Postharvest quality maintenance in fresh fruits and vegetables is greatly influenced by the temperature, relative humidity, and atmospheric composition (oxygen, carbon dioxide, and ethylene concentrations) of their environment. The optimum controlled atmosphere (CA) conditions for maintaining quality between harvest and consumption vary among commodities and cultivars. CA conditions retard loss of chlorophyll (green color), biosynthesis of carotenoids (yellow and orange colors) and anthocyanins (red and blue colors), and biosynthesis and oxidation of phenolic compounds (brown color). Textural quality is affected since the activity of polygalacturonase and solubilization of pectins that cause fruit softening and lignification leading to toughening of vegetables are delayed under CA conditioning. CA also influences flavor quality by reducing loss of acidity, starch to sugar conversion, interconversions of sugars, and biosynthesis of flavor volatiles. Retention of ascorbic acid and other vitamins result in better nutritional quality to fruits and vegetables kept under CA conditions.

The term quality used in reference to fresh fruits and vegetables may refer to market quality, shipping quality, edible quality, desert quality, nutritional quality, internal quality, or appearance quality (1). Different aspects of quality are of primary importance to producers, shippers, sellers and consumers of fresh fruits and vegetables. The rate of postharvest deterioration of flavor and nutritional quality is generally faster than that of appearance and texture quality of fresh produce.

Maintaining the quality of any fresh horticultural commodity begins with producing and selecting a good quality product. Subsequent handling to minimize physical injury, insure proper sanitation, and maintain proper temperature and humidity will contribute to the postharvest maintenance of quality. Once these
requirements have been fulfilled, additional postharvest life may be achieved through modification of the atmosphere surrounding the product. Reducing the oxygen (O$_2$) concentration and/or increasing the carbon dioxide (CO$_2$) concentration can reduce the commodity's respiration and sensitivity to ethylene (C$_2$H$_4$), thereby maintaining its freshness and quality longer than might otherwise be possible. However, if any environmental parameter varies outside the tolerance limit of the product, quality will rapidly decline.

Several aspects of the quality of fresh fruits and vegetables have been recently reviewed (1-8).

Controlled atmosphere (CA) or modified atmosphere (MA) storage refers to reduction of O$_2$ and/or elevation of CO$_2$ to levels different from those in air. The addition of carbon monoxide (CO) or removal of C$_2$H$_4$ may also be involved. CA implies a greater degree of precision in maintaining specified levels of O$_2$ and CO$_2$ than MA.

The beneficial effects of CA in prolonging the postharvest life of apples have been recognized for more than 60 years (9). During that time, a large body of research literature has accumulated, most aimed at identifying optimum CA conditions for various commodities and cultivars. This paper presents an overview of the relatively small portion of this literature that addresses the mechanisms by which CA affects the metabolism of plant tissues and the specific effects of CA on fruit and vegetable quality.

Effects of CA on Postharvest Physiology

Reducing the O$_2$ concentration around fresh fruits and vegetables reduces their respiration rate to an extent that varies with temperature, commodity, cultivar, and physiological age at harvest. Below a minimum of about 1 to 2% O$_2$, a shift from aerobic to anaerobic respiration occurs with a concomitantly increase in CO$_2$ production (10). The reduction in aerobic metabolism associated with reduced O$_2$ levels is apparently not mediated by cytochrome oxidase, which has a $K_m$ value of $10^6$ to $10^7$ M O$_2$ (11,12). It is more likely that reduction of aerobic respiration results from diminished activity of other oxidases such as ascorbic acid oxidase, polyphenol oxidase (PPO), and glycolic acid oxidase, whose affinities for O$_2$ are 5 to 6 times lower than that of cytochrome oxidase (12).

Elevating the CO$_2$ concentration can also have a suppressive effect on respiratory metabolism, depending upon temperature, commodity and cultivar. Levels of CO$_2$ above the limits of tolerance of the particular commodity can also result in accumulation of acetaldehyde and ethanol within the tissues indicating a shift to anaerobic respiration (13). Elevated CO$_2$ atmospheres have been shown to result in accumulation of succinic acid due to inhibition of succinic dehydrogenase activity, and reduced formation of citrate/isocitrate and α-ketoglutarate in apples (14-16), pears (17), and lettuce (18). CO$_2$ levels above 6% stimulated oxidation of malate but suppressed oxidation of citrate, α-ketoglutarate, succinate, fumarate, and pyruvate in mitochondria isolated from apples (19). Ultrastructural changes in 'Bartlett' pear similar to those associated with senescence, such as fragmentation, reduction in size, and changes in shape of mitochondria, were caused by elevated CO$_2$ (20). Kerbel et al. (21) found that 10% CO$_2$ was associated with declines in protein
content and fructose 1,6-bis-phosphate and in the activities of ATP:phosphofructokinase and PPI:phosphofructokinase while levels of fructose 6-phosphate and fructose 2,6-bis-phosphate increased. They concluded that the inhibitory effect of elevated CO₂ on both phosphofructokinases in the glycolytic pathway could account, at least in part, for the observed reduction in respiration.

Respiration is not the only biological activity of plant tissues that requires O₂. Furthermore, since senescence can continue without an increase in respiration, low O₂ must exert its effect on processes other than respiration (22). Oxygen concentrations below about 8% can decrease C₂H₄ production and sensitivity to C₂H₄ of fresh fruits and vegetables (13). The decreased production of C₂H₄ may be due to inhibition of the conversion of 1-aminocyclopropane-1-carboxylic acid (ACC) to C₂H₄ which requires O₂ (23). CO₂ inhibits autocatalytic production of C₂H₄ in climacteric fruits, such as avocado, apple, and tomato. Injurious levels of CO₂ can, however, result in increased production of C₂H₄ (13). Many fresh fruits and vegetables respond to C₂H₄ with accelerated softening, increased abscission and induced physiological disorders, all of which have a direct effect on quality (24).

It is clear that CA profoundly influences the metabolism of plant tissues in several different ways. These effects are reflected, either favorably or unfavorably, in the quality of fruits or vegetables. The extent to which CA is beneficial depends upon the commodity, cultivar, maturity stage, initial quality, concentrations of O₂, CO₂, and C₂H₄, temperature, and duration of exposure to those conditions.

**Effects of CA on Postharvest Quality.**

**Appearance Quality**

**Chlorophyll.** Elevated CO₂ and/or low O₂ levels reduce chlorophyll loss in many fruits and vegetables (7,25). How this occurs is less certain. The disappearance of green color in processed and stored green vegetables is due to the replacement of magnesium in chlorophyll by hydrogen to form colorless phophythin (26-28). High cellular pH caused by elevated CO₂ may reduce the breakdown of chlorophyll to phophythin. Lowered sensitivity of plant tissues to C₂H₄ in the presence of elevated CO₂ and/or reduced O₂ is presumably partly responsible for the reduced chlorophyll breakdown. Wang and Ji (29) found that the retardation of senescence of Chinese cabbage by storage in a 18 O₂ atmosphere was associated with preventing increases in abscisic acid and ACC levels.

**Carotenoids.** Carotenoids are fat-soluble pigments comprised of isoprene units and, in plants, are generally associated with membranes (30). Carotenoids are generally classified as either carotenes, which are structurally related to hydrocarbons, or xanthophylls which are hydroxy, epoxy and oxy derivatives and are frequently esterified. The carotenoids most important in imparting color to fruits and vegetables are derivatives of α- and δ-carotenes and lycopene. Carotenoids vary in their stability but, due to their unsaturated nature, they are generally susceptible to oxidation. Carotenes are important to
nutrition, flavor and appearance as precursors of vitamin A, precursors of some flavor volatiles and as pigments (6).

Low O\textsubscript{2} generally delays or inhibits the synthesis of lycopene, β-carotene, and xanthophylls in tomato fruit (31,32). In sweet pepper, high CO\textsubscript{2} delayed development of red color equally whether combined with 21% or 3% O\textsubscript{2} (33). C\textsubscript{2}H\textsubscript{4} is known to accelerate the biosynthesis of carotenoids (34).

Lipoxygenase appears to catalyze the direct oxidation of certain unsaturated fatty acids with the concurrent bleaching of carotenoids (39). Carotenoids are also sensitive to nonenzymatic oxidation with concurrent loss of color. Carotenoids can lose their color through bleaching after loss of moisture in the presence of O\textsubscript{2} (35,36). The low O\textsubscript{2}, high moisture conditions common in CA may ameliorate some of these changes.

**Anthocyanins.** Anthocyanins are flavonoid, phenolic-based, water-soluble compounds located in the cell vacuole of the epidermal cells of many fruits and vegetables (37). They confer the characteristic red and blue colors of many flowers and fruits and as such are important components of visual quality. The anthocyanins are pH indicators and are red at low pH, colorless at intermediate pH and blue at higher pH. The blue colors at high pH are the result of copigmentation and metal chelation rather than a direct effect of pH. This can result in discoloration of fruits packed in metal containers or handled with metal implements (38).

Anthocyanins accumulate relatively late in the maturation process of fruits. CA conditions, which delay maturation, can thus be expected to delay the development of anthocyanin pigments. This may be mediated through reduced sensitivity to C\textsubscript{2}H\textsubscript{4}, which has been shown to accelerate biosynthesis of anthocyanins (39,41). CA conditions can also alter cellular pH in plant tissues (42) and consequently induce changes in anthocyanins.

O\textsubscript{2} and high temperature were found to be the most important factors in the degradation of anthocyanins in blueberry, cherry, currant, grape, raspberry and strawberry juices (43). Polyphenol oxidases can degrade anthocyanins in the presence of other phenolic substrates such as catechol or chlorogenic acid (44,45). Because polyphenol oxidase is estimated to have a \( K_m \) many times higher than that of cytochrome oxidase, O\textsubscript{2} may become insufficient for its activity at ambient concentrations as high as 2% O\textsubscript{2}. As this level of O\textsubscript{2} is common in CA, preservation of anthocyanins ought to be possible.

**Oxidation of Phenolic Compounds.** Phenolic compounds are widespread throughout the plant kingdom and are prevalent in fruits where they are important contributors to color and flavor (46). Phenolic compounds, particularly flavonoids and derivatives of chlorogenic acid, play a crucial role in the development of a number of postharvest disorders through their oxidation to brown compounds that discolor many fruits and vegetables and substantially reduce their quality. A number of enzymes catalyze the biosynthesis or oxidation of phenolic compounds, among them phenylalanine ammonia lyase (PAL), tyrosine ammonia lyase (TAL), cinnamic acid-4-hydroxylase (C4H), polyphenol oxidase (PPO), and catechol oxidase (CAO). The chemistry
of phenol oxidases in fruits and vegetables has been recently reviewed (47,48). The activities of these enzymes, and thus their mediation of desirable or undesirable changes are affected by CA. Storage of mushrooms in 0% O2 inhibited PPO activity and browning (49). At higher O2 concentrations, browning occurred. CO2 can influence phenolic metabolism at a number of steps (42). CuH4-induced browning in pea seedlings was inhibited by CO2 concentrations above 5% (50). CO2 (20%) inhibited browning of mechanically damaged snap beans and reduced activity of PPO (51). Conversely, 15% CO2 caused brown stain to develop in lettuce, but symptoms developed only after the removal of the CO2 (52). Elevated CO2 (15%) was associated with an increase in PAL activity in lettuce but the authors believed that this was a stress reaction and not the primary cause of browning (52). They speculated that the prevention of symptom development by the presence of CO2 was related to reduced PPO activity, since CO2 has been shown to be a competitive inhibitor of PPO (49). CO2 suppresses the production of phenolic compounds, but CO2 injury (brown stain) scores did not correlate well with total phenolic content in lettuce (52).

Texture Quality

Fruit Softening. The softening of plant tissues is usually accompanied by the breakdown and solubilization of pectic materials and by catabolism of cell wall polysaccharides (2). Polygalacturonases (PG) specifically hydrolyze the β-D-(1,4) linkages between galacturonic residues. Such residues constitute a major structural portion of the middle lamella and their hydrolysis is thought to be largely responsible for fruit softening during maturation and storage (53). The effect of CA storage on firmness has been evaluated for many fruits and vegetables and appears to vary with the commodity (2). Generally, any treatment that retards ripening, such as CA does, retards softening of fruits (54). A 24-hour exposure of snap beans to 40% CO2 reduced titratable acidity and increased pH, apparently due largely to a reduction in malic acid (55). Degradation of pectic substances in the middle lamella increased with increasing pH, which may account for increased softening of snap beans associated with high CO2 (though not with 2.5% O2) exposure (55). The water-soluble polyuronides (WSP) in pears stored in air or in 1% O2 increased substantially during 6 months of storage at 1°C. After removal to air at 20°C, pears previously stored at 1°C showed a decrease in WSP while those stored in 1% O2 showed an increase in WSP (56). Development of a juicy, buttery texture in stored pears is thought to result from an increase in soluble pectic substances in the pulp (57). Anoxic conditions arrested softening, the increase in soluble pectin and the decline in total pectin in Conference pears, perhaps due to an inhibition of the synthesis of wall-degrading enzymes (58). Pectin solubility in high-bush blueberries increased during storage in air, but was unchanged during storage in high CO2 (59). Bananas kept in 2.5% O2 exhibited a larger increase in pectinmethylesterase activity compared to air (22). In the case of avocados, PG activity decreased 40-50% in 2.5% O2, compared to air (60). The appearance of PG was prevented by storing tomatoes in 5% O2 + 5% CO2, but on removal to air, PG was synthesized (61). CA (2%
O₂ + 5% CO₂) storage of kiwifruit at 0°C retarded softening compared to storage in air. In addition, the CA-stored fruit maintained an increased level of water insoluble uronic acids and the associated neutral sugars galactose, arabinose and rhamnose (62). There was no clear relationship between β-galactosidase activity and softening rates of air or CA-stored McIntosh apples (63).

**Toughness of Vegetative Tissue.** Toughening of vegetative tissue during storage appears to be associated with phenolic metabolism and lignification (30). During the key steps of phenolic metabolism, phenylalanine is deaminated by PAL to cinnamic acid. Cinnamic acid can then be hydroxylated into various phenolic compounds. In the presence of O₂, PPO can oxidize these phenolic compounds into quinones which can polymerize into a brown pigment (52). Alternatively, cinnamic acid can be hydroxylated by cinnamic acid-4-hydroxylase to coumaric acid and on to lignin via the shikimic acid pathway (30). Exposure to elevated CO₂ levels can stimulate an increase in PAL, PPO and peroxidase (POD) activities resulting in increased lignification (cell wall thickening) and the accumulation and oxidation of soluble phenolic compounds leading to tissue browning (64). Low O₂ combined with high CO₂ partially reduced CO₂-induced PAL activity and soluble phenolic activity and reduced or retarded brown stain development in iceberg lettuce (65). Lignification is associated with increased PAL and PPO activity in asparagus and can be retarded in 7% CO₂ (66). Holding asparagus spears at 2°C in 15% O₂ + 15% CO₂ retarded lignification and toughening (67,68). High CO₂ (10%) reduced toughening of broccoli (69).

**Flavor Quality**

**Taste.** Taste is the human perception of chemicals in the mouth due to their interaction with receptors on the tongue. Taste consists of four dimensions: sweet, salty, sour and bitter. Taste is affected by odor and texture, which makes it a complicated, subjective quality attribute, difficult to measure objectively (70). In fruits and vegetables, taste is mostly determined by the types and amounts of carbohydrates, organic acids, amino acids, lipids and phenolics (57,71). CA combinations, to the degree that they modify changes in these constituents, can affect the taste of stored fruits and vegetables. Usually, extremely low O₂ or high CO₂ will result in off-flavors and reduced quality due to anaerobic respiration. The specific effect of CA on flavor depends on the crop involved (7).

Both reduced O₂ and elevated CO₂ can slow starch-to-sugar conversion, thus inhibiting the development of sweet flavors. In bananas, phosphatase activity was reduced and sucrose, fructose and glucose accumulated more slowly when kept in 2.5% O₂ relative to those held in air (72). Storage of potatoes in 2.5% O₂ inhibited increases in fructose and glucose and reduced the content of sucrose (73). Low O₂ apparently inhibits the conversion of starch to sugars in potatoes (74). Keeping 'Granex' onions at 1°C in 3% O₂ + 5% CO₂ maintained a higher sugar content and a lower pungency than those kept in air (75). In sweet corn, loss of sucrose was retarded by 2% O₂, but elevated CO₂ (15% or 25%) nullified this benefit (76). Moderate CO₂ levels (up to 5% for brussels sprouts and 7.5% for horseradish) inhibit the
metabolism of sugars. Elevated CO₂, above optimal levels, has been associated with increased sucrose or glucose decomposition in horseradish (3), brussels sprouts (27), and carrots (28). High CO₂ concentrations stimulate respiration in many root crops, perhaps due to injury (29), and this elevated respiration may deplete carbohydrates.

Organic acids and their salts, esters, and glycosides are important both as sources of respiratory energy in the plant cell, and as flavor and aroma compounds, particularly in fruits. Malic acid is a major flavor component in apple, cherry, plum, apricot, broccoli and celery and citric acid is predominant in strawberry and raspberry. Both malic and citric acid are found in tomato and pear and malic and tartaric acid are found in grape. In most fruits organic acids are lost during ripening after harvest (2). Both reduced O₂ and elevated CO₂ can slow the loss of many organic acids, perhaps through interference with the conversion of pyruvate to citrate or through suppression of succinic acid dehydrogenase and the tricarboxylic acid cycle and associated accumulation of succinic acid (2,13,17,80). Different organic acids can be affected differentially by CA (2). Storage of mature-green tomato fruit in 5% O₂ + 5% CO₂ did not influence malic and citric acids (61). The metabolism of radiolabeled citrate in mangoes was suppressed by high CO₂ more than the metabolism of succinate, aspartate, acetate or malate, although all organic acids accumulated compared to controls (81). CA retarded loss of organic acids in stored McIntosh apples. As titratable acidity level is considered a prime quality determinant in apple juice, the authors considered that CA significantly preserved apple quality (82). CA storage of lettuce, spinach and broccoli resulted in lower levels of organic acids, compared to air storage (2).

Although most fruits and vegetables have relatively small amounts of proteins and amino acids, these constituents may play an important role as synergists and primary flavor components, as well as influence oxidation of ascorbic acid and of other flavor compounds (2). Peroxidase has been associated with "off-flavors" in raw vegetables (83). Several amino acids are considered to have unpleasant tastes (84) but glutamic acid is widely used as a flavor potentiator (85). Others are rated as sweet, salty or bitter (86). However, differences in amino acid concentrations during tomato ripening do not appear to be directly related to flavor differences (87). Synthesis of proteins is less in fruits stored in CA than in air (2). In pears (88), cauliflower (89), and lettuce (90) stored in CA this is reflected in a slowed reduction in free amino acids. However, in cherry (91), chestnut (92), and shiitake mushrooms (93), free amino acids were not retained during CA storage. Goodenough et al. (61) found no change during CA storage in the 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 did not interfere with changes requiring enzyme regulation but that it did interfere with de novo enzyme synthesis.

CA can prevent C₂H₄ induced formation of bitter isocoumarins in carrots (94) and can aid in removal of tanins and resulting astringency from persimmons (95,96).
Aroma. Aroma is considered to be much more complex than taste and has many dimensions (97). While the number of compounds conferring aroma in fruits and vegetables is large, they can generally be classified as hydroxy compounds, aldehydes, ketones, acids, esters, sulphur-containing compounds, \( \text{O}_2 \) heterocyclics and pyrazines (97). Several hydrolases and proteases involved in the synthesis of fatty acid and amino acid precursors to volatiles are synthesized or activated during the respiratory climacteric (98-100).

Production of volatiles is lower after CA storage of apples than after air storage (71,101-02). Knee and Hatfield (103) found that low levels of esters in apples stored in low \( \text{O}_2 \) atmospheres were a result of low rates of alcohol synthesis, which they thought was the precursor to esters and aldehydes responsible for apple flavors. This effect was reversible upon removal to air. Very low \( \text{O}_2 \) (about 1%) may suppress development of volatiles after removal to air (104). Fruits picked at the preclimacteric stage and stored in 1 to 2% \( \text{O}_2 \) may lose their ability to produce sufficient volatiles to achieve proper aroma (103). CA storage of apples suppressed production of butanoates, 2-methylbutanoates, pentanoates, and hexanoates, but had little effect on aldehydes and acetates (71). Golden Delicious apples stored 3 to 9 months in 11 combinations of low \( \text{O}_2 \) and high \( \text{CO}_2 \) had measurably lower production of volatiles than apples stored in air (105). Decreasing \( \text{O}_2 \) to 3% had little effect on volatile production, but a further decrease to 1% caused a significant reduction in volatile production. At \( \text{O}_2 \) concentrations above 2%, elevated \( \text{CO}_2 \) became important in reducing volatile production. The relationship between the effects of reduced \( \text{O}_2 \) and elevated \( \text{CO}_2 \) on volatile production was neither additive, nor linear, nor synergistic. There was a residual suppression of volatile production after removal to air, but a 3-week treatment in air at 1°C before removal to shelf temperature partially restored volatile production (105).

Tomato volatiles are important to both aroma and flavor and their concentration increases with ripening (106). Because many of the volatile aroma compounds of tomatoes apparently result from enzymatic breakdown of carotene pigments (107), CA, which delays pigment synthesis, can be expected to delay volatile production.

An inappropriate atmosphere can result in off odors and flavors. Too low \( \text{O}_2 \) or excessive \( \text{CO}_2 \) can cause fermentative metabolism leading to accumulation of ethanol and acetaldehyde. Such off odors can be particularly offensive in broccoli (108).

Nutritional Quality

Vitamins. Vitamins, which are important nutritional components of fruits and vegetables, can also act as antioxidants, pigment relatives and cofactors for numerous enzymatic reactions. They are subject to decomposition after harvest so proper postharvest treatment is crucial to their preservation. The role of vitamins in the postharvest physiology of vegetables has been recently reviewed (6).

Ascorbic acid (vitamin C) is utilized as a cofactor to stabilize the chloroplast stroma, in quenching free radicals and reacting with hydroxy radicals and in the biosynthesis of tartaric acid and oxalic acid (6), important organic acids in grapes, and many vegetables. The effect of CA on ascorbic acid content differs with commodity,
atmosphere and temperature (6). Degradation of ascorbic acid is associated with wilting in green leafy vegetables (109). For many commodities, such as lettuce, parsley, corn salad, Chinese cabbage, spinach, green bean, kale, broccoli, brussels sprouts, apples, red currants, cress, and sweet pepper, 1 to 4% O₂ generally slows ascorbic acid degradation, presumably through prevention of oxidation (6,110-12). Elevated CO₂ can accelerate ascorbic acid degradation in green bananas, potatoes, spinach, asparagus, peas, apples, red currant, corn salad, parsley, cress, sweet pepper, and leeks (6,7,111-15). However, the effect of CO₂ on ascorbic acid depends upon temperature, CO₂ level, and storage time (7). Packaging of spinach and green beans in polyethylene bags prevented ascorbic acid degradation but this was attributed primarily to the maintenance of high relative humidity (116).

There is little vitamin A in fruits and vegetables but carotene, which is a precursor to vitamin A, can be affected by storage conditions (109). Carotenoids are subject to oxidation and to degradation associated with wilting of leafy vegetables (109). CA conditions, which maintain low O₂ and high relative humidity, can be expected to preserve carotenoids. CO₂ (5%) atmospheres accelerated losses of carotenoids in carrots while 7.5% CO₂ resulted in higher carotene levels than at the beginning of storage (7). In leek, 10% CO₂ combined with 1% O₂ resulted in higher carotene levels than at the beginning of storage (117).

Minerals. Fruits and vegetables can be rich sources of minerals important in human nutrition. Minerals are not lost during storage, but can be translocated and concentrated. Thus, low O₂ storage of cauliflower resulted in decreased potassium in the curd compared to the leaf but increased calcium in the curd (7). Low O₂ also favors translocation of molybdenum from the leaves to the curd (7). Significant redistribution of calcium occurred in Cox's Orange Pippin apples during storage but the patterns of redistribution were similar in CA and air-stored samples (118).

Safety Considerations

Plant Pathogens and Mycotoxins. The effects of CA and MA on decay in fruits and vegetables after harvest are difficult to assess due to conflicting reports (119). It is clear that CA/MA can change the general microbial profile of foods (120). CA and MA can delay senescence and maintain the good physiological condition of fresh produce and in this way help maintain inherent resistance to decay organisms. Conversely, inappropriate atmospheres can serve to erode the plant's resistance to microorganisms and in this way increase decay. There is evidence that CA/MA can have a direct suppressive effect on some plant pathogenic microorganisms. Disease suppression can be attributed to both the effect of MA on host resistance and on the altered growth of the pathogen (119). Consequently, the improvement in quality obtained through the use of CA/MA may be in part due to the effect on the physiological condition of the commodity and in part due to the inhibition of spoilage organisms (121). The effects of CA/MA on postharvest pathogens of fruit and vegetables have been reviewed (119,122).
Lowering $O_2$ concentration to 2-3% evidently suppresses pathogen activity very little. Most pathogens are suppressed only at $O_2$ concentrations below 1%, conditions that are damaging to most fruits and vegetables (119). Levels of $CO_2$ commonly used in MA (1-5%) are only moderately suppressive to plant pathogens. Levels of $CO_2$ above 10% have been used successfully to suppress pathogens on those commodities that will tolerate it. Examples are suppression of Botrytis on strawberries and suppression of Botrytis and Monolinia on sweet cherries (119).

In some cases CA/MA can favor development of plant pathogens. This may often be due to the maintenance of high relative humidity associated with established atmospheres, but it has been reported that high $CO_2$ favors growth of gram-positive bacteria (122). Percent decay of tomatoes inoculated with Geotrichum candidum was greater in 3% $O_2$ with or without added $CO_2$ than in air (124). MA can retard periderm formation and wound healing in potatoes, thereby giving pathogens additional time to establish infections and colonize the wound (119).

Mycotoxins are toxic secondary metabolites of fungi, some of which are carcinogenic to animals and humans. Those of major concern are patulin, produced by several species of Aspergillus and Penicillium, and aflatoxin, produced by Aspergillus flavus and other species of Aspergillus. Aflatoxin is found primarily on nuts and patulin can be prevalent on apples (119), pears, and stone fruits (125). Levels of $O_2$ of 2% or higher were only modestly suppressive of $A. flavus$ growth and aflatoxin production. Little suppression was noted in 10% $CO_2$ but 20% or higher was very effective in suppressing fungal growth and aflatoxin accumulation (119).

**Human Pathogens.** Bacteria pathogenic to humans have been isolated from a number of fresh vegetables and in some cases have been responsible for disease (126-31). The environment in a MA package can create a high humidity, low $O_2$ environment that may be favorable to pathogenic microorganisms that would not otherwise thrive on vegetables. Clostridium botulinum was able to grow and produce toxin in the low $O_2$ environment of packaged mushrooms (132). Growth of Listeria monocytogenes is known to be enhanced by elevated $CO_2$ concentrations (133) and has been found on fresh vegetables (129). Another psychrotrophic pathogen, Aeromonas hydrophila, has been isolated from vegetables (127) and could be of concern on products held in chilled, MA conditions (120).

**Future Research Needs**

MA and CA storage, transport, and marketing of fresh fruits and vegetables continue to present a technical challenge and opportunity to researchers and those involved in the fresh produce industry. The gains to be made are substantial, as are the risks. Technical competence in the handling of these commodities will be more important than ever before. In order to ensure that the commodities are handled properly to maintain the highest quality possible while ensuring their safety, the following issues will have to be stressed in future research programs:

1. The effect of CA/MA on quality parameters; rather than evaluating postharvest life only on the basis of appearance, workers should
pay more attention to the effect of CA/MA on texture, flavor, and nutritional quality.

2. The need to determine the likelihood that human pathogens, particularly toxin-producing anaerobes, can grow and produce toxins in MA packages before other spoilage organisms make the produce, either by appearance or by odor, offensive to the consumer.

3. The effects of minimally processing fruits and vegetables on their physiology and deterioration rate and the potential use of CA/MA conditions for their preservation.

4. Efforts to develop a mathematical model that can be used successfully to select the best package for creating and maintaining the optimum MA for each commodity.

5. Research to elucidate the mode of action of reduced O₂ and elevated CO₂ levels on changes in chemical composition of fresh fruits and vegetables.

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