrations. The effect of these atmospheres on the development of several postharvest diseases also was considered. A preliminary report of some of these studies (19) has been published.

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MATERIALS AND METHODS

The postharvest pathogens used in these studies were provided by the junior author. Cultures routinely were stored under refrigeration on potato-dextrose agar slants. The fungi studied, the host from which they were isolated, and the location where they were obtained are listed in Table 1.

The orange (*Citrus sinensis* Osbeck 'Valencia') fruits used in these experiments (grown at the Wolfskill Experimental Orchard, Winters, CA, a facility of the Department of Pomology, University

TABLE 1. Origin of postharvest pathogens used in studies of carbon monoxide suppression of the diseases they cause

Postharvest pathogen	Fruit host	Location
Alternaria alternata (Fr.) Keissler	tomato	California
Ascochyta caricae Pat.	papaya	Hawaii
Botryodiplodia theobromae Pat.	kiwi	California
Botrytis cinerea Pers. ex Fr.	strawberry	California
Colletotrichum gloeosporioides (Penz.) Arx	papaya	Hawaii
Dothiorella gregaria Sacc.	avocado	California
Geotrichum candidum Lk.	citrus	California
Monilinia fructicola (Wint.) Honey	peach	California
Penicillium digitatum Sacc.	citrus	California
P. italicum Wehmer	citrus	California
P. expansum Lk. ex Thom	pear	California
Phomopsis citri Faw.	citrus	California
Phytophthora cactorum (Leb. & Cohn) Schroeter	strawberry	California
Phytophthora parasitica Dastur (Syn. *P. nicotianae* var. *parasitica* [Dastur] Comb.)	papaya	Hawaii
Rhizopus stolonifer (Fr.) Lind.	peach	California
Theilaviopsis paradoxa (d. Seyn.) Hoehn.	pineapple	Hawaii
Verticillium theobromae (Turc.) Mason & Hughes	banana	Egypt
Whetzelinia sclerotiorum (Lib.) Korf & Dumont	apricot	California

TABLE 2. Growth rates of fungi on potato-dextrose agar at 5.5 ± 0.5 and 12.5 ± 0.5 C for the indicated days in various atmospheres

Fungus species	Incubation Temp. (C)	Incubation Time (days)	Mean radial growth rate (mm/day) of colonies in atmospheres composed[w] of: O_2 (%) / CO_2 (%) / CO (%) / N_2 (%)											
			21 / 0 / 0 / 79	19 / 0 / 9 / 72	20 / 5 / 0 / 75	18 / 5 / 9 / 68	17 / 18 / 0 / 65	16 / 18 / 9 / 57	2.3 / 0 / 0 / 97.9	2.3 / 0 / 9 / 88.7	2.3 / 5 / 0 / 92.7	2.3 / 5 / 9 / 83.7	2.3 / 18 / 0 / 79.7	2.3 / 18 / 9 / 70.7
Alternaria alternata	5.5	13	1.3 a[y]	1.2 a	1.2 a	0.6 bc	0.2 d	0.2 d	1.3 a	0.7 b	0.7 b	0.4 cd	0.3 d	0.2 d
	12.5	13	3.6 a	3.4 a	3.3 a	3.3 a	1.3 c	1.1 c	3.8 a	2.1 b	3.4 b	1.4 c	1.4 c	0.6 d
Ascochyta caricae	5.5	12	1.3 b	1.1 bc	1.5 a	0.8 de	0.4 f	0.2 gh	0.9 cd	0.7 e	0.9 cd	0.3 fg	0.1 h	0.1 h
	12.5	11	7.1 a	6.0 b	7.1 a	5.2 c	1.5 f	1.2 f	5.8 bc	2.1 e	5.1 c	3.0 d	1.4 f	1.2 f
Botryodiplodia theobromae[z]	12.5	10	4.0 a	4.0 a	4.2 a	4.3 a	2.9 b	2.9 b	3.4 b	1.3 c	3.7 a	1.9 c	3.1 b	1.9 c
Botrytis cinerea	5.5	8	7.5 ab	7.5 ab	8.4 a	5.0 c	1.0 e	0.6 e	7.2 b	3.8 d	3.9 d	0.4 e	1.1 e	0.3 e
	12.5	4	16.1 ab	15.5 ab	16.8 a	15.7 ab	5.0 d	5.7 d	16.0 ab	10.2 c	14.9 b	9.1 c	5.9 d	4.5 d
Colletotrichum gloeosporioides[z]	12.5	12	2.2 a	2.2 a	2.0 b	1.9 b	0.5 e	0.5 e	2.0 b	1.2 d	1.6 c	1.5 c	0.6 e	0.4 e
Dothiorella gregaria	5.5	15	0.8 a	0.7 ab	0.4 cd	0.2 de	0.1 e	0.1 e	0.7 ab	0.5 bc	0.3 cde	0.2 de	0.1 e	0.1 e
	12.5	12	5.4 bc	5.3 c	6.9 a	6.1 b	3.9 de	4.1 d	5.5 bc	3.0 efg	4.9 c	3.2 efg	3.4 def	2.3 g
Geotrichum candidum	5.5	12	0.9 a	0.9 a	0.9 a	0.9 a	0.6 b	0.5 b	1.0 a	0.4 c	0.9 a	0.4 c	0.6 b	0.4 c
	12.5	12	3.7 b	3.7 b	3.4 b	3.4 b	2.6 c	2.3 c	4.4 a	1.8 d	3.8 b	1.8 d	2.3 c	1.8 d
Monilinia fructicola	5.5	10	1.1 a	0.7 c	1.2 a	1.0 b	0.4 d	0.3 d	0.6 c	0.1 e	0.8 c	0.3 d	0.3 d	0.1 e
	12.5	10	4.2 b	3.4 c	5.0 a	4.4 b	1.3 e	1.1 e	2.4 d	0.2 f	3.7 c	1.0 e	1.3 e	0.1 f
Penicillium digitatum	5.5	15	0.9 a	0.3 b	1.0 a	0.3 b	0.2 b	0.1 b	0.9 a	0.2 b	1.0 a	0.1 b	0.3 b	0.1 b
	12.5	9	4.7 a	1.4 f	4.7 a	1.8 e	2.9 d	0.6 g	4.1 b	0.2 g	4.5 a	0.4 g	3.3 c	0.4 g
Penicillium italicum	5.5	15	0.6 a	0.3 c	0.6 a	0.2 d	0.2 d	0.1 e	0.6 a	0.2 d	0.5 b	0.1 e	0.2 d	0.1 e
	12.5	9	3.5 a	2.0 b	3.2 a	0.8 d	2.1 b	0.4 de	2.3 b	0.2 e	2.4 b	0.4 de	1.3 c	0.4 de
Penicillium expansum	5.5	17	1.4 a	1.1 b	1.5 a	1.1 b	0.5 d	0.5 d	1.4 a	0.8 c	1.0 b	0.2 e	0.5 d	0.2 e
	12.5	8	3.6 a	2.9 b	3.6 a	2.5 b	1.7 c	1.4 c	3.5 a	0.9 c	2.8 b	1.3 c	2.2 b	0.8 c
Phomopsis citri	5.5	15	0.6 ab	0.5 bc	0.6 ab	0.4 c	0.2 d	0.1 d	0.6 a	0.2 d	0.6 a	0.1 d	0.1 d	0.1 d
	12.5	13	2.5 ab	1.8 cdef	2.7 a	1.7 def	2.1 bcd	1.6 ef	2.8 a	1.1 g	2.7 a	1.1 fg	1.9 bcde	0.7 g
Phytophthora cactorum	5.5	13	0.6 a	0.6 a	0.6 a	0.6 a	0.1 c	0.1 c	0.7 a	0.6 a	0.6 a	0.4 b	0.1 c	0.1 c
	12.5	13	2.5 b	2.4 b	2.6 b	2.5 b	0.8 e	0.6 e	3.0 a	1.8 c	2.4 b	2.6 b	1.1 d	0.6 e
Phytophthora parasitica	5.5	12	0.6 a	0.4 b	0.6 a	0.4 b	0.4 b	0.4 b	0.4 b	0.4 b	0.4 b	0.4 b	0.3 b	0.4 b
	12.5	12	4.3 a	4.2 a	4.3 a	4.3 a	2.5 d	2.5 d	3.7 ab	3.3 b	3.6 ab	3.2 bc	2.6 cd	2.6 cd
Rhizopus stolonifer	5.5	8	8.1 b	5.7 d	8.5 b	5.5 d	0.5 f	1.0 f	9.3 a	7.2 c	5.9 d	2.7 e	1.3 f	0.4 f
	12.5	3	22.1 abc	21.8 bcd	23.3 ab	19.0 de	5.8 g	6.8 g	24.8 a	19.4 cde	17.7 e	18.6 e	11.1 f	10.1 f
Thielaviopsis paradoxa[z]	12.5	7	8.5 a	6.2 c	8.3 a	7.0 bd	3.8 def	3.1 f	7.8 ab	4.5 d	7.6 ab	6.2 c	3.4 ef	3.8 def
Verticillium theobromae[z]	12.5	15	1.1 a	0.5 bc	1.0 a	0.2 de	0.2 de	0.1 e	0.7 b	0.1 e	0.4 cd	0.1 e	0.1 e	0.1 e
Whetzelinia sclerotiorum	5.5	6	6.3 a	1.8 d	5.3 b	2.7 c	1.2 e	0.6 ef	3.2 c	0.7 ef	3.5 c	0.8 ef	0.8 ef	0.3 f
	12.5	3	18.8 a	3.9 d	19.8 a	4.0 d	3.4 d	2.8 de	10.0 c	1.4 ef	12.5 b	3.0 d	2.7 de	0.6 f

[w] O_2 levels of 21–16% were air or air diluted with tank CO or CO_2 while 2.3% O_2 was from air diluted with tank N_2, CO_2 and CO.
[x] Each figure is the average of four replicates.
[y] Numbers in horizontal columns followed by the same letter are not significantly different, $P = 0.01$, according to Duncan's multiple range test.
[z] *Verticillium theobromae* showed slight growth in air at 5.5 C; the other fungi showed no growth in air at 5.5 C.

of California) were an orange color when picked. These fruits were placed in storage at 5 C on the day of harvest, and the experiments were started 6 days later.

Lemons (*Citrus limon* Burm. 'Eureka'), which were obtained from a commercial orchard at Visalia, CA, were a yellow color when picked. These fruits were placed in storage at 10 C on the day of harvest, and the experiments were started 5 days later.

Apples (*Malus domestica* Borkh 'Yellow Newtown'), from a packing house in Watsonville, California, had been stored in controlled atmosphere (2–3% O_2 + 5–7% CO_2) at ~4 C for about 90 days. These fruits were stored at 5 C, and experiments were started 3 days later.

Strawberries (*Fragaria chiloensis* Duchesne var. *ananassa* Bailey 'Aiko') were obtained from a commercial shipper at Watsonville, CA. The berries had been placed at 0 C on the day of harvest and were returned to that temperature upon arrival at Davis after 3 hr without refrigeration. Experiment treatments were started within 24 hr after arrival.

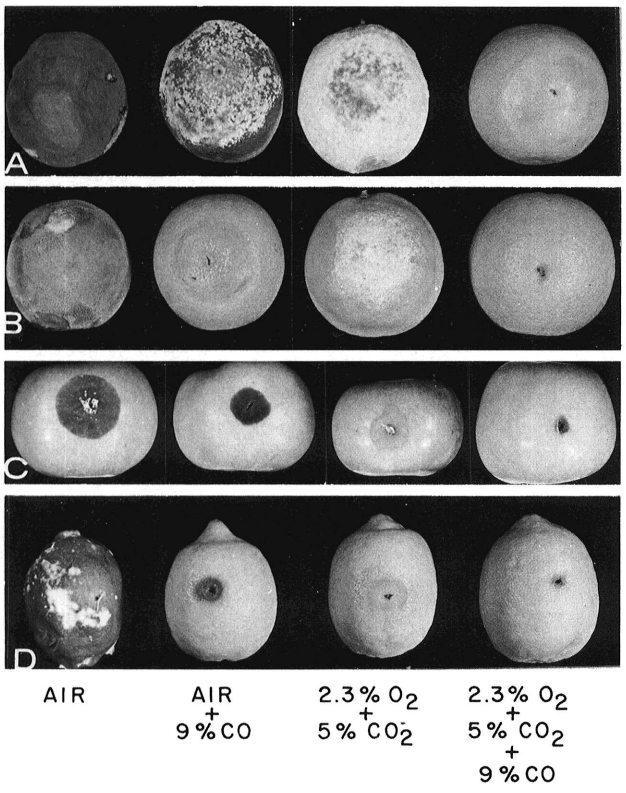

Fig. 1. Fruit rot in different atmospheres. **A,** Oranges after 22 days at 12.5 C following inoculation with *Penicillium digitatum*. **B,** Oranges after 22 days at 12.5 C following inoculation with *P. italicum*. **C,** Apples after 23 days at 5.5 C following inoculation with *P. expansum*. **D,** Lemons after 11 days at 12.5 C following inoculation with *Whetzelinia sclerotiorum*.

To determine the effect of different CAs on the radial growth of the test fungus cultures, four plates (each containing 20 ml of potato-dextrose agar [PDA])were centrally inoculated with 6-mm-diameter mycelial plugs obtained from the edge of a 4- to 10-day-old cultures.

Shaken liquid cultures initially were favored to permit measurement of the dry weight of mycelium. That method was rejected, however, due to problems of restricted gas permeation in the fungal pellets (1,17).

The dishes were vented by positioning a small piece of bent sterilized wire to raise the lid slightly. Plates were placed inside 8.5-L cylindrical glass chambers with aluminum covers fitted with inlet and outlet openings. These openings were connected to lines through which the desired humidified atmospheres flowed continuously. Air, nitrogen, CO_2, and CO, dispensed via capillary flow meters at a pressure of 50 cm of water as described by Claypool and Keefer (12), were mixed as required. In all tests the CO concentration was maintained at 9%, well below the flammable concentration (12%) in air. Gas streams through the chambers were adjusted to a flow rate of 83 ml/min, which was sufficient to avoid respiratory alteration of the atmospheres during tests. Effluent gases from the jars were analyzed periodically by gas chromatography to determine the concentration of O_2, CO_2, and CO. The mixing method was accurate within ± 5% of the final O_2, CO_2, or CO concentration.

Cultures were incubated in controlled atmospheres at 5.5 ± 0.5 C, and 12.5 ± 0.5 C. Colony diameters were measured daily from 3 to 24 days, depending on species and temperature, and growth rates were computed. Data were evaluated by analysis of variance and Duncan's multiple range test.

In preparation for in vivo studies, fruits were washed, surface-sterilized by immersion for 5 min in sodium hypochlorite solution (500 μg/ml), and air-dried. Oranges were inoculated with *Penicillium digitatum* or *P. italicum,* lemons with *Whetzelinia sclerotiorum*, and apples with *P. expansum*. Plugs (6mm in diameter) from a 3- to 6-day-old PDA culture were inserted with a dissecting needle into wounds (1 cm deep) in fruit tissue. Strawberry fruits were inoculated with a needle dipped in *B. cinerea* spore suspension (5×10^6 spore/ml).

Inoculum of *B. cinerea* was prepared by culturing the fungus on PDA in petri dishes. The conidia were harvested after 7 days by adding 20 ml of Tween-80 solution (one drop of Tween-80 in 100 ml of distilled water). Conidial concentration was determined with a Bausch and Lomb Spectronic 20 colorimeter. Absorbance at 490 nm was related to a concentration curve previously established for similar spore suspensions with a hemocytometer.

Inoculated fruits were placed inside 8.5-L cylindrical glass chambers, similar to those described previously. Gas streams were adjusted to 100 ml/min for oranges and lemons, 80 ml/min for apples, and 90 ml/min for strawberries. Atmospheres were: air, air + 9% CO, CA (2.3% O_2 + 5% CO_2), and CA + 9% CO. Uninoculated fruits also were included. Oranges and lemons were held at 12.5 ± 0.5 C for 22 and 11 days, respectively. Apples and strawberries were held at 5.5 ± 0.5 C for 23 and 19 days,

TABLE 3. The rate of rot development (millimeters diameter per day) for inoculated fruit in air and in controlled atmosphere (CA) in presence or absence of 9% CO

Treatments[v]	Oranges[w] *P. digitatum*	Oranges[w] *P. italicum*	Apples[x] *P. expansum*	Lemons[x] *W. sclerotiorum*	Strawberries[y] *B. cinerea*
Air	16.6 a[z]	3.8 a	1.2 a	17.9 a	2.1 a
Air + 9% CO	5.6 b	2.1 b	0.7 b	1.3 c	2.1 a
CA (2.3 O_2 + 5% CO_2)	9.1 c	3.7 a	0.6 b	3.6 b	1.2 b
CA + 9% CO	0.9 d	0.4 c	0.2 c	0.4 c	0.3 c

[v] Inoculated oranges and lemons were held at 12.5 ± 0.5 C for 22 and 11 days, respectively. Inoculated apples and strawberries were held at 5.5 ± 0.5 C for 23 and 19 days, respectively.
[w] Each treatment included three replicates of seven fruits each.
[x] Each treatment included three replicates of 10 fruits each.
[y] Each treatment included three replicates of 35 fruits each.
[z] Numbers in vertical columns followed by the same letter are not significantly different; $P = 0.01$, according to Duncan's multiple range test.

respectively. Every treatment included three replicates of 7–35 fruits each. After the required incubation period, fruits were examined for rot development, the diameters of the rot lesions were measured, and the growth rates were computed. Fifteen judges scored uninoculated fruits on a 0–10 scale for off-flavors. The examined fruits were returned to air at 20 C and reexamined after 3 days.

RESULTS AND DISCUSSION

The effects of the different atmospheres, in the presence or absence of 9% CO, on the radial growth of the fungi in culture are shown in Table 2. It was concluded that:

(i) Addition of 9% CO to air slowed the mycelial growth of certain fungi: by about 70% for *P. digitatum* and *W. sclerotiorum,* about 50% for *P. italicum* and *V. theobromae*, and about 20% for *M. fructicola, P. expansum, P. citri,* and *T. paradoxa*. The growth rates of the other tested fungi were about the same in air and in the 9% CO + air mixture.

(ii) Addition of 5% CO_2 to air slightly slowed the mycelial growth of two tested fungi (about 10% for *C. gloeosporioides* at 12.5 C and for *W. sclerotiorum* at 5.5 C), but it stimulated *M. fructicola* at 5.5 and 12.5 C. The other fungi grew about the same rate in 5% CO_2 as in air.

Growth of all the fungi was slowed in air + 18% CO_2; compared with those in air alone, they ranged from 6% (*R. stolonifer* at 5 C) to 85% (*P. citri* at 12.5 C); and the growth retardation was greater at 5.5 C than at 12.5 C.

(iii) The mycelial growth of certain fungi was reduced significantly from that in air by a low O_2 concentration (2.3%); by about 50% for *M. fructicola, P. parasitica,* and *W. sclerotiorum;* by about 40% for *P. italicum* and *V. theobromae*; and by about 20% for *A. caricae.* On the other hand, atmospheres containing 2.3% O_2 stimulated growth of *G. candidum* and *P. cactorum* by about 20%. The other fungi grew at about the same rate in 2.3% O_2 as in air.

(iv) The slowing of fungus growth in 9% CO generally was much greater if the atmosphere was low in O_2 (2.3%). That combination greatly reduced growth of all the fungi except *P. cactorum* (at 5.5 C). For example, growth reduction was about 95% for *M. fructicola, P. digitatum,* and *P. italicum* at 12.5 C, and about 90% for *W. sclerotiorum.*

(v) When both 9% CO and 5% CO_2 were added to air, mycelial growth generally was slower (except by *B. theobromae, G. candidum,* and *P. cactorum*) than when either was added alone.

(vi) When both 9% CO and 18% CO_2 were added to air, the mycelial growth of all test fungi generally was slower than when either was added alone.

(vii) In most cases, growth was further suppressed when CO_2 (5 or 18%) was added to the 2.3% O_2 + 9% CO atmosphere.

Based on data for the effects of different CAs on the rate of development of fruit rots (Table 3 and Fig. 1), it is evident that adding 9% CO to air or CA atmospheres slowed rot development by *P. digitatum* and *P. italicum* in oranges at 12.5 C or by *P. expansum* in apples during 23 days at 5 C. However, CO (9%) added to a CA was significantly more effective than 9% CO in air. Compared with those in air, the rates of rot development caused by *P. digitatum* in oranges incubated in air + CO, in CA, and in CA + CO were reduced by 67, 45, and 94%, respectively. The rates of rot development of *P. italicum* in oranges in atmospheres of air + CO, in CA, and in CA + CO were reduced by 44, 2, and 90%, respectively. Similarly, the rates of rot development by *P. expansum* in apples in atmospheres of air + CO, in CA, and in CA + CO were reduced by 42, 51, and 78%, respectively, of that in air. The rotted area of apples held in CA (2.3% O_2 + 5% CO_2) did not turn brown (Fig. 1), but when the same fruits later were exposed to air for 24 hr the lesions turned brown normally. It is likely that suppression of browning in CA storage was the consequence of the low O_2 concentration.

Growth of *Whetzelinia sclerotiorum* in lemons during 11 days at 12.5 C was less in 9% CO in air or CA than in air (Fig. 1). In this case, however, the effect of 9% CO added to CA was not significantly better than that of 9% CO in air. The rates of rot development in atmospheres of air + CO, in CA, and in CA + CO were reduced by 93, 80, and 98%, respectively.

Compared with air, CO (9%) in CA caused an 84% suppression of *B. cinerea* development in strawberries during a 19-day period at 5 C. Compared with rot development in air, that in CA alone was reduced 45%. Rates of rot development in fruits held under 9% CO in air were similar to those in fruits held in air alone.

No phytotoxicity was observed in fruits held in any of the atmospheres tested. Off-flavors were negligible or absent in apples stored in different CA conditions (Table 4). Oranges had slight off-flavor, especially under 2.3% O_2 + 5% CO_2, and strawberries developed moderate off-flavors under CA or CA + 9% CO. In general, the off-flavors appeared to be associated with O_2 and CO_2 modification, but not with CO addition. Thus, CO may provide an important improvement in CA storage if future studies confirm the apparent absence of CO-induced off-flavors at useable concentrations. Carbon monoxide forms complexes with cytochrome oxidase and thus inhibits respiration. It is conceivable that CO and low O_2 combinations may be more effective than low O_2 and CO_2 in suppressing respiration without the accumulation of intermediate products associated with off-flavors.

Use of CO in storage or transit atmospheres requires special safety precautions. In air, CO is flammable at concentrations between 12 and 75% (v/v). Therefore, the highest safe concentration for commercial use is probably < 10%. Because it is an odorless poison, transit containers and CA rooms require thorough ventilation before entry. Visual or audible warning devices must be employed in locations where CO might be present.

TABLE 4. Mean scores[w] of off-flavor of orange, apple, and strawberry fruits held in air and in controlled atmosphere (CA) in the presence or absence of 9% CO

Treatments[x]	Oranges	Apples	Strawberries
Air	0.7[y]	0.0[y]	1.3 b[z]
Air + 9% CO	0.3	0.6	1.6 b
CA (2.3% O_2 + 5% CO_2)	2.8	0.5	4.3 a
CA + 9% CO	1.1	0.7	4.4 a

[w] Scores 0–10 indicate increasing off-flavor.
[x] Oranges were held at 12.5 ± 0.5 C for 22 days. Apples and strawberries were held at 5.5 ± 0.5 C for 23 and 19 days, respectively.
[y] No significant difference.
[z] Numbers followed by the same letter are not significantly different; $P = 0.01$, according to Duncan's multiple range test.

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