# Manipulating the Postharvest Environment to Enhance or Maintain Resistance

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It is increasingly common for fresh fruits and vegetables to be marketed at great distances from where they are produced. Marketing fresh produce that is ordinarily out of season may result in large economic benefits to growers, distributors, and retailers and increase consumer choices. For example, stone fruits, pome fruits, and grapes produced in the Southern Hemisphere can be marketed during the northern winter. Kiwi fruits produced in both hemispheres are available throughout the year. Modern storage technology allows some apple cultivars to be marketed year-round. However, if commodities are in storage or in transit for long periods after harvest, they can become diseased or otherwise debilitated if proper care is not taken.

The physiological condition of fruits is extremely important in prevention of disease. High vitality fruits have considerable resistance to microbial attack. Ripening or senescing commodities, on the other hand, may rapidly lose their resistance (26).

The purpose of this paper is to discuss the relation of the postharvest environment and various stresses to the retention of disease resistance in fruits and vegetables. Included are discussions of the effects of the stage of development at harvest on resistance and the ways resistance may be lost or extended.

## NATURE OF POSTHARVEST DISEASE RESISTANCE

It is reasonable to believe that resistance mechanisms in edible parts of fruits and vegetables share the same multifaceted complexity that is found in the plants that produce them. An obvious difference is that harvested fruits are subject to dramatic reductions in resistance as they mature and ripen. Similarly, the edible buds, inflorescences, leaves, petioles, bulbs, roots, and tubers of vegetables are subject to decreasing resistance with time after harvest. The resistance of fruits before ripening may be similar to the resistance that causes some infections to be latent or quiescent (29,30,34,44).

The protective cuticle and the tissue's ability to respond to infection or a wound by producing wound periderm may exclude pathogens (20,33,35). Preformed antimicrobial substances such as catechol and protocatechuic acid, unsaturated lactones, plant glucanases, and chitinases have been associated with defense, as have inhibitors of polygalacturonase or other cell-wall-attacking enzymes (1,25,30).

Infection- or wound-induced substances that appear to play a role in defense include lignin, suberin, and callose, which may thicken or strengthen cell walls (2,5,30,39,42). Peroxidases, polyphenoloxidases, phenolic compounds, glycosides, histones, and phytoalexins are believed to play a role in resistance (19,25). The nature of the stimulus causing wounds or infections to incite the production of these compounds is not known. However, the earliest detectable event to occur following infection or wounding is production of ethylene. It has been suggested that ethylene is the signal for plants to erect defense mechanisms (10).

An important aspect of resistance is the wound-healing capacity of host tissue. During most of the preharvest life, the mechanism of wound healing involves meristematic production of periderm

in response to infection or physical injury (33,35). In apples and many other fruits, healing of wounds by periderm formation ceases before harvest maturity. However, wounds in harvested fruits of *Citrus* spp. heal by formation of a barrier of cells that have walls thickened with ligninlike materials (2,5). Harvested apples and pears have similarly exhibited the formation of thickened cell-wall barriers in living cells near the wounded tissue (20). Ligninlike substances and callose have been associated with the barrier of thickened cell walls. Yellow Newtown apples retained the ability to heal wounds sufficiently to protect against *Botrytis cinerea* Pers. ex Fr. and *Penicillium expansum* Lk. ex Fr. when fruits were wounded after 9 mo in a controlled atmosphere storage (N. F. Sommer, *unpublished results*).

In developing apples, resistance is high during the time of cell division and cell enlargement, and in some fruits, resistance is high during the early portion of the postharvest period. It is informative to compare fruit resistance to respiration rates, particularly in relation to the period from shortly before harvest through the postharvest life of the fruit (13). Most fruits show a respiratory pattern in which the fruit's respiration rate may continue to decline for a time after harvest but will then increase to a maximum at about the time the fruit is optimum for eating. After the climacteric rise, the respiration rate declines as the fruit becomes overripe and obviously very susceptible to disease. Ethylene is produced in large amounts by most fruits during the climacteric period.

Nonclimacteric fruits do not have an increase in the respiration rate associated with ripening. A few, like the sweet cherry, have a ripening sequence very similar to climacteric fruits. Others, such as citrus fruits, may fail to degreen or may degreen and then regreen in a warm humid climate. Under tropical conditions, citrus fruits may normally remain green despite an acceptable eating quality.

Although fruits have been studied most intensively, various nonfruit vegetables (leaves, petioles, stems, buds, bulbs, corms, and roots) also exhibit resistance. Chlorophyll-containing tissues often show a loss of resistance at the time the chlorophyll is being lost as shown by a color change to yellowish green.

## LOSS OF RESISTANCE

Actions during harvesting and handling may cause considerable loss of resistance and reduced maximum storage life during the period between harvest and storage. Common important factors include harvesting at the proper maturity, exposure to ethylene, physical stresses, and moisture loss.

**Harvest maturity.** The stage at which commodities are harvested is an extremely important determinant of the length of the period before loss of resistance. With all other conditions equal, the commodity's maturity determines the extent to which the fruit's postharvest life approaches its maximum genetic potential. Although the term mature is synonymous with ripe in many dictionaries, postharvest scientists make an important distinction between the two. Mature is here defined as "the point in a fruit's life at which it is capable of ripening to a quality acceptable to consumers." Ripe, on the other hand, denotes the point of maximum gustatory quality. If fruits are harvested too early, they may ripen with an entirely unsatisfactory gustatory quality. If fruits are harvested late, their disease-free postharvest life potential may be seriously shortened.

Indices of maturity are selected to better determine time to harvest. California Bartlett pears, for example, utilize firmness, soluble solids, and intensity of the green color as primary determinants. In apples, such information as time from full bloom, heat units during development, the extent of conversion of starch to sugar, soluble solids content, tissue firmness, color, and internal ethylene may all be utilized (18).

**Ethylene exposure.** Exposure to ethylene may cause many commodities to senesce or ripen early (24,26,27,32). Sensitivity of commodities to ethylene varies widely among species. One of the most sensitive is the kiwi fruit. Rapid softening and early appearance of Botrytis rot has resulted from an ethylene concentration as low as 25 ppb (F. G. Mitchell, *personal communication*).

Ripe or rotting fruit in storage may trigger a ripening reaction among all fruits in a package or in nearby packages as a consequence of the ethylene action. Other sources of ethylene to be avoided, in addition to ripe or rotting produce, include exhausts from internal combustion engines, cigarette or other smoke, fluorescent ballasts, and rubber materials subjected to heat or UV light (17). Chilling injury has been reported to cause ethylene production in cucumber fruits (45).

**Physical stress.** Physical injuries (cuts, punctures, bruises, and abrasions) cause an increased respiration rate with greater oxygen consumption and carbon dioxide evolution. Wound ethylene is produced from tissues near the wound, and phenolic substances, suberin, lignin, callose, and other substances associated with wound repair, accumulate (30,40).

**Delayed cooling.** The greatest shortening of a commodity's life commonly results during the elapsed time between harvest and the completion of cooling. The consequences are usually unnoticed by shippers. Instead, the effects of early senescence, ripening, and disease development commonly occur in distant markets where the reasons for reduced vitality and onset of disease is often unknown.

Tests with strawberries showed that cooling delays as short as 2 hr, at a temperature that did not exceed 30 C, noticeably advanced the onset of Botrytis rot when fruits were stored at 5 C during a simulated transit period. Cooling methods can generally be classified as room cooling, forced-air cooling, vacuum cooling, hydrocooling, and package icing. Advantages and disadvantages of different methods are numerous, and their adaptability to various commodities differs. For a general discussion of cooling methods, the reader is referred to Kader et al (18).

## STORAGE ENVIRONMENT

When a fruit or vegetable is separated from the parent plant and is placed in storage, it no longer receives water, minerals, or photosynthates. The living processes of the tissues must be maintained, and energy for the many catabolic and anabolic reactions must be provided by stored reserves. The postharvest life, which usually does not extend long after the commodity loses its disease resistance, is short at ambient temperatures.

**Refrigerated storage and transit.** Low temperatures serve to greatly extend the storage period before disease resistance is lost while also directly suppressing disease-causing organisms (4). For both purposes, the most effective temperature is the lowest that does not damage fruits. Climacteric fruits, such as apples and pears, do eventually undergo changes associated with ripening or senescence and become disease-susceptible, but only after an extended time at 0 C or −1 C.

The lowest temperatures that do not freeze the tissues can be used on non-chilling-sensitive fruits. Other commodities, such as some apple cultivars, are damaged if stored at temperatures below 2–4 C (3). Many commodities of tropical or subtropical origin may suffer chilling injury at temperatures below about 12–14 C (8).

Injury from damaging low temperatures is time-temperature dependent, i.e., the lower the temperature, the more rapid is the onset of injury symptoms in a given species or cultivar. Immature or mature fruits are more sensitive to chilling injury than ripe. At least in some cases, the growing environment may affect the sensitivity to chilling injury, as shown by Yellow Newtown apples from the Watsonville growing area of California, which must be stored at no lower than 3.5 C; yet somewhat lower storage temperatures are possible with apples of the same cultivar from Oregon, Washington, and British Columbia.

**Symptoms of chilling injury vary with different commodities.** Usually tissues are killed as indicated by browning of banana peels or apple flesh, pitting of citrus rinds, and susceptibility to fungi. Some chilling-injured fruits are observed to be especially susceptible to species of *Alternaria, Stemphylium* and *Fusarium*, but these organisms may be rare in nonchilled fruits (37).

**Modified atmospheres.** Modified atmospheres (MA) in storage

or transit are characterized by a decrease in oxygen ($O_2$), an increase in carbon dioxide ($CO_2$) or both. It is called a controlled atmosphere (CA) if the atmosphere composition is maintained nearly constant by frequent adjustment (16,17,36).

Initially, the atmosphere within the chamber is air. To establish the modified atmosphere, oxygen is displaced by nitrogen ($N_2$) gas. Nitrogen gas is sometimes obtained by thermally cracking ammonia into $H_2$ and $N_2$. In that case, $H_2$ reacts with $O_2$ to form water, while $N_2$ is freed from the ammonia. Oxygen may be consumed by catalytic burners or converters which, unfortunately, produce ethylene. Carbon dioxide from gas cylinders or dry ice may be added initially to establish the desired atmosphere. Alternatively, respiration of the commodity may be used to lower $O_2$ and increase $CO_2$ to the desired level. Establishing atmospheres by allowing the commodity to consume $O_2$ and produce $CO_2$ is not desirable, because that method is slow and reduces commodity life.

In operation, some carbon dioxide must be removed because of excessive accumulation from respiration of the fruit or vegetable. Similarly, respiration consumes oxygen and, if the storage is sufficiently airtight, there is a risk of the development of anoxia. Oxygen levels are increased by admitting a sufficient amount of outside air. Carbon dioxide is commonly lowered by passing a portion of the atmosphere through water or lime water which is piped to the exterior. Ethylene and other organic gases may be removed from atmospheres by passing the atmosphere through a scrubber containing potassium permanganate, which has been absorbed into a solid carrier.

Modified atmospheres slow the respiration rate beyond that of low temperature alone. Consequently, in the case of climacteric fruits, the climacteric is delayed and reduced. The period of disease resistance is lengthened to the extent that some apple cultivars may be stored for up to a full year with little rot.

Reducing the level of oxygen in air from the normal 20.8% to about 4% results in a noticeable extension of the storage life of some commodities and evidently increases the period of resistance. Greater effects are achieved at 2 or 1% oxygen. To avoid accidental anoxia, an oxygen level of 2% is often maintained.

Some pathogens, such as *Botrytis cinerea*, grow at near optimum in 4% oxygen. A decrease in the growth rate can be detected at 2%, and growth is reduced nearly 50% at 1% $O_2$ (11). Some modern storages can utilize an oxygen level as low as 1% without undue danger of localized anoxia.

An elevated level of carbon dioxide suppresses respiration of most fruits and vegetables. Carbon dioxide has been used in California for more than 40 yr to suppress disease, mostly caused by *B. cinerea* in transcontinental shipments of strawberries. Control of *B. cinerea* and *Monilinia fructicola* in sweet cherries has similarly used high carbon dioxide atmospheres. The effect of the carbon dioxide is twofold. Some of the disease suppression is due to delaying ripening and the accompanying loss of resistance, whereas some is the direct suppression of fungal growth (11,13,36).

Tolerance of fruits and vegetables to $CO_2$ varies widely. Bartlett pears may be damaged at carbon dioxide levels exceeding about 5%, whereas some apple cultivars tolerate even less. Sweet cherries and strawberries, however, tolerate 12–20%, depending on the cultivar. $CO_2$ injury is believed to be caused by carbon dioxide-induced accumulation of toxic substances, particularly aldehydes and alcohols, in fruit and vegetable tissues (11,16,36).

The inclusion of carbon monoxide (CO) as a component of a modified atmosphere dramatically suppresses the growth of some important pathogens (11,38). Carbon monoxide would likely be in widespread use if the danger from accidental poisoning were not high. Danger from the poisonous gas has caused use to be limited to situations where adequate precautions can be taken such as in refrigerated container ships in trans-Pacific service.

**Humidity.** It has often been assumed that rotting is stimulated by high relative humidity (RH), but that assumption is not necessarily so. High RH may favor the pathogen, as in the case of better spore germination rate (7), or it may favor the host by prolonging retention of resistance (14,31). Van den Berg and Lentz (43) used jacketed storage facilities to obtain 98–100% RH. When temperatures were the same, Brussels sprouts, cabbage, carrots, cauliflower, celery, Chinese cabbage, leeks, potatoes, rutabagas, and apples at 98–100% RH suffered rot equal to or less than that at 90–95% RH. Carrots, parsnips, and rutabagas became soft and shriveled and outside cabbage leaves turned yellow at 90–95% RH but not at 98–100% RH. These results suggest that lower humidity causes advanced senescence and loss of resistance. Further, Littmann (22) reported that water loss hastens ripening in some climacteric fruits.

Botrytis neck rot (*Botrytis* spp.) of onion bulbs was higher at 98–100% RH than at 90–95% (33). However, Grierson and Wardowski (14) pointed out that a mature onion bulb is entering a resting stage and is almost unique in that postharvest curing aims at killing the outer layers of cells by dehydration to provide dry tissues to protect the living bulb.

## FUTURE DEVELOPMENTS

Overcoming the problem of chilling injury to permit use of low temperatures would benefit many commodities dramatically. However, there seems to be little to suggest that the problem will be solved soon. Chilling sensitivity is undoubtedly under genetic control, but for tropical fruits no source of chilling resistance may exist. It is problematic that genetic engineering techniques might permit a genetic solution. Thus far, only small improvements have been made in reducing chilling injury, and those have mostly been in fruits that chill at temperatures below about 3–5 C. Preconditioning fruits or interrupting low temperatures by periods of ambient temperature have sometimes reduced injury symptoms (15).

Maintaining resistance of commodities into the early stages of ripening or senescence might dramatically reduce losses. The possibilities for accomplishing such changes are largely unknown. Chemical treatments that delay ripening are known, however. These include calcium (6,12,28,41), Gibberellin (9), *N*-dimethyl-aminosuccinamic acid (23), and N6-benzyladenine (21). Use of 2,4-dichlorophenoxyacetic acid (39) to slow senescence of citrus fruit calices has reduced stem-end rot caused by *Diplodia natalensis* P. Evans and *Alternaria alternata* (Fr.) Keissler.

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