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Abiotic Stress in Harvested Fruits and Vegetables

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1. Introduction

Harvested fruits and vegetables can be potentially exposed to numerous abiotic stresses during production, handling, storage and distribution (Hodges, 2003). Some of these stresses can be minor in nature, resulting in no quality loss or, in some cases, in quality improvement (Hodges et al., 2005) during distribution. However, when the abiotic stress is moderate or severe, quality losses almost always are incurred at market (Toivonen, 2003a&b). As a consequence it is important to understand the nature and sources for abiotic stresses that affect fruits and vegetables. In addition, with improved understanding, options for better management or resistance become available (Toivonen, 2003b; Toivonen, 2005). One of the challenges facing fruit and vegetable production globally is that regional climate regimes are becoming more unpredictable from year to year. Hence understanding of effects of field abiotic stresses (e.g. drought, extreme temperatures, light and salinity) on postharvest stress susceptibility will become more important since postharvest stresses limit the storage and shelf life potential of fruits and vegetables (Toivonen, 2005). It is the intent of this chapter to first describe the nature of pre- and post-harvest abiotic stress events, delve into their importance for product quality and marketing and then explore the technologies available to begin managing the sensitivity of fruits and vegetables to stresses they encounter in the handling and distribution chain.

2. Major preharvest stresses which influence postharvest abiotic stress response

Abiotic stresses occurring during production can either be the primary cause (direct) for disorders that exhibit themselves during postharvest handling and storage practices or they can influence the susceptibility of a fruit or vegetable to postharvest conditions that cause abiotic stresses resulting in disorders (indirect) (Ferguson et al., 1999). It is important to characterize the relationship between preharvest abiotic stresses occurring during production and postharvest abiotic stresses that the fruit or vegetable is exposed after harvest and during storage and distribution, since the solution to these different problems will be best resolved by focusing on preharvest or postharvest abiotic stress amelioration, respectively. Moderate levels of preharvest stress can potentially work towards enhancing stress resistance of a fruit or vegetable through up-regulating genes and pathways which

renders the tissues cross-tolerant to many stresses (Lesham & Kuiper, 1996; Bowler & Fluhr, 2000) which may occur subsequently in postharvest handling, storage and distribution.

2.1 Drought

The occurrence of drought conditions during production of fruit and vegetable crops is becoming more frequent with climate change patterns (Whitmore, 2000). While much work has been devoted to understanding of drought effects on production and productivity of these crops (Whitmore, 2000), there is limited published literature on the effects of pre-harvest water stress on responses to postharvest stresses and hence on subsequent quality and shelf life. However, the existing literature provides some insight which may lead to better understanding and perhaps also encourage future research.

Water stress during the production phase of some fruits and vegetables may affect their physiology and morphology in such a manner as to influence susceptibility to weight loss in storage. There have been both positive effects reported for field water deficits (stress) in tree fruits and root vegetables. In the case of peaches, it has been shown that lower levels of irrigation results in higher density of fruit surface trichomes and consequent lower weight losses in storage (Crisosto et al., 1994). In addition, two studies have shown that deficit irrigation of apples and pears could reduce water loss of these fruit in subsequent storage (Kilili et al., 1996; Lopez et al., 2011) and this was attributed to reduction in skin permeance of the deficit irrigated fruit (Kilili et al., 1996). Presumably, fruit grown under moderate water stresses imposed by deficit irrigation practices adapt by developing a less water permeable cuticle. In terms of understanding that water deficits can have negative effects on postharvest stress susceptibility, irrigation of apples has been shown to enhance apple size which was associated with lower to water losses during storage (Veličković, 1994). This observation highlights a main concern about using deficit irrigation, which is the reduced size of fruit from such treatments (Lopez et al., 2011). Size of fruit is important, since larger fruit have lower surface area to volume ratios, which confers lower relative water loss (Shibairo et al., 1997). Another negative affect associated with water deficits is the case of root vegetables, such as carrot, where preharvest water stress (watering to 25-75% of soil water field capacity) can weaken the cells, resulting in higher membrane leakage (i.e. cell damage) and consequently greater weight loss in storage (Shibairo et al., 1998b).

Timing of a water stress event can also be very important in determining response to postharvest abiotic stress response. One example is that 'Kensington' mango fruit (*Mangifera indica* L.) will be significantly more susceptible to postharvest chilling injury with exposure to water stress during the cell expansion phase of growth as opposed to being exposed to the stress during cell division or at a time near to harvest maturity (Léchaudel and Joas, 2007). Therefore it is critical to avoid water stress until the fruit has reached maximum size in order to minimize incidence of chilling-induced injury in storage. Water stress, particularly at the tuber forming stage, can also lead to a higher susceptibility of potatoes to postharvest development of black spot disorder (Hamouz et al., 2011). Black spot disorder is correlated primarily to susceptibility of cells in the potatoes to undergo decompartmentation in response to mechanical stress (i.e. bruising) (Stevens and Davelaar, 1997).

2.2 Plant nutrition

There is limited literature regarding the effects of crop nutrition on the susceptibility of fruits and vegetables to postharvest abiotic stress. There is one review dealing with the

effect of preharvest nutrition on postharvest physiology and disorders of fruits and vegetables (Sams and Conway, 2003), however most of the reviewed literature touches on nutrition effects on postharvest biotic stress effects (i.e. disease resistance).

Calcium nutrition during production has been well documented in regard to postharvest disorders of many fruits and some vegetables (Sams and Conway, 2003). Calcium is also been suggested as a putative signalling molecule involved in the development of cross-tolerance to abiotic stresses (Bowler and Fluhr, 2000). Therefore the role of preharvest calcium nutrition is postharvest stress resistance may be complex, and dependent on whether the fruit or vegetable is also exposed to environmental abiotic stresses.

Potassium nutrition has been shown to have a few important effects on postharvest abiotic stress susceptibility of vegetables. In carrots, deficiency in potassium is associated with greater weight loss (desiccation stress) in storage (Shibairo et al., 1998c). At levels below 1 mM potassium in the soil medium, weight loss was directly associated with increased membrane leakage (i.e. damaged cells) in the carrot tissues. Above 1 mM potassium, there were no significant differences in weight loss under standardized storage conditions (Shibairo et al., 1998c). Improved potassium nutrition has also been shown to reduce susceptibility of potatoes to internal bruising in response to mechanical stresses imposed during postharvest handling (Maier et al., 1986; McGarry et al., 1996).

Relatively high preharvest nitrogen is often associated with poor postharvest quality of many fruits and vegetables (Sams and Conway, 2003). In regards to affecting susceptibility to postharvest stress, applying higher than recommended levels of preharvest nitrogen for a specific crop have been linked to storage discoloration susceptibility in both cabbage and potato. In the case of cabbage, it appears that excessive nitrogen fertilization leads to high accumulations of zinc and aluminum and nitrate induced manganese deficiency (Berard et al., 1990). High nitrogen applications in the field resulted in increased incidence and severity of black midrib in cold storage, particularly for the susceptible cultivar, 'Safekeeper' (Berard, 1990). In the case of potatoes, black spot susceptibility (a consequence of bruising; Stevens and Davelaar, 1997) is influenced by nitrogen fertilization, particularly the balance of nitrogen applied in relation to levels of potassium applied (Horneburg and Wirsing, 1995). In contrast nitrogen deficiency or lower than recommended nitrogen application rates will most often results in increased vitamin C content in many fruits and vegetables (Lee & Kader, 2000). Vitamin C content has been tightly linked with storage life potential (Hodges et al., 2001), which is likely a consequence of the importance of this antioxidant nutrient in forestalling oxidative injury that leads to quality losses in storage (Noctor and Foyer, 1998).

2.3 Temperature extremes

Susceptibility to high (heat injury inducing) or low (chill injury inducing) temperatures is known to be reduced by prior exposure of the sensitive fruit or vegetable to low ambient temperatures (Saltveit and Morris, 1990; Wang, 1990). However, if the preharvest temperature leads to chilling induced injury in the field, then susceptibility to postharvest chilling injury can be increased (Morris, 1954). Therefore, the level of the preharvest temperature extreme will be a determinant as to if the exposure will have positive or negative effects on postharvest stress sensitivity.

Extreme high temperatures can occur in the field and apple fruit exposed to direct sunlight can reach in excess of 40 °C (Ferguson et al., 1999). High temperatures during the late season

(leading up to harvest) can enhance susceptibility of apples to superficial scald which develops in storage (Bramlage and Weis, 1997). In contrast, the authors found that low temperatures in the preharvest interval could reduce susceptibility.

2.4 Salinity

Tomatoes grown under high salinity will produce smaller fruit with higher soluble solids (Mizrahi, 1982). Smaller fruit will have higher surface area to volume ratios, hence greater susceptibility to postharvest water loss (i.e. desiccation stress) (Shibairo et al., 1997). While there is no direct information in the literature to confirm that smaller tomato fruit from saline growing conditions would be subject to greater desiccation stress postharvest, firmness declines for tomatoes grown under 3 and 6 dS m⁻¹ salinity levels were increased by 50 to 130%, respectively, at two weeks holding at 20 °C compared with control fruit (Mizrahi et al., 1988).

2.5 Light

It would be considered logical to assume that effects of exposure to high light are difficult to dissociate from effects exposure to high temperatures. However, research has shown that low light (bagging of apples) in the preharvest interval reduced susceptibility of apples to developing superficial scald in cold storage (Barden and Bramlage, 1994) and, in contrast, high ambient temperatures resulted in increased susceptibility (Bramlage and Weis, 1997). Generally, only sun-exposed surfaces of susceptible cultivars of apples develop scald in storage (Ferguson et al., 1999).

In the case of ambient low light, when lettuce is grown under low light which is sub-optimal for photosynthetic activity, shelf life of fresh cut lettuce (i.e. lettuce subjected to mechanical stress) is much shorter than lettuce produced under optimal light conditions (Witkowska & Woltering, 2010). Tomato size is smaller when the crop is grown under ambient low light levels, such as in the early spring season in northern latitudes (Gruda, 2005) and since surface area to volume ratio is greater in smaller fruits, susceptibility to postharvest desiccation stress would increase (Shibairo et al., 1997). Low light also results in lower levels of ascorbate in many greenhouse-grown fruits and vegetables (Gruda, 2005), which would render them less fit to deal with postharvest stresses since ascorbate contents are general directly proportional to relative levels or stress tolerance (Noctor and Foyer, 1998).

3. Postharvest stresses during handling and storage

3.1 Temperature extremes

Postharvest temperature abuse during distribution is an ongoing challenge for many products, particularly those being shipped by air or ocean container (East et al., 2008). Breaks in cool chain temperatures can result in acceleration of climacteric ripening and softening (i.e. reduction in shelf potential) for apples harvested and stored at the pre-climacteric stage of maturity (East et al., 2008). However, those authors also found that temperature breaks had minimal effects on apples harvested and stored at post-climacteric stage of maturity. Fruit harvested at post-climacteric stages of maturity are not generally of concern to industry since those fruit have shorter storage and shelf life potential (Toivonen and Beveridge, 2005).

Chilling injury susceptibility is a significant issue for many crops derived from subtropical and tropical growing regions. Generally fruits, fruit vegetables (fruits which are consumed as

vegetables) and root and tuber crops are chilling sensitive (Kader, 2002; Toivonen, 2010). There is a significant literature pertaining to chilling sensitivity of crops and much effort has been devoted to better understanding of chilling injury mechanisms and approaches to ameliorating the disorder (Wang, 1993; Saltveit, 2003). While there are visible (surface pitting, internal browning) and textural (accelerated softening and development of mealiness) changes often associated with chilling injury (Wang, 1993; Saltveit, 2003), flavour generation capacity has been shown to be a sensitive early indicator of chilling stress effects (Maul et al., 2000).

Use of heat treatments has become popular for disinfestation and disinfection of fruits and vegetables (Lurie, 1998). Appropriately applied levels of heat treatment can also induce temperature tolerance to both high and low temperatures (Lurie, 1998). However, when excessively harsh heat treatments are applied, heat-induced damage can occur.

3.2 Low O₂ and high CO₂

Managing postharvest handling and storage atmospheres to avoid low O₂ or high CO₂ stress is a constant concern and the problem is more severe when handling products in modified atmosphere (MA) packages as opposed to controlled atmosphere (CA) systems since temperature is often not as easily controlled in the MA packages as the produce moves through a distribution chain (Toivonen, 2003a; Toivonen et al., 2009). As such, the importance atmospheric stress in postharvest systems deserves significant discussion.

While low O₂ levels are well-known to induce stress-induced changes in metabolism and resultant metabolite accumulations (Kanellis et al., 2009), acute low oxygen injury is not expressed until the tissue is re-aerated (Biemelt et al., 1998) and a consequent uncontrolled oxygen burst (consisting of hydrogen peroxide and other radicals) occurs, resulting in lipid peroxidation, protein denaturation and membrane injury (Blokchina et al., 2001, 2003). Different fruits and vegetables have varying thresholds for low O₂ stress, dependent on anatomy, temperature, physiological age, presence of supplemental gases (e.g. CO₂, CO, SO₂, C₂H₄) and duration of exposure (Kader and Saltveit, 2003; Kanellis et al., 2009). Threshold limits for low O₂ tolerance can range from approximately 10 kPa partial pressure (for early potatoes and asparagus) down to approximately 1 kPa partial pressure (for mushroom, broccoli, and chipping potatoes), assuming that the produce is cooled to its recommended temperature when it is placed into that atmosphere (Kader and Saltveit, 2003). When a fruit or vegetable is converted to fresh-cut format, it generally becomes tolerant to lower levels of oxygen.

One of the most notable effects of high CO₂ levels in postharvest handling is to competitively inhibit ethylene binding and action hence delaying ripening in climacteric fruits (Kanellis et al., 2009). High CO₂ will directly inhibit succinate dehydrogenase, thus impairing the functioning of the tricarboxylic acid cycle and aerobic respiration. There are numerous physiological disorders that can be attributed to high CO₂ stress, including black heart of potatoes (Davis, 1926), brown heart or core in apples and pears (Meheriuk et al., 1994), surface bronzing in apples (Meheriuk et al., 1994) and brown stain of lettuce (Kader and Saltveit, 2003). High CO₂ can also modulate chilling stress, ethylene induced disorders and susceptibility to pathogenic attack (Kader and Saltveit, 2003).

3.3 Mechanical injury

There are two types of mechanical injury that can be incurred during harvest and handling of fruits and vegetables; 1) cuts or punctures, and 2) impacts leading to bruises. Cuts can

lead to transitory increases in respiration, ethylene production, phenolics production and cell deterioration near the site of the injury (Toivonen and DeEll, 2002 ; Toivonen et al., 2005). Several factors influence the severity and size of bruising sustained, including maturity, water potential, tissue or cellular orientation at the site of the injury, shape of the object imparting the bruising force, energy and angle of the impact, and temperature of the product (Miller, 2003).

Cut type injuries are most prevalent in fresh-cut fruit and vegetable products (Toivonen and DeEll, 2002). Severity of response to cutting is very much dependant on the tissue characteristics, maturity of the fruit or vegetable of interest, the coarseness or sharpness of the cutting implement used and the temperature at which the cutting is done (Toivonen and DeEll, 2002). Cut injuries occur during the harvest process of many fruits and vegetables and is more severe in machine-harvested as compared with hand-harvested product (Miller, 2003). Products such as tomatoes, pickling cucumber, snap beans, green peas, potatoes, garlic can sustain significant damage during machine harvest, whereas asparagus, Brussels sprouts, leafy greens and head lettuce are more tolerant (Miller, 2003). Cutting associated disorders are primarily visualized as cut-edge browning or blackening, but may also include yellowing in green tissues and whitening on carrots (Toivonen and DeEll, 2002).

Impact caused injuries are associated with loading of product for transport, events during transport (particularly when uneven or rough roads or lanes are encountered), during unloading and throughout packaging and processing lines (Miller, 2003). Impact bruising has been shown to induce significant levels of ethylene production in mature-green tomatoes, with the levels produced being concomitant with the number of impacts sustained (MacLeod et al., 1976). Both physically visible internal damage and slight declines in ascorbic acid content of the fruit were observed in response to the impact events imposed on the fruit. Impact bruising leads to development of internal black spots in potato tubers (Stevens and Vavelaar, 1997).

3.4 Desiccation

Loss of water leading to deterioration in fruit and vegetable tissues is a common issue for postharvest handling and distribution (Ben-Yehoshua and Rodov, 2003). In addition to wilting (Ben-Yehoshua and Rodov, 2003), water stress can lead to accelerated senescence or ripening which are expressed as softening of tissues, membrane deterioration and yellowing (Lurie et al., 1986; Burden et al., 1994). As mentioned previously, one of the main characteristics of a fruit or vegetable that defines susceptibility to water loss is surface area to volume ratio (Shibairo et al., 1997b). Burton (1982) described a range of surface area to volume ratios from as low as 0.2 cm^{-1} in winter cabbage or turnip to as high as $50\text{-}100 \text{ cm}^{-1}$ in leafy vegetables, explaining differences in water loss characteristics in these very different types of vegetables. In beans, the density of hairs on the cuticle can modulate rates of water loss to some extent and damage to these hairs will lead to increased losses (Hoffman, 1967). In other fruits and vegetables, lenticel density or epicuticular wax thickness can modulate water loss (Ben-Yehoshua and Rodov, 2003).

The driving force for water loss is the vapour pressure deficit (vpd), which is the relationship that describes the difference in water activity of the fruit or vegetable and the water activity of the atmosphere surrounding it (Ben-Yehoshua and Rodov, 2003). The greater the vapour pressure deficit, the greater the water loss. Three postharvest handling principles are important in minimizing water loss of any fruit or vegetable; 1) warm product

loses water faster than cool product when placed into a cool room, hence the importance of rapid precooling before storage, 2) delays in cooling will lead to longer exposures to higher vapour pressure deficit conditions, hence timely cooling after harvest is of utmost importance, and 3) storing product at the coldest storage temperature and highest relative humidity possible will minimize water loss (Toivonen, 2010). Following these principles will result in the least desiccation stress for any fruit or vegetable.

4. Effects of abiotic stresses on plant metabolism

4.1 Metabolic changes Induced by stress

Heat stress induces metabolic changes associated with heat shock protein accumulations which are known to confer persistent levels of stress resistance in heat-exposed produce (Wang et al., 2004). Heat stress can also inhibit the production and accumulation of lycopene (Hall, 1964). The duration and temperature of exposure will determine if such an effect will occur, but tomato fruit exposed to 32 °C continuously will not turn red, remaining yellow even at full ripeness.

Chilling stress results in the accumulation of lipid peroxidation products, superoxide anions and hydrogen peroxide and also to losses in flavor volatile production in sensitive fruits and vegetables (Wang, 1993; McDonald et al., 1996; Maul et al., 2000). Chilling stress affects ethylene metabolism (Wang & Adams, 1982; Obenland et al., 2008), leading to accelerated softening. It also modifies cell wall metabolism, with resultant up-regulation of cell wall dismantling enzymes such as pectin methylesterase and endopolygalacturonase (Nilo et al., 2010).

There are two distinct phases for response to exposure to anaerobic or anoxic atmospheres. The first phase involves the metabolic shift induced by impairment of the mitochondrial electron transport chain by limitation of the primary electron acceptor, molecular O₂ (Hanhijärvi and Fagerstedt, 1994). The resultant impairment has been well-characterized as declines in ATP levels, pyruvate dehydroxylase activity and cytoplasmic pH (Kader and Saltveit, 2003). These conditions lead to an increase in pyruvate decarboxylase, alcohol dehydrogenase and lactate dehydrogenase activities (Kader and Saltveit, 2003). Anaerobic respiration is induced and there is an accumulation in acetaldehyde, ethanol, ethyl acetate and/or lactate (Purvis, 1997). In addition, the impairment of the mitochondrial electron transport chain results in electron leakage and consequent generation of superoxide anions and hydrogen peroxide in the cells which can be decomposed by existing cellular antioxidant systems (Blokchina et al., 2001). Ascorbate and glutathione levels can also increase during an anoxic or hypoxic event (Biemelt et al., 1998). Any or all of these changes are indicators of oxygen stress in fruit and vegetable tissues and affect quality attributes. However, actual injury to the tissue does not occur until the second phase, where the fruit or vegetable is returned to higher O₂ atmospheres. On return to aerobic atmospheres, rates of oxygen radical production in the impaired electron transport chain becomes accelerated, leading to great accumulations of superoxide anion, hydrogen peroxide and hydroxyl radical that cannot be fully decomposed by existing antioxidant protection systems and consequent lipid peroxidation and protein denaturation ensues, leading to membrane damage, enzymatic browning and cell death (Blokchina et al., 2001, 2003).

Kubo et al. (1990) found that different fruits and vegetables responded in different ways to high CO₂. Those fruits and vegetables showing no change in O₂ uptake (respiration) in response to 60% CO₂ exposure did not show any change in ethylene production. Those

showing a decline in respiration generally also showed a decline in ethylene production, except banana (Kubo et al., 1990) and those which showed a significant increase in respiration also showed an increase in ethylene production (cucumber, eggplant, podded pea, spinach and iceberg lettuce). This suggests that these latter vegetables were more sensitive to CO₂ stress than the other fruits and vegetables tested. Mathooko et al. (1998) determined that CO₂ stress-induced ethylene biosynthesis was likely regulated at a post-transcriptional level and it involves the *de novo* synthesis of novel protein(s). They also identified that protein phosphorylation and dephosphorylation processes as being required in one or more of the steps leading to the induction of ACC synthase, which is the last enzyme in the ethylene biosynthesis pathway.

Initial response to wounding stress is characterized with a progressive accumulation of ACC synthase, ACC and ethylene production in tomatoes and this lasts for up to 2 hours, but if the cut tomatoes are held over longer durations, ethylene production declines (Kende and Boller, 1981). However, both ACC synthase and ACC continue to accumulate, indicating that there is a capacity to produce ethylene, but transformation of ACC to ethylene is blocked or inhibited (Kende and Boller, 1981). Wounding has also been shown to induce phenolic accumulation through up-regulation of phenylalanine ammonia lyase (PAL) (Ke and Saltveit, 1989). This up-regulation of PAL was associated with wound-induced ethylene production. Other metabolites increase in response to bruising or wounding stress, including isocoumarin in carrots (Lafuente et al., 1996), anthocyanins in midribs of red-pigmented lettuce (Ferrerres et al., 1997), methanethiol, allyl isothiocyanates and dimethyl disulfide in cabbage (Yano et al., 1986; Chin and Lindsay, 1993), six-carbon aldehydes and alcohols in cut peppers (Wu and Liou, 1986) and suberin in tomatoes and bean pods (Dean and Kolattukudy, 1976). Some of the metabolic shifts are mediated by stress response messengers (e.g. phenolics, suberin and isocoumarin accumulation) and others are a direct consequence of cellular disruption that occurs during wounding or bruising (e.g. methanethiol, allyl isothiocyanate and dimethyl sulphide accumulations).

Desiccation stress has been shown to cause some metabolic changes in fruits and vegetables. In carrots, desiccation stress at extreme handling conditions (i.e. at 13 °C) led to increases in osmotic potential, which are a function of free sugars in the roots (Shibairo et al., 2002). Increase in osmotic potential in response to water loss was most likely explained by increases in polysaccharide hydrolyzing enzymes activities in response to the stress. Hence, enzymes such as polygalacturonase and pectinesterase may increase in activity leading to loss of cell wall structure and concomitant increases in soluble sugars (Inari et al., 2002). This may explain at least a component of the loss of firmness that has been observed with carrots as they lose water (Shibairo et al., 2002). This hypothesis is borne out by results of work with cucumbers where water stress resulted in up-regulation of polygalacturonase activity, suggesting that water loss itself was not the only factor in causing softening of stressed fruit (Kubo et al., 2000). Another aspect of water stress is induction ethylene production (Kubo et al., 2000), which may explain why water stress leads to accelerated ripening in bananas (Burdon et al., 1994) and accelerated senescence in bell peppers (Lurie et al. 1986).

4.2 Effects on quality

Postharvest abiotic stressors can lead to numerous quality problems in fruits in vegetables, including scald, core and flesh browning of fruits, sweetening, pitting, water-soaking appearance, abnormal ripening, russetting and tissue softening (Hodges et al., 2005). Stress can also result in the losses of nutrient constituents in the fruit or vegetable, with vitamin C

loss being the most sensitive indicator of stress exposure (Noctor & Foyer 1998; Pignocchi & Foyer, 2003; Ioannidi et al., 2009).

4.3 Mechanisms for abiotic stress response at the biochemical and molecular levels

Response to all abiotic stresses can be acute and sub-acute in nature, where acute responses represent cases where cell death is a direct result and sub-acute responses represent cases where the stress leads to induction of adaptive changes in biochemical and gene expression (Toivonen, 2005). Many reactive oxygen species (ROS), particularly hydrogen peroxide, behave as signalling agents to trigger biochemical changes at the gene expression level (Jaspers & Kangasjärvi, 2010). In general, abiotic stressors will induce perturbations in the fruit or vegetable cellular homeostasis which will then result in the increased generation of ROS in the apoplast, mitochondria, peroxisomes, cytoplasm, chloroplasts and endoplasmic reticulum (Jaspers & Kangasjärvi, 2010). The ability of the cell to initially cope will depend largely on the endogenous free radical scavenging capacity (Mittler, 2002).

When free radical generation exceeds the endogenous scavenging capacity, the ROS interact with sensors, for which the full nature are not currently understood, that will initiate mitogen activated-protein kinase (MAPK) cascade reactions and also directly up-regulate transcription factors and calcium/calmodulin kinases (Mittler, 2002; Jaspers & Kangasjärvi, 2010). The MAPK cascade reaction will activate various transcription factors that enable *de novo* production of ROS, ROS scavenging systems, accumulation of heat shock proteins, and modulate NADPH supply in the cell (Mittler, 2002). Some of the MAPK cascade paths have been also shown to be linked specifically to ethylene production (Jaspers & Kangasjärvi, 2010), which is probably why ethylene production seems to be intrinsic to most stress responses. However, not all stressors produce identical response pathways, and so there is still a lot of work to be done in mapping of stress response networks (Jaspers & Kangasjärvi, 2010).

Chilling, bruising and cutting injuries all lead to increased activities of cell wall hydrolysing enzymes (polygalacturonase and pectinmethylesterase), which accounts for accelerated softening and abnormal ripening that occurs in response to those abiotic stresses (Van linden et al., 2008). Water stress will also lead to accelerated softening (Kubo et al., 2000), and that response has been associated with the induction of ethylene production in response to water stress. It quite likely that the effect of all these stresses on up-regulating the cell wall hydrolysing enzymes and consequently accelerating softening is an ethylene-mediated response.

Accumulation of heat shock proteins (HSPs) which are mediated via transcription factor activation downstream of the MAPK cascade (Mittler, 2002) have been reported to enhance persistent levels of stress resistance in affected tissues (Sabehat et al., 1996). HSPs are thought to be an important factor for protein folding, assembly, translocation and degradation under normal, stress free conditions (Wang et al., 2004). HSPs have also been linked to stabilization of proteins and membranes, and enabling protein refolding under stress conditions. As a consequence HSPs are thought to have a pivotal function of protecting plant tissues against stress by maintaining cellular homeostasis.

5. Approaches to ameliorate abiotic stress sensitivity

5.1 Treatments to enhance stress resistance

Numerous postharvest treatments have been evaluated for enhancing abiotic stress resistance of fruits and vegetables (Toivonen, 2003b). Generally, temperature modulation

(including intermittent warming), extreme atmospheres (high O₂, CO₂ and low O₂), growth regulators, anti-transpirants, antioxidant dips, growth regulators, nitric oxide and ethanol have been tested (Toivonen, 2003b). Application of treatments in combination can often improve the stress resistance level to the fruit or vegetable (Toivonen, 2005 & 2009).

One treatment that has not been widely studied to date is the concept of gradual cooling to enhance resistance to chilling injury. Gradual cooling (2 °C per day) has been shown to reduce susceptibility of tomato to chilling injury, presumably by cooling slowly enough to allow the inherent stress resistance systems to develop before actual chilling temperatures were reached (Gálvez et al., 2010). The approach is perhaps more amenable to commercial practice than some others tested (i.e. intermittent warming).

While there has been significant effort placed on developing treatments to enhance postharvest abiotic stress resistance in fruits and vegetables, the efforts have only resulted in incremental success (Toivonen, 2004). This is largely due to the fact that stress response and resistance is a very complex matrix of processes and pathways, which are not fully understood at this point in time (Toivonen, 2005; Jaspers & Kangasjärvi, 2010). Hence, it is very difficult to design effective treatments to achieve the resistance required for any or all abiotic stresses that a fruit or vegetable may encounter during harvest, handling, storage and distribution.

Hot or warm water treatments have been shown to minimize cutting induced injuries in fresh-cut products (Lurie, 1998). Such treatments may also be used to control chilling injury via induction of heat shock proteins (Collins et al., 1995; Sabehat et al., 1996). Warm water treatment has also been shown to reduce sensitivity to irradiation in cut and packaged lettuce (Fan et al., 2003). Each product has a differing tolerance to temperature and so such treatments must be developed case by case for each vegetable or fruit of interest. The key is apply a sublethal temperature exposure, in order to enhance the adaptive response of the fruit or vegetable tissue (Saltveit, 2003).

Another approach is to apply conditioning treatments to enhance chill stress tolerance. This has been shown to provide enhanced chilling stress in several fruits and vegetables (Saltveit, 1991; Wang, 1993). It also has the advantage over heat treatments in that the risk of causing acute injury during treatment is very low.

Atmospheric treatments are quite often beneficial to controlling response to postharvest stresses. Modified or controlled atmospheres have been shown to help minimized chilling injury in a number of fruits and vegetables (Wang, 1993). However, it must be noted that in some cases, application of a controlled atmosphere led to detrimental effects on the fruit (e.g. asparagus, cucumber, limes, sweet bell peppers). Therefore, a case by case evaluation is required to determine if secondary stress is induced by the atmosphere treatments.

Growth regulator applications can also potentially enhance stress resistance, particularly for fruits and vegetables which are prone to show accelerated ripening or senescence in response to stress (Baldwin, 2003). Accelerated ripening or senescence is most often mediated by ethylene production in response to the stress. As consequence anti-ethylene products such as aminovinylglycine (AVG) and 1-methylcyclopropene (1-MCP) could enhance storage or shelf if ethylene production in response to stress was a main concern (Baldwin, 2003; Blankenship and Dole, 2003). Other growth hormones, such as methyl jasmonate (which promotes leaf senescence), can enhance chilling resistance in avocado, grapefruit, bell peppers and zucchini squash (Meir et al., 1996; Wang, 1994). Absciscic acid has been demonstrated to reduce chilling-induced injury in some crops (Wang, 1993). Other growth regulators have been suggested for use in preventing senescence in leafy vegetables (e.g. 2, 4-D), however their practical application is limited.

Quite often a single stress resistance enhancing treatment may not confer optimal resistance levels to all postharvest stresses encountered (Toivonen, 2003b). Therefore it may be productive to consider application of a combination of two or more stress tolerance enhancing treatments to achieve optimal levels of resistance (Toivonen, 2005 & 2009). There are several examples in the literature which show the added benefit of applying treatment combinations (Toivonen, 2009).

5.2 Germplasm selection

There have been some reports on the selection of germplasm and cultivars from breeding programs that will have greater postharvest stress resistance and hence better storage capability. Hodges et al. (2001) were able to show that a cultivar which was more susceptible to yellowing was so because of differences in balance of antioxidant systems in the tissues, which resulted in higher accumulations of ROS, particularly hydrogen peroxide. They hypothesized that the higher levels of ROS were directly causal of the yellowing of the chlorophyll in the spinach leaves. A similar relationship was found for a broccoli cultivar resistant to yellowing when compared with a cultivar highly susceptible to yellowing during storage (Toivonen & Sweeney, 1997). Apple cultivars which have resistance to developing browning in response to cutting have greater levels of apoplastic antioxidant enzymes and lower levels of ROS in the apoplast after cutting than cultivars with lower levels of antioxidant enzymes (Toivonen et al., 2003). While measures of antioxidant enzymes and ROS levels can be instructive to understand the basis for difference in stress tolerance in selections of a breeding population, they are too labour intensive to consider for incorporation as selection tools into a breeding program.

In vitro selection is an approach where plant cells of a fruit or vegetable of interest are tissue-cultured and exposed to a stressor, taking surviving cells to regenerate new plants having a superior level of stress resistance (Rai et al., 2011). This approach has been highly successful to regenerate germplasm of many crop plants which can be regenerated via tissue culture techniques. *In vitro* selection is much less expensive approach than molecular engineering and laboratories can easily be set up almost anywhere in the world having access to basic utilities, using inexpensive technology (Rai et al., 2011). The fact that the approach relies on the cells to survive in response to the applied stress means that the complexity of the stress response network is incorporated into the plants regenerated in this way.

5.3 Use of molecular probes for marker - assisted breeding

There are a large number of genes and proteins associated with stress tolerance in plants and so the best approach to identifying stress tolerant lines is apply the stress of interest and perform quantitative trait loci (QTL) analyses (Foolad, 1999). This approach may be used with intact plants and/or harvested plant parts, generally using the plant part which is of interest in the breeding improvement strategy (Foolad, 1999). The approach requires analysis of adaptive changes in QTL expression as opposed to constitutive expression (Collins et al., 2008). A stress protocol, to which target fruit or vegetable will be exposed, must be established to provide clear differentiation between resistant and susceptible lines. However, as stated earlier, the stress response is complex and so success using QTLs will require interdisciplinary effort, integrating biochemistry, gene mapping and phenotyping activities to allow reliable interpretation and successful use of adaptive QTLs for selecting for stress resistance (Collins et al., 2008).

5.4 Molecular engineering

Molecular engineering for stress resistance in fruits and vegetables is limited due to two major factors; 1) the complexity of the stress response network (Toivonen, 2005; Jaspers & Kangasjärvi, 2010) means that modulating the stress resistance with single gene insertions is unlikely, and 2) methods to successfully transform many important fruit and vegetable crops have yet to be developed (Rai et al., 2011). One area where there has been some advance is insertion of anti-freeze genes to protect against low temperature injury (Kole & Hall, 2008). However, the future advances will require a better basic knowledge of the stress response network and control points at the molecular level. This approach may be a helpful adjunct to adaptive QTL analysis, since insertion of a putatively important gene may alter the adaptive QTL profile and provide a probe to better understand the functional changes induced by a stress (Collins et al., 2008).

5.5 Improved postharvest harvest and handling protocols

Most existing postharvest handling and storage procedures are generally not considered to be stress-inducing, except in cases where quality issues arise (Toivonen, 2009). However, there is increasing information in the research literature that suggests that there are significant stresses that could be modulated during the postharvest continuum. It is often difficult to avoid low temperature stress, since most produce is refrigerated as a necessary step to control spoilage and preserve food safety (Toivonen, 2009).

Simple modifications to postharvest handling systems can sometimes result in significant reduction in stress exposure and consequently result in storage and/or shelf life extension. One of the most successful strategies is the application of plastic film packaging or wraps to prevent desiccation, resulting in significant improvements and shelf life and quality of many fruits and vegetables (Ben-Yehoshua and Rodov, 2003). In many cases, modified atmosphere packaging is considered to largely control humidity around product and thus prevent moisture loss of fresh-cut and whole fruits and vegetables (Toivonen et al., 2009). Also, anti-transpiration coatings have been shown to be effective for maintaining quality through control of water loss (Baldwin, 2003). In regards to maintaining water content on the retail shelf, the application of misting systems can 'recharge' the vegetable and in so doing maintain quality over longer durations at less than ideal storage temperatures (Barth et al., 1990; Shibairo et al., 1998).

While rapid cooling is generally recommended to preserve quality, delayed or gradual cooling may be useful to chilling sensitive crops to allow them to acclimatize or adapt to storage and handling conditions. Delays in cooling of apples after harvest can be used to reduce the development of low temperature stress induced disorders in 'Honeycrisp' apples (DeLong et al., 2004). Similarly, delays in cooling can reduce CO₂-induced internal browning in 'Braeburn' apples (Toivonen et al., 2003). Recently, slow cooling at a rate of 2 °C per day from 12 °C to 4 °C of tomatoes has shown promise to reduce chilling injury when stored at the lower temperature (Gálvez et al., 2010).

6. Conclusions

Abiotic stresses are significant determinants of quality and nutritional value of fruits and vegetables during harvest, handling, storage and distribution to consumer. Crop management can have a significant influence on susceptibility to stress. In addition, climate change has created additional environmental variables which may influence postharvest

stress susceptibility of fruits and vegetables. While breeding is underway for many crops to develop stress resistance that will allow them to adapt to climate change, it is not clear that breeding for stress resistance in the field will also extend stress resistance characteristics to the harvested portion. It is important understand the basis of molecular and biochemical response networks to various stresses encountered in the field and in the postharvest continuum to better evaluate the benefits that abiotic stress during production may yield for postharvest abiotic stresses.

The focus of effort should probably be on use of breeding or directed breeding to enhance stress tolerance in fruits and vegetables, as opposed to genetic engineering. This is because stress response networks are extremely complex and, as such, specific target transformations may be insufficient to confer significant increase in stress tolerance. An important aspect of the breeding and selection approach is that there must be stressors applied in reproducible ways to allow the breeder to identify expression of stress resistance since that characteristic is adaptive, rather than constitutive, in nature. The researcher must determine whether the adaptive stress response is best tested in the field, greenhouse or test tube.

In the context of postharvest handling treatments, there is some indication that such approaches may benefit in enhancing tolerance and thereby extending shelf and nutritional life of fruits and vegetables. However, again there is a limited amount of basic understanding to help guide the development of approaches to reliably confer useful levels of stress tolerance to stresses in general, and, more importantly, to specific stresses that a product is known to be subjected to during its normal distribution.

7. References

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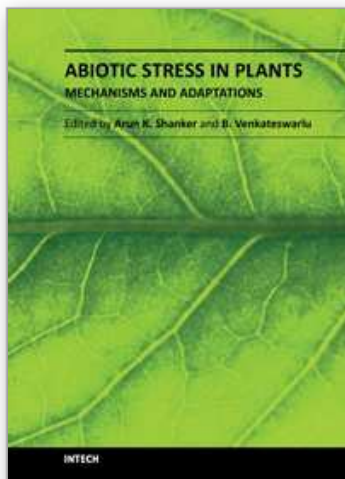
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World population is growing at an alarming rate and is anticipated to reach about six billion by the end of year 2050. On the other hand, agricultural productivity is not increasing at a required rate to keep up with the food demand. The reasons for this are water shortages, depleting soil fertility and mainly various abiotic stresses. The fast pace at which developments and novel findings that are recently taking place in the cutting edge areas of molecular biology and basic genetics, have reinforced and augmented the efficiency of science outputs in dealing with plant abiotic stresses. In depth understanding of the stresses and their effects on plants is of paramount importance to evolve effective strategies to counter them. This book is broadly divided into sections on the stresses, their mechanisms and tolerance, genetics and adaptation, and focuses on the mechanic aspects in addition to touching some adaptation features. The chief objective of the book hence is to deliver state of the art information for comprehending the nature of abiotic stress in plants. We attempted here to present a judicious mixture of outlooks in order to interest workers in all areas of plant sciences.

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