Responses of Horticultural Commodities to High Carbon Dioxide as Related to Modified Atmosphere Packaging

Christopher B. Watkins

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SUMMARY. The tolerances of horticultural commodities to CO_2 are outlined, as are also the associated biochemical and physiological aspects of differences in tolerance between and within commodity types. These tolerances are related to responses to the use of modified atmosphere packaging (MAP) during storage. Commodities vary widely in their responses to elevated CO_2, and low tolerance to the gas limits its use to maintain quality in some cases. Standard recommendations are generally those established to extend the storage period of any given commodity as long as possible, and safe atmospheres may differ substantially for shorter term exposures used in MAP. Use of MAP for storage of minimally processed products represents an important example of this, as storage periods and quality attributes required for commercial marketing of cut products can be very different from those of the whole product. Factors such as cultivar and postharvest treatment before imposing high CO_2 can influence responses of commodities to CO_2, but are rarely considered in cultivar selection or in commercial application. A better understanding of the physiology and biochemistry of commodity responses to CO_2 is required for increased use of MAP.

The focus of this paper is on CO_2 effects as they pertain to modified atmosphere packaging. In an associated paper, Beaudry (2000) has described factors associated with responses of horticultural commodities to low O_2, but under MAP conditions elevated CO_2 is also a major factor influencing quality of fruit and vegetables. Indeed, it is often the elevated CO_2 in addition to, or rather than, the low O_2 that exerts beneficial or detrimental effects.

The postharvest tolerances of most commercially important fruit and vegetables to high CO_2 concentrations have been established, the general goal being to identify the safe concentrations (in conjunction with the accompanying O_2 concentration) that will result in maximum commodity storage life without injury. When a fruit or vegetable is subjected to atmospheres outside safe limits at any temperature/time combination, damage may be manifested as irregular ripening, initiation and/or aggravation of certain physiological disorders, development of off-flavors, and increased susceptibility to decay.

Tolerances of commodities to high CO_2 levels are affected by both metabolic and physical factors. Responses of horticultural commodities to CO_2 can vary dramatically among species, cultivars and strains, organ types, and developmental stages, and can be either unwanted or highly desirable, depending on the product. Generally it is assumed that CO_2 directly affects respiration and associated metabolic pathways, as well as pathways involved in secondary metabolism such as production of ethylene, pigments, phenolics, and volatiles (Beaudry, 1999; Kader, 1997a). However, physical effects such as skin thickness that influence gas exchange will affect gaseous equilibrium between the outside and inside of the tissue and thereby influence the susceptibility of products to injury (Burton, 1974). Therefore, the recommended storage atmospheres represent ones that are safe for the overall population of intact fruit or vegetables rather than for individuals, whose physiology can vary greatly.

The objectives of this presentation are to outline the tolerances of horticultural commodities to CO_2, to describe the associated biochemical and physiological aspects of differences in tolerance between and within commodity types, and to focus on how these variables relate to the use of MAP during storage. The fungistatic effects of CO_2 on decay incidence in MAP (DeVries-Paterson et al., 1991) are not considered here.

Tolerances of horticultural commodities to carbon dioxide

Sources of information for recommended CO_2 (and O_2) concentrations for most horticultural commodities include Beaudry (1999), Kader (1997a), references cited by Kader and Watkins (2000), and the Proceedings from the International Controlled Atmosphere Conferences held every 4 years (e.g., Gorny, 1997; Kader, 1997b; Kupferman, 1997; Saltveit, 1997).

These recommendations generally represent the conditions that will result in maximum storage life of each commodity. However, it is also useful to examine the differences in tolerances to CO_2 among commodities. An extremely wide range of CO_2 concentrations beyond which injury occurs exists for different commodities (Table 1). Whereas 2% CO_2 represents the upper level for lettuce, some berryfruit, figs and cherimoya can tolerate 25% or higher. It should be noted that these limits have been identified by storing commodities for maximum periods, and therefore may be lower than those that are safe for short-term storage. Understanding the reasons for differences in susceptibility to CO_2 injury may yield information that can be used to expand uses of MAP and other uses of CO_2 such as disinfestation treatments and decay control.

Effects of CO_2 on metabolism

At the metabolic level, more information exists for effects of O_2 than for CO_2 because of the extensive research that has been carried out on anoxia and hypoxia in many different plant materials (Ratcliffe, 1995). In contrast, information about the effects of high CO_2 is largely limited to fruit and vegetables after harvest. Overall, there are many similarities between the effects of low O_2 and high CO_2 on metabolism, with most effects being suppression of various metabolic processes (Beaudry, 1999; Kader, 1997a). The following exceptions are evident.

- Respiration is usually inhibited by low O_2, but can be inhibited, unaffected or stimulated by high CO_2 in the storage environment (Mathooko, 1996a). The stimulation of respiration may represent stress responses by the tissue.
- 1-Aminocyclopropane-1-carboxylic acid (ACC) synthase activity is inhibited by both low O_2 and high CO_2. However, while ACC oxidase activity is inhibited by low O_2, it is stimulated and inhibited by low and high CO_2 concentrations, respectively (Mathooko, 1996b).
- Activity of phenylalanine ammonia lyase (PAL), an enzyme involved in phenolic metabolism, is inhibited by low O_2 but is enhanced by high CO_2 in some (Prusky et al., 1996), but not all, tissues (Holcroft et al., 1998).
- High CO_2 is a competitive inhibitor of ethylene action (Burg and Burg, 1967).

Research on high CO_2 effects on metabolism has focused on the primary metabolic pathways, such as glycolysis, fermentation, TCA cycle, and the mitochondrial respiratory chain. A complete cataloging of the effects of high CO_2 on individual enzymes will not be provided here, but rather, broad statements and identifications of differences between the action of low O_2 and high CO_2 will be made. High CO_2 appears to do the following.

- Increase carbon flux through glycolysis and maintain energy levels in the cell. Activation of glycolysis may not involve the same enzymes as those affected by low O_2, especially the phosphofructokinases, PPi-PFK and ATP-PFK (Kerbel et al., 1990). Also, pyruvate kinase and pyruvate decarboxylase activities are affected differently by low O_2 and high CO_2 (Silva, 1998).
- Increase carbon flux through the fermentation pathway, although activation of pyruvate decarboxylase (PDC) and alcohol dehydrogenase (ADH) is less evident in high CO_2 than in low O_2 treatments (Ke et al., 1995).
- Result in accumulation of the TCA cycle intermediate, succinate, in CO_2, but not in O_2-treated tissues. This accumulation, which is thought to be toxic to plant cells (Hulme, 1956), may be related to the inhibition of succinate dehydrogenase (SDH) activity (Frenkel and Patterson, 1973; Ke et al., 1993). Succinate accumulation could also result, however, from activation of the glyoxylate cycle (Yang et al., 1998), the γ-aminobutyrate shunt (Satya Narayan and Nair, 1986), and/or phosphoenolpyruvate carboxylase activity (Bisbis et al., 1997).
- Enhance the alternative pathway by induction and/or activation of the alternative oxidase, and inhibition of the cytochrome pathway by suppression of cytochrome oxidase activity, although treatment effects can be diverse according to physiological state of the tissue, harvest season, temperature, and CO_2 concentration (Lange and Kader, 1997a).

Both CO_2 and O_2 may affect enzyme activities by changing the rates of degradation and/or synthesis, activation and/or inactivation, substrate and cofactor availability, or a combination of these processes. In addition, CO_2 may cause complex interactions in tissues, including changes in the kinetics of allosteric proteins (Mitz, 1979).

Table 1. CO_2 limits beyond which injury will occur for selected horticultural crops. (Modified from Herner (1987), Kader (1997b), and Saltveit (1997)).

CO_2 (%)	Commodity
1	Onion (long term) (*Allium cepa* L.)
2	Lettuce (crisphead) (*Lactuca sativa* L.)
	Pear (*Pyrus communis* L.)
3	Artichoke (*Cynara scolymus* L.)
	Tomato [*Lycopersicon esculentum* (L.) Mill.]
5	Apple (most cultivars) (*Malus×domestica* Borkh.]
	Apricot (*Prunus armeniaca* L.)
	Carrot (*Daucus carota* L.)
	Cauliflower (*Brassica oleracea* L. Group Botrytis)
	Cucumber (*Cucumis sativus* L.)
	Grape (*Vitis vinifera* L.)
	Nashi (*Pyrus serotina* Rehd.)
	Olive (*Olea europaea* L.)
	Orange [*Citrus sinensis* (L.) Osb.]
	Peach (clingstone) [*Prunus persica* (L.) Batsch]
	Potato (*Solanum tuberosum* L.)
	Pepper (bell) (*Capsicum annuum* L.)
7	Banana (*Musa* sp.)
	Bean (green snap) (*Phaseolus vulgaris* L.)
	Kiwifruit [*Actinidia deliciosa* (A. Chev) C.F. Liang et A.R. Ferguson var. *deliciosa*]
8	Papaya (*Carica papaya* L.)
10	Asparagus (*Asparagus officinalis* L.)
	Brussels sprouts (*Brassica oleracea* L. Group Gemmifera)
	Cabbage (*Brassica oleracea* L. Group Capitata)
	Celery [*Apium graveolens* L. *dulce* (Mill.) Pers.]
	Grapefruit (*Citrus paradisi* Macf.)
	Lemon (*Citrus jambhiri* Lush.)
	Lime (*Citrus limettioides* Tan)
	Mango (*Manifera indica* L.)
	Nectarine [*Prunus persica* (L.) Batsch Group Nectarine]
	Onion (short term) (*Allium cepa* L.)
	Peach (freestone)
	Persimmon (*Diospyros kaki* L.)
	Pineapple [*Ananas comosus* (L.) Merr.]
	Sweetcorn (*Zea mays* L.)
15	Avocado (*Persea americana* Mill.)
	Broccoli (*Brassica oleracea* L. Group Italica)
	Lychee (*Litchi chinensis* Sonn.)
	Plum (*Prunus×domestica* L.)
	Pomegranate (*Punica granatum* L.)
	Spinach (*Spinacia oleracea* L.)
	Sweetsop (*Annona squamosa* L.)
20	Cantaloupe (muskmelon) (*Cucumis melo* L.)
	Durian (*Durio zibethinus* Murr.)
	Mushroom (*Agaricus bisporus* L.)
	Rambutan (*Nephelium lappaceum* L.)
25	Blackberry (*Rubus* L. subg. *Rubus* Watson)
	Blueberry (*Vaccinium corymbosum* L.)
	Fig (*Ficus carica* L.)
	Raspberry (*Rubus idaeus* L.)
	Strawberry (*Fragaria ×ananassa* Duch.)
30	Cherimoya (*Annona cherimola* Mill.)

Enzyme activities may also be affected by acidification of the cytoplasm by O_2 and CO_2. Oxygen effects may be associated with stimulation of lactic dehydrogenase, while those of CO_2 are usually ascribed to the generation of carbonic acid and subsequent lowering of the intracellular pH (Burton, 1974). The pH changes in the cytoplasm could affect the activity of several key enzymes in situ. Theoretical considerations indicate that acidification will occur at CO_2 concentrations above 5% (Bown, 1985). However, strong evidence for lowering of pH in
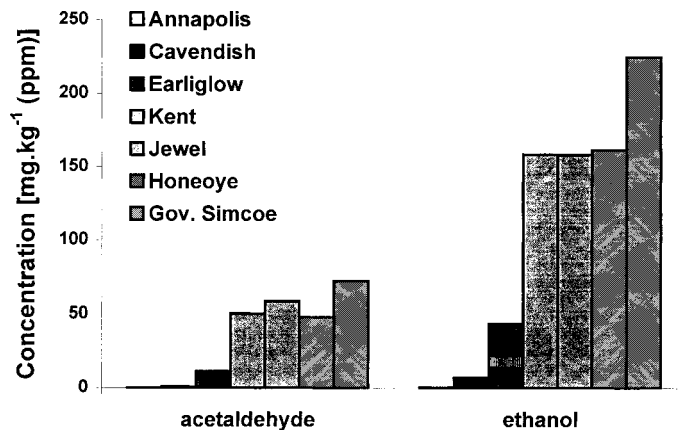
Fig. 1. Acetaldehyde and ethanol concentrations in seven strawberry cultivars when exposed to 20 kPa CO_2 for 7 d (modified from Watkins et al., 1999). No detectable acetaldehyde or ethanol were found for 'Annapolis'. Data are means of three replications per cultivar, and cultivar differences are significant at $P \leq 0.001$.

CO_2-treated tissues is not easily obtained, especially in bulky fruit tissues, although Lange and Kader (1997b) found that 20% to 40% CO_2 decreased the in vivo pH of avocado. Decreases in cytoplasmic pH have been indicated by nuclear magnetic resonance (NMR) measurements (Siriphanich and Kader, 1986). Indirect evidence for acidiosis has also been obtained by γ-aminobutyrate accumulation in CO_2-treated tissue since it is produced by the decarboxylation of glutamate in a proton-consuming glutamate decarboxylation reaction stimulated by lower cell pH (Ke et al., 1993). However, in vivo cellular pH may remain fairly constant because of buffering capacity; this capacity may vary among tissue types and the overall importance of acidification in tissue responses to high CO_2 is not yet certain.

Factors affecting tolerances of horticultural commodities to CO_2

CULTIVAR. Cultivar effects on susceptibility of commodities to CO_2 injury have been noted, e.g. in lettuce (Lopez-Galvez et al., 1996) and in apples (Wilkinson and Fidler, 1973). These have rarely been used to investigate the mechanisms of CO_2 action, although Ke et al. (1993) found no differences in metabolism of organic and amino acids in cultivars of crisphead

lettuce with varying tolerances to the gas. Recently, we have identified two groups of strawberry cultivars that vary widely in their responses to elevated CO_2 as indicated by accumulation of the fermentation products, acetaldehyde and ethanol (Fig. 1) (Watkins et al., 1999). When treated with 20% CO_2 for up to 9 d, cultivars such as 'Annapolis' and 'Cavendish' did not accumulate appreciable levels of fermentation products. In contrast, cultivars such as 'Honeoye' and 'Kent' accumulated large amounts of acetaldehyde and ethanol. These different responses not only provide useful material to investigate CO_2 effects on metabolism (Fernández-Trujillo et al., 1999), but also have implications for use of MAP. The marketplace usually rejects produce with accumulations of fermentation products and associated off-flavor development. Cultivars such as 'Annapolis' and 'Cavendish' would be regarded commercially as tolerant, whereas 'Honeoye' and 'Kent' would be considered as intolerant to high CO_2 conditions, respectively. Differences among cultivar responses could impact recommendations arising from MAP studies.

POSTHARVEST FACTORS. Tolerances of commodities to CO_2 are affected by its concentration and the storage temperature and length of exposure to the gas. The optimal CO_2 and O_2 concentrations may be different for products under MAP conditions than for typical CA storage. For example, some commodities are able to withstand very high CO_2 concentrations for short periods, e.g. up to 60% for asparagus (Corrigan and Carpenter, 1993) and 20% to control chilling injury in peaches and nectarines (Lurie, 1992). Tolerances of commodities can be higher at lower temperatures than higher temperatures, e.g. beneficial CO_2 concentrations for asparagus are 10% to 14% at 0 to 3 °C and 5% to 9% at 3 to 6 °C, and for chili pepper are 15% to 20% at 5 °C and 0% to 5% at 10 °C (Saltveit, 1997).

Other factors that may be related

to CO_2 tolerance under MAP conditions have been revealed by the occurrence of CO_2-related disorders during controlled atmosphere storage in a number of new commercial apple cultivars such as 'Braeburn', 'Empire' and 'Fuji'. Storage losses from these disorders have stimulated research that illustrates several important features of CO_2 tolerance. Susceptibility of apples to CO_2 injury is affected by the following.

• The timing of exposure of fruit to elevated CO_2 during CA storage. Apples are more susceptible to CO_2 injury during the first several weeks of CA storage. When 'Empire' apples are exposed to 5% CO_2 for 4 week intervals during normal CA storage conditions of 2% CO_2 and 2% O_2, most injury occurs during the first 4 weeks (Watkins et al. 1997). Elgar et al. (1998) found similar results for 'Braeburn'.

• Storage time in air before exposure to elevated CO_2. If 'Empire', 'Braeburn' or 'Bramley's Seedling' apples are kept in air storage for as little as 4 to 5 d before exposure to elevated CO_2, susceptibility to injury declines markedly (Fig. 2) (Colgan et al., 1999; Elgar et al., 1998; Watkins et al., 1997).

• Postharvest treatment with the antioxidant diphenylamine (DPA). DPA, which is widely used as a postharvest drench to prevent a physiological disorder known as superficial scald, can prevent CO_2-induced injury (Fig. 2) (Burmeister and Dilley, 1995; Watkins et al. 1997).

The implication of these studies is that in addition to cultivar effects, storage conditions, delays before application of MAP, and/or postharvest chemical treatment can affect tolerance of horticultural products to CO_2. Therefore, research on MAP of apples, for example, carried out with freshly harvested or stored fruit, with or without DPA treatment could result in different conclusions being reached for either fresh or minimally processed products.

Effects of minimal processing

A rapid increase in marketing of minimally processed products has led to a concomitant increase in application of MAP technologies (Gorny, 1997). Minimal processing can have
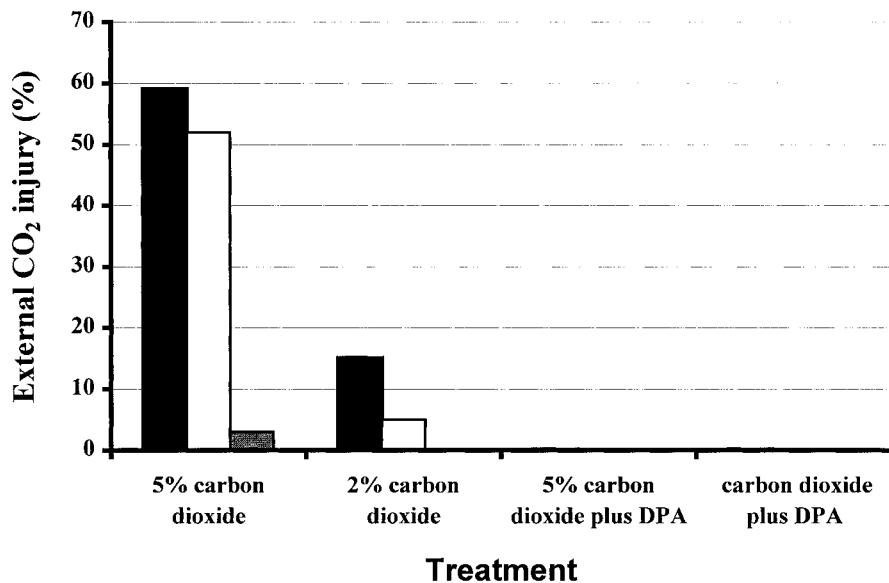
Fig. 2. External CO_2 injury of 'Empire' apple fruit, treated with either water or 5.9 mM diphenylamine (DPA) at harvest, and placed in air storage [2.2 °C (36 °F)] for 1d (black bars), 4 d (white bars) or 7 d (grey bars) before being exposed to 2% or 5% CO_2 (in 2% O_2) for 20 weeks. Data are provided for two combined orchard lots of fruit (modified from Watkins et al., 1997).

very direct effects on the tolerances of products to CO_2 by disrupting physical barriers between the external and internal environments, and removing

Table 2. Comparisons of CO_2 tolerance for selected whole and fresh cut fruits and vegetables. (Modified from Gorny (1997), Herner (1987), Kader (1997b), Kader et al. (1989), and Saltveit (1997)).

Commodity	CO_2 concn (%) beyond which injury occurs	
	Whole	Fresh cut
Broccoli	15	9
Cabbage	10	20
Cantaloupe	20	20
Carrot	5	20
Kiwifruit	7	10
Lettuce	2	10
Mushroom	20	20
Onion	1	15
Peach	5–10	12
Pear	2	10
Pepper	5	10
Spinach	15	13
Strawberry	25	12

the primary limitation imposed by skin resistance to gas diffusion. Accordingly, one might expect tolerances to CO_2 to differ greatly between whole and minimally processed products. Table 2 shows that CO_2 concentrations, beyond which injury symptoms occur on fresh cut products, can be higher than, equal to or lower than that for symptom development on whole products. These differences can occur for at least two important reasons.

• Storage conditions for processed products can differ greatly from those for whole products. Storage periods are typically much shorter for processed products than for whole products. A cut product has greater surface area, and is potentially subject to greater water loss, more damaged sites, higher respiration and ethylene production rates, and higher microbial growth. While MAP can delay these events (Gorny, 1997), the cut product is more metabolically active than the whole product, as well as being more prone to decay, and therefore shorter lived.

• The attributes of importance to the consumer, and hence the optimum atmosphere for storage to provide these attributes, can be different for each type of product. In strawberry, higher CO_2 concentrations are recommended for whole berries than for slices; CO_2 concentrations of 15% to 20% that maintain firmness and reduce decay, also result in bleaching of the internal flesh color (Gil et al., 1997). Such bleaching is not a marketing limitation for a whole product but is not acceptable for slices (Wright and Kader, 1997). In contrast, for lettuce, higher CO_2 concentrations are recommended for minimally processed lettuce than for the whole product. Whole lettuce can be damaged by disorders known as brown stain, and heart leaf injury, and/or accumulations of fermentation products, at CO_2 concentrations as low as 2% (Mateos et al., 1993a, 1993b). In the processed product, however, elevated CO_2 prevents browning associated with the midribs and cut surfaces (Lopez-Galvez et al., 1996; Mateos et al., 1993a, 1993b).

In addition, effects of cultivar, such as those described earlier for whole products, will be important in evaluating responses of cut products. Examples already shown include products as diverse as lettuce (Lopez-Galvez et al., 1996) and apple (Kim et al., 1993). Lopez-Galvez et al. (1996) have also investigated effects of storage periods of whole products before processing. To date, however, no attention has been given to the possible effects of storage or postharvest chemical usage on tolerances of minimally processed products to elevated CO_2. Data presented earlier on effects of DPA and delayed exposure to CO_2 on responses of whole apple to the gas suggest that these effects could be substantial.

Commercially, there seems to be little recognition and perhaps even less interest in dealing with variations in product responses related to cultivar or postharvest effects on a day to day basis. A one-size-fits-all process is preferred, but failure to recognize these effects could result in misleading conclusions about efficacy of a process under investigation, or to variable responses to a process after it put into practice.

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