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Ripening and Postharvest Storage of 'Soft Fruits'

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ABSTRACT

The terms 'soft fruit' have been used to refer to different commodities including strawberries, blueberries and several species of the genus *Rubus*. Most work in 'soft fruit' ripening regulation has been done on strawberry. Auxin has been shown to be a repressor of several ripening-associated genes which led to hypothesize that reduction in auxin levels in the receptacle could activate those genes. Despite that, some evidence suggest that that is only part of the story and that other factors are also involved in the regulation of 'soft fruits' ripening process. Softening is one of the most dramatic changes observed in 'soft fruit' ripening. Early reports on strawberry stated that the average molecular size of hemicelluloses greatly declines during ripening. In contrast, later work showed that pectin size is reduced while only slight depolymerization occurs in hemicellulosic polymers. Pectin metabolism has recently shown to be a major modification accompanying softening in species of the genus *Rubus*. Contrarywise, a reduction in glucan content and downshifts in hemicellulose molecular size are the main changes observed in blueberry. Extension of 'soft fruit' postharvest life has been an ongoing challenge. Strategies to reduce 'soft fruit' losses include selection of firmer genotypes and optimum postharvest handling procedures. A single postharvest technique is unlikely to fully control postharvest losses but new tools such as UV radiation, heat treatments or chitosan coatings may be added to the overall management plan (cooling conditions, modified atmospheres) to further delay softening and prevent decay losses. Biotechnology may be useful to address some of the concerns about bramble quality attributes (e.g. increased fruit firmness, improved flavor) and engineered resistance may be a sustainable method to control *Botrytis cinerea*.

Keywords: blackberry, blueberry, decay, postharvest, quality, raspberry, softening, strawberry

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INTRODUCTION

The terms 'soft fruit' comprise different commodities such as strawberries, blueberries, blackberries, raspberries and their hybrids (Manning 1993). This grouping does not have a botanical basis and includes species from different families with very diverse fruit structures. However, their fruits have several characteristics that make the grouping useful at least from a postharvest technological angle. They are characterized by a high metabolic rate and a very short shelf life (Salunkhe and Desai 1984; Kader 2002). Fresh 'soft fruits' are highly accepted by consumers but their high perishability determines that a significant percentage of the production is used for processing in the manufacture of jams, yoghurts, sauces, juices, flavorings and other products. In terms of growth pattern, there are also significant differences between 'soft fruits' and other commodities. In many fruits, ripening is triggered once growth is over, but strawberries, blueberries, blackberries and raspberries continue to become larger simultaneously with the ripening process. 'Soft fruits' typically have a blue or red color due to the accumulation of anthocyanins (Manning 1993). Although these pigments are almost ubiquitous in horticultural crops, relatively high levels are usually observed in 'soft fruits'

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(Dugo *et al*. 2001). Besides, their role determining the esthetic properties of the fruits, anthocyanins are antioxidants (Wang *et al*. 1996) and several works have suggested that 'soft fruit' consumption could have beneficial effects towards the prevention of several chronic and degenerative diseases associated with oxidative damage (Heinonen *et al*. 1998; Meydani 2001). In addition, 'soft fruits' are generally rich in ascorbic acid (Lee and Kader 2000) and phenolic acids (Zadernowski *et al*. 2005) which have also been associated with disease prevention (Cozzi *et al*. 1997). Blueberry and raspberry fruit rank high in antioxidant activity among fresh fruits (Wu *et al*. 2004). Lau *et al*. (2005) showed that blueberry supplementation was beneficial in both forestalling and reversing the deleterious effects of aging on neuronal communication and behavior. It has been reported that a low dietary intake of fruits and vegetables doubles the risk of most types of cancer and markedly increases the risk of heart disease and cataracts as compared to high intake (Ames *et al*. 1993). This has led to a much greater concern of consumers about food nutritional value and has probably contributed to the increased popularity of 'soft fruits' in the last few years.

PRODUCTION

In terms of production, strawberry is the most important crop in the 'soft fruit' group. Its worldwide production is estimated in 3.5 million M Tons (**Table 1**) though this value could be underestimated due to the uncertainty of Chinese production volumes. The production volume of other berries such as blueberries and raspberries is low relative to total 'soft fruit' production (**Table 1**) but has rapidly increased in the last ten years (50% and 80%, respectively).

GENERAL FEATURES OF THE PRINCIPAL 'SOFT FRUITS'

Strawberries

Strawberry belongs to the family *Rosaceae*. Its name derives form the Latin '*fragans*', which is associated with the characteristic aroma of the fruits (Branzanti 1989). Approximately 150 species of the genus *Fragaria* are widespread around the world but the cultivated strawberry *Fragaria* × *ananassa* Duch. is considered to have arisen in France in the 18th century from a chance cross involving the North American or meadow strawberry *F. virginiana* (L.) Duch. with the Chilean strawberry *F. chiloensis* Duch. (Branzanti 1989). The strawberry is considered a false fruit since the edible structure originates from the expansion of the flower base (the receptacle) as a pseudocarp (Aharoni and O'Connell 2002). The fruits show a rapid growth, reaching full size approximately 20-60 days after anthesis, depending on the environmental conditions (Perkins-Veazie and Huber 1987). Growth kinetics show a different pattern hanging on the cultivar considered: in some cases, simple sigmoid curves have been reported (Forney and Breen 1985; Stutte and Darnell 1987) while in other cases double sigmoid patterns have been described (Archbold and Dennis 1984; Perkins-Veazie and Huber 1987). Fruit size is influenced by the position in the inflorescence: primary fruits are bigger than secondary and tertiary ones (Moore *et al*. 1970). Growth rates of primary and secondary fruit are similar but the latter has a longer lag phase to initiate active growth thus attaining a reduced final size. Removal of primary fruit causes an increase in secondary fruit size indicating that fruits in the same inflorescence compete for resources. Fruit size is also positively correlated with the size and number of achenes formed thus showing that good pollination is a key factor determining fruit yield and quality. The ripening process occurs very rapidly and includes modifications in flavor, color and texture (Manning 1993). Strawberry fruit has a high respiration rate (50-100 ml CO_2 kg^{-1} h^{-1} at 20ºC) and the reduction of metabolic activity is crucial to delay fruit deterioration (Mitchell 1992). Fruit quality is determined by several factors including appearance, color, shape, size, firmness, taste (mainly determined by soluble solids, organic acids and volatile compounds) and nutritional value (vitamin C) (Kader 1991; Mitcham 1996). Soluble solids over 7% and acidity under 0.8% are recommended (Kader 1999). The calyx should show a green and fresh appearance (Mitchell *et al*. 1996).

Brambles

Blackberries, dewberries, raspberries and their hybrids, collectively referred to as "brambles", are a diverse group of species and hybrids included in the genus *Rubus* (Rieger 2005). They are members of the *Rosaceae* family, closely related to strawberry in the subfamily *Rosoideae*. *Rubus* is a highly diverse genus of flowering plants in the world, with 12 subgenera, some of which group hundreds of species (Antonius-Klemola 1999). Commercial *Rubus* crops include red (*R. idaeus* L.), black (*R. occidentalis* L.) and purple (hybrid between red and black) raspberries, blackberries (*Rubus* spp. and hybrids), cloudberries (*R. chamaemorus* L.) and Andean blackberries (*Rubus* spp.) (Thompson 1997). Boysenberries (*Rubus idaeus* L. × *Rubus ursinus* Cham. & Schldl) are hybrids between raspberries and blackberries (Bushman *et al*. 2004). In all brambles, the fruit is an aggregate structure composed of drupelets with a fleshy mesocarp and a hard endocarp consisting of sclereids or fibers and containing the true seed held together by a receptacle. Each drupelet is supplied with assimilate and water by a separate vascular arrangement and contains a single seed (Iannetta *et al*. 1999). A morphological difference between raspberry and boysenberry is that the drupelets of the latter lack the fine hairs on the fruit surface that raspberry has, and appears smooth and shiny. Another difference is that the boysenberry retains the receptacle at harvest while it abscises in the case of raspberry. Fruit development occurs rapidly, taking only 30-50 days for most raspberries, and 40-60 days for boysenberries. The fruits are mature when they have completely developed their typical color, and are easily detached from the plant. These characteristics are commonly used as maturity indices. All brambles require frequent pickings over a period of a few weeks. If the berries are picked too soon, berry size will be reduced. Furthermore, since sugars accumulate until late ripening, early harvests will significantly reduce flavor (Mitcham *et al*. 2006). To harvest at peak quality, berries should be picked every 2-3 days. Harvesting should be done when the fruits are not wet to reduce decay, a major problem limiting postharvest life. Picking should be done gently and the berries should be placed into shallow containers to minimize physical damage (Hardenburg *et al*. 1990).

Table 1 Strawberry, blueberry and raspberry world production (Thousand M Tons) in the last 10 years (Adapted from FAOSTAT, 2006).

Product \ Year	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005
Strawberry	2,752	2,760	2,867	3,186	3,299	3,204	3,215	3,335	3,546	3,530
Blueberry	137	150	137	211	237	237	222	245	241	241
Raspberry	321	319	355	400	408	432	471	442	485	483
Other berries	510	510	573	463	618	630	626	642	647	652
TOTAL	3,620	3,739	3,932	4,260	4,562	4,503	4,534	4,664	4,919	4,906

Blueberry

Blueberries are members of the *Ericaceae* family, genus *Vaccinium* (Kron *et al*. 2002). Demand for blueberries has increased in recent years and fresh-market prices have been relatively stable. To meet growing consumer demand, commercial blueberry acreage in the US increased more than 60% in the past 15 years (Demchak *et al*. 2005). Production has more than doubled since the late 1970's. Major increases have occurred in Michigan (where more than 40% of the commercial acreage is located) and in the southeastern United States (Demchak *et al*. 2005). Interest in blueberry as a crop has also increased in other countries and the western states of the United States. The fruit is an epigynous or "false" berry (Rieger 2005). This means that the fruit is berry-like but derived from an inferior ovary unlike true berries that derive from superior ovaries. The "button" on the far end of the fruit is actually the calyx scar. Fruit development occurs for about 2 to 3 months after bloom and depends on cultivar, weather, and plant vigor (Prodorutti *et al*. 2007). They have a low ethylene production (0.1-1.0 μl kg^{-1} h^{-1} at 5°C) (Mitcham *et al*. 2006). Size continues to increase after fruit turns blue due mainly to water uptake. Blue color is the most frequently used maturity index (Mitcham *et al*. 2006). The fruit turns from green to pink and then gradually to a full blue color when ripe. Ripe berries will remain attached for several days or weeks, and sugars will continue to accumulate.

HOW IS RIPENING REGULATED IN BERRY FRUITS?

Little is known about the mechanisms that regulate berry fruit ripening (Trainotti *et al*. 2005). Most 'soft fruits' show low ethylene production and sensitivity and are considered non-climacteric though there has been some debate about their correct categorization (Lipe 1978; Walsh *et al*. 1983; Burdon and Sexton 1993). At present, no single growth regulator appears to play a positive role analogous to that played by ethylene in the ripening of climacteric fruits. Application of 0.5-1 μL L^{-1} 1-methylcyclopropene delays color changes (Jiang *et al*. 2001) and, as occurs in climacteric fruit, an increased synthesis of ethylene receptors takes place in strawberries during ripening (Trainotti *et al*. 2005). However, the effects are not as pronounced as observed in other fruits (Blankenship and Dole 2003; Bower *et al*. 2003; Sozzi and Beaudry 2007). Furthermore, several ripening specific genes have shown to be ethylene-insensitive or even be repressed by the hormone (Civello *et al*. 1999; Trainotti *et al*. 2001; Castillejo *et al*. 2004). Consequently, it is currently assumed that ethylene is not a fundamental hormone regulating ripening in strawberry. In the case of raspberries, increased ethylene production has been reported during ripening (Burdon and Sexton 1990), an unexpected pattern for non-climacteric fruits. Reduction of ethylene synthesis rates using the ethylene production inhibitor aminoethoxyvinylglycine reduced the rate of abscission zone weakening while treatments of green fruit with 1-methylcyclopropene showed that a key role of endogenous ethylene is associated with the abscission of the fruit receptacle (Iannetta *et al*. 1999, 2000). Some controversy has also arisen regarding the correct classification of blueberry. Some authors classified blueberries as climacteric (Ismail and Kender 1969; Mitcham *et al*. 2006) while others considered the fruit as non-climacteric (Frenkel 1972). In many climacteric fruits, the physiological importance of ethylene lays in the assurance that several aspects of fruit ripening may be manipulated by controlling ethylene production or perception. In blueberries, the technological implications of the categorization are not crucial since the fruits should be harvested fully ripe to avoid a reduction in their organoleptic characteristics. Blueberries depend on the plant for assimilates during ripening and are commercially unacceptable if not "vine ripened" since flavor does not improve after harvest.

Abscisic acid (ABA) is another hormone which has been suggested to be involved in ripening regulation of fruits (Jiang and Joyce 2003). Strawberry ripening can be stimulated by treatment with 10^{-4}-10^{-5} mol L^{-1} ABA. However, Jiang and Joyce (2003) reported that the ABA effects on anthocyanin accumulation and enhanced strawberry fruit color development are ethylene-mediated. In other fruits, promotion of fruit ripening by ABA also seems to be mediated by ethylene.

Auxin is the phytohormone that has been shown to play the most dramatic role in berry fruit ripening to date. Early studies showed that fruit receptacle growth is regulated by the achenes and that applications of synthetic auxins can resume growth in deachened fruits. However, it is currently thought that auxins have a role far beyond growth and also influence fruit ripening. This was proposed by Given *et al*. (1988) who showed that achene (a source of endogenous auxin) removal from green fruit accelerates the ripening process while application of naphthaleneacetic acid retards it. Later, Aharoni *et al*. (2002) demonstrated that the expression of many ripening-specific genes can be down-regulated by treatments with 0.5 mM indole-3-acetic acid and that several ripening-specific genes are induced following the removal of the achenes. The model proposed then established that auxins, mainly produced in the achenes, repress the ripening progress and that the subsequent reduction in the levels of the hormone leads to an activation of the genes required for ripening. The "auxin as a ripening repressor" model might explain part of the hormonal regulation and ripening control in non-climacteric fruits. The completion of such a model still requires further studies. For instance, it is not completely clear how auxin is distributed from the achenes to the receptacle. Auxin, as well as other native plant growth regulatory compounds, can be transported passively in vascular tissues. However, there is also an active cell-to-cell auxin flow (Bennett *et al*. 1998) known as polar transport. The PIN-FORMED (PIN) protein family is a group of plant transmembrane proteins with a predicted function as secondary transporters. PINs have been shown to play a rate-limiting role in the catalysis of efflux of the plant growth regulator auxin from cells, and their asymmetrical cellular localization determines the direction of cell-to-cell auxin flow (Zažĭmalová *et al*. 2007). The potential involvement of specific PIN family members in auxin distribution in strawberry fruit is not known as yet. Furthermore, the potential formation of biologically inactive conjugates of IAA in the receptacles or the involvement of other pathways that could degrade or permanently inactivate IAA by oxidation (Woodward and Bartel 2005) has not been analyzed in detail. IAA biosynthesis, metabolism, and transport ensure that appropriate auxin levels are in place to orchestrate plant development but the way auxin affects gene expression in the receptacle is another aspect that needs to be revealed. Recent genetic and molecular studies in *Arabidopsis* have revealed a crucial intracellular auxin signaling pathway in which a ubiquitin-dependent proteolytic system has a key role in sensing and transducing the hormone signal to transcriptional programs (Dharmasiri and Estelle 2004; Dharmasiri *et al*. 2005). A structural model of auxin perception by the receptor (TIR1) has been proposed (Tan *et al*. 2007). The way these elements fit into the auxin-mediated ripening regulation has not yet been investigated. Looking into these aspects would be useful to strengthen the model of strawberry fruit "auxin ripening regulation". Whether or not auxin plays an important role in repressing ripening-related genes in other 'soft fruits' has not been explored so far and it might be another interesting research area.

Despite the potential role of auxins in strawberry fruit ripening regulation, this does not explain the induction of many ripening-associated genes (Civello *et al*. 1999; Aharoni *et al*. 2002). Interestingly enough, different genes usually up-regulated during ripening were shown to be induced by oxidative stress (Aharoni *et al*. 2002). Some of those genes encode protective enzymes such as ferritin (9-fold induction under oxidative stress), detoxyfying enzymes such as glutathione-*S*-transferases (4-fold induction), and pathogenesis related proteins such as harpin-induced protein (3-fold induction). Thus, active gene expression may be induced to cope with oxidative stress conditions during ripening. Alternatively, the strawberry ripening transcriptional program may be – at least in part – considered an oxidative stress-induced process. While several advances have provided some clues about the regulation of fruit ripening in some non-climacteric commodities, many of the aspects involved in such regulation remain obscure and require further work.

CELL WALL DISASSEMBLY IN 'SOFT FRUITS'

Controlled softening is desirable in order to attain consumption maturity but an excessive loss of firmness is one of the main factors limiting marketing, transportation and retail of fresh 'soft fruits'. Fruit firmness is affected by several factors. It may change due to altered hydrostatic pressure (turgor) within fruit cells (Shackel *et al*. 1991; King *et al*. 2000; Salentijn *et al*. 2003). Membrane damage and dehydration, and mesocarp cell enlargement could be involved in textural changes in some fruits (Sexton *et al*. 1997; Waldron *et al*. 2003). However, fruit textural changes are thought to be, at least in part, a consequence of changes in the composition and architecture of the cell wall (Brummell and Harpster 2001). The second factor that makes 'soft fruit' postharvest management difficult is the high susceptibility to decay. Postharvest diseases can be caused by different fungi such as *Botrytis cinerea*, *Rhizopus stolonifer*, *Mucor mucedo* and *Colletotrichum acutatum* (Maas 1984; Paulus 1990; Terry and Joyce 2000). The last two organisms are less common while *Rhizopus* rot can be easily controlled by storing the fruit at 0ºC since the fungus does not develop at this temperature. However, that is not the case for *Botrytis cinerea* which continue to grow and cause disease even under low temperature storage (Maude 1980; Agrios 2005). Several studies have been carried out in order to characterize the infection caused by *Botrytis* in plant tissues (Elad 2004). The fungus produces several cell wall degrading enzymes at early stages of colonization and some *Botrytis* polygalacturonases are virulence factors. For instance, mutant *Botrytis* strains lacking *Bcpg1* were shown to be less virulent than wild type *Botrytis* (ten Have *et al*. 1998). Furthermore, reduced susceptibility to *Botrytis* was observed in plants over-expressing a polygalacturonase inhibiting protein (PGIP) (Powell *et al*. 2000; Agüero *et al*. 2005). Consequently, both excessive softening and postharvest decay – the two most important problems limiting 'soft fruit' postharvest life – seem to be associated with cell wall modifications. While extensive degradation of cell wall polymers may lead to a massive softening of the fruit tissues, these changes could also contribute to increase decay susceptibility by reducing the strength of the cell wall, a main barrier against tissue colonization by plant pathogens (Vorwerk *et al*. 2004).

Plant cell walls are highly complex, dynamic and organized structures composed of polysaccharides, proteins and phenolic compounds, as well as of some ions (Carpita and Gibeaut 1993; Carpita and McCann 2000). The biochemical basis of plant cell wall organization depends on the species considered. Many studies analyzing changes in the cell wall of different fruits have reported that pectins, hemicelluloses and, possibly, the amorphous regions of cellulose undergo structural modifications during fruit growth and ripening (Brummell and Harpster 2001; Brummell 2006). Tomato fruit has been used as a model for cell wall metabolism during ripening, partly because of its importance as a food crop species, its diploid inheritance, and its ease of seed and clonal propagation (Giovannoni 2001; White 2002; Giovannoni 2004). Furthermore, the efficient sexual hybridization, a relatively short generation period and the availability of several ripening mutants displaying dramatically reduced ripening-associated modifications of the cell wall and arrested softening have contributed to its use as a model system and the subsequent generation of an extensive literature describing tomato softening (Steele *et al*. 1997; Brummell and Harpster 2001; White 2002). However, the "cell wall modification program" may not be a highly conserved process (Sozzi 2004) and it is unclear to what extent our understanding of cell wall composition and disassembly in model fruits could be successfully extrapolated to other commodities such as 'soft fruits'. In contrast to tomato fruit, 'soft fruit' enlargement continues throughout development. A fine and concerted balance between cell wall synthesis and degradation generates a structure that can support the growth of individual cells (Cosgrove *et al*. 2002), but ultimately allowing the dramatic disassembly accompanying the ripening process (Rose *et al*. 2004). Several studies have been carried out to understand cell wall metabolism in some 'soft fruits' such as strawberries (Neal 1965; Barnes and Patchett 1976; Knee *et al*. 1977; Huber 1984; Koh and Melton 2002; Rosli *et al*. 2004). Huber (1984) reported that hemicelluloses of strawberry fruit are depolymerized during ripening while only small changes are detected in pectin size. Rosli *et al*. (2004) analyzed ripening-related cell wall changes in three strawberry varieties and found that pectin size was reduced, but only slight depolymerization was observed in hemicelluloses. Jiménez-Bermúdez *et al*. (2002) reported reduced softening and pectin depolymerization in strawberries with antisense expression of the pectate lyase gene thus suggesting that pectin matrix disassembly is a key determinant of fruit softening. Different studies have reported the compositional changes of boysenberry, raspberry and blueberry during growth and ripening (Given *et al*. 1986; Monro and Lee 1987; Porter 1988; Plowman 1991; Perkins-Veazie and Nonnecke 1992; Perkins-Veazie *et al*. 2000) but there are very few investigations performed on cell wall metabolism (Redgwell *et al*. 1997; Stewart *et al*. 2001). Although cell wall changes associated with fruit development do not proceed in discrete stages and cell wall disassembly is a consequence of highly regulated changes occurring in a continuum, Vicente *et al*. (2007a) suggested that temporal changes in boysenberry cell wall degradation includes at least 3 stages: (a) an early stage (green to 75% red) associated with cellulose and cross-linking glycan metabolism; (b) an intermediate period characterized by a clear increase in pectin solubilization without depolymerization, in which arabinose is lost (75-100% red); and (c) a final stage characterized mainly by a reduction of galactose and a great increase in pectin depolymerization. In raspberry, a similar pattern was observed: no depolymerization of hemicelluloses during development, an increase in α-arabinofuranosidase activity consistent with a loss of arabinose from the cell wall, an increased solubilization of arabinose-rich polyuronides in later stages and a final dramatic depolymerization of all the pectic fractions at the red ripe stage (Vicente *et al*. 2007b). In blueberry, the early and intermediate ripening stages have been associated with significant hemicellulose depolimerization and the solubilization of pectins and hemicelluloses; as ripening progresses, increased arabinose solubilization takes place in both pectins and hemicelluloses (Vicente *et al*. 2007c). No pectic solubilization was detected in late ripening but a clear downshift in hemicellulose throughout development is apparent.

One aspect that has not received enough attention is the interaction between different fruit ripening-associated processes. Some research suggests that the interrelation among ripening traits might be much more profound than expected (Vicente *et al*. 2007d). For instance, the down-regulation of PL gene from strawberry fruit led to a decrease in fruit softening but, in addition to the modification in fruit firmness, several independent antisense RNA suppressed PL lines produced fruits with reduced ascorbic acid content (Agius *et al*. 2003). This led the authors to suggest that D-galacturonic acid (GalA) derived from pectin was reduced to L-galactonic acid which in turn was readily converted to ascorbate (Valpuesta and Botella 2004). Several related processes, such as the internalization of the GalA precursors from the apoplast to the mitochondria – where the final oxidative step of ascorbate synthesis occurs – have not been clearly demonstrated. Any how, these observations suggest a primary involvement of cell wall metabolism-derived products in non-wall traits such as vitamin C biosynthesis.

POSTHARVEST RECOMMENDATIONS

Lack of storage potential is one of the main barriers to fresh fruit production on a large commercial scale. 'Soft fruit' quality declines rapidly after harvest (Bower *et al*. 2003). All berries should be harvested near to the ripe stage as eating quality does not improve after harvest. Careful handling to reduce physical damage is extremely important. During the hot season it is recommended to perform the harvest operations during the coolest hours of the day. Picking usually takes place every two days but it might be necessary to carry out daily harvests during the production peak. Harvested fruit should be carefully placed in the containers to prevent physical damage. Furthermore, diseased or wounded berries should be removed to avoid cross contamination. In general, 'soft fruits' show a relatively high respiration rate. In order to reduce the fruit softening rate, metabolic activity, and fungal development, it is crucial to rapidly cool the fruit after harvest. Cooling operations should not be delayed more than one hour after picking. Cooling delay increases softening and changes in sugars, organic acids and vitamin C (Nunes *et al*. 1995). The longest storage life is attained by storing the fruit at 0ºC and 90-95% relative humidity (Mitcham *et al*. 2006). Even under these conditions, shelf life is still fairly short: 1-2 weeks for strawberries and blueberries, and 2-5 days for raspberries, blackberries and hybrids. 'Soft fruits' have low ethylene production rates (< 0.1 µl C_2H_4 kg^{-1} h^{-1} at 20°C). Even when the responses to ethylene are not very dramatic, fruit deterioration may be accelerated by ethylene (Bower *et al*. 2003) reducing the storage life of the fruits (Wills and Kim 1995). Removal of the hormone from storage facilities can reduce the incidence of postharvest diseases (El-Kazzaz *et al*. 1983).

Controlled atmosphere (CA) and modified atmosphere packaging (MAP) can supplement proper temperature management and translate into reduced qualitative and quantitative losses of 'soft fruits'. In a CA, the air is replaced with a mixture of gases (mainly integrated by high CO_2 and low O_2), the proportion of each component being fixed when the mixture is introduced. The gaseous mixture is maintained at the original level throughout the distribution cycle and, consequently, a CA requires constant monitoring and regulation of the gas composition. In contrast, the MAP techniques involve the use of plastic films that limit gas diffusion leading to enrichment on CO_2 and a reduction in the O_2 content. Either the pack is flushed with the required gas mix or the produce is sealed within the pack with no modification to the atmosphere. Subsequent respiration of the produce and the gas permeability of the packaging allow an equilibrium-modified atmosphere to be reached. The final gaseous composition will depend on a series of factors such as the weight of product packed, storage temperature, and commodity respiration rate, cultivar and ripening stage. In addition, the exchange of gases between the container atmosphere and the exterior will be affected by the difference in concentration inside and outside the packages, the exposed surface and the permeability of the selected film. Reduced decay incidence and severity, and retardation of senescence, along with associated biochemical and physiological changes (e.g., slowed down respiration and softening) are the main benefits of CA and MAP. 'Soft fruits' are relatively tolerant to high CO_2 partial pressures (Watkins *et al*. 1999). CO_2-enriched atmospheres (10-20% in air) are used to extend the postharvest life of strawberries (Smith 1992; Holcroft and Kader 1999a, 1999b). In blueberries, the respiration rates decrease with increasing CO_2 but are little affected by changes in O_2 (Song *et al*. 1992). Thus, optimal storage conditions are 17-18% CO_2 and 9% O_2 (Kim *et al*. 1995). In raspberries, decay is significantly reduced when the fruit are stored in gaseous mixtures containing 10% O_2 and 15% CO_2 (Haffner *et al*. 2002). After transfer from a CA or MAP to air, residual effects such as reduction of respiration and ethylene production rates, accumulation of ethanol, maintenance of flesh firmness and retardation of flesh color development can still be detected (Li and Kader 1989).

In strawberries, the standard method of CO_2 treatment is to completely enclose pallet loads of cold fruit in sealed plastic bags, pull a slight vacuum and add CO_2 to create a 12 to 15% CO_2 gas mixture within the pallet bag. In blueberries, fruit are first enclosed in clamshells and then placed in cardboard boxes with a microperforated or microporus film (with very high gas transmission rates) overwrap sealed to the boxes before adding the CO_2 gas mixture.

In Australia, Day (1998, 2005) recommended the application of a novel high oxygen MAP (> 60% O_2 plus 10-20% CO_2) for the retailing of fresh commodities such as berries, together with a 30 µm oriented polypropylene with antimist coating as packaging material. Under high oxygen CA and high oxygen MAP conditions, anaerobic fermentation is prevented and moisture loss and microbial growth may be significantly inhibited. Superatmospheric oxygen levels have been suggested to be helpful in maintaining the sensorial, nutritional, and microbial quality of different 'soft fruits' (Ayala-Zavala *et al*. 2007; Zheng and Wang 2007, and references cited therein).

ALTERNATIVE STRATEGIES TESTED TO MAINTAIN 'SOFT FRUIT' QUALITY

Extension of 'soft fruit' postharvest life has been an ongoing challenge, as a significant proportion of fresh berries still fail to reach the consumer. Strategies for reducing 'soft fruit' losses include selection of firmer genotypes and optimum postharvest handling procedures. A single postharvest technique is unlikely to fully cut down postharvest losses. In the last few years there has been an increase in the search for alternative methods such as short postharvest heat treatments, UV-C irradiation, chitosan coatings or treatments with natural compounds. Those methods could complement refrigeration benefits. In addition, biotechnology may be useful to improve fruit quality attributes (e.g. flavor), to reduce the softening rate or to decrease the susceptibility against *Botrytis cinerea* (Orlando *et al*. 1997). Overexpression of genes coding for proteins with antifungal activity seems a promising strategy for future work in 'soft fruit' species (Dolgov *et al*. 1999). Many groups have focused on the development or adjustment of these strategies that might also reduce the use of hazardous chemicals in the postharvest environment.

Heat treatments

The use of heat treatments is effective to reduce decay and delay some ripening-associated processes in several fruits (Lurie 1998; Paull and Chen 2000). In strawberry, postharvest heat treatments (45°C, 3 h) with air, in combination with refrigerated storage were useful to reduce the incidence of *Botrytis cinerea* and delay softening without causing negative modifications in sugar and organic acid levels (Vicente *et al*. 2002). Several factors seem to be involved in the reduction of the susceptibility to pathogens in heat-treated fruits. Heat treatments directly affect *Rhizopus stolonifer* and *Botrytis cinerea* by reducing the germination rate of the conidia (Pan *et al*. 2004). In addition, heat treatments may modify fruit physiology and indirectly affect pathogen incidence. Those changes in fruit physiology include an increased polyphenol oxidase activity, reduced cell wall degradation (which could affect tissue penetration and colonization) and increased enzymatic and non-enzymatic protection against reactive oxygen species (Vicente *et al*. 2006). Moreover, during heat treatments, there is a marked increase in the levels of salicylic acid which has been shown to be involved in defense responses signaling in plants (Vicente 2004). Postharvest heat treatments were also tested in boysenberry: exposure of the fruits to 45ºC for 1 h with a subsequent refrigerated storage also reduced fruit damage and softening (Vicente *et al*. 2004). García *et al*. (1995, 1996) described that hot water dips were also useful to control pathogens in strawberry.

UV irradiation

Postharvest UV-treatments consist of exposing the commodities for a certain period to radiation between 200 and 300 nm (usually 254 nm) (Civello *et al*. 2006). UV-C radiation has several effects on fruits and vegetables. First, it has a germicide effect and can be used to control pathogens present on the surface of the commodities. Effective control of postharvest decay by UV-C treatments (0.5-4.5 kJ m^{-2}) has been reported in strawberry (Baka *et al*. 1999; Nigro *et al*. 2000; Marquenie *et al*. 2002, 2003a; Pan *et al*. 2004) and boysenberry (Vicente *et al*. 2004). In addition to the direct role of UV radiation on pathogens, several lines of evidence suggest that the reduction in disease incidence and severity observed in UV-C-treated tissues results at least in part from an activation of defense response mechanisms in the commodities such as the induction of pathogenesis-related proteins and the accumulation of phytoalexins (Nigro *et al*. 2000; Marquenie *et al*. 2003b). Other effects reported in fruits in response to UV-C treatments include delayed ripening and reduced firmness loss. Doses of 1 kJ m^{-2} or 4.1 kJ m^{-2} UV-C radiation reduced strawberry fruit softening (Baka *et al*. 1999; Pan *et al*. 2004). Also, UV-C treatments increased antioxidant accumulation in grapes and boysenberries (Vicente *et al*. 2004) suggesting that they could be used to increase the nutritional value of some commodities. UV radiation only brought about minor modifications in fruit quality attributes associated with flavor, such as total sugars and acidity (Baka *et al*. 1999; Pan *et al*. 2004; Vicente *et al*. 2004). In some cases, excessively long treatments or very high UV-C doses caused detrimental effects such as calyx discoloration and drying in strawberries (Marquenie *et al*. 2002).

Both heat treatments and UV-C irradiation have proven to be useful to supplement the benefits of refrigeration, maintain quality and reduce postharvest losses. However, most of the experiments have been performed in a laboratory scale. Many aspects remain to be clarified and further evaluation and research are required before these methods are fully adopted in a commercial scale. Some important issues requiring further attention include optimizing fruit handling, reduction of operation (treatment) times, equipment design for continuous processes (e.g. UV-irradiation and/or water/air HT) and assurance of homogeneous doses.

Chitosan coatings

Chitosan (poly-*N*-acetylglucosamine, a polymer of β-1,4-D-glucosamine) is a biodegradable animal-derived compound obtained commercially by alkaline deacetylation of chitin (Muzzarelli and Muzzarelli 2002). Chitosan has shown to be useful as an edible coating and natural antimicrobial agent capable of inducing plant defense responses (Rabea *et al*. 2003). In strawberries, it acts as a barrier to gas diffusion and inhibits pathogenic fungi development, thus delaying ripening and improving storability (El Ghaouth *et al*. 1991a, 1991b, 1992a, 1992b). Preharvest spray applications or postharvest dips in a chitosan solution protect strawberry and other 'soft fruits' from decay (Aharoni and Barkai-Golan 1987; El Ghaouth *et al*. 1997; Reddy *et al*. 2000; Han *et al*. 2004; Hernández-Muñoz *et al*. 2006; Ribeiro *et al*. 2007). Chitosan coatings also increase firmness retention and delay changes in the external color (Han *et al*. 2004; Hernández-Muñoz *et al*. 2006).

Other supplemental treatments

Other technologies also increase antimicrobial protection during 'soft fruit' storage and transit. In addition, fruit quality-related attributes may be improved. Treatments that showed to be successful at a laboratory scale include different natural compounds (e.g., methyl jasmonate and essential oils; Archbold *et al*. 1997; Chanjirakul *et al*. 2006, 2007; Tzortzakis 2007), ethanol (Karabulut *et al*. 2004a; Chanjirakul *et al*. 2006, 2007), benzoic acid (Lattanzio *et al*. 1996), ozone (Barth *et al*. 1995), nitric oxide (Wills *et al*. 2000) and biological control (Helbig 2002; Wszelaki and Mitcham 2003; Karabulut *et al*. 2004b). Further research to optimize and scale up those treatments would be of interest.

FINAL REMARKS

Although there has been some controversy over 'soft fruits', they are usually classified as non-climacteric fruits because ethylene does not show a major role in ripening regulation. Auxin has shown to be a repressor of several ripening-associated genes; however, further research is needed to achieve a model based on auxin regulation. Issues such as auxin transport to the receptacle, auxin catabolism and the signal transduction pathways involved in the regulation of the ripening-associated genes need to be elucidated. Recent advances in the identification of auxin transporters and receptors in model plants may facilitate further analysis of these topics. Whether or not that plant growth regulator plays a major role in repressing ripening-related genes in other 'soft fruits' has not been explored yet and it might be an interesting research area. In addition, the identification of other effectors involved in the regulation of auxin-independent genes is another interesting topic to explore.

Understanding cell wall metabolism in 'soft fruits' is of great interest since it affects the two most important factors limiting the postharvest life of the fruits: excessive softening and susceptibility to opportunistic pathogens. Pectin matrix disassembly has shown to be a major feature accompanying softening in strawberry, raspberry and boysenberry. In contrast, the temporal sequence of cell wall disassembly in blueberry included an early stage associated with the solubilization of pectin while later in development a reduction in glucan content and downshift in hemicellulose, but not in pectin, took place.

In 'soft fruits', characterized by a high metabolic rate and a very short shelf life, the extension of postharvest life has been an ongoing challenge since a significant percentage of fresh berries fail to reach the consumer. The importance of proper cooling and refrigeration in 'soft fruits' cannot be overstated. Nevertheless, a single postharvest technique is unlikely to fully control postharvest losses but new tools such as UV radiation, heat treatments, chitosan coatings or treatments with natural compounds may be added to the overall management plan (cooling conditions, MAP) to further delay softening and prevent severe decay losses. Biotechnology may be also useful to improve fruit quality attributes, and to decrease the softening rate and the susceptibility against *Botrytis cinerea*.

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