# BIOCHEMICAL AND PHYSIOLOGICAL BASIS FOR EFFECTS OF CONTROLLED AND MODIFIED ATMOSPHERES ON FRUITS AND VEGETABLES

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☐ VARIOUS ASPECTS of controlled-atmosphere (CA) and modified-atmosphere (MA) transport and storage have been reviewed during the past few years, including responses of fruits and vegetables to CA (Lipton, 1975; Smock, 1979; Isenberg, 1979; Brecht, 1980; Kader, 1980; Dewey, 1983). Burton (1974; 1978) discussed some of the biophysical, biochemical, and physiological aspects of modified atmospheres in relation to quality maintenance of fruits and vegetables. Lougheed et al. (1978) and Jamison (1980) summarized the effects of hypobaric (low-pressure) storage on horticultural crops. Dewey (1983) and Bartsch and Blanpied (1984) reviewed requirements for structure and operation of CA facilities.

Much research has been directed toward determination of the optimum CA conditions for a large number of fruits and vegetables and specific cultivars of each commodity (Dewey et al., 1969; Dewey, 1977; Richardson and Meheriuk, 1982). As of May 1985, the number of published reports dealing with MA reached about 4,000 (Morris et al., 1971; Murr et al., 1974; Kader and Morris, 1977; 1981; Kader, 1985b). But less than 10% of these reports dealt with the mode of action of reduced oxygen and elevated carbon dioxide concentrations, i.e., the biochemical and physiological basis for MA effects on fruits and vegetables.

Generally, the effect of reduced $O_2$ and/or elevated $CO_2$ on reducing respiration rate has been assumed to be the primary reason for the beneficial effects of CA on fruits and vegetables. This is an oversimplification, since postharvest deterioration of fresh produce can be caused by many factors in addition to high respiration rate, including: metabolic changes (biochemical changes associated with respiratory metabolism, ethylene biosynthesis and action, and compositional changes); growth and development (anatomical and morphological changes); physical injuries; water loss; physiological disorders; and pathological breakdown. This article will discuss the possible direct and indirect effects of CA on each of these causes of deterioration.

## Respiratory Metabolism

Lowering the $O_2$ level around fresh fruits and vegetables reduces their respiration rate in proportion to the $O_2$ concentration, but a minimum of about 1–3% $O_2$, depending on the commodity, is required to avoid a shift from aerobic to anaerobic respiration. Under such conditions, the glycolytic pathway replaces the Krebs cycle as the main source of the energy needed by the plant tissues. Pyruvic acid is no longer oxidized but is decarboxylated to form acetaldehyde, $CO_2$, and, ultimately, ethanol; this results in development of off-flavors and tissue breakdown. Although the $O_2$ level at which anaerobic respiration occurs may be as low as 0.2% within the plant cell, the gradient of $O_2$ concentration from that point to the external atmosphere requires maintenance of about 1–3% $O_2$ around the commodity, depending on its respiration ($O_2$ consumption) rate and gas diffusion characteristics of the dermal and subdermal tissues of the specific cultivar of a given commodity.

Robinson et al. (1975) measured respiration ($CO_2$ production) rates in air and in 3% $O_2$ at 0, 10, and 20°C of 30 fresh vegetables and soft fruits. They found a reduction of respiration rate in 3% $O_2$ relative to that in air of 10–46% at 0°C and 20–60% at 10 or 20°C. The decrease in respiration rate in response to reduced $O_2$ levels (of not less than about 2%) is not the result of suppression of the basal metabolism mediated by cytochrome oxidase, which has a Km value of $10^{-8}$ to $10^{-7}$ M $O_2$ (Burton, 1978; Solomos, 1982). Rather, it appears that such reduction stems from the diminution of the activity of other oxidases (such as polyphenol oxidase, ascorbic acid oxidase, and glycolic acid oxidase) whose affinity for $O_2$ may be 5–6 times lower than that of cytochrome oxidase (Solomos, 1982). Further reduction in $O_2$ concentration, to a level influencing uptake by cytochrome-c oxidase, could have marked effects upon the metabolism of the stored material, possibly beneficial though not necessarily so, with danger of anaerobiosis in part of the material (Burton, 1978).

Elevated $CO_2$ concentrations also reduce the respiration rate of fresh fruits and vegetables, but above a level of about 20% or higher, depending on the commodity and the $O_2$ concentration, $CO_2$ can result in accumulation of ethanol and acetaldehyde within the tissues. $CO_2$ concentrations of about 10% resulted in formation of aldehyde and ethanol in black currants (Smith, 1957), mango fruits (Lakshminarayana and Subramanyam, 1970), and citrus fruits (Davis et al., 1973), indicating a shift toward anaerobic respiration. The effects of reduced $O_2$ and elevated $CO_2$ on respiration rate and the shift from aerobic to anaerobic respiration are additive: 10% $CO_2$ added to air influences respiratory metabolism to about the same extent as a 2% $O_2$ atmosphere, and the combination of 2% $O_2$ + 10% $CO_2$ has double the effect of either component alone.

Storage of fruits and vegetables in 5–20% $CO_2$ can cause changes in the activities of specific enzymes of the respiratory metabolism and may have an uncoupling effect on oxidative phosphorylation. Studies of the effects of high $CO_2$ levels on Krebs cycle intermediates and enzymes have shown accumulation of succinic acid due to inhibition of succinic dehydrogenase activity in apples (Hulme, 1956; Knee, 1973; Monning, 1983), pears (Frenkel and Patterson, 1973), and lettuce (Brecht, 1973). Shipway and Bramlage (1973) found that $CO_2$ levels above 6% stimulated malate oxidation and suppressed oxidation of citrate, $\alpha$-ketoglutarate, succinate, fumarate, and pyruvate in mitochondria isolated from apples. Ultrastructural changes in 'Bartlett' pears stored in CA, including fragmentation, reduction in size, and changes in shape of mitochondria, were reported by Frenkel and Patterson (1977). The ultrastructural changes caused by elevated $CO_2$ were similar to those associated with senescence.

Monning (1983) reported that elevated $CO_2$ inhibited glycolysis and succinic dehydrogenase activity and reduced formation of citrate/isocitrate and $\alpha$-ketoglutarate, but that malic dehydrogenase activity was not influenced by exposing apple tissue to 10% $CO_2$. There are no published reports concerning the effects of high $CO_2$ levels on the glycolytic enzymes. Such information, especially for phosphofructokinase and pyruvic kinase, which are important regulatory enzymes in the glycolytic pathway, would help elucidate the mode of action of $CO_2$ on the respiratory metabolism.

## Ethylene Biosynthesis and Action

Reduced $O_2$ levels below 8% decrease ethylene production by fresh fruits and vegetables and reduce their sensitivity to ethylene. Burg and Burg (1967; 1969) demonstrated that $O_2$ is required for ethylene production and action. At 2.5% $O_2$,

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ethylene production is halved and fruit ripening is retarded. At 3% $O_2$, the binding of ethylene is reduced to about 50% of that in air (Burg and Burg, 1967). Under anaerobic conditions, the conversion of 1-aminocyclopropane-1-carboxylic acid (ACC) to ethylene is inhibited; this results in accumulation of ACC in the tissue, since earlier steps in ethylene biosynthesis from methionine occur in the absence of $O_2$ (Yang, 1985). Lau et al. (1984) found that storage of 'Golden Delicious' apples in 2.5% $O_2$ suppressed internal ethylene concentration and ACC accumulation. The extent of ACC accumulation was closely related to the subsequent flesh softening and increase in internal ethylene concentration, and these processes were suppressed in CA-stored fruit.

Elevated $CO_2$ levels can reduce, promote, or have no effect on ethylene production rates by fruits, depending on the commodity and the $CO_2$ concentration. It appears that the increase in ethylene production by some commodities during and/or following exposure to $CO_2$ occurs only when the $CO_2$ concentration is high enough to cause physiological injury to the tissue. It is not known whether this high-$CO_2$-stress–induced ethylene is due to a partial shift from aerobic to anaerobic conditions or to other mechanisms.

Chaves and Tomas (1984) observed a reduction in ethylene production by 'Granny Smith' apples following exposure to 20% $CO_2$ for 2 hr. This treatment increased the ACC content of the tissue, indicating a possible effect of elevated $CO_2$ on the enzyme system responsible for the conversion of ACC into ethylene.

$CO_2$ prevents or delays many responses of fresh fruits and vegetables to ethylene. These responses, which can be detrimental to quality, include accelerated softening, increased abscission, and induced physiological disorders (Kader, 1985a). The presence of 10% $CO_2$ abolishes the biological activity of 1 ppm ethylene (Burg and Burg, 1967), but the effectiveness of elevated $CO_2$ levels is reduced at higher ethylene concentrations. In certain fruits, $CO_2$ accumulates in the intercellular space and functions as a natural ethylene antagonist (Yang, 1985). The mode of action of $CO_2$ in inhibiting or reducing ethylene effects is not known, but Burg and Burg (1967) suggested that $CO_2$ competes with ethylene for the binding site. Beyer (1985) reported that $CO_2$ can affect ethylene metabolism by inhibiting ethylene oxidation to $CO_2$ through a feedback inhibition mechanism.

Although low $O_2$ and/or high $CO_2$ concentrations reduce ethylene production rates and render fresh fruits and vegetables less susceptible to its action, harmful concentrations of ethylene can still accumulate under CA conditions, especially for those fruits that normally produce high levels of ethylene such as ripening apple, pear, avocado, cherimoya, and kiwifruit. In such cases, an effective system of ethylene removal from the CA storage room can significantly reduce softening rate and delay deterioration (Kader, 1980).

## Compositional Changes

Many of the compositional changes which occur in harvested fruits and vegetables influence their color, texture, flavor, and nutritive value. While some of these changes are desirable, others are detrimental to the quality of the commodity. CA can influence the rate of compositional changes, as illustrated by the following examples.

• **Color.** Loss of chlorophyll (green color) and biosynthesis of carotenoids (yellow and orange colors) and anthocyanins (red and blue colors) are slowed down in fruits and vegetables kept in CA (Wankier et al., 1970; Wang et al., 1971; Isenberg, 1979; Smock, 1979). Knee (1980) reported that the rate of chlorophyll degradation in peel and cortex of apples was half maximal at 2.5–4% $O_2$. Goodenough and Thomas (1980) found that the storage of tomatoes in 2.5–4% $O_2$ + 4% $CO_2$ for up to 2 mo at 12.5°C resulted in reduction in chlorophyll loss and lycopene synthesis. Anthocyanin development is delayed in plums kept in 2% $O_2$ + 5% $CO_2$, relative to those kept in air at 10 or 20°C (Kader, unpublished data).

Elevated $CO_2$ can result in detrimental effects on color of some commodities during CA storage and following transfer to air. Examples include uneven red color development in tomatoes picked at the mature-green stage and kept in more than 5% $CO_2$; appearance of grayish-yellow color in cauliflower upon cooking following exposure to 15% $CO_2$; and migration of anthocyanins (red color) toward the external tissues of strawberries kept in 30% $CO_2$ for 2 days or longer. Brown discoloration of external or internal tissues can occur as a result of high $CO_2$ and/or reduced $O_2$ levels beyond those that are tolerated by a given commodity. Nassar (1966) and Yahia et al. (1983) found that elevated $CO_2$ concentrations (5–15%) increased browning of grapes.

Murr and Morris (1974) reported that 0% $O_2$ was needed to arrest o-phenol oxidase activity and brown discoloration of the cap in mushrooms. $CO_2$ concentrations above 5% enhanced discoloration, even when suppressing o-phenol oxidase activity. On the other hand, Buescher and Henderson (1977) found that 10–30% $CO_2$ delayed brown discoloration of mechanically damaged tissue in green beans via its decrease of phenolics content, phenolase activity, and oxidation of phenolics. The effect of elevated $CO_2$ on inhibition of phenolics production and polyphenol oxidase activity was also observed in lettuce tissue (Siriphanich and Kader, 1985a). However, once the lettuce tissue was removed to air, browning resumed.

• **Texture.** CA conditions delay fruit ripening and softening. For example, Knee (1980) found that the rates of flesh softening and soluble polyuronide formation in apples were half maximal at 2.5–4.0% $O_2$. Goodenough et al. (1982) reported that the appearance of polygalacturonase was prevented by storing mature-green tomatoes in 5% $O_2$ + 5% $CO_2$ for up to 8 weeks at 12.5°C. On removal of the tomatoes to ambient conditions, polygalacturonase was synthesized and fruit softening and red pigmentation resumed. The rate of kiwifruit softening during storage at 0°C for up to 24 weeks was significantly reduced in fruits exposed to 2% $O_2$ + 5% $CO_2$ relative to those kept in air (Arpaia et al., 1985); elevated $CO_2$ had a greater effect on firmness retention than reduced $O_2$. Elevated $CO_2$ atmospheres slow down the softening rate of strawberries and bush berries. The effect of $CO_2$ on firmness retention is often noticeable after transfer of the berries to air.

CA can also influence the textural quality of nonfruit vegetables. Lipton (1975) reported that 12 ± 2% $CO_2$ retarded toughening of asparagus spears kept at 4°C or lower. Storing broccoli in 10% $CO_2$ for up to 2 weeks at 5°C made it more tender relative to broccoli kept in air; this tenderization seems to be related to $CO_2$-mediated increase in pH of the tissue (Lipton and Harris, 1974). Reduced $O_2$ had little effect on tenderness of asparagus or broccoli (Lipton, 1975). The mechanism of CA effects on texture of fresh fruits and vegetables is not fully understood and merits further investigation.

• **Flavor.** Changes in carbohydrates, organic acids, proteins, amino acids, lipids, and phenolic compounds can influence the flavor of fresh fruits and vegetables. Starch-to-sugar conversion, which is undesirable in table and processing potatoes kept at 2°C, can be slowed down by storage in 5–20% $CO_2$ or in less than 3% $O_2$, but such treatments may increase sprouting (Burton, 1974). Sherman and Ewing (1983) found that storage of potatoes in 2.5% $O_2$ at 1°C prevented the increase in reducing sugars and improved the chip color relative to potatoes kept in air. Elevated $CO_2$ can also reduce the rate of sugar-to-starch conversion, which is undesirable in peas and sweet corn. Goodenough and Thomas (1981) found that CA conditions slowed down the losses in sugars and organic acids in tomatoes during storage at 12.5°C for up to 2 mo. Goodenough (1982) observed an increase in glucose, fructose, and citric acid and a decrease in starch and malic acid in tomatoes kept in 5% $O_2$ + 5% $CO_2$. However, there was no change in the multiple form pattern of several respiratory enzymes, including alcohol dehydrogenase, malic enzyme, isocitrate dehydrogenase, phosphogluconate dehydrogenase, glucose-6-phosphate dehydrogenase, and NADH dehydrogenase. He suggested that CA allowed changes which rely on enzyme regulation but prevented events which involve *de novo* enzyme synthesis.

CA storage reduced losses in acidity in fresh fruits. A 2.5% $CO_2$ atmosphere maintained a higher titratable acidity in 'Golden Delicious' apples during an 8-mo storage period (Lau and Looney, 1982). Brecht et al. (1982) reported that 2% $O_2$ + 5% $CO_2$, which extended the preprocessing storage life of clingstone peaches by 1–3 weeks beyond air storage, maintained fresh firmness and acidity (lower pH). Nassar (1966) found that 5–15% $CO_2$ resulted in accumulation of $\alpha$-amino butyric and succinic acids and reduction of aspartic and glutamic acids in grapes.

Increased pH (decreased acidity) following exposure to elevated $CO_2$ has been reported in several vegetables, including broccoli and cauliflower (Lipton, 1975). Siriphanich and Kader (1986) reported that immediately following removal of lettuce tissue from 5–15% $CO_2$ atmospheres, an increase in acidity and a decrease in pH occurred, but that soon thereafter the opposite trend was observed. It is not known whether this pH increase is just a consequence of $CO_2$ effects on normal metabolism or is a direct reaction by plant tissue to counteract the acidic effects of $CO_2$.

Li and Hansen (1964) found that pears kept in 2% $O_2$ + 2% $CO_2$ at −1 to 0°C maintained their capacity for protein synthesis better than those stored in air. CA conditions prevent ethylene-induced formation of isocoumarin, with resultant bitter flavor, in carrots (Burton, 1974; Kader, 1985a). Exposure of persimmons to 50–70% $CO_2$ for 24 hr at 20–25°C results in removal of astringency without tissue softening (Matsou and Ito, 1977).

CA storage, especially for extended durations, can decrease the production rate of volatiles by apples, pears, and other fruits. Knee and Hatfield (1981) studied the interconversion of short-chain aliphatic alcohols, aldehydes, and esters of apples kept in air or 2% $O_2$ and found that the low levels of esters in apples from low-$O_2$ atmospheres were a consequence of low rates of alcohol synthesis. This effect is reversible after removal of apples from CA storage. However, fruits picked at the preclimacteric stage and stored in 1–2% $O_2$ for long durations may lose their capacity to produce the required concentrations of volatiles to attain a good aroma.

Off-flavors can develop in any fresh fruit or vegetable if it is exposed to $O_2$ and/or $CO_2$ levels that result in anaerobic respiration and formation of ethanol and acetaldehyde. For example, undesirable odor occurred in broccoli kept in less than 0.5% $O_2$ or more than 15% $CO_2$ (Kasmire et al., 1974). Although the accumulated ethanol and acetaldehyde can be removed from plant tissues by aeration, the extent of removal depends on the duration of exposure to CA conditions which allow the shift from aerobic to anaerobic respiration.

● **Nutritive Value.** Generally, CA storage results in better retention of ascorbic acid in fresh fruits and vegetables than storage in air. Ascorbic acid losses in spinach kept in 4% $O_2$ + 9% $CO_2$ were about 50% of the losses in spinach stored in air (McGill et al., 1966). Wang (1983) reported that 1% $O_2$ was very effective in retaining ascorbic acid content of Chinese cabbage, in delaying losses in sugars and chlorophyll contents, and in extending the storage life at 0°C to 5 mo, compared to less than 3 mo in air.

## Growth and Development

Sprouting of potatoes, onions, garlic, and root crops greatly reduces their utilization value and accelerates deterioration. Rooting of onions and root crops is also undesirable. Asparagus spears continue to grow after harvest; elongation and curvature (if the spears are held horizontally) are accompanied by increased toughness and decreased palatability.

Sprouting of potatoes is inhibited by exposure to 15% $CO_2$ at 10°C, but 2–5% $CO_2$ stimulated sprouting. Reduced $O_2$ atmospheres (2–4%) encouraged potato sprouting (Burton, 1974). Sprouting and rooting were inhibited when onions were kept in 3% $O_2$ + 5–10% $CO_2$ at 1°C (Isenberg, 1979). Storage in 2.5% $O_2$ inhibited sprouting and rooting of carrots, but increased decay problems. Root hair growth was suppressed by 1% $O_2$ or lower concentrations. Isenberg (1979) suggested that CA may influence the levels of endogenous growth regulators which control sprouting and rooting of propagules. However, the mechanism involved is yet to be elucidated. $CO_2$ levels above 10% and $O_2$ levels below 5% prevent wound healing through periderm formation on potatoes (Lipton, 1975).

Elongation of cut asparagus spears is inhibited by elevated $CO_2$. Holding asparagus spears at 2°C in 15% $O_2$ + 15% $CO_2$ significantly retarded opening of the leaf scales on the tip and lignification which results in increased toughness (Lipton, 1975; Isenberg, 1979). An atmosphere containing 1% $O_2$ and/or 5% $CO_2$ prevented cap opening of mushrooms for up to 5 weeks at 0°C. Sporophore elongation was greatly reduced in mushrooms kept in 15% $CO_2$ or 0.25–1% $O_2$ (Murr and Morris, 1974; Burton, 1974; Isenberg, 1979).

## Physical Injuries

Various types of physical damage such as surface injuries, impact bruising, and vibration bruising are major contributors to deterioration. These injuries not only are unsightly but also accelerate water loss, provide loci for fungal infection, and stimulate $CO_2$ and ethylene production by the commodity. While CA has no direct effect on incidence of physical injuries, some indirect effects on their consequences are possible. As mentioned above, CA conditions can interfere with the wound-healing processes in potatoes. Both reduced $O_2$ (less than 5%) and elevated $CO_2$ (especially above 10%) have been shown to reduce suberization and prevent periderm formation in potato tubers (Wigginton, 1974; Lipton, 1975).

Certain CA combinations inhibit or at least reduce brown discoloration of physically injured tissues as a result of their effects on phenolic metabolism. Carbon monoxide at 2–3% has also been shown to inhibit brown discoloration of cut surfaces in lettuce and other commodities (Kader, 1983). CA can reduce physical-stress-induced increase in $CO_2$ and ethylene production rates.

## Water Loss

Water loss can be one of the main causes of deterioration, since it not only results in direct quantitative losses (loss of salable weight), but also causes losses in appearance (due to wilting and shriveling), texture (softening, flaccidity, limpness, loss of crispness and juiciness), and nutritional quality. CA does not directly influence rate of water loss, but its possible effects on reducing periderm formation in commodities such as potatoes and sweet potatoes render them more susceptible to water loss. On the other hand, the need for a gas-tight environment for CA storage and transport often results in significantly higher relative humidity around the commodity and consequently reduced water loss compared to air storage.

## Physiological Disorders

Fresh fruits and vegetables are subject to numerous physiological disorders which result from exposure to undesirable temperatures and/or levels of ethylene, $CO_2$, and $O_2$. CA conditions may alleviate, induce, or aggravate these physiological disorders, as illustrated by the following examples:

● **Disorders Alleviated by CA.** Elevated $CO_2$ (5–20%) has been shown to reduce severity of chilling-injury symptoms in several commodities, including okra, chili pepper, avocado, peach, and 'Fuyu' persimmons. Mencarelli et al. (1983) reported that 1, 2, or 4% $O_2$ ameliorated chilling injury on squash fruits kept at 2.5°C. CA conditions reduced the severity of certain physiological disorders such as scald on apples and pears (Smock, 1979). Elevated $CO_2$ and/or reduced $O_2$ levels can significantly reduce ethylene-induced physiological disorders, such as russet spotting of lettuce and flesh translucency of kiwifruit (Kader, 1985a).

● **Disorders Aggravated by CA.** Elevated $CO_2$ in combination with ethylene induced white core inclusions in kiwifruit (Arpaia et al., 1985). Exposure of some chilling-sensitive commodities, such as cucumber, bell pepper, and mature-green tomato, to CA conditions at chilling temperatures aggravates the chilling-injury symptoms.

● **Disorders Induced by CA.** Exposure of fresh fruits and vegetable to $O_2$ levels below or $CO_2$ levels above their tolerance limits results in various physiological disorders, including impaired ripening of climacteric fruits such as tomato, melons, and plum; internal browning of lettuce, celery, cabbage, apple, pear, peach, and other commodities; external brown discoloration of tomato skin, pepper calxy, and lettuce; and surface pitting of cucumber, mushroom, apple, and pear. However, the mechanisms by which reduced

$O_2$ and/or elevated $CO_2$ induces these physiological disorders are not known.

Elevated $CO_2$ concentrations inhibit the activity of succinic dehydrogenase, resulting in accumulation of succinic acid, a toxicant to plant tissues (Hulme, 1956; Williams and Patterson, 1964; Frenkel and Patterson, 1973). But this observation does not provide an adequate explanation for $CO_2$-induced brown stain on lettuce, since Brecht (1973) found the accumulation of succinic acid in lettuce kept in air + 5% $CO_2$ to be greater at 10 and 15°C than at lower temperatures, while $CO_2$ injury was much more severe at the lower temperatures.

In a study of $CO_2$ effects on phenolic metabolism in lettuce tissue, Siriphanich and Kader (1985a) found that 15% $CO_2$ induced phenylalanine ammonia lyase activity which correlated well with the development of brown stain. Phenolics production and polyphenol oxidase activity were reduced in the presence of $CO_2$; but once the lettuce tissue was removed to air, phenolic oxidation resumed and brown stain symptoms became visible. Siriphanich and Kader (1985b) reported that 15% $CO_2$ prevented the development of cinnamic acid-4-hydroxylase in lettuce tissue. Subsequent removal of $CO_2$ did not allow the enzyme development to proceed, whereas total phenolic content increased and browning occurred. Thus, the effect of $CO_2$ on inhibition of lettuce-tissue browning does not appear to involve this enzyme. Subjecting lettuce tissue to 15% $CO_2$ at 0°C for 6 days resulted in a decrease of about 0.4 and 0.1 pH unit in the cytoplasm and vacuole, respectively. However, once the lettuce was removed to air, an increase in pH was noted (Siriphanich and Kader, 1986). The authors also found that lettuce kept in air had a higher glucose-6-phosphate content than $CO_2$-treated lettuce. Exposure of lettuce to light at 0°C reduced $CO_2$ injury by about 50% relative to tissue kept in the dark. The possible involvement of reduced energy supply in $CO_2$ injury of lettuce merits further investigation.

## Pathological Breakdown

One of the most common and obvious symptoms of deterioration results from the activity of bacteria and fungi. Attack by most organisms follows physical injury or physiological breakdown of the commodity. In a few cases, pathogens can infect apparently healthy tissues and become the primary cause of deterioration. In general, harvested fruits and vegetables exhibit considerable resistance to potential pathogens during most of their postharvest life. The onset of ripening in fruits and senescence in all commodities results in their becoming susceptible to infection by pathogens. CA conditions delay senescence, including fruit ripening, and consequently reduce susceptibility of fruits and vegetables to pathogens. On the other hand, CA conditions unfavorable to a given commodity can induce physiological breakdown and render it more susceptible to pathogens.

CA may also directly influence the pathogens and reduce postharvest decay problems. The $O_2$ and $CO_2$ concentrations required to inhibit growth and/or spore germination vary with the species of fungi, but, generally, $O_2$ levels below 1% and/or $CO_2$ levels above 10% are needed to significantly suppress fungal growth (El-Goorani and Sommer, 1981). However, not all fresh fruits and vegetables will tolerate such concentrations of $O_2$ and $CO_2$ without physiological injury.

Elevated $CO_2$ (10–20%) has been shown to be effective in suppressing fruit rot in strawberries (El-Kazzaz et al., 1983), blackberries (Morris et al., 1981), and other berries, as well as cherries, fresh figs, and other fruits that tolerate such $CO_2$ levels (El-Goorani and Sommer, 1981).

Carbon monoxide (CO) at 5–10% is a fungistatic gas which suppresses fungal growth. Its relative effectiveness depends on the pathogen and is greatly enhanced when it is combined with less than 5% $O_2$ (El-Goorani and Sommer, 1981; Kader, 1983). Yahia et al. (1983) found that a combination of 2% $O_2$ + 10% CO was as effective as the currently used $SO_2$ treatment in controlling decay of grapes kept at 0°C for up to 4 mo and caused less browning and bleaching than $SO_2$. The mechanism of CO action in suppressing fungal growth is not known. It may affect the physiology of the fungus, or the host, or both. Peiser et al. (1982) found that $^{14}CO$ is metabolized in lettuce tissue to primarily $^{14}CO_2$, which is the precursor of acid-stable products with malate as the predominant product.

## Need More Research on Mechanism

It is clear from this review that CA can influence directly or indirectly all causes of postharvest deterioration of fresh fruits and vegetables and consequently their quality and postharvest life. Although much research has been done to find the optimum $O_2$ and $CO_2$ levels for each commodity and cultivar within a commodity, the mode of action of reduced $O_2$ and elevated $CO_2$ is still largely unknown. It is hoped that greater research efforts will be directed in the future toward improving our understanding of how reduced $O_2$ and elevated $CO_2$ levels influence respiratory metabolism, ethylene biosynthesis and action, and compositional changes related to quality attributes of fresh fruits and vegetables. Such information will no doubt help in expanding the use of CA or MA during transport and storage of perishable commodities.

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