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Review

Effects of superatmospheric oxygen levels on postharvest physiology and quality of fresh fruits and vegetables

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Abstract

Exposure to superatmospheric O_2 concentration may stimulate, have no effect, or reduce rates of respiration and ethylene production, depending on the commodity, maturity and ripeness stage, O_2 concentration, storage time and temperature, and concentrations of CO_2 and C_2H_4 present in the atmosphere. In some plant organs, cyanide-resistant respiration is enhanced by elevated O_2 atmospheres. Ripening of mature-green, climacteric fruits was slightly enhanced by exposure to 30–80 kPa O_2, but levels above 80 kPa retarded their ripening and caused O_2 toxicity disorders on some fruits. High O_2 concentrations enhance some of the effects of ethylene on fresh fruits and vegetables, including ripening, senescence, and ethylene-induced physiological disorders (such as bitterness of carrots and russet spotting on lettuce). While superatmospheric O_2 concentrations inhibit the growth of some bacteria and fungi, they are much more effective if combined with elevated (15–20 kPa) CO_2, which is a fungistatic gas.

Keywords: Ethylene; Oxygen toxicity; Pathological breakdown; Physiological disorders; Respiration; Ripening

1. Introduction

Oxygen concentrations greater than 21 kPa (induced through high O_2 atmospheres or hyperbaric atmospheres) may influence postharvest physiology and quality maintenance of fresh horticultural perishables either directly or indirectly via altered CO_2 and C_2H_4 production rates. Increased O_2 concentrations around and within the commodity result in higher levels of free radicals that can damage plant tissues (Fridovich, 1986). Sensitivity to O_2 toxicity varies among species and developmental stages.

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Day (1996) discussed the rationale behind, and the potential applications for, the use of novel gas mixtures (i.e. high oxygen, argon, and nitrous oxide) for the modified atmosphere packaging (MAP) of fresh prepared produce. He stated that high O_2 levels are effective at inhibiting enzymic discoloration, preventing anaerobic fermentation reactions, and influencing aerobic and anaerobic microbial growth.

Oxygen is colorless, odorless, and tasteless, so O_2 enrichment cannot be detected by the human senses. Superatmospheric O_2 levels can accelerate combustion of all materials. Thus, special care must be taken in designing and using packaging machines and gas-flushing systems to avoid ignition sources when high O_2 concentrations are utilized (British Compressed Gases Association, 1998).

In this report we will review published information and some unpublished data on responses of fresh fruits and vegetables to superatmospheric O_2 concentrations alone and in combination with elevated CO_2 atmospheres.

2. Respiratory metabolism

Exposure to superatmospheric O_2 levels may stimulate, have no effect, or reduce rates of respiration, depending on the commodity, maturity and ripeness stage, O_2 concentration, time and temperature of storage, and the CO_2 and C_2H_4 concentrations. Kidd and West (1925), Blackman (1928), Blackman and Parija (1928) were among the first to describe the intricate relationship between apple ripening, O_2 tension and respiratory activity. Kidd and West (1934) found that 100 kPa O_2 accelerated the onset of the climacteric rise in apples. Choudhury (1939) found no change in respiration of artichoke kept in superatmospheric O_2, while carrot respiration rose with every increase in O_2 concentration from 6.2 to 98.6 kPa.

The effects of O_2 concentrations above those in air were studied by Biale (1946) with avocado, a climacteric fruit, and by Biale and Young (1947) with lemon, a non-climacteric fruit. The response of the avocado fruit to 50 and 100 kPa was a

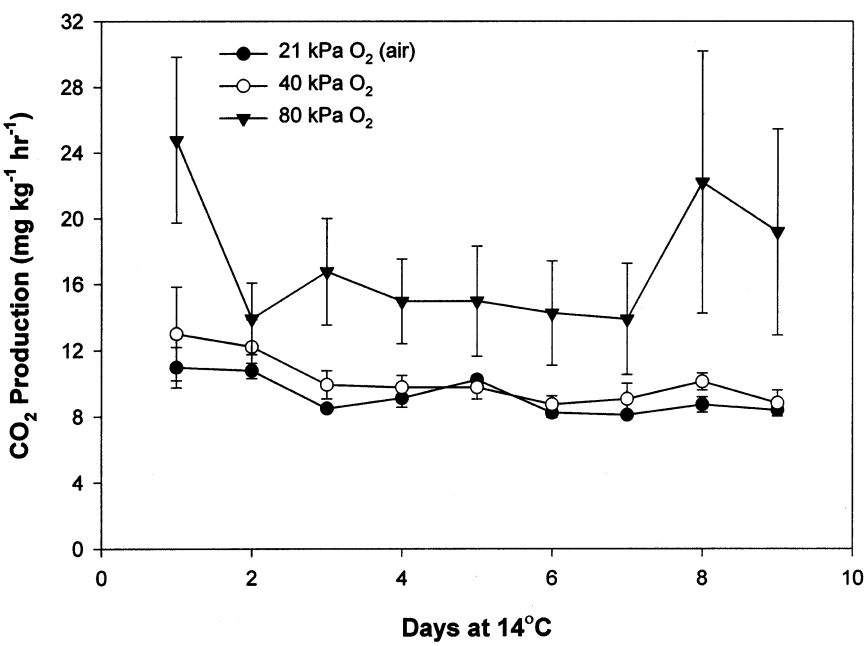

Fig. 1. Effects of superatmospheric O_2 levels on respiration rates of grapefruit kept at 14°C.

rather small acceleration of the onset of the climacteric rise. With lemon fruit, superatmospheric O_2 levels (34.1, 67.5, and 99.2 kPa) induced a pronounced increase in the respiratory rate. We recently found that an 80 kPa O_2 atmosphere stimulated respiration rates of grapefruit kept at 14°C (Fig. 1) (Chairat et al., 1999, unpublished data). In contrast, superatmospheric O_2 atmospheres (30, 50, 75, and 100 kPa) had no marked effect on respiration of cherries or apricots (Claypool and Allen, 1948).

The respiration of 'Wickson' plums was stimulated in proportion to the increase in O_2 concentration. However, in 100 kPa O_2, the respiration rates in several experiments at different temperatures were lower than at 70 kPa O_2 (Claypool and Allen, 1951). Maxie et al. (1958) worked with the same cultivar of plums and reported that, the respiration rate at 40 kPa O_2, was maximal. It declined in a lower O_2 concentration, while staying at the same level at a higher concentration. The respiration rate of tissue slices was similar to that of whole fruit suggesting that diffusion or availabilty of O_2 was not limited by either the skin or the pulp. High O_2 levels accelerated the onset of the climacteric in control plums but had no added stimulatory effect on ethylene-treated fruit.

Barker and Mapson (1955) observed a marked inhibition of CO_2 production by potato tubers kept at 1°C in 100 kPa O_2 for 38 days and attributed this to a block in the TCA cycle between citrate and α-ketoglutarate. Brown discoloration of the flesh increased with time of exposure to the 100 kPa O_2. Burton (1974) reported that 100 kPa O_2 did not influence cytochrome-c-oxidase but it stimulated polyphenol oxidase and ascorbic acid oxidase, 2–3-fold relative to air-stored potatoes. Chin and Frenkel (1976) found that exposing potato tubers to 100 kPa O_2 with 10 μl l^{-1} C_2H_4 markedly enhanced their respiratory rise accompanied by an increase in peroxides.

Gorny and Kader (1998, unpublished data) found that exposure of 'Bartlett' pear slices to 40, 60, or 80 kPa O_2 decreased their respiration rates during 4 days at 10°C, but did not influence skin color and flesh firmness. Lu and Toivonen (2000) reported that exposure of whole 'Spartan' apples to 100 kPa O_2 for 12 days at 1°C before slicing resulted in lower respiration, browning, and softening rates of the slices than in those made from air-stored apples during storage at 1°C for 2 weeks.

Janes et al. (1981) reported that the development of CN-resistant repiration in potato tubers kept at 2°C was greatly enhanced by high O_2 concentrations. The respiration that developed in the cold was maintained even at 22°C in 100 kPa O_2 but not at lower O_2 concentrations. The alternate respiratory path is enhanced by high O_2 and lowered by low O_2 levels in whole potato tubers, tissue slices and in mitochondrial preparations made from these tubers.

Theologis and Laties (1982a,b) confirmed the effects of O_2 and C_2H_4 in inducing the alternative path as a part of a larger rise in the respiration of bulky storage organs. The total rise in respiration evoked by C_2H_4 is mediated by a system with an O_2 requirement much higher than that of cytochrome oxidase, while the ethylene induced development of the alternative path depends on a system with a still higher O_2 requirement.

Laties (1998) reviewed CN-resistant respiration. He emphasized that in avocado fruit, when O_2 tension is reduced slowly from 100 kPa O_2 the respiratory isotherm is biphasic, whereas when the concentration is dropped rapidly the isotherm is monophasic, with $K_m^{O_2}$ appropriate for cytochrome oxidase. He hypothesized that the slow depletion of O_2 allows for the intermediation of biochemical processes, and perhaps the regulation of gene expression. An O_2-sensitive negative feedback system was postulated by Tucker and Laties (1995) to be responsible for the fundamental control of respiration rate at O_2 concentrations in excess of that saturating the terminal oxidase. These authors also stressed that the low affinity, high $K_m^{O_2}$ arm of the biphasic respiration isotherm they observed has nothing to do with the effect of O_2 on ethylene synthesis or ethylene action, since this biphasic pattern is evident equally in preclimacteric and climacteric fruit. Tucker and Laties (1995) described the enhancement of the CN-resistant, alternative respiratory pattern by O_2 concentrations greater than 21 kPa (air). At superatmospheric concentrations, O_2 has other roles,

such as enhancing the production of reactive O_2, which damages the cytoplasm and inhibits various metabolic activities, leading to deterioration of produce quality.

The physiological role of the alternative oxidase was suggested by Purvis and Shewfelt (1993) to be reduction of the potential production of reactive O_2 species during and after exposure of plant tissues to stress. Purvis (1997) demonstrated that mitochondria isolated from the pericarp of green bell pepper fruit produced superoxide in buffers aerated with 100 kPa O_2. ADP and uncouplers of the electron transport chain reduced the production of superoxide. Disulfiram, an inhibitor of the alternative oxidase enhanced superoxide production. Purvis (1997) suggested that during normal respiration some reactive O_2 species (superoxide and hydrogen peroxide) are produced by the respiratory electron transport chain, but antioxidants such as vitamins C and E are present in sufficient concentration to prevent damage to the phospholipids and proteins of the membrane. In stressed plant tissue, the supply of respiratory substrates to the mitochondria increases and the respiratory electron transport chain cannot handle the increased flow of electrons. Under these conditions, more reactive O_2 species are produced than there are antioxidants to destroy them, which leads to damage to the phospholipids and proteins. The alternative path provides a means for oxidation of substrates at the stress-induced increased level without excessive production of reactive O_2 species, and therefore the antioxidants present are able to prevent damage.

3. Ethylene biosynthesis and action

Creech et al. (1973) reported that 'Russet Burbank' potato tubers stored in 80 kPa $O_2 + 12$ kPa CO_2 produced ethylene at a much higher rate than those kept in air at 7°C. 'Bartlett' pears kept in 100 kPa O_2 and 20°C had higher rates of ethylene production, chlorophyll degradation, and softening than those kept in air (Frenkel, 1975). Morris and Kader (1975) reported that 30 and 50 kPa O_2 atmospheres accelerated ethylene production and ripening of mature-green and breaker tomatoes stored at 20°C. In contrast, exposure to 80 or 100 kPa O_2 reduced ethylene production rates and delayed ripening of mature-green and breaker tomatoes at 20°C (Fig. 2).

Ethylene production rates of muskmelons kept at 100 kPa O_2 at 20°C did not increase above those of fruits held in air, but were enhanced in response to 10 μl l^{-1} C_2H_4 added to 100 kPa O_2 (Altman and Corey, 1987).

ACC oxidase follows an ordered binding mechanism in which it first binds to O_2 and then to ACC. However, when the O_2 concentration was increased from 21 to 100 kPa there was little influence on the apparent K_m for ACC (Yip et al., 1988).

Gorny and Kader (1998, unpublished data) found that exposure of pear slices to 40, 60, or 80 kPa O_2 decreased ethylene production rates by 7, 13, or 27%, respectively, relative to air control, during 4 days at 10°C (Fig. 3).

4. Compositional changes

4.1. Pigments and color

Biale and Young (1947) reported that the change in lemon color from green to yellow was markedly accelerated by high O_2 levels. However, exposure to 99.2 kPa O_2 also induced rapid peel breakdown. At 18°C, cherries and apricots held in 100 kPa O_2 were slightly less ripe (as indicated by color) at the end of 10 days than those held in air (Claypool and Allen, 1948). Oxygen at 30, 50, and 75 kPa hastened 'Wickson' plum ripening at 20°C, while 100 kPa O_2 delayed color changes associated with ripening (Claypool and Allen, 1951).

High O_2 (50 kPa) increased the rate of degreening of 'Hamlin' oranges, but 50 kPa $O_2 + 5$–10 μl l^{-1} ethylene did not accelerate the degreening response over ethylene alone (Jahn et al., 1969).

Li et al. (1973) reported that ripening of tomatoes at 12–13°C was accelerated in 40–50 kPa O_2 compared with air. Lycopene synthesis in *rin* tomatoes was stimulated in fruits kept in 60 or 100 kPa O_2 in the presence of 10 μl l^{-1} C_2H_4 (Frenkel and Garrison, 1976).

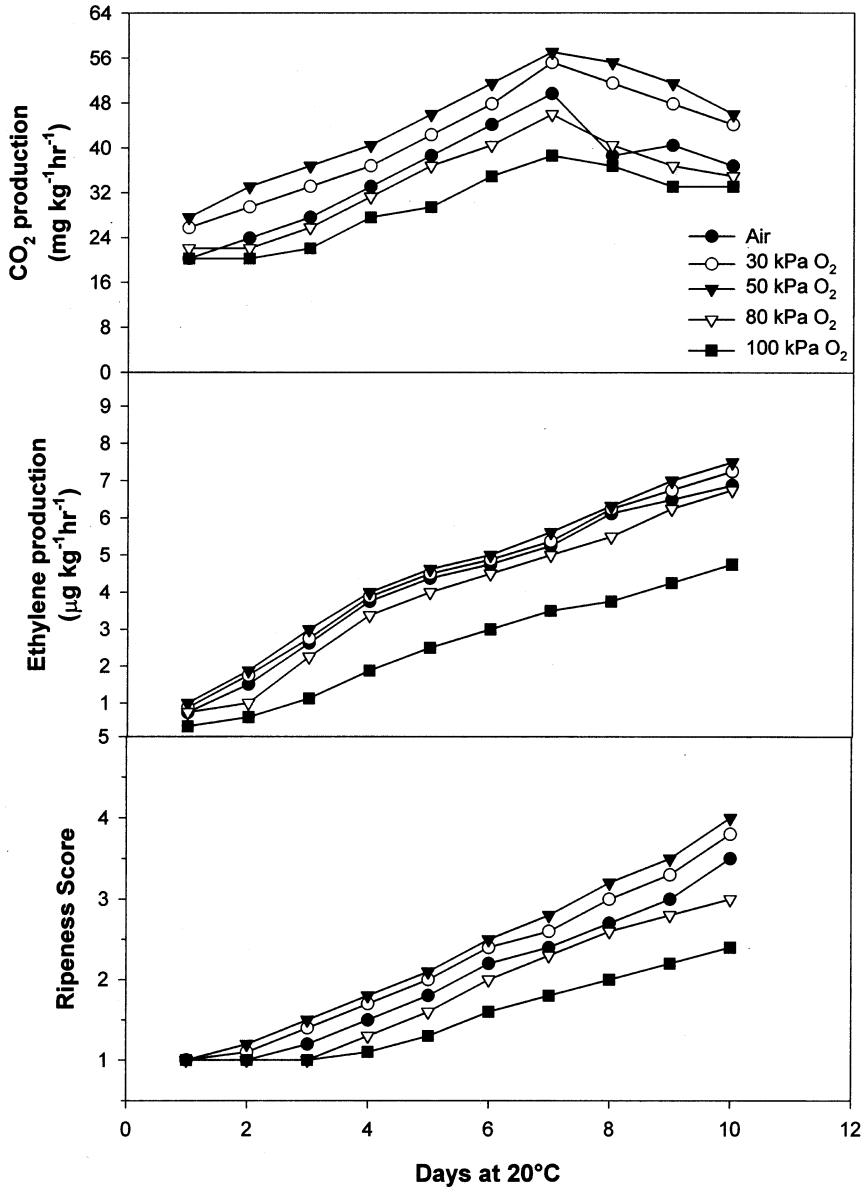

Fig. 2. Effects of superatmospheric O_2 levels on rates of respiration, ethylene production, and ripening of mature-green tomatoes kept at 20°C; ripeness score: 1, mature-green; 2, breaker; 3, light-pink; 4, dark pink.

Buescher and Doherty (1978) found that 100 kPa O_2 enhanced color development in *nor* tomatoes held in the dark, but it was detrimental to ethephon-induced color development in both *rin* and *nor* tomatoes exposed to light.

Storage in 40–80 kPa O_2 may have practical application for improving the color of endocarp and juice in some orange cultivars kept for 4 weeks at 15°C (Houck et al., 1978). Aharoni and Houck (1980) exposed oranges for 4 weeks at 15°C to 40 or 80 kPa O_2, followed by 2 additional weeks in air. Fruits kept in 80 kPa O_2 had the palest rind, but their endocarp and juice were the deepest orange. The response was intermediate for

oranges kept in 40 kPa. We observed undesirable changes from yellow to orange in grapefruit exposed to 40 or 80 kPa O_2 levels (Ben Yehoshua et al., 1999, unpublished data).

Aharoni and Houck (1982) reported that 40 or 80 kPa O_2 deepened the red color (due to anthocyanin synthesis) of flesh and juice of all three blood-orange cultivars tested. Total soluble solids, titratable acidity, and pH of the juice were not affected.

4.2. Phenolics and tissue browning

Tissue browning due to oxidation of phenolic compounds by polyphenol oxidase results from loss of compartmentalization within the cells when

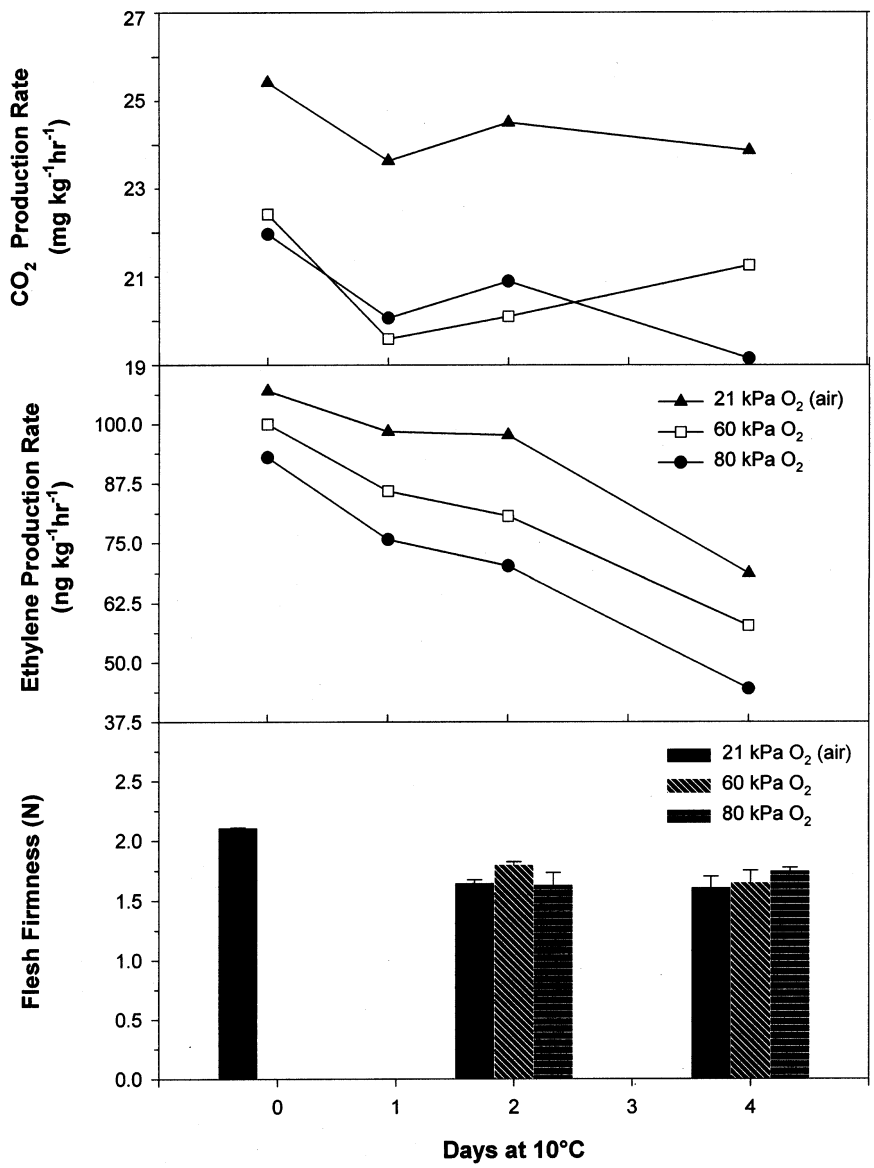

Fig. 3. Effects of superatmospheric O_2 levels on rates of respiration, ethylene production, and softening of 'Bartlett' pear slices kept at 10°C for 4 days.

exposed to physical and/or physiological stresses. There are very few published reports on the effects of elevated O_2 on enzymatic browning. Over 10 days at 5°C, an atmosphere of 80 kPa O_2 + 20 kPa CO_2 did not increase browning of MA-packaged, shredded lettuce compared with that resulting from exposure to air + 20 kPa CO_2 (Heimdal et al., 1995). Day (1996) hypothesized that high O_2 levels may cause substrate inhibition of polyphenol oxidase (PPO) or alternatively, high levels of colorless quinones formed may cause feedback inhibition of PPO. Lu and Toivonen (2000) observed a slower browning rate during storage at 1°C for 2 weeks of slices made from 'Spartan' apples that had been kept in 100 kPa O_2 for 12 days at 1°C prior to cutting compared with those kept in air. Gorny and Kader (1998, unplublished data) found that exposure of 'Bartlett' pear slices to 40, 60, or 80 kPa O_2 for 4 days at 10°C did not influence their browning rate compared with slices kept in air.

4.3. Volatile compounds and aroma

Elevated O_2 atmospheres may affect synthesis and accumulation of some volatile compounds associated with respiratory metabolism, including fermentative metabolites such as acetaldehyde, ethanol and ethyl acetate (Solomos et al., 1997; Whitaker et al., 1998). In a preliminary study on responses of grapefruit to superatmospheric O_2 (Ben Yehoshua et al., 1999, unpublished data) we observed that exposure to 80 kPa O_2 with or without 15 kPa CO_2 resulted in lower concentrations of ethyl acetate (less off-flavor) in the grapefruit kept at 5 or 15°C for 2 weeks than in those exposed to 15 kPa CO_2-enriched air. It appears that high O_2 levels reduce the negative effects of high CO_2 concentrations and may allow their use for decay control.

Yahia (1991) found that poststorage exposure to 100 kPa O_2 at 3.3°C for up to 4 weeks was not effective in enhancing volatile formation in 'McIntosh' apples that had been stored in 3 kPa O_2 + 3 kPa CO_2 at 3.3°C for up to 9 months. Rosenfeld et al. (1999) found that highbush blueberries packaged in 40 kPa O_2 and stored at 4 and 12°C for up to 17 days had similar sensory quality to those packaged in air.

4.4. Vitamins and nutritional quality

Very little information is available on effects of elevated O_2 levels on concentrations of vitamins, minerals, dietary fiber, and phytonutrients in fresh intact and fresh-cut fruits and vegetables. Barker and Mapson (1952) reported that ascorbic acid content of potato tubers kept in 100 kPa O_2 was lower than in those stored in air. Day et al. (1998) reported that high O_2 MAP had beneficial effects on the retention of ascorbic acid and degree of lipid oxidation. They also stated that high O_2 MAP, in comparison with low O_2 MAP, did not decrease antioxidant levels in prepared lettuce.

5. Growth and development

The potential effects of superatmospheric O_2 levels on elongation and curvature of asparagus and sprouting of onions and potatoes should be investigated in view of the findings of Abdel-Rahman and Isenberg (1974) that 40 kPa O_2 increased sprouting and rooting of 0°C-stored carrots.

6. Physiological disorders

Kidd and West (1934) showed that storage of 'Bramley's Seedling' apples in 100 kPa O_2 can be detrimental. After 4 months at 4°C, symptoms included mealy flesh and browning of skin and flesh. Storage of 'Granny Smith' apples in 70 kPa O_2 at 0°C for 1 month did not accelerate the severity of sunscald (Lurie et al., 1991). Solomos et al. (1997) reported that 'Gala' and 'Granny Smith' apples exposed to 100 kPa O_2 developed extensive injury akin to that which occurs under 1 kPa or lower O_2 atmospheres. The activity of *cis*-aconitase in the fruit was inhibited by 100 kPa O_2, thereby disrupting the TCA cycle. This in turn caused an increase in ethanol production.

Production of farnesene and trienol, related to development of storage scald, increased in apples kept in 100 kPa O_2 atmospheres at 0°C for up to 3 months. 'Granny Smith' apples stored under 100 kPa O_2 were completely 'bronzed' after 3 months

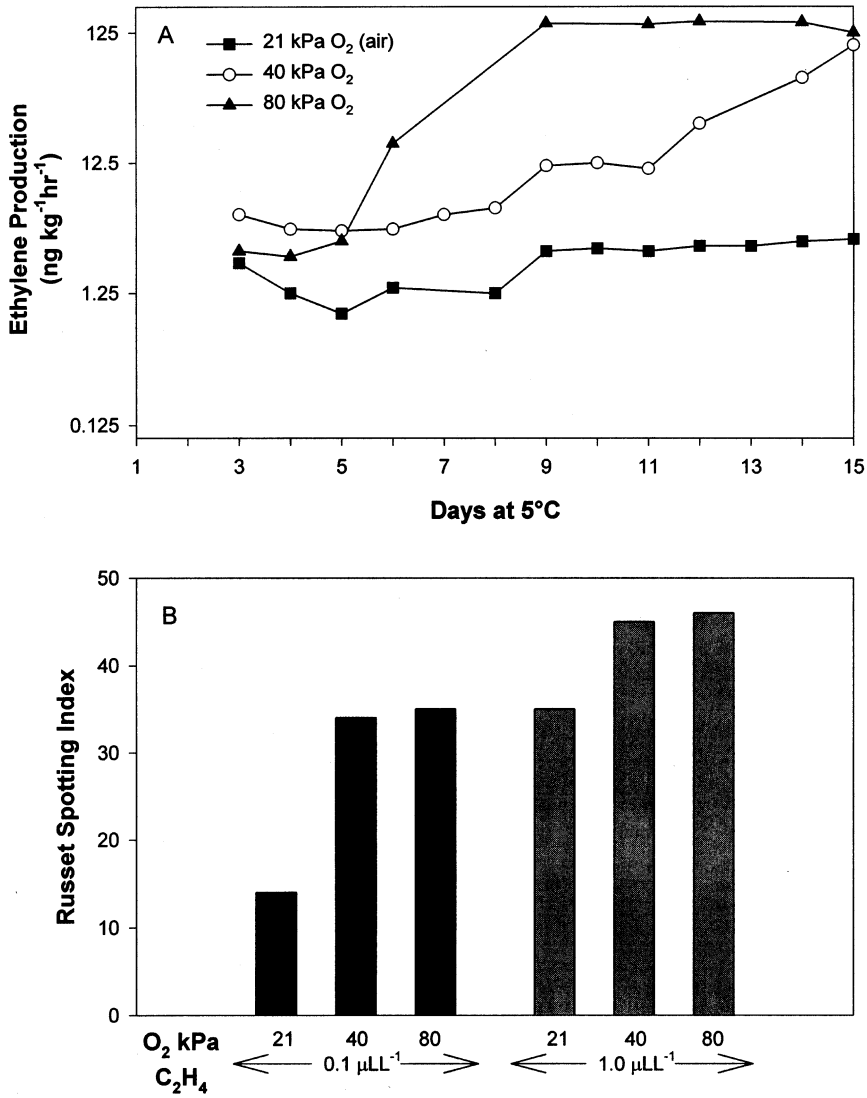

Fig. 4. Effects of superatmospheric O_2 levels on ethylene production by lettuce (A) and response of the tissue to ethylene action (russet spotting) after 10 days at 5°C (B).

and contained high ethanol concentrations (Whitaker et al., 1998).

An atmosphere of 100 kPa O_2 potentiated the effect of 0.5 µl l^{-1} C_2H_4 on isocoumarin formation in carrots, resulting in a 5-fold increase over that found in carrots treated with C_2H_4 in air (Lafuente et al., 1996). Superatmospheric O_2 levels increased ethylene production and the incidence and severity of pink rib and C_2H_4-induced russet spotting on lettuce (Klaustermeyer and Morris, 1975) as shown in Fig. 4 (Klaustermeyer et al., 1975, unpublished data). Mature-green tomatoes exposed to 80 or 100 kPa O_2 for more than 5 days exhibited dark-brown spots on their skin. The severity of this high-O_2 injury depended on duration of exposure at 20°C and type of wax used on the tomatoes (Kader and Morris, 1975, unpublished data).

7. Responses of microorganisms

Growth rate and growth efficiency as well as the respiration rates of living organisms are dependent on O_2 tension (Harrison, 1976). Above the 'critical level' in air these parameters are not affected by the O_2 concentration, but growth is inhibited below the critical level as well as at toxic high O_2 tensions. Obligate anaerobes are injured even by 0.1 kPa O_2 concentrations.

Bert (1878) reported that compressed air at 15–44 atmospheres preserved meat and raw eggs for several days at room temperature. He ascribed this preservation effect to the high O_2 and not to the high pressure. Indeed many of the microorganisms, bacteria, yeasts and molds in various foods were found to be killed by hyperoxygenation (Bert, 1878). High O_2 causes damage to living organisms (Bean, 1945; Zobell and Hittle, 1967). However, different organisms vary greatly in their sensitivity to O_2 partial pressure. Toxicity of O_2 in the obligate anaerobes may be associated with the formation of hydrogen peroxide, which cannot be removed in the absence of catalase (Zobell and Hittle, 1967). In the case of some anaerobes it has been suggested that O_2 may inhibit their growth through the autooxidation of cytochromes.

Among the many factors that may help explain the toxicity of hyperbaric O_2 are the unfavorable effects on the oxidation-reduction potential of the system, the oxidation of certain enzymes especially those having sulfhydryl groups or disulfide bridges and the accumulation of injurious reactive O_2 species (ROS). Gerschman (1964), Haugaard (1968) suggested, in addition to ROS, lipid peroxidation as a cause of O_2 toxicity. However, the major explanation for O_2 toxicity is the formation of superoxide radicals (O_2^-), which are destructive to some components of cell metabolism. Cells synthesize the enzyme superoxide dismutase (SOD) to remove these radicals. Gregory and Fridovich (1974) found that high O_2 tensions enhanced SOD content in. *E coli* and this corresponded with increased resistance to hyperbaric O_2. In *Bacillus subtili* grown at high O_2 tensions, catalase was induced, but not SOD, and there was no enhanced protection against hyperbaric O_2. Gregory and Fridovich (1974) found two distinct SODs in *E. coli*. One, of these contains iron, is present in cells grown at low levels of O_2, and is not induced by O_2. The other SOD contains manganese, is absent in anaerobically grown cells, and is induced by O_2. The iron containing SOD protects against exogenous superoxide radicals, while the manganese-containing SOD, which is inducible by O_2, protects against endogenous superoxide radicals formed under hyperbaric O_2 tensions.

Microorganisms have developed strategies, such as the induction of other enzymes that decompose ROS, to avoid their lethal damage. Studies on the effects of O_2 stress on *S. typhimurium*, *E. coli*, and *L. lactis* have identified the presence of inducible multigene systems, which destroy ROS, and proteins that serve to repair oxidative damage at of 30–37°C (Demple and Halbrook, 1983; Sanders, 1997). However, no information is available regarding such induction of repair systems at lower temperatures.

Caldwell (1965) found that exposure of bacteria and fungi to 10 atm O_2 for 8 h suppressed their growth completely. On return to air, the fungi began to grow after a variable delay period, whereas the bacterial cultures, with one exception, resumed growth immediately. Robb (1966) reported that 52 of 103 species of fungi exposed to high O_2 concentrations at 10 atm pressure, for 7 days resumed growth after treatment. Of these, 22 species recovered after 14 days exposure. After a lag period between decompression and recovery, the growth rates were the same as those of untreated colonies. Among this group of 22 fungi that recovered from exposure to 10 atm O_2 for 14 days were the following important pathogens: *Aspergillus flavus*, *A. niger* and six other *Aspergillus* species, as well as six species of *Penicillium*. Among the 30 species of fungi that were resistant to exposure for 7 days, but not to 14 days were the following fungi: *Aspergillus ochraceus*. *Candida albicans*, *Penicillium* species, *Colletotrichum dematium*, and *Verticillium lateritium*. More detailed investigation of the reaction of *Fusarium solani*, *Rhizopus arrhizus*, *Mucor racemosus*, and *M. plumbeus* showed that the lag periods of growth generally increased with increasing exposure times. The extinction points, i.e. the exposure

that killed all replicates, varied and at exposures approaching the extinction point there was selective survival either of spores or of strains in the last three fungi of those listed above.

Day (1996) suggested that high O_2 atmospheres could be advantageous for MAP by directly inhibiting the decay causing organisms, particularly fungi on soft fruits. More recently, Gonzalez-Roncero and Day (1998) reported that 99 kPa O_2 alone did not prevent the growth of any of the following microorganisms: *Pseudomonas fragi*, *Aeromonas hydrophila*, *Yersinia enterocolitica*, and *Listeria monocytogenes*. They found that growth of *P. fragi* and *A. hydrophila* was inhibited by 14 and 15%, respectively. The combination of 80 kPa O_2 and 20 kPa CO_2 was more effective in inhibiting growth of all the organisms tested at 8°C than either alone.

Amanatidou et al. (1999) reported the effect of elevated O_2 and CO_2 on the surface growth of various microorganisms associated with vegetables and including several human pathogens. They found that exposure to 80–90 kPa O_2 generally did not inhibit microbial growth strongly, but caused a significant reduction in the growth rate of some of the microorganisms tested (e.g. *Salmonella enteritidis*, *S. typhimurium* and the biological control yeast, *Candida guilliermondii*.) Among the ten microbial species studied, growth of some was even stimulated. Carbon dioxide at 10–20 kPa was effective in significantly reducing the growth of *Pseudomonas fluorescens* and *S. enteritidis*. However, the combined application of 80–90 kPa O_2 together with either 10 or 20 kPa CO_2 had an inhibitory effect on the growth of all microorganisms. In general, a notable prolongation of the lag phase and a reduction in the final population density was observed. The most prominent effect though was the complete inhibition of the growth of yeast antagonists. Amanatidou et al. (1999) concluded that when high O_2 or high CO_2 are applied alone, the inhibitory effect on microbial growth is highly variable. Stronger and much more consistent inhibition of microbial growth was obtained when the two gases are used in combination. Amanatidou et al. (2000) found that a combination of 50 kPa $O_2 + 30$ kPa CO_2 prolonged the shelf life by 2–3 days of sliced carrots compared to storage in air.

In a preliminary experiment we checked the effects of various concentrations of O_2 with and without 15 kPa CO_2 on the decay of grapefruit. The only effective reduction of decay appeared with 80 kPa O_2, or its combination with 15 kPa CO_2, but not with 40 kPa O_2, or its combination with 15 kPa CO_2. It is interesting that 100 kPa O_2 enhanced the *Penicillium* decay of grapefruit (Kader and Ben Yehoshua, 1999, unpublished data).

Wszelaki and Mitcham (1999), Wszelaki et al. (1999), Wszelaki and Mitcham (2000) found that 80–100 kPa O_2 inhibited the in vitro growth of *Botrytis cinerea* on strawberries. However, only 100 kPa O_2 inhibited growth of this fungus more than 15 kPa CO_2 in air, and only after a 14-day exposure. No residual effect on in vitro fungal growth was observed upon transfer to air. Botrytis rot on strawberry fruit was reduced during 15 days of storage at 5°C in 80–100 kPa O_2, but some fermentative metabolism was induced. Addition of 15 kPa CO_2 to air or to 40 kPa O_2 was effective as a fungistatic atmosphere without detrimental effects on fruit quality during storage for 7 days at 5°C. These data indicate that the high O_2 atmospheres had an effect on the fruit as well as the fungus, resulting in greater effect in vivo than in vitro.

8. Future research needs

It is clear from the limited published information on effects of elevated O_2 levels on postharvest physiology and quality of fresh fruits and vegetables that much more research is needed to answer the following questions:

1. What are the mechanisms by which superatmospheric O_2 levels influence rates of CO_2 and C_2H_4 production by climacteric fruits, non-climacteric fruits, and non-fruit vegetables?
2. Do high O_2 atmospheres ameliorate or aggravate chilling injury and other physiological disorders?
3. Can superatmospheric O_2 levels reduce elevated CO_2-induced disorders and off-flavors?
4. How do high O_2 concentrations alone and in combination with elevated CO_2 levels influence

growth of decay-causing bacteria and fungi and human pathogens (food safety related)?
5. What are the effects of beneficial elevated O_2 levels alone and in combination with elevated CO_2 levels on textural, flavor, and nutritional quality of target commodities?
6. Is there any relationship between tolerance of the commodity tissues to high O_2 concentrations and their total antioxidant capacity?

Based on the answers, it will be possible to identify the situations in which use of elevated O_2 alone or in combination with elevated CO_2 atmospheres might be a useful supplement to maintaining the optimum range of temperature and relative humidity during postharvest handling to maintain fresh produce quality.

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