Responses of Horticultural Commodities to Low Oxygen: Limits to the Expanded Use of Modified Atmosphere Packaging

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SUMMARY. The application of low oxygen through modified atmosphere packaging (MAP) is a technique used successfully to preserve the visual quality of lettuce and some other commodities. The expansion of use of low O_2 via MAP to preserve quality of most commodities is limited by technical difficulties achieving target O_2 concentrations, adverse physiological responses to low O_2, and lack of beneficial responses to low O_2. Low O_2 often is not used simply because the physiological responses governed by the gas are not limiting quality maintenance. For instance, shelf life may be governed by decay susceptibility, which is largely unaffected by low O_2 and may actually be exacerbated by the conditions encountered in hermetically sealed packages. Physiological processes influenced by low O_2 and limit storability are discussed. The interdependence of O_2 concentration, O_2 uptake by the product, and temperature are discussed relative to requirements for packaging films.

An important goal in some modified atmosphere packaging (MAP) systems is to generate an atmosphere sufficiently low in O_2 to influence the metabolism (e.g., softening, chlorophyll degradation, tissue browning, senescence) of the product being packaged such that storability and / or shelf life is extended. For some products, modifying both O_2 and CO_2 may be desirable and indeed, when the O_2 partial pressure in packages is altered, so too must be that of CO_2 by virtue of the system. In this presentation, however, comments will primarily be confined to the ramifications of O_2 modification; a discussion of the influence of CO_2 in MAP environments on metabolism is presented by Watkins (2000).

The expansion of MAP use in the future will, to some extent, require that technical and physiological limitations surrounding the application of low O_2 environments be overcome. Technical challenges remain, for instance, in developing packages that maintain O_2 partial pressures within tolerance levels as packages undergo changes in temperature and humidity.

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Challenges also remain in ameliorating and / or avoiding adverse physiological responses to low O_2. Also, the lack of beneficial responses of some commodities to low O_2 partial pressures reduces impetus to expand use of MAP.

If low O_2 is desired for packaged fruits or vegetables, knowledge of the effect of package characteristics (film type, film thickness, film area, product weight), product respiration, and environmental parameters (temperature and humidity) on the O_2 partial pressure obtained in the package and the effect of this atmosphere on the quality and physiology of the enclosed product is essential. For instance, if O_2 levels decline below partial pressures required to sustain aerobic respiration, then fermentation and, potentially, off-flavors may result. Alternatively, if O_2 levels are not low enough, then responses to these atmospheres may inadequately improve storability. A range of nondamaging O_2 (and CO_2) levels have been published for a number of fruits and vegetables (Beaudry, 1999; Kader, 1997a; Kupferman, 1997; Richardson and Kupferman, 1997: Saltveit, 1997), minimally processed products (Gorny, 1997), and flowers and ornamentals (Reid, 1997) and are summarized (Table 1).

Technical limitations to low O_2 application

A film or package restricts gas exchange. Modified atmospheres are generated through the natural process of respiration by the enclosed product, which reduces O_2 concentration and increases CO_2 concentration under restricted gas exchange through the film barrier. Two somewhat different strategies for regulating gas exchange to achieve desired gas partial pressures exist. The first strategy uses continuous films that control movement of O_2 and CO_2 into or out of the package. The second strategy uses perforated films with small holes or microperforations as the primary route of gas exchange. For both routes of gas exchange, the reduction in O_2 partial pressure and increase in CO_2 partial pressure create gradients that, according to Fick's Law, cause O_2 to enter and CO_2 to exit the package. Steady-state (constant) O_2 levels are achieved in the package when the O_2 uptake by the product is equal to that permeating into the package, a situation that exists only when the respiratory rate is constant (Cameron et al., 1989; Jurin and Karel, 1963; Tomkins, 1962). As for O_2, steady-state CO_2 levels in the package are achieved when CO_2 production by the product equals CO_2 escape from the package. This process can be augmented by adjusting the mix of gases in the package headspace at the time of package sealing.

At steady-state, O_2 uptake can be depicted as follows:

$$r_{O_2} = (p_{o,O_2} - p_{i,O_2}) \times P_{O_2} A / Wl \qquad [1]$$

here r_{O_2} is the respiration rate ($mol \cdot kg^{-1} \cdot s^{-1}$) for oxygen, p_i and p_o are, respectively, the partial pressure in kPa (1.0 kPa ≈ 1% of an atmosphere) of gases outside and inside the package (p_{o,O_2} is 21 kPa (21%) O_2 and p_{i,O_2} is the steady-state O_2 level in the package headspace), A is the area (m^2) of the package exposed to gas transfer, W is the weight (kg) of the produce, and l is the thickness (m) of the packaging film. P_{O_2} is the O_2 permeability ($mol \cdot m^{-1} \cdot m^{-2} \cdot kPa^{-1} \cdot s^{-1}$), respectively, for the continuous or perforated film, which increases exponentially with temperature (Beaudry et al., 1992). The steady-state levels of both O_2 and CO_2 are dependent on the interaction of respiration of the product and the permeability properties of the packaging film (Beaudry et al., 1992; Cameron, et al., 1989; Jurin and Karel, 1963). For continuous films, because the permeability of CO_2 is usually 2 to 8 times higher than that of O_2, the sum of O_2 and CO_2 concentrations is less than 20% to 21% unless the RQ is of the same magnitude (or greater) as the ratio of CO_2 to O_2 permeability. For perforated films, since the permeability of perforations to CO_2 is only 20% less than to O_2, the sum of O_2 and CO_2 concentrations is usually only slightly less than 21%, the concentration of O_2 external to the package, unless the RQ is significantly greater than 1, in which case, the sum would be larger than 21%. Steady-state conditions are not always reached in packages, however, and part of the design process includes assessing and predicting the dynamic changes in package headspace. Dynamic models have been developed to do just this (Hertog et al., 1998).

Temperature is an extremely important consideration in package design. As temperature increases, the O_2 and CO_2 permeability of many packaging films increases markedly. A temperature sensitivity factor known as the energy of activation (Ea) describes the temperature sensitivity of the permeation of O_2 and other gases through films and has units that are expressed in kiloJoules (kJ) per mole of molecules undergoing the interaction. The value of the Ea for O_2 permeation through low density polyethylene (LDPE) is about 38 $kJ \cdot mol^{-1}$ (Cameron et al., 1994), which yields a 2.5-fold (250%) increase in permeability between 0 and 15 °C. A higher Ea would relate to a greater change in permeability over the temperature range and a lower Ea indicates a lower temperature responsiveness. In contrast to permeation through continuous films, the permeation of gases through perforations has an extremely low temperature sensitivity factor, being about equivalent to 4.3 $kJ \cdot mol^{-1}$ and so gas exchange through perforations in a package undergoes only a 10% increase with temperature in the range depicted.

The respiratory response of plant material to O_2 concentration also has a temperature sensitivity that can be mathematically described using saturation-type curves. A standard means of expressing the dependence of a reaction (O_2 uptake) on a substrate (O_2) is the Michaelis-Menton model (Cameron et al., 1994; Hertog et al., 1998), which is primarily applied to specific enzymatic reactions, although other models have been used. The model is expressed as follows:

$$r_{O_2} = (V_{max}\, p_{i,O_2}) / (K_m + p_{i,O_2}) \qquad [2]$$

where r_{O_2} is O_2 uptake ($mol \cdot kg^{-1} \cdot s^{-1}$), V_{max} ($mol \cdot kg^{-1} \cdot s^{-1}$) is the maximal rate of O_2 uptake, p_{i,O_2} is the partial pressure (Pa) of O_2 in the package, and K_m is the O_2 partial pressure in the package at 50% of V_{max}. For some products, the skin and / or flesh may offer significant resistance to gas movement, so the terms apparent K_m or $K_{1/2}$ are often substituted for K_m since it includes the gradient from the interior to the exterior of the plant tissues (Cameron et al., 1994, 1995).

Importantly, V_{max} can be assigned a temperature sensitivity factor in a manner similar to the process of permeation (Cameron et al., 1994). This factor can be termed the apparent E_a or E_a^{app} with higher values reflecting greater changes in respiration over a given temperature range. The maximal rate of respiration for most fruit and vegetable products has an Eaapp

between 60 and 90 kJ·mol^{-1}, undergoing a 4- to 6-fold increase from 0 to 15 °C (32 to 59 °F) (Beaudry et al., 1992; Cameron et al., 1994, 1995; Lakakul et al., 1999). This means that product respiration increases at two or three times the rate of LDPE permeability and thirty times the rate of perforation permeability with increasing temperature. A situation where respiratory demand for O_2 increases faster than O_2 permeation presents problems with maintaining adequate O_2 when the package undergoes a temperature increase and is an example of a significant limitation with regard to package O2, namely, maintaining target gas levels. The imbalance in the temperature sensitivity of respiration and permeation was recognized by early workers in the field (Tomkins, 1962; Workman, 1959) and later modeled (Cameron et al., 1994; Hertog et al., 1998).

Theoretically, there are several ways of solving the temperature problem. One method is to use a polymer film with a higher temperature sensitivity factor for O_2 transmission. High O_2 permeability, highly temperature sensitive films are now available and are being used commercially on a limited scale (Clarke and De Moor, 1997; Lange, 2000). Another solution to the MAP temperature problem is to develop a package system that senses either the environment or the physiological status of the enclosed product and responds by increasing the permeability to O_2 (Cameron et al., 1993). Such sense-and-respond packaging is technically difficult to develop, although some progress has been made at least conceptually (Smyth et al., 1999). A third approach to solve the MAP temperature problem is to design packages to function at the highest temperatures typically encountered in the distribution and retail cool chain and, as far as possible, maintain control over the temperature of the packaged product, thereby adapting to the limitations imposed by the film. This simple solution, first suggested by Tomkins (1962) and Workman (1959), has been adopted by most companies using MAP. Generally, the lowest temperature feasible is maintained, since temperature has a much more significant influence on preserving quality than the application of low O_2 (Kays, 1997).

The effect of temperature and other factors on package O_2 can be determined or predicted using mathematical models (Cameron et al., 1994; Hertog et al., 1998). The models depend on combining information that includes the effect of temperature on film permeability (Eq. 1) with information that includes the effects of temperature and O_2 on respiration (Eq. 2). The models permit us to predict package O_2 as a function of temperature, product weight, surface area, and film thickness. By setting Eq. 1 equal to Eq. 2 and solving for the O_2 partial pressure in MA packages, the following model can be developed (Cameron et al., 1994):

$$p_{i,O_2} = 1/2\{[(K_{1/2} + (Wl/P_{O_2}A)V_{max} - p_{o,O_2})^2 + 4p_{o,O_2}K_{1/2}]^{1/2} - [K_{1/2} + (Wl/P_{O_2}A)V_{max} - p_{o,O_2}]\} \quad [3]$$

Models have been published for whole apples, apple slices (Lakakul et al., 1999), blueberries (Beaudry et al., 1992, Cameron et al., 1994), chicory leaves (Hertog et al., 1998), broccoli florets (Cameron et al., 1995), lettuce leaves (Cameron et al., 1995), strawberry (Joles, 1993), tomato (Hertog et al., 1998), and raspberry (Joles, 1993; Joles et al., 1994).

In addition to respiratory responses to package atmospheres, nondetrimental exposure criteria for O_2 and CO_2 are important pieces of information for package design and the interpretation of the package O_2 models. If O_2 levels get too low, fermentation results, which is linked to the development of off-flavors and / or tissue damage (Kays, 1997). The lower O_2 limit for most commodities generally increases with temperature (Beaudry et al., 1992; Cameron et al., 1994, 1995; Yearsley et al., 1996).

Finally, the variation one might encounter in the respiration rate of the product and the variation in film or pore permeability should be factored into design criteria. Variation in broccoli respiration and package permeability has been measured and the effect on package O_2 levels modeled (Cameron et al., 1993; Talasila et al., 1994). For any package design, there is an estimable risk of the package O_2 falling below the lower O_2 limit tolerated by the product, resulting in fermentation. By reducing the variability of package parameters and targeting effective, but adequate O_2 concentrations well above the lower O_2 limit, the risk of inducing fermentation in packages can be minimized.

Once all of the above information has been accumulated, it should be possible to design packages with a reasonably predictable performance. For instance, packages can be designed to maintain aerobic O_2 levels at the highest temperature to which they will be exposed, thus avoiding fermentative conditions at all temperatures. Alternatively, they can be designed to generate low O_2 levels only at high temperatures. A package O_2 model such as the one specified can also be used to predict very specific package criteria. For instance, the thickness ranges that protect against fermentation can be established for specific film types (Lakakul et al., 1999). It should also be noted that combination packages can be designed that use both perforation and film polymer pathways for gas exchange (Fishman et al., 1996).

Combined perforation / permeation MAP has have features of both systems and the attainable atmosphere combinations are in-between those of packages dependent on permeation only and those dependent on diffusion through perforations only (Beaudry, 1999; Lee, 1994). These packages would attain a sort of 'middle ground' in terms of O_2 and CO_2 transmission in that the temperature sensitivity for permeation and the discrimination between O_2 and CO_2 is somewhere between those for perforated packages and hermetic packages.

Physiological limitations to low O2 application

The application of MAP to preserve the quality of harvested plant products is limited in part by adverse and / or nonbeneficial physiological responses to the atmospheres. Plant responses to modified O_2 levels have generally been well-characterized and include responses at the levels of primary and secondary metabolism (Kader, 1997b). Of the primary metabolic responses to low O_2, beneficial reactions include a reduction in respiration (i.e., O_2 uptake), which can be manifested as a reduction in starch degradation and sugar consumption. Reduced respiration is often interpreted as reflecting a reduction in global metabolism (Kays, 1997). An important negative response to low O_2 is the induction of fermentation, as has been mentioned previously, and the diversion of carbon in glycolysis to acetaldehyde, ethanol, and lactate. Generally, the lower limit of O_2 content in the atmosphere is considered to be the O_2

level at which fermentation is induced (Yearsley et al., 1996). The O_2 level at the induction point for fermentation can be termed the fermentation threshold. The fermentation threshold is not always the lower O_2 limit in commercial practice, however, when benefits due to O_2 levels near or below the fermentation threshold outweigh the loss in flavor or other quality parameters. This is true for fresh-cut lettuce, in particular, a situation that will be later detailed.

Of the secondary metabolic responses to low O_2, important beneficial reactions include a reduction ethylene synthesis and perception, reduced chlorophyll degradation, reduced cell wall degradation, and reduced phenolic oxidation. Reduced ethylene effects can be manifested as changes in primary and secondary metabolism. The low O_2-induced reduction in ethylene action likely comprises the most widely useful aspect of low O_2 application and forms the basis for the controlled-atmosphere (CA) storage of climacteric fruit (Solomos, 1997). It should be noted that many of the plant responses to low O_2 are altered by the presence of CO_2 (Silva, 1998; Watkins, 2000; Yang and Chinnan, 1988).

Negative secondary metabolic responses to low O_2 include reduced aroma biosynthesis for fruit including apple, banana, pear, peach, strawberry, and other crops (Mattheis and Fellman, 2000; Shamaila et al., 1992), and the possibility of off-flavor generation (Kays, 1997). The determination as to whether a particular plant organ can be favorably affected by reduced O_2 concentration depends upon the balance obtained between positive and negative responses. The following discussion details the influence of O_2 on primary and secondary metabolic pathways important to fruit and vegetable quality, with emphasis on respiratory suppression.

RESPIRATION. A reduction in the rate of respiration by the application of low O_2 atmospheres has often been stated as a rationale for the use of CA and MAP. The premise has been that reducing the respiration rate reduces the rate of deterioration of the tissues, thereby extending storage life (Burton, 1974; Herner, 1997). The basis for this argument originally stems from work by Kidd and West (1914, 1927) on seed and fruit storage. The suggestion that reduced O_2 can be applied for the purpose of reducing respiration cannot be broadly applied, however, because, for many crops, a reduction in respiration by low O_2 is accompanied by the induction of fermentation. For those commodities in which a significant reduction in respiration is possible without the induction of fermentation, the impact is often not directly on the respiratory machinery, but on ethylene action (Solomos, 1997). The following analysis of respiratory behavior serves to illustrate these points.

If one assumes that a significant reduction in respiratory (i.e., metabolic) activity is needed to add sufficient value to offset the expenses incurred in the application of MAP technologies to reduce O_2, then there is some point at which investment in the technology is balanced by the added value. For the sake of argument, a level of 50% reduction in respiration is suggested to be associated with sufficient enhancement of shelf life (i.e., value) such that the cost of the extra handling and materials resulting from MAP will be recovered. While this level of respiratory inhibition is arbitrary, it is coincident with the $K_{1/2}$, a physiologically significant parameter, and serves as a benchmark for the purpose of discussion.

There are two terminal oxidases that use O_2 as a substrate in this final step in respiration: cytochrome c oxidase (CytOx) and the alternative, cyanide-insensitive, oxidase (AltOx). CytOx has a very high affinity for O_2, having a K_m of 0.1% to 0.15% O_2 in the atmosphere external to the cell, while the AltOx has much lower affinity for O_2, as reflected by its K_m of 1% to 3% O_2 (Mapson and Burton, 1962; Solomos, 1977a). CytOx is typically present and functioning in most tissues, whereas the AltOx is not always present and is commonly modulated at the molecular level or by allosteric effectors (Vanlerberghe and McIntosh, 1997). The simultaneous operation of both oxidases may make respiratory responses to O_2 difficult to interpret. Additionally, even if only CytOx were active, the external O_2 level at which O_2 uptake is 50% of its maximum will likely be considerably higher than 0.15% due to flesh and skin resistances to gas diffusion.

As noted previously, the $K_{1/2}$ includes the gradient between the interior and exterior of the plant organ and can be substantially higher than the K_m. The $K_{1/2}$ for various plant parts is often in the 0.25% to 5% O_2 range and exhibits a temperature dependence, increasing with increasing temperature (Cameron et al., 1995; Hertog et al., 1998; Joles, 1993; Yearsley et al., 1996). The temperature dependence of the $K_{1/2}$ is a result of an increase in the gradient of O_2 with temperature, rather than a shift in the K_m since the K_m is relatively constant within the range of physiologically relevant temperatures (Yearsley, et al., 1996). The relatively high $K_{1/2}$ causes the curve describing the dependence of O_2 uptake on O_2 concentration to be rather broad for whole plant organs, especially those held at elevated temperatures, but very sharp for single cells and other tissues with little diffusive resistance (Fig. 1). For the remainder of the paper, discussion regarding the fermentation threshold and the $K_{1/2}$ will pertain to O_2 levels in the package atmosphere (p_{i,O_2}) in that this value represents that of concern to the commercial storage operator and is the quantity most often expressed in papers on the topic of atmosphere tolerances.

It is worth mentioning that the control of O_2 uptake may not be strictly controlled at the level of CytOx and AltOx. A hypothetical system that senses the O_2 concentration in plant tissues and regulates carbon flux has been suggested (Mapson and Burton, 1962; Solomos, 1997b). While such a system would help explain the rather broad nature of O_2-dependent curves obtained for glycolytic processes in some tissues (Silva, 1998; Solomos, 1997b), definitive proof is lacking. In some instances, skin and flesh resistances have been suggested to cause broad O_2-dependent respiratory curves (Tucker and Laties, 1985).

A convenient way to collect the respiratory data required to calculate the $K_{1/2}$ and the fermentation threshold involves enclosing the desired product in packages composed of films of known permeability for a given temperature (Beaudry et al., 1992). The weight of the plant material and the thickness of the film can be varied in order to generate a range of O_2 atmospheres. After some days, the O_2 and CO_2 levels reach steady-state at which time the rates of flux of O_2 and CO_2 through the package are essentially equal to their rate of uptake and pro-

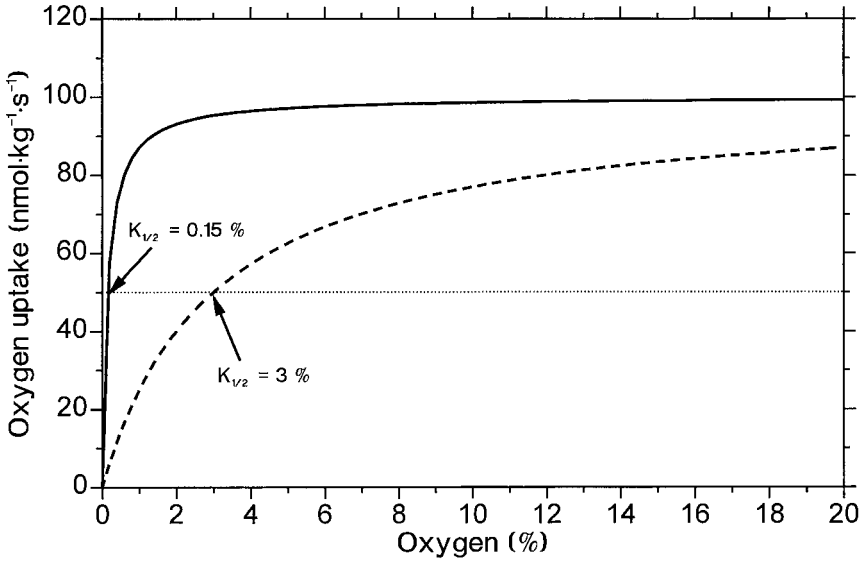

Fig. 1. Hypothetical respiratory responses to O_2 for a respiratory system of low diffusive resistance exhibiting a $K_{1/2}$ of about 0.15% O_2, representative of single cells or tissues, and a tissue with significant diffusive resistance to gas exchange with an $K_{1/2}$ of 3% O_2.

duction, respectively. At steady-state, O_2 uptake, CO_2 production, and a relative indicator of fermentation, the respiratory quotient (RQ), can be determined as a function of the package O_2 concentration (Fig. 2). By fitting the respiratory data with a Michaelis-Menton equation, the $K_{1/2}$ can be determined. The fermentation threshold can be considered to be the O_2 level below which, the RQ increases (Beaudry et al., 1992).

The difference between the $K_{1/2}$ for O_2 uptake and the fermentation threshold can be used as a criterion for deciding whether low O_2 will provide a beneficial response in terms of restricting respiration and slowing metabolism for the purpose of improving storability. If, for instance, the fermentation threshold is much lower than the apparent K_m, then a greater than 50% reduction in respiration and attendant metabolic activities can be achieved without the threat of fermentation, thereby, in concept, safely enabling improved storability via metabolic suppression. This range of O_2 levels might be termed the safe working atmosphere with respect to respiratory reduction. On the other hand, if the fermentation threshold is near or above the $K_{1/2}$, it could be argued that little or no advantage due to reduced metabolic activity can be achieved by reducing O_2 since the tissues would be compromised by fermentative activity. In the latter case, there would be no safe working atmosphere.

Two examples of the commodities having no safe working atmosphere include strawberry fruit and asparagus spears. In an unpublished study in which the respiratory rate of strawberry was determined using packages, the $K_{1/2}$ was determined to be about 1% O_2 at 20 °C, but fermentation was evident below about 1.2% O_2 (Fig. 2). Similar data are available for asparagus held at 0 °C, where the $K_{1/2}$ is about 1% O_2 and the fermentation threshold is 1.2% O_2 (Silva, 1998). Based on these data, use of low O_2 for the purpose of respiratory suppression would not be advisable. In fact, low O_2 storage is not recommended for either of these plant materials to extend shelf life (Table 1). This is consistent with commercial practice in that little to no low O_2 storage of either commodity occurs.

An example of a rather broad safe working atmosphere was found for apple fruit, although it was dependent upon the stage of fruit development (Fig. 3). Mature, but nonripening 'Empire' apple fruit were treated with 1-methylcyclopropene (1-MCP), an inhibitor of ethylene action (Serek et al., 1995; Sisler and Blankenship, 1996) to keep them in a preclimacteric stage of development, or were left untreated before packaging. Packaged fruit were held at 20 °C for 14 d. Ripening of

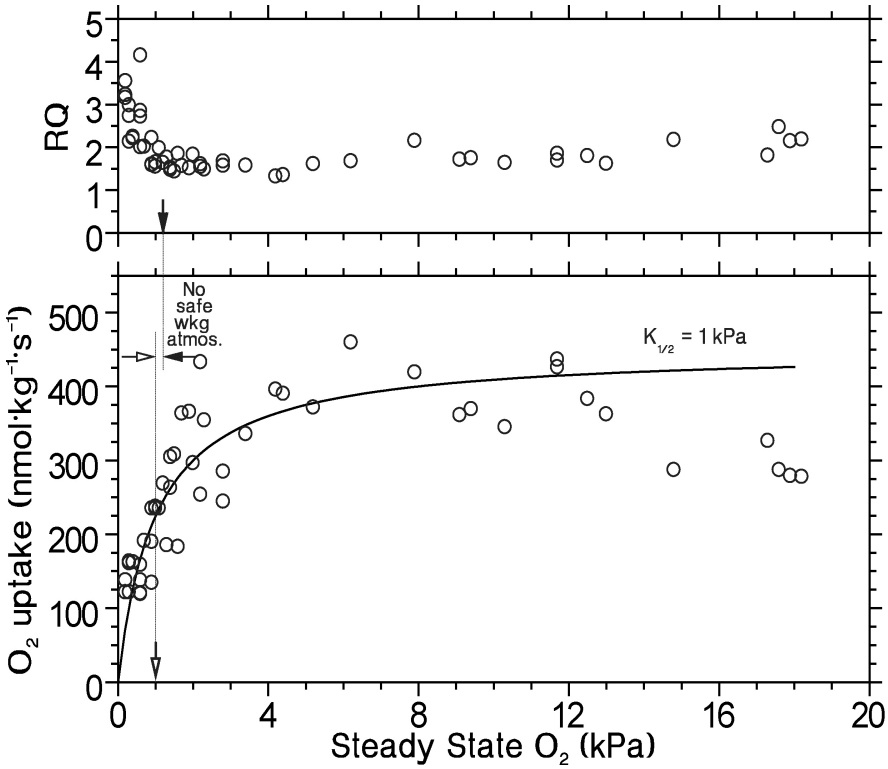

Fig. 2. Respiratory response to O_2 and the associated RQ of strawberry fruit held at 22 °C (72 °F) for 5 d in LDPE packages (data previously unpublished). The vertical arrow in the upper graph depicts the lower O_2 limit based on the increase in fermentative activity at lower O_2 concentrations. The vertical arrow in the lower graph indicates the $K_{1/2}$ of the fitted line. The fact that the lower O_2 limit exceeds the $K_{1/2}$ is taken to indicate that there is no safe working atmosphere.

Table 1. Oxygen (O_2) limits below which injury can occur for selected horticultural crops held at typical storage temperatures (from Beaudry, 1999; Gorny, 1997; Kader, 1997a; Kupferman, 1997; Richardson and Kupferman, 1997; Saltveit, 1997). Those commodities in bold are considered to have very good to excellent potential to respond to low O_2. The O_2 limit does not always refer to the fermentation threshold, but may relate to discoloration or other disorder.

O_2 (%)	Commodity
≤0.5	Broccoli (*Brassica oleracea* L. Group Italica)
	Lettuce (chopped greenleaf, redleaf, Romaine and iceberg; *Lactuca sativa* L.)
	Mushroom (*Agaricus bisporus* L.)
	Pear (sliced) (*Pyrus communis* L.)
	Spinach (*Spinacia oleracea* L.)
1	Apple (sliced) (*Malus ×domestica* Borkh.)
	Apricot (*Prunus armeniaca* L.)
	Atemoya (*Annona squamosa ×cherimola*)
	Avocado (*Persea americana* Mill.)
	Banana (*Musa* L.)
	Brussels sprouts (*Brassica oleracea* L. Group Gemmifera)
	Broccoli (florets)
	Cantaloupe (muskmelon; *Cucumis melo* L.)
	Cherimoya (*Annona cherimola* Mill.)
	Cherry (sweet; *Prunus avium* L.)
	Chicory (*Cichorium intybus* L.)
	Cranberry (*Vaccinium macrocarpon* Ait.)
	Cucumber (*Cucumis sativus* L.)
	Grape (*Vitis vinifera* L.)
	Kiwifruit (*Actinidia deliciosa* (A. Chev) C.F. Liang et A.R. Ferguson var. *deliciosa*)
	Lettuce (chopped butterhead, crisphead)
	Litchi (Lychee) (*Litchi chinensis* Sonn.)
	Nectarine [*Prunus persica* (L.) Batsch Group]
	Onion (bulb; *Allium cepa* L.)
	Peach [*Prunus persica* (L.) Batsch]
	Plum (*Prunus ×domestica* L.)
	Rambutan (*Nephelium lappaceum* L.)
	Sweetsop (*Annona squamosa* (L.))
1.5	Apple (most cultivars)
	Pear (most cultivars)
2	Artichoke (*Cynara scolymus* L.)
	Blackberry (*Rubus* L. subg. Rubus Watson)
	Cabbage (*Brassica oleracea* L. Group Capitata)
	Cauliflower (*Brassica oleracea* L. Group Botrytis)
	Carrot (shredded and cut) (*Daucus carota* L.)
	Celery [*Apium graveolens* L. dulce (Mill.) Pers.]
	Corn (sweet) (*Zea mays* L.)
	Durian (*Durio zibethinus* Murr.)
	Fig (*Ficus carica* L.)
	Mango (*Manifera indica* L.)
	Olive (*Olea europaea* L.)
	Papaya (*Carica papaya* L.)
	Pepper (green bell and chilli; *Capsicum annuum* L.)
	Pineapple [*Ananas comosus* (L.) Merr.]
	Pomegranate (*Punica granatum* L.)
	Raspberry (*Rubus idaeus* L.)
	Strawberry (*Fragaria ×ananassa* Duch.)
	Tomato [*Lycopersicon esculentum* (L.) Mill.]
2.5	Blueberry (*Vaccinium corymbosum* L.)
	Cabbage (shredded)
3	Apple (some cultivars)
	Cantaloupe (cubed or sliced)
	Grapefruit (*Citrus paradisi* Macf.)
	Pear (some cultivars)
	Persimmon (*Diospyros khaki* L.)
	Potato (*Solanum tuberosum* L.)
4	Mushrooms (sliced)
5	Bean (green snap) (*Phaseolus vulgaris* L.)
	Lemon (*Citrus jambhiri* Lush.)
	Lime (*Citrus limettioides* Tan.)
	Orange [*Citrus sinensis* (L.) Osb.]
10	Asparagus (*Asparagus officinalis* L.)
14	Orange (sections)

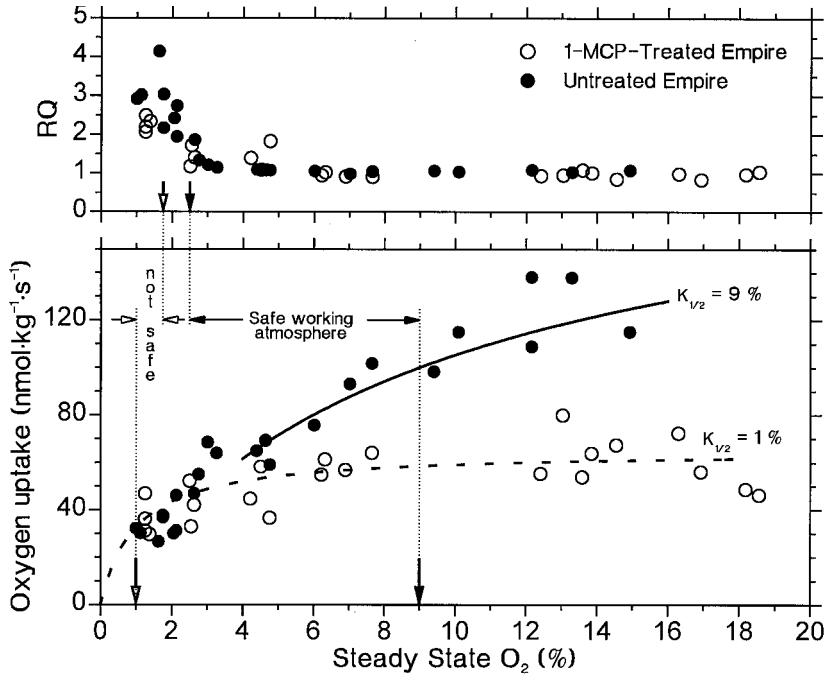

Fig. 3. Respiratory response to O_2 and the associated RQ of mature, unripe (1-MCP-treated) and ripening (untreated) apple fruit held at 22 °C (72 °F) for 14 d in LDPE packages (data previously unpublished). The vertical arrow in the upper graph depicts the lower O_2 limit based on the increase in fermentative activity at lower O_2 concentrations. The vertical arrow in the lower graph indicates the $K_{1/2}$ of the fitted line. The fact that the lower O_2 limit exceeds the $K_{1/2}$ for unripe fruit is taken to indicate that there is no safe working atmosphere for fruit of this developmental stage. The fact that the $K_{1/2}$ exceeds the lower O_2 limit for ripening fruit is taken to indicate that there is a substantial safe working atmosphere for fruit of this developmental stage.

apple fruit is inhibited by a single exposure to 1-MCP for as long as 30 to 40 d at room temperature (Beaudry, unpublished data; Fan et al., 1999). Untreated fruit ripened normally within 5 to 6 d. The 1-MCP-treated fruit showed no outward signs of ripening throughout the study as judged by changes in green and yellow coloration or firmness loss such that the fruit were considered to be in a nonripening state. The respiratory curve for the nonripening fruit exhibited a $K_{1/2}$ of about 1% O_2 and a Vmax of about 65 nmol·kg^{-1}·s^{-1} (Fig. 3). The fermentation threshold was about 2% O_2. Thus, there was no safe working atmosphere for nonripening fruit. The implication is that for nonripening fruit, low O_2 benefits are not due to respiratory suppression, but are primarily due to effects on ethylene action, which is consistent with previous assessments (Burg and Burg, 1967; Solomos, 1997b). Ripening fruit, however, had a $K_{1/2}$ of about 9% O_2 and a Vmax of about 200 nmol·kg^{-1}·s^{-1}. The increased respiratory rate at high O_2 levels indicated that the fruit were undergoing climacteric respiratory enhancement associated with ripening. The fermentation threshold was about 2.5% O_2, yielding a safe working atmosphere of nearly 6.5% in breadth between 2.5% and 9% O_2. A similar response to O_2 was found for 'Jonathan' apple fruit, which had a safe working atmosphere of about 6% in breadth between 1% and 7% O_2 (data not shown). Insofar as the permeabilities of the apple fruit skin and flesh are not known to shift dramatically during the early stages of ripening (Park, 1990), this shift in $K_{1/2}$ and Vmax may reflect the induction and extensive use of the alternative oxidase as ripening commenced, an observation supported by previous research on other climacteric crops (Cruz-Hernandez and Gomez-Lim, 1995), but not yet confirmed. In any case, ripening fruit in which climacteric respiration has been induced would be expected to respond to reduced O_2 levels by a reduction in O_2 uptake and associated oxidative metabolism at an O_2 level well above the fermentation threshold. In keeping with this expectation is the long history of successful low O_2 storage of apple fruit (Kidd and West, 1927, 1945). In the apple industry, CA storage is a relatively common practice and typically results in a doubling or trebling of shelf life relative to refrigerated air storage (Fidler, 1965).

A similar, large safe working atmosphere is present for tomato fruit (data not shown), which respond positively to low O_2 levels. Unlike apple fruit, however, there was a safe working atmosphere for both unripe, mature fruit as well as ripening fruit. The $K_{1/2}$ increased from 3% to 9% O_2 during ripening and the fermentation threshold remained unchanged at about 1% O_2 (data not shown). Low O_2 atmospheres significantly delay the onset of tomato ripening and slow ripening once underway (Yang and Chinnan, 1988). Despite the rather broad safe working atmosphere for tomato, advantages gained by respiratory suppression and the reduction in ethylene action by low O_2 may be minimized by decay and bruising (Allen and Allen, 1950; Isenburg, 1979; Saltveit, 1997). In that O_2 concentrations above the fermentation threshold have little effect on the activity of most decay organisms (Brown, 1922), low O_2 would not directly suppress decay. Additionally, marketing is such that extending storage life of tomato fruit for would do little to add value to the crop. Tomato production is already year-round, with no discernible breaks in fresh product availability.

Safe working atmospheres 3.5% and 2% O_2 in width were found for broccoli and blueberries, respectively (data not shown). Broccoli respond to reduced O_2 in a favorable fashion (Makhlouf et al., 1989a, 1989b; Tian et al., 1994), exhibiting a longer storage life in terms of green color retention. A benefit for low O_2 on blueberries has been reported (Frisina et al., 1988), while others report little to no benefit (Ceponis and Cappellini, 1985; Smittle and Miller, 1988). Blueberry fruit are highly susceptible to decay and this feature often limits storability rather than the rate of fruit metabolism per se (Ceponis and Cappellini, 1985).

The lack of a safe working atmosphere for respiratory suppression may provide a mechanistic understanding as to why low O_2 atmospheres do not extend storage life in many horticul-

tural commodities. A clear exception appears to be preclimacteric apple fruit, for which respiratory suppression could be damaging, but because ethylene plays a significant role in ripening and senescence, low O_2 is effective in improving storability. Alternatively, the presence of a safe working atmosphere does not necessarily mean that the commodity is appropriate for the implementation of low O_2 atmospheres. Largely this is due to factors other than respiratory (i.e., metabolic) rate that limit storability.

ETHYLENE. Low O_2 is known to exert marked effects on ethylene biosynthesis (Abeles et al., 1992; Makhlouf et al., 1989a, 1989b). The $K_{1/2}$ of 1-aminocyclopropane carboxylic acid oxidase (ACO), the enzyme responsible for the last step in the enzymatic production of ethylene from 1-aminocyclopropane carboxylic acid (ACC) has been variously reported as falling within the range of 1.4% to 10% (Abeles et al., 1992). The requirement for O_2 is dependent on the concentration of the other substrate, ACC, due to the fact that ACO is a bisubstrate enzyme. As ACC levels increase, the K_m of the enzyme for O_2 declines. The mechanism is considered to be ordered bisubstrate with ACO first binding O_2, then binding ACC (Abeles et al., 1992).

Oxygen has also been reported to exert an effect on C_2H_4 perception (Burg and Burg, 1967) although this has been disputed (Abeles et al., 1992). Therefore, the effect of reduced O_2 may be due to reducing ethylene sensitivity in addition to its effect on biosynthesis. The general observation for climacteric tissues, however, is that O_2 concentrations that would normally not inhibit respiration in the mature green fruit still reduce the rate of ripening. For example, 'Empire' apple, fruit held in 3% O_2 and 22 °C that were maintained in a preclimacteric, nonripening state by 1-MCP treatment exhibited little reduction in respiration (Fig. 3). However, apple ripening can be significantly retarded by this concentrations of O_2 relative to higher O_2 levels (Sfakiotakis and Dilley, 1973). Thus, even if O_2 does not directly impinge on ethylene perception as suggested by Abeles et al. (1992), climacteric tissue responses make it appear so. Further, for nonripening climacteric fruit, it appears that the primary function of low O_2 is to suppress ripening through ethylene action, as opposed to general metabolic suppression via respiratory inhibition.

Low O_2 atmospheres have been used most commonly in commercial CA facilities to minimize ethylene-dependent responses attendant to ripening of climacteric fruit, but this goal may not always be compatible with MAP for consumer packages. For instance, while the initiation of ripening can be prevented very effectively by MAP, it is not commonly used for this purpose since it is the ripe or nearly ripe fruit that must be packaged to permit immediate consumption by the consumer. Ripe fruit are generally less responsive to inhibition of ethylene action than the preclimacteric fruit and more susceptible to handling damage and decay. The increased risks for quality loss likely do not justify the increased costs of packaging. More potential for incorporation of MAP to control ripening exists, perhaps, for lightly processed products, which require packaging anyway, or for whole fruit at the packinghouse or distributor level (Watkins et al., 1998).

PLANT PIGMENTS. Low O_2 has important effects on metabolism other than those on respiration and ethylene action that can have significant impacts on quality of plant products at both the distributor and consumer level. Low O_2 reduces the rate of degreening due to chlorophyll loss and inhibits browning reactions catalyzed by polyphenol oxidase (PPO). Chlorophyll loss, a desirable trait for many climacteric fruit, results in a quality loss for many vegetable products. Chlorophyll degradation in green vegetables can be inhibited by low O_2 (Makhlouf et al., 1989a). This response is probably partly due to inhibition by O_2 of ethylene-mediated promotion of senescence and perhaps by the direct action of O_2 in limiting the reaction of pheophorbide a oxygenase (Matile et al., 1999). The argument for the involvement of ethylene in the degreening process is strong for broccoli. Broccoli degreening can be inhibited by low O_2 (Makhlouf et al., 1989a), which reduces ethylene synthesis (Makhlouf et al., 1989b) and can be enhanced by added ethylene or the ethylene analogue propylene (Tian et al., 1994). Further, broccoli degreening is inhibited by the specific inhibitor of ethylene action, 1-MCP (Ku and Wills, 1999; Mir and Beaudry, unpublished data).

By far, the bulk of low O_2 use in consumer MA packages is for the purpose of reducing browning of the cut surfaces on lightly processed products, primarily lettuce and salad mixes. Cutting results in the mixing of cellular contents so that the various phenolic substrates such as mono-, di- and triphenols (Mayer and Harel, 1979) come into contact with PPO, leading to the formation of high molecular weight polymers and complexes with amino acids and proteins, resulting in the formation of brown pigments. The K_m for O_2 in tissue browning has been variously reported as ranging from 6% to 10% (Mapson and Burton, 1962; Mayer and Harel, 1979). Smyth et al. (1998) demonstrated that O_2 levels below 2% and above the fermentation threshold of about 0.5% reduced the rate of browning in lettuce. The concentration of O_2 in commercial packages of lettuce and salad products is often below the fermentation threshold (Cameron et al., 1995; Peiser et al., 1997). However, the fermentation of lettuce, if not severe, results in very few off-flavors (Smyth et al., 1998).

VOLATILES. The production of volatile esters, which contribute to characteristic aromas of a number of fruit including apple, banana, pear, peach, strawberry, and others are affected by atmosphere modification (Mattheis and Fellman, 2000; Shamaila et al., 1992; Song et al., 1998). This topic will be discussed in detail (Mattheis and Fellman, 2000) in these workshop proceedings. Production of aroma compounds that confer characteristic odors is generally suppressed by low O_2, in part by the action of O_2 on ethylene action in climacteric fruits, but also likely via action of O_2 on oxidative processes, including respiration, required for substrate production. Many volatiles that do not contribute to aroma are also suppressed by low O_2. In apple and pear, for instance, low O_2 may also alter terpenoid metabolism such that the production of α -farnesene (a semivolatile sesquiterpene that induces superficial scald) is reduced (Huelin and Murray, 1966). In general, most products recover from moderate low O_2 suppression of aroma volatile production and eventually develop characteristic flavors. Importantly, however, for consumer MA packages using low O_2, aroma suppression immediately precedes con-

sumption and may limit consumer acceptance.

Conclusions

The ability to modify the atmosphere surrounding plant products by sealing the plant material in permeable polymeric films has led to the development of MAP applications for bulk and consumer-sized products. MAP dates back to the middle to late 1940s when packages were first evaluated for their capability to reduce O_2 levels sufficiently to slow the ripening of apple fruit. The primary limitation of MAP application noted in the early studies was technical in nature, specifically being the lack of consistent control of O_2 concentration in the package, which was a problem compounded by the lack of adequate temperature control. While temperature management has improved markedly, O_2 control still remains a primary concern. Recent developments in packaging models, the advent of temperature-compensating films, and the prospects for the development of sense-and-respond packaging suggests that this limitation may eventually diminish. The physiological limitations presented by fruit and vegetable products have proven less tractable than the technological limitations mentioned, and little progress has been made in this area apart from quantifying the ability of plant material to withstand low O_2 stresses and recover from low O_2 exposure. Furthermore, many, if not most, plant tissues do not respond favorably to low O_2 to a sufficient extent to warrant the use of MA packaging for the purpose of reducing the O_2 concentration in the atmosphere surrounding the product (see also Table 1). With regard to those plant materials that do respond positively to low O_2, knowledge of plant responses to O_2 at the level of primary and secondary metabolism is limited. We have much to look forward to in terms of additional progress in resolving technical and physiological limitations to low O_2 application to expand the use of MAP in food preservation.

Literature cited

Abeles, F.B., P.W. Morgan, and M.E. Saltveit, Jr. 1992. Ethylene in plant biology. 2nd ed. Academic Press, San Diego, Calif.

Allen, A.S. and N. Allen. 1950. Tomato-film findings. Modern Packaging 23:123–126, 180.

Beaudry, R.M. 1999. Effect of O_2 and CO_2 partial pressure on selected phenomena affecting fruit and vegetable quality. Postharvest Biol. Technol. 15:293–303.

Beaudry, R.M., A.C. Cameron, A. Shirazi, and D.L. Dostal-Lange. 1992. Modified atmosphere packaging of blueberry fruit: Effect of temperature on package oxygen and carbon dioxide. J. Amer. Soc. Hort. Sci. 117:436–441.

Brown, W. 1922. On the germination and growth of fungi at various temperatures and in various concentrations of oxygen and carbon dioxide. Ann. Bot. 36:257–283.

Burg, S.P. and E.A. Burg. 1967. Molecular requirements for the biological activity of ethylene. Plant Physiol. 42:114–152.

Burton, WG. 1974. Some biophysical principles underlying the controlled atmosphere storage of plant material. Ann. Appl. Biol. 78:149–168, 1974.

Cameron, A.C., R.M. Beaudry, N.H. Banks, and M.V. Yelanich. 1994. Modified-atmosphere packaging of blueberry fruit: Modeling respiration and package oxygen partial pressures as a function of temperature. J. Amer. Soc. Hort. Sci. 119:534–539.

Cameron, A.C., W. Boylan-Pett, and J. Lee. 1989. Design of modified atmosphere packaging systems: Modelling oxygen concentrations within sealed packages of tomato fruits. J. Food Sci. 54:1413–1416, 1421.

Cameron, A.C., B.D. Patterson, P.C. Talasila, and D.W. Joles. 1993. Modeling the risk in modified-atmosphere packaging: A case for sense-and-respond packaging, p. 95–102. In: M.E. Saltveit (ed.). CA'93 Proceedings. vol. 1. NRAES-71, Ithaca, N.Y.

Cameron, A.C., P.C. Talasila, and D.J. Joles, 1995. Predicting the film permeability needs for modified-atmosphere packaging of lightly processed fruits and vegetables. HortScience 30:25–34.

Ceponis, M.J. and R.A. Cappellini. 1985. Reducing decay in fresh blueberries with controlled atmospheres. HortScience 20:228–229.

Clarke, R. and C.P. De Moor. 1997. The future in film technology: A tunable packaging system for fresh produce, p. 68–75. In: J. Gorny (ed.). CA'97 Proceedings. vol. 5. Fresh-cut fruits and vegetables and MAP. Univ. Calif. Postharvest Hort. Ser. 19.

Cruz-Hernandez, A. and M.A. Gomez-Lim. 1995. Alternative oxidase from mango is differentially regulated during fruit ripening. Planta 197:569–576.

Fan, X., S.M. Blankenship, and J.P. Mattheis. 1999. 1-methylcyclopropene inhibits apple ripening. J. Amer. Soc. Hort. Sci. 124:690–695.

Fidler, J.C. 1965. Controlled atmosphere storage of apples, p. 1–7. In: Proc. Inst. Refrig., Natl. College for Heating, Ventilation, Refrig. and Fan Eng., London, England.

Fishman, S., V. Rodov, and S. Ben-Yehoshua. 1996. Mathematical model for perforation effect on oxygen and water vapor dynamics in modified-atmosphere packages. J. Food Sci. 61:956–961.

Frisina, J., L Barrand, C. Cooper, C. Little, and K. Clayton-Greene. 1988. Blueberry storage trials progress report for 1987/1988. Hort. Res. Inst., Knoxfield, Australia.

Gorny, J.R. 1997. A summary of CA and MA requirements and recommendations for fresh-cut (minimally-processed) fruits and vegetables, p. 30–66. In: J. Gorny (ed.). CA'97 Proceedings. vol. 5. Fresh-cut fruits and vegetables and MAP. Univ. Calif. Postharvest Hort. Ser. 19.

Hertog, M.L.A.T.M., H.W. Peppelenbos, R.G. Evelo, and L.M.M. Tijskens. 1998. A dynamic and generic model of gas exchange of respiring produce: the effects of oxygen, carbon dioxide and temperature. Postharvest Biol. Technol. 14:335–349.

Herner, R.C. 1987. High CO_2 effects on plant organs, p. 239–253. In: J. Weichman (ed.). Postharvest physiology of vegetables. Marcel Dekker, Inc., New York.

Huelin, F.E. and K.E. Murray. 1966. a-Farnesene in the natural coating of apples. Nature (London) 210:1260–1261.

Isenberg, F.M.R. 1979. Controlled atmosphere storage of vegetables. Hort. Rev. 1:337–394.

Joles, D.W. 1993. Modified-atmosphere packaging of raspberry and strawberry fruit: Characterizing the respiratory response to reduced O_2, elevated CO_2 and changes in temperature. MS thesis. Mich. State Univ., E. Lansing.

Joles, D.W., A.C. Cameron, A. Shirazi, P.D. Petracek, and R.M. Beaudry. 1994. Modified-atmosphere packaging of 'Heritage' red raspberry fruit: Respiratory response to reduced oxygen, enhanced carbon dioxide, and temperature. J. Amer. Soc. Hort. Sci. 119:540–545.

Jurin, V. and M. Karel. 1963. Studies on control of respiration of McIntosh apples by packaging methods. Food Technol. 17:104–108.

Kader, A.A. 1997a. A summary of CA requirements and recommendations for fruits other than apples and pears, p. 1–36. In: A. Kader (ed.). CA'97 Proceedings. vol. 2. Fruits other than apples and pears. Univ. Calif. Postharvest Hort. Ser. 17.

Kader, A.A. 1997b. Biological bases of O_2 and CO_2 effects on postharvest life of horticultural perishables, p. 160–163. In: M.E. Saltveit (ed.). CA'97 Proceedings. vol. 4. Vegetables and ornamentals. Univ. Calif. Postharvest Hort. Ser. 18.

Kays, S.J. 1997. Postharvest physiology of perishable plant products. Van Nostrand Reinhold, N.Y.

Kidd, F. and C. West. 1914. The controlling influence of carbon dioxide in the maturation,

dormancy and germination of seeds. Proc. Royal Soc. London, B 87:408–421.

Kidd, F. and C. West. 1927. A relation between the concentration of oxygen and carbon dioxide in the atmosphere, rate of respiration, and length of storage of apples. Food Invest. Board Rep. London for 1925, p. 41–42.

Kidd, F. and C. West. 1945. Respiratory activity and duration of life of apples gathered at different stages of development and subsequently maintained at constant temperature. Plant Physiol. 20:467–504.

Ku, V.V.V. and R.B.H. Wills. 1999. Effect of 1-methylcyclopropene on the storage life of broccoli. Postharvest Biol. Technol. 17:127–132.

Kupferman, E. 1997. Controlled atmosphere storage of apples, p. 1–30. In: E.J. Mitcham (ed.). CA'97 Proceedings. vol. 3. Apples and Pears. Univ. Calif. Postharvest Hort. Ser. 16.

Lakakul, R., R.M. Beaudry, and R.J. Hernandez. 1999. Modeling respiration of apple slices in modified-atmosphere packages. J. Food Sci. 64:105–110.

Lange, D.L. 2000. New film technologies for horticultural products. HortTechnology 10(3):487–490.

Lee, L.J. 1994. Analysis, design, evaluation and modelling of bulk packaging systems under optimal modified atmosphere for storage and transportation of fruits and vegetables. PhD diss. Laval Univ., Quebec, Canada.

Makhlouf, J., C. Willemot, J. Arul, F. Castaigne, and J.-P. Emond. 1989a. Long-term storage of broccoli under controlled atmosphere. HortScience 24:637–639.

Makhlouf, J., C. Willemot, J. Arul, F. Castaigne, and J.-P. Emond. 1989b. Regulation of ethylene biosynthesis in broccoli flower buds in controlled atmospheres. J. Amer. Soc. Hort. Sci. 114:955–958.

Mapson, L.W., and W.G. Burton. 1962. The terminal oxidases of potato tuber. Biochem. J. 82:19–25.

Matile, P., S. Hörtensteiner, and H. Thomas. 1999. Chlorophyll degradation. Annu. Rev. Plant Physiol. 50:67–95.

Mattheis, J.P. and J.K. Fellman. 2000. Impacts of modified atmosphere packaging and controlled atmospheres on aroma, flavor and quality of horticultural commodities. HortTechnology 10(3):507–510.

Mayer, A.M. and E. Harel. 1979. Polyphenol oxidases in plants. Phytochemistry 18:193–215.

Park, Y.M. 1990. Gas exchange in apples: pathways for gas exchange, changes in resistance to gas diffusion during fruit development and storage, and factors affecting the changes. PhD diss. Cornell Univ., Ithaca, N.Y.

Peiser, G., G. López-Gálvez, and M. Cantwell. 1997. Changes in off-odor volatiles of salad products during storage, p. 23–28. In: J. Gorny (ed.). CA'97 Proceedings. vol. 5. Fresh-cut fruits and vegetables and MAP. Univ. Calif. Postharvest Hort. Ser. 19.

Reid, M.S. 1997. A summary of CA and MA requirements and recommendations for ornamentals and cut flowers, p. 129–136. In: M.E. Saltveit (ed.). CA'97 Proceedings. vol. 4. Vegetables and ornamentals. Univ. Calif. Postharvest Hort. Ser. 18.

Richardson, D.G. and E. Kupferman. 1997. Controlled atmosphere storage of pears, p. 31–35. In: E.J. Mitcham (ed.). CA'97 Proceedings. vol. 2. Apples and pears. Univ. Calif. Postharvest Hort. Ser. 16.

Saltveit, M.E. 1997. A summary of CA and MA recommendations for harvested vegetables, p. 98–117. In: M.E. Saltveit (ed.). CA'97 Proceedings. vol. 4. Vegetables and ornamentals. Univ. Calif. Postharvest Hort. Ser. 18.

Serek, M, E.C. Sisler, and M.S. Reid. 1995. 1-Methylcyclopropene, a novel gaseous inhibitor of ethylene action, improves the life of fruits, cut flowers and potted plants. Acta Hort. 394:337–345.

Sfakiotakis, E.M. and D.R. Dilley. 1973. Induction of autocatalytic ethylene production in apple fruits by propylene in relation to maturity and oxygen. J. Amer. Soc. Hort. Sci. 98:504–508.

Shamaila, M., W.D. Powire, and B.J. Skura. 1992. Analysis of compounds from strawberry fruit stored under modified atmosphere packaging (MAP). J. Food Sci. 5:1173–1176.

Silva, S. 1998. Regulation of glycolytic metabolism in asparagus spears (*Asparagus officinalis* L.), PhD thesis. Mich. State Univ., E. Lansing.

Sisler, E. and S. Blankenship. 1996. Patent No. 5,518,988. Method of counteracting an ethylene response in plants. 21 May 1996.

Smittle, D.A. and W.R. Miller. 1988. Rabbiteye blueberry storage life and fruit quality in controlled atmospheres and air storage. J. Amer. Soc. Hort. Sci. 113:723–728.

Smyth, A.B., J. Song, and A.C. Cameron. 1998. Modified atmosphere packaged cut iceberg lettuce: Effect of temperature and O_2 partial pressure on respiration and quality. J. Agr. Food Chem. 46:4556–4562.

Smyth, A.B., P.C. Talasila, and A.C. Cameron. 1999. An ethanol biosensor can detect low-oxygen injury in modified atmosphere packages of fresh-cut produce. Postharvest Biol. Technol. 15:127–134.

Solomos, T. 1977a. Cyanide-resistant respiration in higher plants. Ann. Rev. Plant Physiol. 28:279–97.

Solomos, T. 1997b. Effects of hypoxia on the senescence of horticultural crops, p. 138–148. In: M.E. Saltveit (ed.). CA'97 Proceedings. vol. 4. Vegetables and ornamentals. Univ. Calif. Postharvest Hort. Ser. 18.

Song, J., W. Deng, L. Fan, J. Verschoor, and R. Beaudry. 1998. Aroma volatiles and quality changes in modified atmosphere packaging, p. 85–95. In: J.R. Gorny (ed.). CA'97 Proceedings. vol. 4. Vegetables and ornamentals. Univ. Calif. Postharvest Hort. Ser. 18.

Smyth, A.B., J. Song, and A.C. Cameron. 1998. Modified-atmosphere packaged cut iceberg lettuce: effect of temperature and O2 partial pressure on respiration and quality. J. Agr. Food Chem. 46:4556–4562.

Talasila, P.C., A.C. Cameron, and D.W. Joles. 1994. Frequency distribution of steady-state oxygen partial pressures in modified-atmosphere packages of cut broccoli. J. Amer. Soc. Hort. Sci. 119:556–562.

Tian, M.S., C.G. Downs, R.E. Lill, and G.A. King. 1994. A role for ethylene in the yellowing of broccoli after harvest. J. Amer. Soc. Hort. Sci. 119:276–281.

Tomkins, R.G. 1962. Film packaging of fresh fruit and vegetables—The influence of permeability. Inst. Packaging Conf. Guide 1961, Larkfield, Maidstone, Kent, England. p. 64–69.

Tucker, M. and G. Laties. 1985. The dual role of oxygen in avocado respiration: Kinetic analysis and computer modeling of diffusion-affected respiratory oxygen isotherm. Plant Cell Environ. 9:117–127.

Vanlerberghe, G.C. and L. McIntosh. 1997. Alternative oxidase: from gene to function. Annu. Rev. Plant Physiol. 48:703–34.

Watkins, C.B. 2000. Responses of horticultural commodities to high carbon dioxide as related to modified atmosphere packaging. HortTechnology 10(3):501–506.

Watkins, C.B., P.L. Brookfield, H.J. Elgar, and S.P. McLeod. 1998. Development of a modified atmosphere package for export of apple fruit, p. 586–592. In: S. Ben-Yehoshua (ed.). Proc. 1997 Intl. Congr. Plastics Agr. Laser Pages Publ. Ltd., Jerusalem, Israel.

Workman, M. 1959. The status of polyethylene film liners to provide modified atmosphere for the storage of apples. Eastern Fruit Grower 23:6,10–14.

Yang, C.C. and M.S. Chinnan. 1988. Modeling the effect of O_2 and CO_2 on respiration and quality of stored tomatoes. Trans. Amer. Soc. Agr. Eng. 31:920–925.

Yearsley, C.W., N.H. Banks, S. Ganesh, and D.J. Cleland. 1996. Determination of lower oxygen limits for apple fruit. Postharvest Biol. Technol. 8(2):95–109.