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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 O\textsubscript{2} and high CO\textsubscript{2}

Managing postharvest handling and storage atmospheres to avoid low O\textsubscript{2} or high CO\textsubscript{2} 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 O\textsubscript{2} 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 (Blokhina et al., 2001, 2003). Different fruits and vegetables have varying thresholds for low O\textsubscript{2} stress, dependent on anatomy, temperature, physiological age, presence of supplemental gases (e.g. CO\textsubscript{2}, CO, SO\textsubscript{2}, C\textsubscript{2}H\textsubscript{4}) and duration of exposure (Kader and Saltveit, 2003; Kanellis et al., 2009).

Threshold limits for low O\textsubscript{2} 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 CO\textsubscript{2} levels in postharvest handling is to competitively inhibit ethylene binding and action hence delaying ripening in climacteric fruits (Kanellis at al., 2009). High CO\textsubscript{2} 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 CO\textsubscript{2} 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 CO\textsubscript{2} 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 50-100 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
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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 (Blokhina 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 (Blokhina 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 (Ferrerers 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). Abscisic 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 higher 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 orders 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

Baldwin, E.A. (2003). Coating and Other Supplemental Treatments to Maintain Vegetable Quality. In: Postharvest Physiology and Pathology of Vegetables, 2nd Edition, J.A. Bartz & J. K. Brecht (Eds.), 413-456, Marcel Dekker, Inc, ISBN 0-8247-0687-0, New York

Barden, C.L. & Bramlage, W.J. (1994). Separating the Effects of Low Temperature, Ripening, and Light on Loss of Scald Susceptibility in Apples Before Harvest. Journal of the American Society for Horticultural Science, Vol. 119, No. 1 (February 1994), pp. 54-58, ISSN 0003-1062

Barth, M.M.; Perry, A.K.; Schmidt, S.J. & Klein, B.P. (1990). Misting Effects on Ascorbic Acid Retention in Broccoli During Cabinet Display. Journal of Food Science, Vol. 55, No. 4 (July 1990), pp. 1187-1188, ISSN 1365-2621

Ben-Yehoshua, S. & Rodov, V. (2003). Transpiration and Water Stress. In: Postharvest Physiology and Pathology of Vegetables, 2nd Edition, J.A. Bartz & J. K. Brecht (Eds.), 111-159, Marcel Dekker, Inc, ISBN 0-8247-0687-0, New York

Berard, L.S. (1990). Effect of Nitrogen Fertilization on Stored Cabbage. I. Development of Physiological Disorders on Tolerant and Susceptible Cultivars. Journal of Horticultural Science, Vol. 65, No. 3 (May 1990), pp.289-296, ISSN 1462-0316

Berard, L.S.; Senecal, M. & Vigier, B. (1990). Effects of Nitrogen Fertilization on Stored Cabbage. II. Mineral Composition in Midrib and Head Tissues of Two Cultivars. Journal of Horticultural Science, Vol. 65, No. 4 (July 1990), pp.289-296, ISSN 1462-0316

Biemelt, S.; Keetman, U. & Albrecht, G. (1998). Re-Aeration Following Hypoxia or Anoxia Leads to Activation of Antioxidant Defense System in Roots of Wheat Seedlings. Plant Physiology, Vol. 116, No. 2 (February 1998), pp. 651-658, ISSN 0032-0889
Blankenship, S.M. & Dole, J.M. (2003). 1-Methylcyclopropene: A Review. *Postharvest Biology and Technology*, Vol. 28, No. 1 (April 2003), pp. 1-25, ISSN 0925-5214

Blokhina, O.B.; Chirkova, T.V. & Fagerstedt, K.V. (2001). Anoxic Stress Leads to Hydrogen Peroxide Formation in Plant Cells. *Journal of Experimental Botany*, Vol. 52, No. 359 (June 2001), pp. 1179-1190, ISSN 0022-0957

Blokhina, O.; Virolainen, E. & Fagerstedt, K.V. (2003). Antioxidants, Oxidative Injury and Oxygen Deprivation Stress: a Review. *Annals of Botany*, Vol. 91, No. 2 (January 2003), pp. 179-194, ISSN 0305-7364

Bowler, C. & Fluhr, R. (2000) The Role of Calcium and Activated Oxygens as Signals for Controlling Cross-Tolerance. *Trends in Plant Science*, Vol. 5, No. 6 (June 2000), pp. 241-246, ISSN 1360-1385

Bramlage, W.J. & Weis, S.A. (1997). Effects of Temperature, Light and Rainfall on Superficial Scald Susceptibility in Apples. *HortScience*, Vol. 32, No. 5 (August 1997), pp. 808-811, ISSN 0018-5345

Burdon, J.N.; Dori, S.; Lomaniec, E.; Marinansky, R. & Pesis, E. (1994). The Post-harvest Ripening of Water Stressed Banana Fruits. *Journal of Horticultural Science*, Vol. 69, No. 5 (September 1994), pp. 799-804, ISSN 1462-0316

Burton, W.G. (1982). *Postharvest Physiology of Food Crops*. Longman Group Ltd, ISBN0-582-46038-7, London.

Chin, H.-W.; Lindsay, R.C. (1993). Volatile Sulfur Compounds Formed in Disrupted Tissues of Different Cabbage Cultivars. *Journal of Food Science*, Vol. 58, No. 4 (July 1993), pp. 835-830, 841, ISSN 1750-3841

Collins, N.C.; Tardieu, F. & Tuberosa, R. (2008). Quantitative Trait Loci and Crop Performance under Abiotic Stress: Where Do We Stand? *Plant Physiology*, Vol.147, No. 2 (June 2008), pp. 469-486, ISSN 0032-0889

Collins, G.G.; Nie, X.L. & Slatveit, M.E. (1995) . Heat Shock Protein and Chilling Injury of Mung Bean Hypocotyls. *Journal of Experimental Botany*, Vol. 46, No. 7 (July 1995), pp. 795-802, ISSN 0022-0957

Crisosto, C.H.; Johnson, R.S.; Luza, J.G. & Crisosto, G.M. (1994). Irrigation Regimes Affect Fruit Soluble Solids Concentration and Rate of Water Loss of ‘O’Henry’ Peaches. *HortScience*, Vol. 29, No. 10 (October 1994), pp. 1169-1171, ISSN 0018-5345

Davis, W.B. (1926). Physiological Investigation of Black Heart of Potato Tuber. *Botanical Gazette*, Vol. 81, No. 3 (May 1926), pp. 323-338, ISSN 0006-8071

Dean, B. & Kolattukudy, P.E. (1976). Synthesis of Suberin During Wound-Healing in Jade Leaves, Tomato Fruit, and Bean Pods. *Plant Physiology*, Vol. 58, No. 3 (September 1976), pp. 411-416, ISSN 0032-0889

Delaquis, P.J.; Stewart, S.; Cliff, M.; Toivonen, P.M. & Moys, A.L. (2000). Sensory quality of Ready-to-Eat Lettuce Washed in Warm, Chlorinated Water. *Journal of Food Quality*, Vol. 23, No. 6 (December 2000), pp. 553-563, ISSN 1745-4557.

DeLong, J. M.; Prange, R.K. & Harrison, P.A. (2004). The Influence of Pre-Storage Delayed Cooling on Quality and Disorder Incidence in ‘Honeycrisp’ Apple Fruit. *Postharvest Biology and Technology*, Vol. 34, No. 3 (December 2004), pp. 353-358, ISSN 0925-5214 (Erratum Version)

East, A.R.; Tanner, D.J.; Maguire, K.M. & Mawson, A.J. (2008). The Influence of Breaks in Storage Temperature on ‘Cripps Pink’ (Pink Lady™) Apple Physiology and Quality. *HortScience*, Vol. 43, No. 3 (June 2008), pp. 818-824, ISSN 0018-5345
Abiotic Stress in Harvested Fruits and Vegetables

Fan, X.; Toivonen, P.M.A.; Rajkowski, K.T. & Sokorai, K.B. (2003). Warm Water Treatment in Combination with Modified Atmosphere Packaging Reduces Undesirable Effects of Irradiation on the Quality of Fresh-Cut Iceberg Lettuce. *Journal of Agricultural and Food Chemistry*, Vol. 51, No. 5 (January 2003), pp. 1231-1236, ISSN 0021-8561

Ferguson, I.B.; Volz, R. & Woolf, A. (1999) Preharvest Factors Affecting Physiological Disorders of Fruit. *Postharvest Biology and Technology*, Vol.15, No. 3 (March 1999), pp. 255-262, ISSN 0925-5214

Ferreres, F.; Gil, M.I.; Casteñer, M. & Tomás-Barberán, F.A. (1997). Phenolic Metabolites in Red Pigmented Lettuce (*Lactuca sativa*). Changes with Minimal Processing and Cold Storage. *Journal of Agricultural and Food Chemistry*, Vol. 45, No. 11(November 1997), pp. 4249-4254, ISSN 1520-5118

Foolad, M.R. (1999). Genetics of Salt Quantitative and Cold Analysis Tolerance in Tomato: and QTL Mapping. *Plant Biotechnology*, Vol. 16, No. 1 (March 1999), pp. 55-64, ISSN 0289-5770

Fukumoto, L.R.; Toivonen, P.M.A. & Delaquis, P.J. (2002). Effect of Wash Water Temperature and Chlorination on Phenolic Metabolism and Browning of Stored Iceberg Lettuce Photosynthetic and Vascular Tissues. *Journal of Agricultural and Food Chemistry*, Vol. 50, No. 16 (June 2002), pp. 4503-4511, ISSN 0021-8561

Gálvez, A.B.; García, M.V.; Corrales, J.C.; López, A.C. & Valenzuela, J.A.L. (2010). Effect of Gradual Cooling Storage on Chilling Injury and Phenylalanine-Lyase Activity in Tomato Fruit. *Journal of Food Biochemistry*, Vol. 34, No. 2 (April 2010), pp. 295-307, ISSN 1745-4514

Gong, Y.; Toivonen, P.M.A.; Lau, O.L. & Wiersma, P.A. (2000). Response of Anaerobic Metabolism to Delaying Controlled Atmosphere Storage in Braeburn Apples. *HortScience*, Vol. 35, No. 3 (June 2000), pp. 411, ISSN 0018-5345

Gruda, N. (2005). Impact of Environmental Factors on Product Quality of Greenhouse Vegetables for Fresh Consumption. *Critical Reviews in Plant Sciences*, Vol. 24, No. 3, pp. 227-247, ISSN 0735-2689

Hall, C.B. (1964). The Effect pf Short Periods pf High Temperature pn the Ripening pf Detached Tomato Fruits. *Proceedings of the American Society for Horticultural Science*, Vol. 84, pp. 501-506.

Hamouz, K.; Bečka, D. & Morava, J. (March 2011). Effect of Environmental Conditions on the Susceptibility to Mechanical Damage of Potatoes. In: *Agris On-Line Papers in Economics and Informatics*. 30.03.2011. Available from http://www.aagraria.cz/yhledavac/detail.php?id=116921&iSub=518&sHighLight=a gria&PHPSESSID=997764de5509230f23dc06268b7b8344

Hanhijärvi, A.M. & Fagerstedt, K.V. (1994). Comparison of Effect of Natural and Experimental Anoxia on Carbohydrate and Energy Metabolism in *Iris pseudocorus* rhizomes. *Physiologia Plantarum*, Vol. 90, No. 3 (March 1994), pp. 437-444, ISSN 1399-3054

Hodges, D.M. (2003). *Postharvest Oxidative Stress in Horticultural Crops*, Food Products Press, ISBN 1-56022-962-4, New York, USA

Hodges, D.M.; Lester, G.E.; Munro, K.D. & Toivonen, P.M.A. (2005). Oxidative stress: Importance for Postharvest Quality. *HortScience*, Vol. 39, No. 5 (August 2005), pp. 924-929, ISSN 0018-5345

Hodges, D.M.; Wismer, W.V. & Forney, C.F. (2001). Antioxidant Responses in Leaves of Two Cultivars of Spinach (*Spinacia oleracea* L.) Differing in Their Senescence Rates.
Hoffman, J.C. (1967). Morphological Variations of Snap Bean Pods Associated with Weight Loss and Wilting. *Proceedings of the American Society of Horticultural Science*, Vol. 91, pp. 294-303

Horneburg, B. & Wirsing, F. (1995). The Tendency of Potato Tubers to Black Spot. 2. Influence of Fertilizer Application and Irrigation on the Expression of Black Spot. *Kartoffelbau*, Vol. 46, No. 8 (August 1995), pp. 318-320, ISSN 0022-9156

Inari, T.; Yamauhi, R.; Kato, K. & Takeuchi, T. (2002). Changes in Pectic Polysaccharides during the Ripening of Cherry Tomato Fruits. *Food Science and Technology Research*, Vol. 8, No. 1 (March 2002), pp. 55-58, ISSN 1344-6606

Ioannidi, E.; Kalamaki, M.S.; Engineer, C.; Pateraki, I.; Alexandrou, D.; Mellidou, I.; Giovannoni, J. & Kanellis, A.K. (2009). Expression Profiling of Ascorbic Acid-Related Genes During Tomato Fruit Development and Ripening and in Response to Stress Conditions. *Journal of Experimental Botany*, Vol. 60, No. 2 (February 2009), pp. 663-678, ISSN 1460-2431

Jaspers, P. & Kangasjärvi, J. (2010). Reactive Oxygen Species in Abiotic Stress Signalling. *Physiologia Plantarum*, Vol. 138, No. 4 (April, 2010), pp. 405-413, ISSN 0031-9317

Kader, A.A. (2002). Postharvest Biology and Technology: An Overview. In: *Postharvest Technology of Horticultural Crops*, A.A. Kader (Ed.), 39-47, University of California Agriculture and Natural Resources Communications Services, ISBN 1-879906-51-1, Oakland, CA

Kader, A.A. & Saltveit, M.E. (2003). Atmosphere Modification. In: *Postharvest Physiology and Pathology of Vegetables, 2nd Edition*, J.A. Bartz & J. K. Brecht (Eds.), 229-246, Marcel Dekker, Inc, ISBN 0-8247-0687-0, New York

Kanellis, A.K.; Tonutti, P. & Perata, P. (2009). Biochemical and Molecular Aspects of Modified and Controlled Atmospheres. In: *Modified and Controlled Atmospheres for Storage, Transportation and Packaging of Horticultural Commodities*, E. Yahia (Ed), 553-567. CRC Press, ISBN 978-1-4200-6957-0, Boca Raton, FL.

Ke, D. & Saltveit, M.E. (1989). Wound-Induced Ethylene Production, Phenolic Production and Susceptibility to Russet Spotting in Iceberg Lettuce. *Physiologia Plantarum*, Vol. 76, No. 3 (July 1989), pp. 412-418, ISSN 1399-3054

Kende, H. & Boller, T. (1981). Wound Ethylene and 1-Aminocyclopropane-1-Carboxylate Synthase in Ripening Tomato Fruit. *Planta*, Vol. 151, No. 5 (May 1981), pp. 476-481, ISSN 0032-0935

Kilili, A.W.; Behboudian, M.H. & Mills, T.M. (1996). Postharvest Performance of ‘Braeburn’ Apples in Relation to Withholding of Irrigation at Different Stages of the Growing Season. *Journal of Horticultural Science*, Vol. 71, No. 5 (September 1996), pp. 693-701, ISSN 1462-0316

Kole, C. & Hall, T.C. (2008). *Compendium of Transgenic Crop Plants: Transgenic Temperate Fruit and Nuts*. Blackwell Publishing Ltd, ISBN 978-1-405-16924-0, Hoboken, NJ, USA

Kubo, Y.; Inaba, A. and Nakamura, R. (1990) Respiration and C3H4 Production in Various Harvested Crops Held in CO2-Enriched Atmospheres. *Journal of the American Society for Horticultural Science*, Vol. 115, No. 6 (November 1990), pp. 975-978, ISSN 0003-1062

Kubo, Y.; Xue Y.B.; Nakatsuka, A.; Mathooko, F. M.; Inaba, A.; Nakamura, R. (2000). Expression of a Water Stress-Induced Polygalacturonase Gene in Harvested...
Abiotic Stress in Harvested Fruits and Vegetables

Cucumber Fruit. *Journal of the Japanese Society for Horticultural Science*, Vol. 69, No. 3 (September 2000), pp. 273-279, ISSN 0013-7626

Lafuente, M.T.; López-Gálvez, G.; Cantwell, M. & Yang, S.F. (1996). Factors Influencing Ethylene-Induced Isocoumarin Formation and Increased Respiration in Carrots. *Journal of the American Society for Horticultural Science*, Vol. 121, No. 3 (May 1996), pp. 537-542, ISSN 0003-1062

Léchaudel, M. & Joas, J. (2007). An Overview of Preharvest Factors Influencing Mango Fruit Growth, Quality and Postharvest Behaviour. *Brazilian Journal of Plant Physiology*, Vol. 19, No. 4 (October-December 2007), pp.287-298, ISSN 1677-0420

Lesham, Y.Y. & Kuiper, P.J.C. (1996) Is There a GAS (General Adaptation Syndrome) Response to Various Types of Environmental Stress? *Biologia Plantarum*, Vol. 38, No. 1 (March 1996), pp. 1-18, ISSN 0006-3134

Lopez, G.; Larrigaudière, C.; Girona, J.; Behboudian, M.H. & Marsal, J. (2011). Fruit Thinning in ‘Conference’ Pear Grown Under Deficit Irrigation: Implications for Fruit Quality at Harvest and After Cold Storage. * Scientia Horticulturae*, Vol. 129, No. 1 (May 2011), pp. 64-70, ISSN 0304-4238

Lurie, S.; Shapiro, B. & Ben-Yehoshua, S. (1986). Effects of Water Stress and Degree of Ripeness on Rate of Senescence of Harvested Bell Pepper Fruit. *Journal of the American Society for Horticultural Science*, Vol. 111, No. 6 (December 1986), pp. 880-885, ISSN 0003-1062

Lurie, S. (1998). Postharvest Heat Treatments of Horticultural Crops: Commodity Responses. *Postharvest Biology and Technology*, Vol.14, No. 3 (November 1998), pp. 257-269, ISSN 0925-5214

MacLeod, R.F.; Kader, A.A. & Morris, L.L. (1976). Stimulation of Ethylene and CO₂ Production of Mature-Green Tomatoes by Impact Bruising. *HortScience*, Vol. 11, No. 6 (December 1976), pp. 604-606, ISSN 0018-5345

Maier, N.A.; Dahlenburg, A.P. & Frensharn, A.B. (1986). Potassium Nutrition of Irrigated Potatoes in South Australia. 3. Effect on Specific gravity, Size and Internal Bruising of Tubers. *Australian Journal of Experimental Agriculture*, Vol. 26, No. 6 (November/December 1986), pp. 737-744, ISSN 1836-0939

Mathooko, F.M.; Inaba, A. & and Nakamura, R. (1998). Characterization of Carbon Dioxide Stress-Induced Ethylene Biosynthesis in Cucumber (*Cucumis sativus* L.) Fruit. *Plant and Cell Physiology*, Vol. 39, No. 3 (March 1998), pp. 285-293, ISSN 0032-0781

Maul, F.; Sargent, S.A.; Sims, C.A.; Baldwin, E.A.; Balaban, M.O. & Huber, D.J. (2000). Recommended Storage Temperatures Affect Tomato Flavor and Aroma Quality. *Journal of Food Science*, Vol. 65, No. 7 (October 2000), pp. 1228-1237, ISSN 1750-3841

McDonald, R.E.; McCollum, T.G. & Baldwin, E.A. (1996). Prestorage Heat Treatments Influence Free Sterols and Flavor Volatiles of Tomatoes Stored at Chilling Temperature. *Journal of the American Society for Horticultural Science*, Vol. 12s, No. 3 (May 1996), pp. 531-536, ISSN 0003-1062

McGarry, A.; Hole, C.C.; Drew, R.L.K. & Parsons, N. (1996). Internal Damage in Potato Tubers: A Critical Review. *Postharvest Biology and Technology*, Vol. 8, No. 4 (September 1996), pp. 239-258, ISSN 0925-5214

Meheriuk, M.; Prange, R.K.; Lidster, P.D. & Porritt, S.W. (1994). *Postharvest Disorders of Apples and Pears*. Agriculture Canada, ISBN 0-662-21237-1, Ottawa, Canada

Meir, S.; Philosoph-Hadas, S.; Lurie, S.; Droby, S.; Akerman, M.; Zauberman, G.; Shapiro, B.; Cohen, E. & Fuchs, Y. (1996). Reduction of Chilling Injury in Stored Avocado,
Grapefruit, and Bell Peppers by Methyl Jasmonate. *Canadian Journal of Botany*, Vol. 74, No. 6 (June, 1996), pp. 870-874, ISSN 1916-2790

Miller, A.R. (2003). Harvest and Handling Injury: Physiology, Biochemistry, and Detection, In: *Postharvest Physiology and Pathology of Vegetables, 2nd Edition*, J.A. Bartz & J. K. Brecht (Eds.), 177-208, Marcel Dekker, Inc, ISBN 0-8247-0687-0, New York

Mittler, R. (2002). Oxidative Stress, Antioxidants and Stress Tolerance. *TRENDS in Plant Science*, Vol. 7, No. 9 (September 2002), pp. 405-410, ISSN 1360-1385

Mizrahi, Y. (1982). Effect of Salinity on Tomato Fruit Ripening. *Plant Physiology*, Vol. 69, No. 4 (April 1982), pp. 966-970, ISSN 0032-0889

Mizrahi, Y.; Taleisnik, E.; Kagan-Zur, V.; Zohar, Y.; Offenbach, R.; Matan, E. & Golan, R. (1988). A Saline Irrigation Regime for Improving Tomato Fruit Quality Without Reducing Yield. *Journal of the American Society for Horticultural Science*, Vol. 113, No. 2 (April 1988), pp. 202-205, ISSN 0003-1062

Morris, L.L. (1954). Field and Transit Chilling of Fall-Grown Tomatoes. In: *Proceedings of the Conference on Transportation of Perishables*, 101-105, University of California, Davis, CA, USA.

Nilo, R.; Saffie, C.; Lilley, K.; Baeza-Yates, R.; Cambiazo, V.; Campos-Vargas, R.; González, M.; Meisel, L.A.; Retamales, J.; Silva, H; Orellana, A. (2010). Proteomic Analysis of Peach Fruit Mesocarp Softening and Chilling Injury Using Difference Gel Electrophoresis (DIGE). *BMC Genomics*, Vol. 11, No. 43 (January 2010), ISSN 1471-2164

Noctor, G. & Foyer, C.H. (1998). Ascorbate and Glutathione: Keeping Active Oxygen Under Control. *Annual Review of Plant Physiology and Plant Molecular Biology*, Vol. 49, (June 1998), pp. 249–279, ISSN 0601-0249

Obenland, D.M.; Vensel, W.H. & Hurkman, W.J. (2008). Alterations in Protein Expression Associated with the Development of Mealiness in Peaches. *Journal of Horticultural Science & Biotechnology*, Vol. 83, No. 1 (January 2008), pp. 85–93, ISSN 1462-0316

Pignocchi, C. & Foyer, C.H. (2003). Apoplastic Ascorbate Metabolism and Its Role in the Regulation of Cell Signalling. *Current Opinion in Plant Biology*, Vol. 6, No. 4 (August 2003), pp. 379-389, ISSN 1369-5266

Purvis, A.C. (1997) The Role of Adaptive Enzymes in Carbohydrate Oxidation by Stressed and Senescing Plant Tissues. *HortScience*, Vol. 32, No. 7 (December 1997), pp. 1165-1168, ISSN 0018-5345

Rai, M.K.; Kalia, R.K.; Singh, R.; Gangola, M.P. & Dhawana, A.K. (2011). Developing Stress Tolerant Plants Through In Vitro Selection - An Overview of the Recent Progress. *Environmental and Experimental Botany*, Vol. 71, No. (2011), pp. 89–98, ISSN

Saltveit, M.E. (1991). Prior Temperature Exposure Affects Subsequent Chilling Sensitivity. *Physiologia Plantarum*, Vol. 82, No. 4 (August 1991), pp. 529-536, ISSN 1399-3054

Saltveit, M.E. (2003). Temperature Extremes, In: *Postharvest Physiology and Pathology of Vegetables, 2nd Edition*, J.A. Bartz & J. K. Brecht (Eds.), 457-483, Marcel Dekker, Inc, ISBN 0-8247-0687-0, New York

Saltveit, M.E. & Morris, L.L. (1990). Overview of Chilling Injury of Horticultural Crops. In: *Chilling Injury of Horticultural Crops*, C.Y. Wang (Ed.), 3-15, CRC Press, ISBN 0-8493-5736-5, Boca Raton, FL, USA

Sams, C.E. & Conway, W.S. (2003). Preharvest Nutritional Factors Affecting Postharvest Physiology, In: *Postharvest Physiology and Pathology of Vegetables, 2nd Edition*, J.A.
Bartz & J. K. Brecht (Eds.), 161-176, Marcel Dekker, Inc, ISBN 0-8247-0687-0, New York

Sabehat, A.; Weiss, D. & Lurie, S. (1996). The Correlation Between Heat-Shock Protein Accumulation and Persistence and Chilling Tolerance in Tomato Fruit. *Plant Physiology*, Vol. 110, No. 2 (February 1996), pp. 531-537, ISSN 0032-0889

Shibairo, S.I.; Upadhyaya, M.K. & Toivonen, P.M.A. (1997). Postharvest Moisture Loss Characteristics of Carrot (*Daucus carota* L.) Cultivars During Short-Term Storage. *Scientia Horticulturae*, Vol. 71, No. 1-2 (November 1997), pp. 1-12, ISSN 0304-4238

Shibairo, S.I.; Upadhyaya, M.K. & Toivonen, P.M.A. (1998a). Replacement of Postharvest Moisture Loss by Recharging and its Effect on Subsequent Moisture Loss During Short-Term Storage of Carrots. *Journal of the American Society for Horticultural Science*, Vol. 123, No. 1 (January 1998), pp. 141-145, ISSN 0003-1062

Shibairo, S.I.; Upadhyaya, M.K. & Toivonen. P.M.A. (1998b). Influence of Preharvest Water Stress on Postharvest Moisture Loss of Carrots (*Daucus carota* L.). *Journal of Horticultural Science and Biotechnology*, Vol. 73, No. 3 (May 1998), pp. 347-352, ISSN 1462-0316

Shibairo, S.I.; Upadhyaya, M.K. & Toivonen, P.M.A. (1998c). Potassium Nutrition and Postharvest Moisture Loss in Carrots (*Daucus carota* L.) *Journal of Horticultural Science and Biotechnology*, Vol. 73, No. 6 (November 1998), pp. 862-866, ISSN 1462-0316

Shibairo, S.I.; Upadhyaya, M.K. & Toivonen, P.M.A. (2002). Changes in Water Potential, Osmotic Potential, and Tissue Electrolyte Leakage During Mass Loss in Carrots Stored Under Different Conditions. *Scientia Horticulturae*, Vol. 95, No. 1-2 (August 2002), pp.13-21, ISSN 0304-4238

Stevens, L.H. & Davelaar, E. (1997). Biochemical Potential of Potato Tubers To Synthesize Blackspot Pigments in Relation to Their Actual Blackspot Susceptibility. *Journal of Agricultural and Food Chemistry*, Vol. 45, No. 11 (November, 1997), pp. 4221-4226, ISSN 0021-8561

Toivonen, P.M.A. (2003a). Effects of Storage Conditions and Postharvest Procedures on Oxidative Stress in Fruits and Vegetables. In: *Postharvest Oxidative Stress in Horticultural Crops*, D.M. Hodges (Ed.), 69-90, Food Products Press, ISBN 1-56022-962-4, New York

Toivonen, P.M.A. (2003b). Postharvest Treatments to Control Oxidative Stress in Fruits and Vegetables. In: *Postharvest Oxidative Stress in Horticultural Crops*, D.M. Hodges, (Ed.), 225-246. Food Products Press, ISBN 1-56022-962-4, New York

Toivonen, P.M.A. (2005). Postharvest Storage Procedures and Oxidative Stress. *HortScience*, Vol. 39, No. 5 (August 2005), pp. 938-942, ISSN 0018-5345

Toivonen, P.M.A. (2009). Benefits of Combined Treatment Approaches to Maintaining Fruit and Vegetable Quality. *Fresh Produce*, Vol. 3, No. 1 (December 2009), pp. 58-64, ISSN 1749-4788

Toivonen, P.M.A. (2010). Postharvest Physiology of Vegetables, In: *Handbook of Vegetables and Vegetable Processing*, Y.H. Hui, N. Sinha, J. Ahmed, E.O. Evranuz and M. Siddiq (Eds.), 199-220, Wiley-Blackwell Publishing, ISBN 978-0-8138-1541-1, Ames, IA

Toivonen, P.M.A. & Beveridge, T.H.J. (2005). Maturity, Ripening and Quality Relationships. In: *Produce Degradation: Pathways and Prevention*. O. Lamikanra, S.H. Imam & D.O. Ukuku (Eds.), 55-77. CRC Press, ISBN 0-8493-1902-1, Boca Raton, FL
Toivonen, P.M.A.; Brandenburg, J.S. & Luo, Y. (2009) Modified Atmosphere Packaging for Fresh-cut Produce. In: Modified and Controlled Atmospheres for Storage, Transportation and Packaging of Horticultural Commodities, E. Yahia (Ed), 463-489. CRC Press, ISBN 978-1-4200-6957-0, Boca Raton, FL

Toivonen, P.M.A. & DeEll, J.R. (2002). Physiology of Fresh-Cut Fruits and Vegetables, In: Fresh-Cut Fruits and Vegetables: Science, Technology, and Market, O. Lamikanra, (Ed.), 91-123, CRC Press, ISBN 1-58716-030-7, Boca Raton, FL

Toivonen, P.M.A.; Hampson, C. & Stan, S. (2005). Apoplastic Levels of Hydroxyl Radicals in Four Different Apple Cultivars are Associated with Severity of Cut-Edge Browning. Acta Horticulturae, Vol. 682, (June 2005), pp. 1819-1824, ISSN 0567-7572

Toivonen, P.M.A.; Hampson, C.; Neilsen, D.; Neilsen, G. & Stan, S. (2003). Relationship of Antioxidant Protection Systems to Browning or Flesh Browning-Related Disorders of Different Cultivars of Apples (Malus x domestica) and in Response to Phosphorus and Calcium Nutrition. HortScience, Vol. 38, No. 3 (June 2003), pp. 798, ISSN 0018-5345

Toivonen, P.M.A. & Sweeney, M. (1997). Differences in Chlorophyll Loss at 13°C for Two Broccoli (Brassica oleracea L.) Cultivars Associated With Antioxidant Enzyme Activities. Journal of Agricultural and Food Chemistry, Vol. 46, No. 1 (January 1997), pp. 20-24, ISSN 1520-5118

Van linden, V.; Ndaka Sila D.; Duvetter, T.; De Baerdemaeker , J. & Hendrickx, M. (2008). Effect of Mechanical Impact-Bruising on Polygalacturonase and Pectinmethylesterase Activity and Pectic Cell Wall Components in Tomato Fruit. Postharvest Biology and Technology, Vol. 47, No. 1(January 2008), pp. 98–106, ISSN 0925-5214

Veličković, M. (1994). The Influence of Irrigation of Fruit Weight Change of Some Major Cultivars During Refrigerated Storage. Review of Research Work at the Faculty of Agriculture, Belgrade. Vol. 39, No. 1, pp. 139-143, ISSN 0522-8530

Wang, C.Y. (1993) Approaches to Reducing Chilling Injury of Fruits and Vegetables. Horticultural Reviews, Vol. 15, pp. 63-95, ISSN 0163-7851

Wang, C.Y. (1994). Reduction of Chilling by Methyl Jasmonate. Acta Horticulturae, Vol. 368, pp. 901-907, ISSN 0567-7572

Wang, C.Y. & Adams, D.O. (1982). Chilling-Induced Ethylene Production in Cucumbers (Cucumis sativus L.). Plant Physiology, Vol. 69, No. 2 (February 1982), pp. 424-427, ISSN 0032-0889

Wang, W.; Vinocur, B.; Shoseyov, O. & Altman, A. (2004). Role of Plant Heat-Shock Proteins and Molecular Chaperones in the Abiotic Stress Response. Trends in Plant Science, Vol. 9, No. 5 (May 2004), pp. 244-252, ISSN 1360-1385

Witkowska, I. & Woltering, E.J. (2010) Pre-Harvest Light Intensity Affects Shelf-Life of Fresh-Cut Lettuce. Acta Horticulturae, Vol. 877, pp. 223-227, ISSN 0567-7572

Whitmore, J.S. (2000). Drought Management on Farmland, Kluwer Academic Publishers, ISBN 0-7923-5998-4, Dordrecht, The Netherlands

Wu, C.-M. & Liou, S.-E. (1986). Effect of Tissue Disruption on Volatile Constituents of Bell Peppers. Journal of Agricultural and Food Chemistry, Vol. 34, No. 4 (July 1986), pp. 770-772, ISSN 1520-5118

Yano, M.; Saijo, R. & Ota, Y. (1986). Inhibition of Browning and Ethylene Production in Shredded Cabbage by Isothiocyanates. Journal of the Japanese Society for Horticultural Science, Vol. 55, No. 2 (June 1986), pp. 194-198, ISSN 1882-3351
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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