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Review

Chilling injury in peach and nectarine

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Abstract

Peaches and nectarines ripen and deteriorate quickly at ambient temperature. Cold storage is used to slow these processes and decay development. However, low temperature disorders, chilling injury classified as internal breakdown, limit the storage life of peaches and nectarines under refrigeration. The onset of chilling injury symptoms determines the postharvest storage/shipping potential because their development reduces consumer acceptance. Chilling injury is genetically influenced and triggered by a combination of storage temperature and storage period. It manifests itself as fruit that are dry and have a mealy or woolly texture (mealiness or woolliness), or hard textured fruit with no juice (leatheriness), fruit with flesh or pit cavity browning (internal browning), or with flesh bleeding (internal reddening). In this review, we describe what is known about the etiology of each of these types of chilling injury symptoms as well as the biochemical processes in the fruit tissue responsible for their development. We also report on pre- and postharvest manipulations or treatments that can affect the time of appearance or severity of chilling injury symptoms.

Keywords: *Prunus persica* L.; Storage; Physiological disorders; Internal browning; Flesh browning; Internal reddening; Leatheriness; Mealiness; Woolliness

Contents

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1. Introduction

Peaches [*Prunus persica* (L.) Batsch] and nectarines [*P. persica* (L.) Batsch, var. nectarina] belong to the Rosaceae family and are thought to have originated in China (Salunkhe and Desai, 1984). Chinese literature dates cultivation of the peach in China to 1000 B.C. and it was probably carried from China to Persia. Peach, at one time called "Persian apple", quickly spread from there to Europe. In the 16th century, it was established in Mexico and in the 18th century Spanish missionaries introduced the peach to California, which turned out to be the most important production area after China and Italy (LaRue, 1989).

Like other stonefruit, peaches and nectarines, both closely related (Brady, 1993), have a characteristic, lignified endocarp (pit or stone) that encloses the seed, a fleshy mesocarp and a thin exocarp. However, nectarine cells have smaller intercellular spaces than peaches and are, therefore, denser. In addition, they lack pubescence on the skin, which is controlled by a single gene (Lill et al., 1989). On the basis of the separation of the stone from the flesh, peaches and nectarines can be divided into two groups: freestone and clingstone. In addition, based on the amount of softening of the flesh that occurs during ripening, peaches and nectarines can be either of a melting or non-melting type. Melting fruit will soften to below 8N firmness, while non-melting fleshed fruit will soften to 16N or higher. Polygalacturonase (PG) activity has been reported to be different between these two peach types (Lester et al., 1996). Most cultivars have yellow flesh, but white-fleshed cultivars have always been known and are being increasingly planted and currently are 30% of the plantings of the yellow flesh cultivars. The peel of both types may be highly colored due to the accumulation of anthocyanin. Peaches and nectarines with low, medium or high acid concentrations are also available (Genard et al., 1999). Peach fruit is rich in ascorbic acid (vitamin C), carotenoids (provitamin A), and phenolic compounds that are good sources of antioxidants (Tomás-Barberán et al., 2001; Byrne, 2002).

Currently, world production of peaches and nectarines stands at 11 million tonnes, with the three major producing countries being China, Italy and the United States in the Northern hemisphere and Chile, South Africa and Australia in the Southern hemisphere. All of these different combinations of fruit types – peach or nectarine, clingstone or freestone, yellow or white flesh, low, medium or high acidity – are available as freshly harvested fruit from April through September in the Northern Hemisphere and from November to March in the Southern Hemisphere.

Peaches and nectarines ripen and deteriorate quickly at ambient temperature. Therefore, cold storage is used to slow these processes and decay development. However, chilling injury (CI) limits the storage life of peaches and nectarines under low temperature. It has been widely reported that the expression of CI symptoms, especially flesh browning or internal browning, develops faster and more intensely when susceptible fruit are stored at temperatures between 2.2 and 7.6 °C (killing temperature zone) than those stored at 0 °C or below but above their freezing point (Harding and Haller, 1934; Smith, 1934; Crisosto et al., 1999a). These symptoms mainly develop during fruit ripening after cold storage, and the problem is not noticed until the fruit reaches customers (Bruhn et al., 1991; Crisosto et al., 1995). Therefore, fruit maximum storage life can be achieved near or below 0 °C, depending on the soluble solids content of the fruit.

2. Chilling injury (CI) symptoms

CI visual symptoms develop within 1 or 2 weeks when fruit are stored at 2–5 °C compared to 3 weeks or more at 0 °C (Anderson, 1979; Lill et al., 1989; Crisosto et al., 1999a). CI is genetically influenced and triggered by a combination of storage temperature and storage period (Mitchell, 1987; Crisosto et al., 1999a). It manifests itself as dry, mealy, woolly (lack of juice) or hard textured fruit with no juice (leatheriness), flesh or pit cavity browning, and flesh bleeding or internal reddening (Fig. 1). In the more advanced stages, chilling injured fruit also show flesh tissue separation and cavity formation. This is more frequently observed in white flesh peach cultivars.

The maturity at which peaches are harvested greatly influences their ripening, ultimate flavor and market life quality potential (Von Mollendorff, 1987; Lill et al., 1989; Crisosto et al., 1997). While some researchers found that the more immature the fruit were picked, the higher the incidence of mealiness (Harding and Haller, 1934; Ekstein, 1984; Kailasapathy and Melton, 1992; Fernandez-Trujillo et al., 1998), others reported that ripe fruit were more susceptible to mealiness than immature fruit (Deshpande and Salunkhe, 1964; Guelfat-Reich and Ben Arie, 1966; Salunkhe et al.,

Fig. 1. Three physiological disorders that occur in peaches and nectarines following storage. (A) Mealiness or woolliness; (B) internal browning (upper fruit are healthy); (C) internal reddening (upper fruit are healthy).

1968). In some studies (Von Mollendorff et al., 1989, 1993), fruit became soft when they developed mealiness, while in others (Ben Arie and Sonego, 1980), fruit never reached eating softness after storage. In studies using Fresno USDA-group yellow flesh peach and nectarine cultivars in California, low maturity was associated with earlier flesh browning development and late maturity was associated with mealiness and a flesh texture deterioration development (Crisosto et al., 1997). In the last decade, 135 selections and 120 cultivars were evaluated in the Fresno USDA evaluation program and it was found that in most cultivars mealiness and flesh browning symptoms were observed. In most of these cultivars onset of mealiness symptoms occurred prior to the development of flesh browning. Some cultivars from this group only developed mealiness symptoms, and only a few cultivars developed flesh browning without mealiness. However, in all of the cases, flavor was compromised approximately 5 days prior to visual CI symptoms (Crisosto and Labavitch, 2002).

Flesh bleeding, expressed as an intense red color development of the flesh, usually radiating from the pit, may be a problem in some peach cultivars. This symptom is an important cause of rejection for canning peaches because of cosmetic reasons. Contrary to mealiness and flesh browning, flesh bleeding does not affect fruit taste and is becoming more common on chilling susceptible and non-susceptible cultivars, particularly in the new release cultivars due to their abundant red pigment concentration. Development of flesh bleeding in some of the newly released cultivars has been associated with fruit maturity and it appears not to be a CI symptom.

With the number of different cultivars available and with a 6-month availability of freshly harvested fruit, the question may be asked as to why storage for the length of time that causes CI is necessary? The answer is that marketing and shipment, either within a large country such as China or the United States, or export to other countries can require a lengthy storage period. The Southern hemisphere producing countries that ship their fruit out of season to the Northern hemisphere, need 4–6 weeks of storage of their fruit as do exports from the United States to the far east. European producers shipping within Europe may require 3–4 weeks of storage. Therefore, understanding and preventing the causes of CI in peaches and nectarines is of economic, as well as scientific interest.

3. Biological basis of chilling injury

Numerous studies of the biochemical basis for mealiness have identified factors, which may be important in the development of the symptoms, although considerable discrepancy exists between results. Compared to juicy fruit, mealiness has been found associated with a reduction in pectin methylesterase (PME) activity (Buescher and Furmanski, 1978), or with an increase (Ben Arie and Sonego, 1980), or with unchanged levels (Obenland and Carroll, 2000; Zhou et al., 2000a). Similarly, exo-polygalacturonase (exo-PG) activity was reduced in mealy fruit in some studies (Zhou et al., 2000a), or showed no correlation with mealiness in others (Artes et al., 1996). A reduction in endo-PG activity during cold storage has been commonly observed (Buescher and Furmanski, 1978; Ben Arie and Sonego, 1980; Artes et al., 1996; Zhou et al., 2000a), although mealiness develops not in cold storage but during the subsequent ripening period at warm temperatures (Buescher and Furmanski, 1978). If on the other hand, the cold period exceeds a certain critical length, or the ripening period is short, no increase in endo-PG activity occurs during ripening and mealiness results (Ben Arie and Sonego, 1980). During the ripening period fruit may develop mealiness properties with low extractable juice, but upon extended ripening become juicy (Von Mollendorff and de Villiers, 1988; Von Mollendorff et al., 1989, 1993). However, this apparent restoration of free juice may be due to tissue breakdown and senescence processes. In mealy fruit the most easily extractable cell wall pectins (soluble in water or chelator) are reduced in amount and are of higher molecular weight and viscosity than in ripened, juicy fruit (Buescher and Furmanski, 1978; Von Mollendorff and de Villiers, 1988; Dawson et al., 1992; Lurie et al., 1994; Zhou et al., 2000a). The degree of methylesterification of pectin may also be altered (Ben Arie and Lavee, 1971; Lurie et al., 2003). Cell wall pectin participates in the wall in cell-to-cell adhesion, which is accomplished largely by calcium cross-linking between partially de-methylesterified homogalacturonan in the middle lamella (Jarvis et al., 2003; Vincken et al., 2003). It has been suggested that changes to pectin metabolism cause mealiness either by cell fluids forming calcium-pectate gel complexes with high molecular weight pectin in the middle lamella (Ben Arie and Lavee, 1971; Zhou et al., 2000b), or that

the decreased intercellular adhesion in mealy fruit reduces cell rupture during biting and chewing, preventing release of cellular contents (King et al., 1989; Brummell et al., 2004).

Other enzymes and cell wall proteins are beginning to be examined in relation to the development of mealiness in peaches. Endo-l,4-glucanase activity and mRNA are increased following chilling temperature storage, while fruit from treatments which delay the appearance of mealiness do not have this increase (Zhou et al., 2000c). Expansin protein and mRNA decreased as peaches became mealy (Obenland et al., 2003). Other enzymes including endo-1,4-β-mannase, β-galactosidase and α-arabinosidase had lower activities in mealy fruit than in ripe, juicy fruit (Brummell et al., 2004).

The other CI symptom that gives fruit a dry texture and uneven ripening is leatheriness. Some fruit remain firm and others become soft after a few days at 20 °C following cold storage. In general, soft fruit with dry texture are mealy (woolly), while the firm fruit with dry texture are leathery (Luza et al., 1992). Under the electron microscope the leathery fruit show a high degree of cell wall thickening compared with mealy or juicy fruit (Luza et al., 1992). A study of three harvests, early, commercial and late, of 'Huangjin' peaches found that the early harvested fruit were those that developed leatheriness (Ju et al., 2000). These peaches did not soften as much as juicy or mealy fruit. The enzyme activities of the ethylene synthesis pathway (ACC synthase and ACC oxidase) were lower in these fruit as well as the cell wall modifying enzymes PG and β-galactosidase, while insoluble pectin content remained higher than in juicy or mealy fruit. A more recent study examined cell wall polymer depolymerization, cell wall polysaccharide sugar composition, enzyme activity and tissue physical characteristics during the development of leatheriness (Brummell et al., 2004). Increasing time of cold storage was used to induce increasing severity of CI symptoms in order to examine which changes in cell wall polymers or enzyme activities precede or accompany the symptom developments. After 3 or 4 weeks in cold storage, some fruit developed a leathery texture. This was similar to mealiness but free juice was even lower and flesh browning higher in these fruit than in mealy fruit, and the texture of the flesh was firm rather than grainy (Brummell et al., 2004). Fruit developing leatheriness had reduced amounts of chelator-soluble pectin and greater amounts of tightly bound matrix PG, similar to mealy fruit. In terms of molecular weight distribution of chelator-soluble pectin, leathery fruit showed a greater arrest of depolymerization than mealy fruit. Relative to mealy fruit of the same length of storage, leathery fruit possessed lower activities of exo-PG, endo-PG, endo-1,4-β-mannase, β-galactosidase and α-arabinosidase. The activities of PME and endo-1,4-β-glucanase were similar in fruit with both disorders (Brummell et al., 2004).

The appearance of internal browning in the fruit flesh, or flesh browning, occurs sooner at temperatures of 2–5 °C than at the optimal storage temperature of 0 °C. In fact, less flesh browning developed at −0.5 °C than at +0.5 °C (Ceretta et al., 2000). The disorder may be related to tissue deterioration or senescence, which leads to changes in membrane permeability and the interaction between phenols and polyphenol oxidase, which are generally found in separate compartments in the cell. Kader and Chordas (1984) found that the browning potential of peaches depended on the total amount of phenolic compounds present in the fruit and the level of activity of polyphenol oxidase. Manabe et al. (1979) similarly found that the level of polyphenols differed among cultivars of white-fleshed peach. Controlled atmosphere (CA) storage was found to alleviate or prevent the development of this disorder in some cultivars (Retamales et al., 1992; Streif et al., 1992; Crisosto et al., 1995; Ceretta et al., 2000). In addition, during normal air storage, a lack of juiciness indicative of either mealiness or leatheriness is observed before flesh browning develops to any degree (Crisosto et al., 1999b).

In many cultivars of peaches and nectarines there are cells near the stone, which contain anthocyanin and when fruit is halved the appearance is often of red rays extending out from the center, which contains the pit (flesh bleeding). Following extended storage these sharply delineated areas of cells disappear and the whole area around the pit has a reddish appearance. This red coloration can also extend throughout the flesh when the disorder is severe. There has been almost no research conducted on the causes of this disorder. It has been noted in some studies, along with enumeration of other disorders appearing in fruit, but with no further details. It may be a consequence of tissue senescence, since it is inversely correlated with decrease in

organic acids in the tissue (Lurie, unpublished data). Additional evidence for this is that CA storage was found to prevent the development of this disorder (Lurie et al., 1992; Retamales et al., 1992). Or it may be a consequence of the arrest of normal ripening, since the ethylene action inhibitor, 1-methylcyclopropene (1-MCP), greatly enhanced the development of this disorder (Dong et al., 2001). However, the application of exogenous ethylene during 0 °C storage for 30 days did not affect the development of internal reddening or flesh bleeding (Crisosto et al., 2001; Palou et al., 2003).

4. Genotype influence on chilling injury

There is a large variation among different selections and/or cultivars of peaches and nectarines as to their susceptibility to CI when stored at either 0 or 5 °C (Crisosto et al., 1999a). This variation may be valuable to geneticists and breeders to develop stonefruit cultivars free of CI, to understand the genetic inheritance of CI and to isolate the genes responsible. In a large-scale study in California, 25 cultivars of nectarines and 32 cultivars of peaches were evaluated for their storage potential. Early season yellow-fleshed cultivars, both peaches and nectarines, were less susceptible to CI than later season cultivars (Crisosto et al., 1999a; Lurie, unpublished data), although this was not the case in white-fleshed cultivars. In a newly released group of cultivars that are being developed from a new genetic pool, the susceptibility to CI is becoming random (Crisosto et al., 1999a, 2003; Crisosto, 2002). In general, nectarine cultivars were less susceptible to CI than the peach cultivars. Also, the melting flesh peach cultivars were more susceptible to CI than the firmer non-melting flesh cultivars (Brovelli et al., 1999; Crisosto et al., 1999a). Non-melting flesh cultivars have reduced endo-PG activity (Lester et al., 1996). The genetic locus for freestone appears to contain a cluster of endo-PG genes (Callahan et al., 2004; Peace et al., 2005).

5. Methods of delaying chilling injury

The onset of CI symptoms determines the postharvest storage/shipping potential because their development reduces consumer acceptance (Crisosto et al., 1997). In addition, the disorders are internal and generally not observed by consumers until consumption at home. Susceptibility to CI varies according to genetic background (Harding and Haller, 1934; Anderson, 1979; Hartmann, 1985; Crisosto et al., 1999a), maturity (Von Mollendorff, 1987; Ju et al., 2000) and orchard factors (Crisosto et al., 1995, 1997). Several treatments to delay and limit development of this disorder have been tested such as warming interruptions during cold storage (Anderson, 1979; Nanos and Mitchell, 1991) plant growth regulators (Zilkah et al., 1997), controlled atmosphere environment (Anderson et al., 1969; Kajiura, 1975; Wade, 1981; Lurie et al., 1992; Streif et al., 1992; Ceretta et al., 2000; Garner et al., 2001), and controlled delayed cooling (Ben Arie et al., 1970; Lill, 1985; Nanos and Mitchell, 1991; Fernandez-Trujillo and Artes, 1997; Zhou et al., 2000c, 2001a; Crisosto et al., 2004). There are a number of preharvest and post-harvest manipulations that can be used to delay the onset of the CI symptoms that will be discussed below.

5.1. Fertilizer practice

The lack of relationship between nitrogen and CI development during storage in peach and nectarine was demonstrated on a detailed and extensive evaluation from 1980 to 1995 at the Kearney Agricultural Center (Daane et al., 1995). During this work, leaf nitrogen levels reached 2.2, 2.6, 3.2 and 3.6% across different fertilization treatments. Calcium has been involved in numerous biochemical and morphological processes in plants and has been implicated in many disorders of considerable economic importance to production and postharvest quality. However, different foliar calcium sprays have not been used successfully to affect peach storage quality. Work over the last 15 years in California using several commercial calcium foliar sprays on peach and nectarine (applied every 14 days, starting 2 weeks after full bloom and continuing until 1 week before harvest) showed no effect on the onset of CI symptoms (Crisosto et al., 2000).

5.2. Irrigation regimes

Despite the important role of water in fruit growth and development, few specific studies have been done on the influence of the amount and the timing of

water applications on peach postharvest performance (Prashar et al., 1976; Crisosto et al., 1994). An early report indicated that when trees were allowed to grow without irrigation during the growing season on a shallow soil under California conditions, fruit developed a mealy texture during cold storage (Uriu et al., 1964). The regulated irrigation deficit (RID) technique has been evaluated for peach performance in different production areas (Girona, 2002). In general, this technique imposes a moderate stress (30–50% evapotranspiration (ET)) to reduce vegetative growth and save water use (4–30%) at a given physiological stage without affecting yield. In California, during three seasons, the influence of three different irrigation regimes applied 4 weeks before harvest on 'O'Henry' peach postharvest performance was evaluated (Crisosto et al., 1994). The irrigation regimes (50, 100 and 150% ET applied 4 weeks before harvest) decreased 'O'Henry' peach size and increased SSC, but it did not affect CI development during 2, 4 and 6 weeks in storage at 0 or 5 °C. Recently in California, RID and partial root zone drying (PRD) were evaluated on white flesh peaches growing under California conditions (Goldhamer et al., 2002). PRD involves inducing partial stomata closure by exposing some part of the root zone to continual soil drying. After 2 years of evaluations, fruit quality was not affected by the PRD and the RID treatments.

5.3. Crop load and fruit size

In most cultivars, fruitlet thinning when done properly increases fruit size while also reducing total yield, thus a balance between yield and fruit size must be achieved (Day, 1997; Costa and Vizzotto, 2000). In California during two seasons, large (~275 g), medium (~175 g) and small (~125 g) 'O'Henry' peaches were stored in either air, 5% CO_2 + 2% O_2, or 17% CO_2 + 6% O_2 at 3.3 °C. Large size 'O'Henry' peach fruit benefited more from the 17% CO_2 + 6% O_2 than from 5% CO_2 + 2% O_2 or air storage atmosphere treatments. Large, medium and small 'Elegant Lady' peaches were stored in air or 17% CO_2 + 6% O_2 at either 0 or 3.3 °C. Fruit size, storage atmosphere and temperature all had significant effects on CI development. Small peaches stored in air at 0 °C had a longer market life than large fruit. At both storage temperatures, large size 'Elegant Lady' and 'O'Henry' fruit had a longer market life under CA than under air storage. However, at 3.3 °C small size 'Elegant Lady' fruit in CA showed browning in the flesh. This suggests that 17% CO_2 + 6% O_2 may induce flesh browning in small size 'Elegant Lady' peaches. In both years, lack of juiciness (mealiness/leatheriness) was found before the development of flesh browning as was observed in other tests. Thus, market life was dependent on the incidence of mealiness/leatheriness rather than flesh browning (Crisosto et al., 1999b).

5.4. Canopy position

Fruit quality measured at harvest and during storage for several peach and nectarine cultivars varied according to fruit canopy positions in different production areas (Marini et al., 1991; Crisosto et al., 1997; Iannini et al., 2002; Luchsinger et al., 2002). In California, the overall incidence of mealiness and flesh browning in fruit from the high crop load was low, intermediate in fruit from the commercial crop load, and the highest in fruit from the low crop load (Crisosto et al., 1997). Fruit that developed in the more shaded inner canopy positions have a greater incidence of CI than fruit from the high light outer canopy positions. Thus, fruit from the outer canopy have a longer potential market life, especially in susceptible cultivars. The use of more efficient training systems which allows for more sunlight penetration into the center and lower canopy areas is recommended to reduce the number of shaded fruit, thus extending postharvest life (Crisosto et al., 1997). Summer pruning and leaf removal around the fruit increases fruit light exposure and, when performed properly, can increase market life (Day, 1997; Forlani et al., 2002).

5.5. Plant growth regulators (PGR)

Studies both in Israel and in California have explored the effect of preharvest application of gibberellin on pectin hydrolyzing enzymes and fruit mealiness development in stonefruit (Zilkah et al., 1997; Crisosto, unpublished data). Results showed that preharvest application of gibberellin significantly reduced CI in nectarine fruit when the compound was applied at the end of the pit hardening stage in concentrations from 50 to 100 mg/l a.i. Gibberellin was also applied to a Chinese peach cultivar, 'Feicheng', at the end of pit hardening, and flesh browning after 0 °C storage

was decreased if the concentration was 100 mg/1 a.i., but not if it was 50 (Ju et al., 1999). Gibberellin also increases fruit firmness and fruit size, because it delays fruit maturity and the fruit remain on the tree longer (Zilkah et al., 1997; Ju et al., 1999). However, there may be a problem the following year with the percentage of buds that are flower buds. If the reduction is not too drastic this may be beneficial, because generally peaches and nectarines need hand thinning, which is labor intensive and expensive.

An inhibitor of ethylene synthesis, aminoethoxyvinylglycine (AVG), also delayed fruit development and increased firmness when applied in the orchard (Ju et al., 1999). When used as a postharvest dip it slowed the rate of fruit softening (Byers, 1997). A combination of gibberellin at pit hardening and AVG given 2 weeks before harvest enhanced storability of 'Feicheng' peaches and allowed 2 extra weeks of storage before flesh browning developed during after-storage ripening (Ju et al., 1999). However, a recent report on 'Arctic Snow' nectarines found that AVG delayed harvest and enhanced fruit firmness, but encouraged the development of internal reddening and leatheriness in 1 °C storage (McGlasson et al., 2005). In contrast the untreated fruit became mealy. The AVG treated fruit stored more poorly than control fruit. Adding ethylene to the storage atmosphere (1 °C) delayed the appearance of the disorders. Possible reasons for this are described in the ethylene section below.

5.6. Controlled atmosphere (CA)

Most studies of CA storage of peaches and nectarines have found that lowering O_2 and raising CO_2 in the storage atmosphere conferred benefit on the fruit and delayed or prevented the appearance of mealiness, internal reddening and flesh browning (Lurie, 1992; Retamales et al., 1992; Crisosto et al., 1995; Levin et al., 1995; Zhou et al., 2000c). The CO_2 component appears to be critical for delaying the onset of CI (Anderson et al., 1969; Kajiura, 1975; Wade, 1981). Original recommendations for CA conditions for peaches and nectarines were similar to those for some apple cultivars; 3–5% CO_2 + 1–2% O_2 at 0 °C (Anderson et al., 1969; Kader, 1986). However, recent studies have found that higher levels of CO_2 will delay appearance of CI symptoms better than the original recommendations. Exposure to 10% CO_2 + 10% O_2 for 6 weeks has been reported to prevent CI in the nectarine cultivars 'Fantasia', 'Flavortop', and 'Flamekist' (Lurie, 1992). It has been demonstrated that 'Fantasia' nectarines stored in air plus 10–20% CO_2 were juicy and had good flavor after 5 weeks at 0 °C storage (Burmeister and Harman, 1998). CA conditions of 6% O_2 + 17% CO_2 have been reported to be beneficial for peaches and nectarines shipped from Chile (Retamales et al., 1992; Streif et al., 1992). In California, the major benefits of CA during storage/shipment are retention of fruit firmness and ground color, and reduction of flesh browning development. CA conditions of 6% O_2 + 17% CO_2, the best combination, at 0 °C have shown a limited benefit for reduction of mealiness during shipments for yellow flesh cultivars (Crisosto et al., 1999a) and white flesh cultivars (Garner et al., 2001). As mealiness is the main CI symptom rather than flesh browning, the use of CA technology in California cultivars has been limited. The CA efficacy is related to cultivar, preharvest factors (Von Mollendorff, 1987; Crisosto et al., 1997), temperature, fruit size (Crisosto et al., 1999b), marketing period and shipping time (Crisosto et al., 1999a). The use of the modified atmosphere packaging (MAP) technique has been tested in several peach cultivars (Zoffoli et al., 2002) without success. Despite high CO_2 levels that were reached during cold storage, flesh mealiness and flesh browning development limited the potential benefits of this technology. In some commercial cases when box liners (MAP) were used, the incidence of decay increased because of lack of proper cooling and condensation during transportation.

Increasing CO_2 and decreasing O_2 in the atmosphere around the fruit tissue has profound effects on cellular metabolism. It reduces the respiration rate of fruit and vegetables (Kader, 1986). However, low oxygen may cause external symptoms such as skin browning and even black pitting on the skin. The internal damage is associated near the skin and surrounding the stone. In both cases, well-defined grayish brown or brown areas are formed. These areas are not associated with mealy tissues and can occur anytime during cold storage (Kader, 1986). Ke et al. (1993) proposed that elevated CO_2 influences respiration rates by regulating carbon flux through the TCA cycle. High CO_2 appears to increase carbon flux through glycolysis, maintain energy levels in the cell and enhance the alternative electron pathway by inducing and/or activating alterna-

tive oxidase and inhibiting cytochrome oxidase activity (Watkins, 2000). CA can also affect the activity of the enzymes involved in ethylene synthesis. ACC oxidase requires CO_2 and O_2 for its activity (Poneleit and Dilley, 1993). Therefore, ethylene is inhibited during storage in CAs, but will recover following removal to air. CA also affects the cell wall degrading enzymes that are responsible for fruit disassembly and whose imbalance or inhibition is associated with mealiness development. At the end of CA storage the activities of pectin esterase and PG were lower than following regular air storage at 0 °C (Zhou et al., 2000c). However, both the activity and mRNA abundance of both enzymes increased during after storage ripening to a greater extent in fruit that had been stored in CA than in fruit stored in air. This recovery of enzyme activity enabled pectin molecules to be cleaved quickly during ripening and led to normal fruit softening and development of juiciness.

5.7. Ethylene and ethylene inhibitors

Ethylene is generally thought to be harmful during storage, inducing fast softening, ripening and deterioration in fruit. However, presence of ethylene during cold storage may not be a problem for peaches and nectarines, and indeed may be beneficial (Zhou et al., 2001a; Palou et al., 2003). Brecht and Kader (1982) found that treatment of 'Fairlane' or 'Flamekist' nectarines with ethylene during 0 °C storage had no effect on rate of color change or softening during storage or subsequent ripening at 20 °C. In prolonged cold storage, maintaining the ability of the fruit to produce ethylene, or adding exogenous ethylene to the storage atmosphere, may help prevent CI. Nectarines developing mealiness were found to be deficient in their ability to produce ethylene (Zhou et al., 2001b). Delayed storage (for nectarines) and intermittent warming (IW) (for peaches) maintained the ability of the fruit to produce ethylene concomitantly with preventing mealiness development (Fernandez-Trujillo and Artes, 1997; Zhou et al., 2001a,b). Exposing the fruit to exogenous ethylene during storage at 0 °C enhanced ethylene production after storage, thereby promoting the sequence of cell wall disassembly necessary for normal ripening (Dong et al., 2001). The ethylene at 0 °C did not lead to fruit softening during storage. Adding 3 ppm ethylene, a concentration measured in some postharvest environments, to 'O'Henry' peaches during 0 and 5 °C storage delayed mealiness development (Crisosto et al., 2001). In another study by the same group flesh mealiness was decreased in 'Elegant Lady' peaches by adding ethylene to the storage atmosphere, though not consistently (Palou et al., 2003). The conclusion was that no benefit would be conferred by scrubbing ethylene from storage rooms, but it was not clear that benefit would occur from adding ethylene.

The use of ethylene inhibitors such as 1-MCP in peaches and nectarines has been tested by several research groups. For example, blocking ethylene action with 1-MCP appeared to prevent normal ripening of several peaches and nectarines after cold storage (Dong et al., 2001; Crisosto, unpublished data). Nectarine fruit treated with 1-MCP developed severe flesh mealiness and reddening and had lower expressible juice compared to control fruit or fruit treated with ethylene during 0 °C storage (Dong et al., 2001). Both the mRNAs of the ethylene synthesis pathway, ACC synthase and ACC oxidase, as well as enzymes of cell wall disassembly were decreased in 1-MCP treated fruit. Peaches treated with 1-MCP were firmer than untreated fruit after 5 °C storage, but had more severe flesh browning than control fruit (Fan et al., 2002). It appears that ethylene is essential for proper ripening of peaches and nectarines after storage.

5.8. Intermittent warming (IW) and controlled delayed cooling

Delayed storage, sometimes termed controlled ripening, involves holding the fruit in warm conditions for 1 or 2 days after harvest before placing them in 0 °C storage. Intermittent warming (IW) involves placing the fruit immediately in cold storage, but removing them to 20 °C for a day every 10–14 days. These temperature manipulations can affect the performance of peaches and nectarines in storage. O'Reilly (1947) reported preventing mealiness in peaches if they were held for 2–5 days at 24 °C before storage at 0 and 4.4 °C. IW has also been found to delay or prevent CI. Ben Arie et al. (1970) reported control of chilling symptoms in 'Elberta' peaches if the fruit were warmed to 20 °C for 2 days every 2 weeks during 6 weeks storage at 0 °C. Lill (1985) showed that IW was effective at temperatures as low as 12 °C, but that at this temperature the length of the warming period had to be longer than

if the warming temperature was 20 °C. More recently IW of peaches was tested with and without modified atmosphere packaging (Fernandez-Trujillo and Artes, 1997). IW of 1 day at 20 °C every 6 days gave an extra week of storage at 0.5 °C before CI appeared. Ethylene production was stimulated by the IW regime. In another study where IW for 2 days at 20 °C was applied every 12 days during 0 °C storage, mealiness was also prevented (Zhou et al., 2001a). The mRNAs of ACC oxidase and ACC synthase were induced by this treatment and ethylene production at 0 °C was higher in these fruit than in control fruit. IW also increased the activity of PG (Artes et al., 1996), thereby allowing for normal softening after storage.

Delaying storage of peaches for 2 or 3 days at 26 °C extended their storage life at 0 °C by 10–15 days (Guelfat-Reich and Ben Arie, 1966). Scott et al. (1969) found that holding fruit at 20 °C for 2 days prior to 7 weeks storage at −0.5 °C reduced CI considerably but was not as effective as IW. Two days of delayed storage at 20 °C prior to storage at 0 °C for 42 days prevented CI in 'Flavortop' nectarines (Zhou et al., 2000c). Examination of the cell wall components of these fruit compared to control fruit showed that the 2 days began the process of cell wall disassembly which continued slowly during storage, so that at the end of storage the distribution of the pectin between soluble and insoluble fractions and the size of the polymers in the different classes was similar to that of fruit ripened without storage (Zhou et al., 1999, 2000a). Control fruit after storage showed less solubilization of the pectin and larger polymers in the soluble fraction. This increased cell wall disassembly often led to delayed storage fruit being softer than control fruit (Retamales et al., 1992; Zhou et al., 2000c). In addition, although it helped to prevent mealiness it had no effect on internal browning and sometimes enhanced internal reddening (Retamales et al., 1992).

A commercial controlled delayed cooling or preconditioning treatment was developed to extend peach (*P. persica*) market life of the most popular California and Chilean peach cultivars (Crisosto et al., 2004). A 24 to 48-h cooling delay at 20 °C was the most effective treatment for extending market life of CI susceptible peaches and nectarines without causing fruit deterioration. This treatment increased minimum market life by up to 2 weeks in the cultivars tested. Weight loss and softening occurred during the controlled delayed cooling treatments, but did not reduce fruit quality. Detailed monitoring of these fruit quality changes during the delayed cooling period and proper use of fungicides is highly recommended for success in this fruit delivery system. Rapid cooling after preconditioning is important to stop further fruit deterioration such as flesh softening, senescence, decay and weight loss. Controlled delayed cooling can also be used to pre-ripen susceptible and non-susceptible peaches and nectarines in order to deliver a "ready to buy" product to the consumer.

6. The genetic long-term approach

While certain treatments can be used to reduce the incidence of CI, the underlying mechanisms of genetic control are unclear. In the last decade, a program at the Kearney Agricultural Center has evaluated approximately 255 peach and nectarine selections and cultivars for their susceptibility to CI. Certain cultivars appear more susceptible than others, indicating that the symptoms have a significant genetic component, though the genetic differences between low and high susceptible genotypes are not known. Peach breeding would benefit from the ability to identify at the seedling stage those genotypes not prone to CI, which marker-assisted selection (MAS) could provide. To develop this tool and gain a better understanding of the genetic control of CI, we have undertaken a classical and molecular genetics approach, using two related and genetically variable populations of peach (Peace et al., 2005). During three seasons, mealiness occurred after 5 °C storage in both populations only within freestone melting flesh (FMF) progeny, which is intuitive since a simple definition of mealiness is flesh that is dry, which requires that fruit have passed through the melting stage. Further analysis of mealiness was conducted on a subset of the progeny consisting of only those that were FMF, since clingstone non-melting flesh (CNMF) progeny may carry genes for high mealiness susceptibility that are masked. CI traits were affected by various non-genetic factors, such as year and storage duration (Peace et al., 2005). Considering those factors that were consistent between the two populations, mealiness and flesh browning were greatest in 2002 and for the 3-week storage duration, and flesh bleeding was greatest in white CNMF fruit and for the 2-week storage duration. Despite these

non-genetic influences on the incidence of CI, the traits were quite consistent within each progeny (highly significant genotype effects), such that the heritability of each of the symptoms was moderate. This indicates that there is considerable genetic control of CI in this germplasm, a promising result for the identification of quality trait loci (QTLs) and the development of MAS for these traits.

7. Conclusions

The different expressions of CI symptoms commercially affect visual and flavor quality of peaches and nectarines, therefore limiting their marketing and consumption in spite of their high nutritional value. This problem is the main limitation on fruit consumption of ripe peaches and nectarines. The onset of CI symptoms in susceptible cultivars is temperature plus time of exposure dependent but also has a genetic component. To maintain fruit quality during marketing, the susceptibility of the cultivar to CI should be taken into account and strategies to bring to market the highest quality fruit should be pursued. It is important to encourage growers, shippers, receivers and handlers to apply the current information on short-term solution techniques available to reduce CI symptom development. In this regard, ripening protocols to assure fruit ripening prior to consumption have been developed for shippers, handlers, store produce managers and consumers. These are similar to the techniques described in the section on delayed storage. However, for a long-term solution to the problem of CI in peaches and nectarines, basic research programs to understand the genetic and biochemical basis of CI's genetic control by using available molecular genetic technologies should be economically supported.

Because peach consumer quality cannot be improved after harvest, it is important to understand the role of preharvest factors in market life. Unfortunately, too little research has been conducted on this topic. Preharvest factors often interact in complex ways depending on cultivar characteristics, stage of development and season. We believe that the orchard quality potential for each cultivar can be achieved only by understanding the role of preharvest factors in consumer acceptance and postharvest life potential. Therefore, research to identify cultivar market life and the role of preharvest factors (orchards and climatic conditions) in the development of CI should be encouraged.

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