ELSEVIER

Postharvest Biology and Technology 21 (2000) 7–20

Postharvest Biology and Technology

www.elsevier.com/locate/postharvbio

Postharvest responses to high fruit temperatures in the field

A.B. Woolf *, I.B. Ferguson

HortResearch, Private Bag 92169, Auckland, New Zealand

Received 10 June 2000; accepted 21 August 2000

Abstract

The impact on postharvest responses, of preharvest exposure of fruit and vegetables to direct sunlight, with associated high tissue temperatures, is reviewed. Fruit and vegetable flesh temperatures well above 40°C have been recorded in direct sunlight in a wide range of crops in both hot and temperate climates. These high temperatures, both in terms of diurnal fluctuations and long-term exposure, can result in differences in internal quality properties such as sugar contents, tissue firmness, and oil levels, as well as in mineral content differences. Fruit with different temperature histories will also respond differently to postharvest low temperatures and heat treatments used for insect disinfestation. For example, avocado fruit from exposed sites on a tree have less chilling injury, whereas more chilling damage is found in exposed tissues of citrus and persimmons. Mechanisms of high temperature effects on postharvest responses are discussed, including the role of heat shock proteins, membrane damage, and skin characteristics. Differences in exposure of fruit on the tree may be responsible for much of the wide variation commonly found in fruit with regard to at-harvest quality, ripening and postharvest behaviour. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Field heat; Fruit; Heat treatments; Chilling injury; Sun exposure; Heat shock; Postharvest quality

1. Introduction

Postharvest heat treatments can modify postharvest responses of fruit and vegetables, and serve as quarantine treatments (Lurie, 1998). If these heat treatments are effective, then can high temperatures experienced by fruit on the tree prior to harvest have a similar postharvest effect? This question has led to a re-examination of the effects of high preharvest flesh temperatures of the fruit on a range of postharvest quality properties and processes. For example, there may be a protective action of preharvest high temperatures in increasing tolerance of fruit to both low and high temperature postharvest treatments (reduced chilling and heat injury). As early as the middle of last century, a number of researchers showed that high fruit flesh temperatures occur in the field (e.g. Hopp, 1947; Schroeder and Kay, 1961; Schroeder, 1965). They even postulated that these temperatures may have important implications for postharvest responses such as induced thermotolerance (Schroeder, 1965). However, these possible implications have not often been investigated.

---

* Corresponding author: Tel.: + 64-9-8154200 fax: + 64-9-8154202.

E-mail address: awoolf@hort.cri.nz (A.B. Woolf).

PII: S0925-5214(00)00161-7

Along with the effects of high preharvest fruit temperatures on postharvest temperature responses, we aim to bring together other sun exposure-related information such as effects on maturity, ripening and disorders of fruit and vegetables. In reviewing this research area, some definitions and explanations are necessary.

1.1. *Effects of temperature on growth versus high fruit temperatures*

Temperature is a major factor in determining fruit growth rates, fruit development, and quality properties such as sugar contents of fruit. We are limiting the scope of this review to the specific effects of *high* temperatures experienced by the fruit and the subsequent effects on postharvest behaviour.

1.2. *How do we define heat?*

There is no precise definition in this context. However, for our purposes, we focus on temperatures which have been shown to be effective in postharvest treatments, either in reducing chilling injury or in establishing tolerance to higher disinfesting temperatures. Such temperatures seem to range between about 38 and 42°C (e.g. apple, Lurie and Klein, 1990; papaya, Paull and Chen, 1990; tomato, Lurie and Klein, 1991; avocado, Woolf et al., 1995). There has been insufficient research on lower temperatures (e.g. approx. 30°C) to reach any conclusions about their effectiveness, although Woolf et al. (1995) found that 34°C was effective in reducing chilling injury in avocado fruit. Many of the characteristic responses to high temperatures, such as induction of heat shock proteins (hsps), can occur at much lower temperatures than the 38–42°C range (e.g. in apple cells, Bowen, 2000).

1.3. *There may be a difference between short and long-term high temperature experience*

In considering postharvest responses, there may be differences in the effects resulting from long-term, multiple or continuous exposure to high temperatures during fruit growth, and those from high fruit temperatures at or immediately prior to harvest (e.g. fruit going into cold storage with flesh at elevated temperatures). For example, long-term exposure is more likely to result in morphological and developmental differences.

1.4. *Light and temperature effects can be confused*

The effects of light and temperature on pre- and postharvest fruit quality properties have not been separated. High fruit temperatures measured in the field have been strongly associated with direct exposure to sunlight (e.g. in 'Braeburn' apple fruit; Ferguson et al., 1998). Conversely, studies on shading and exposure may have temperature components in addition to those of light. For example, high light intensity has been associated with high sugar and anthocyanin levels and low acidity in grapes (Kliewer and Smart, 1989), and it affects sugar levels, texture, and taste and flavour attributes in apple fruit (Palmer, 1989). Temperature components of these effects have not been identified (Palmer, 1993). Light will have an influence on important postharvest fruit properties such as pigmentation and skin structure. We appreciate the light component of temperature responses in the field, but are not specifically addressing them in this review.

2. Temperatures of fruit in the field

2.1. *Temperature measurements*

In tropical and sub-tropical fruit, high flesh temperatures may arise as much from the ambient air temperature as from direct exposure to the sun. Few published temperature recordings of fruit flesh are available for tropical crops, but the preharvest temperature experience of fruits such as papaya can affect postharvest heat sensitivity. Higher mean minimum and maximum air temperatures (range: 17–31°C) three days before harvest were significantly correlated with increased resistance of papaya fruit to damage from a 49°C heat treatment used for disinfestation (Paull, 1995). The other feature of tropical climates which may influence fruit heat response, is that temperatures may fluctuate less than in hot dry or temperate climates. Whether this is important is not known. However, diurnal temperature fluctuations of up to 35°C occur in sun-exposed apple and avocado flesh in temperate climates (Ferguson et al., 1998; Woolf et al., 1999a) and must require impressive homeostatic control of cell metabolism.

In the hot, dry climate of California, flesh temperatures of melon and tomato fruits exposed to sunlight and air temperatures of above 30°C can reach temperatures of between 40°C and 50°C (Schroeder, 1965). In a similar climate in Australia, grape skin temperatures of up to 12°C above air temperatures have been recorded (Kliewer and Lider, 1968; Smart and Sinclair, 1976). Three basic results, which apply to other fruits, were demonstrated in this early work. (1) Direct sunlight can result in fruit flesh temperatures of up to 15°C above air temperature; (2) There may be a large (e.g. 15°C) thermal gradient across fruit from the exposed to the shaded sides; (3) Darker pigmented skin will result in higher fruit temperatures: red tomato fruit can be 4–8°C warmer than green fruit under the same conditions (Schroeder, 1965); black-skinned avocado fruit had higher flesh temperatures (max $>$ 40°C) than green-skinned fruit (max $<$ 40°C) (Schroeder and Kay, 1961).

Measurements of fruit temperatures in temperate climates have shown that high air temperatures are not necessary for the fruit flesh to reach temperatures over 40°C (Table 1). For instance, apple, avocado, tomato and squash fruit flesh temperatures above 40°C have been recorded in fruit under direct sunlight, but with air temperatures of less than 30°C (Hopp, 1947; Ferguson et al., 1998; Woolf et al., 1999a). Air temperatures in a pea pod rose substantially above air temperature (12–15°C higher) under direct sunlight, but were only a couple of degrees above air when not in sunlight (Hopp, 1947). In many studies, only skin temperatures have been measured, and again in apples, these under direct sunlight can reach up to 12°C above ambient (Thorpe, 1974; Kotzé et al., 1988; Parchomchuk and Meheriuk 1996; Wünsche et al., 2000). In most studies, temperature differences across fruit, from sun to shaded sides, have been shown to reach as great as 10–15°C, a magnitude modelled by Thorpe (1974) in apple fruit.

Table 1
Temperatures measured in fruit flesh or on the skin, in relation to air temperatures[a]

Fruit/vegetable	Air temperature (°C)	Tissue	Flesh or skin temperature (°C)		Reference
			Exposed	Unexposed	
Tomato	28	Flesh	41		Hopp, 1947
	40	Flesh	50		Schroeder, 1965
Watermelon	33	Flesh	42		Schroeder, 1965
Canteloupe	36	Flesh	44	30	Schroeder, 1965
Apple	27	Skin	41	30	Thorpe, 1974
		Skin	44		Kotzé et al., 1988
	25	Skin	38		Parchomchuk and Meheriuk, 1996
	23	Flesh	36	27	Ferguson et al., 1998
Grape	41	Skin	47	34	Kliewer and Lider, 1968
Avocado (NZ)	23	Flesh	43	27	Woolf et al., 1999a
Avocado (Israel)	26	Flesh	45	30	Woolf et al., 2000
Pea	28	Int. air	36		Hopp, 1947
Squash	24	Flesh	36		Hopp, 1947
Pineapple	30	Flesh	40		Chen and Paull, 2000
Papaya	30	Skin	45		Paull (pers comm)

[a] 'Exposed' refers to temperatures measured in tissue directly exposed to the sun and 'Unexposed' refers to temperatures in unexposed (shaded) tissues.

2.2. Water status, water loss and wind

Water loss from plant tissues leads to evaporative cooling. Differences in evaporative cooling potential between bulky fruit tissues and leafy tissues explain why fruit reach such high temperatures while leaves do not. Smart and Sinclair (1976) provide a useful model of the effect of organ diameter and wind velocity on flesh temperature. They show that fruit with larger diameters will become hotter because the radiation absorbed varies with fruit radius and convective heat loss (i.e. increasing air speed reduces temperature). Where a plant, or fruit, is under water stress, then fruit temperatures will increase. For example, water stress from high temperatures and low soil moisture can lead to increased sun-scald of cranberries (Croft, 1995). When a steep temperature gradient across apple fruit was artificially established, movement of water occurred from the warm to the cool side, leading to 'wilting' on the warm side (Curtis, 1937; Lessler, 1947). This process was also observed in tomatoes, but not in oranges or potatoes (Curtis and Clark, 1938). This difference was attributed to the lack of continuous air spaces through the latter two organs, water vapour being the supposed medium of water migration. Water supply through the fruit stalk results in a cooling effect. Harvesting fruit breaks this supply, and fruit exposed to the sun after harvest therefore are more prone to heat damage than fruit still attached to the tree. For example, lime fruit attached to the tree can be 8–10°C lower than fruit picked into boxes and exposed to the sun (Davenport and Campbell, 1977).

Water loss from different sides of the fruit is variable. For instance, Maguire et al. (1999) found that although there was variability in permeance measurements around the fruit, there was no obvious relationship with blush (sun exposure). However, in measurements on whole citrus fruit, Purvis (1984) observed lower diffusive resistance (i.e. higher permeability) on the sun-exposed sides of fruit.

Another factor influencing fruit water loss and surface temperatures is air movement. In modelling apple temperatures, Thorpe (1974) showed that a wind speed increase from 0.3 to 4.0 $\mathrm{m\,s^{-1}}$ resulted in a temperature drop of 5°C at the fruit surface.

Even stems and petioles have temperatures elevated above air temperature, although not as much as large fruit (Hopp, 1947). Stems may become hotter than leaves, although less than fruits, with transpiration and water flow being intermediate between the two former organs. Temperature differences across petioles and stems may influence water replenishment of fruits and leaves (Curtis, 1937).

2.3. Tissue type

Different fruit types will attain different temperatures, and this is related to the ability of the fruit tissue to conduct heat. In modelling apple heating under radiant energy, Thorpe (1974) recognised that the heat conductivity of the flesh tissue was important, and Turrell and Perry (1957) showed that even among four citrus fruit types, there were significant differences among thermal conductivity coefficients ($0.78–1.17 \times 10^3\ \mathrm{Cal\,s^{-1}\,cm^{-1}\,°C^{-1}}$). The water content of the citrus fruit at harvest influenced the specific heat of the citrus tissues (Turrell and Perry, 1957). Skin thickness and type will also influence temperature. For example, citrus peel has a lower density than fruit flesh, with 30–50% of the peel volume being air space. This leads to the thermal conductivity coefficient of the peel being about 10% of that of the whole fruit (Turrell and Perry, 1957). A consequence is that it effectively acts as an insulating layer.

3. Relationships between fruit temperatures and quality at harvest

3.1. Harvest disorders increased by exposure

A number of important postharvest fruit disorders are caused or increased by preharvest sun exposure (Table 2). These disorders are often visible or detectable at the time of harvest, or soon afterwards; many are affected in some way by low temperature storage.

Table 2
Disorders associated with exposure of fruit to direct sunlight on fruit in the field

Fruit	Disorder	Symptoms	Reference
Apple	Solar injury	Skin discoloration, pigment breakdown	Parchomchuk and Meheriuk, 1996
Apple	Sunburn	Skin discolouration, pigment breakdown	Bergh et al., 1980; Wünsche et al., 2000
Apple	Watercore	Water soaking of flesh	Marlow and Loescher, 1984
Avocado	Sunburn	Skin browning	Schroeder and Kay, 1961
Cranberry	Sun scald	Tissue breakdown	Croft, 1995
Lime	Stylar end breakdown	Juice vesicle rupture	Davenport and Campbell, 1977
Pineapple	Flesh translucence	Water soaking of flesh	Paull and Reyes, 1996; Chen and Paull, 2000

Sunburn (or solar injury) is the most common temperature-induced disorder reported in fruit and vegetables, most likely because it is readily observed on the skin. It is less affected by postharvest conditions, but is worth recording here because it is a consequence of high skin temperatures. Factors which increase the propensity for sunburn are high light intensity, high air temperatures (e.g. apples; Bergh et al., 1980, Parchomchuk and Meheriuk, 1996), and increased water stress (e.g. cranberries; Croft, 1995). Sunburn can be viewed as exceeding the possible beneficial effects of sun exposure.

Early signs of sunburn include yellowing or bleaching of the skin (apple, Bergh et al., 1980; avocado, Woolf et al., 1999b), and a corky or roughened fruit surface (avocado, Schroeder and Kay, 1961). Another measure of skin damage is reduced photosynthetic activity, measured by reduced chlorophyll fluorescence (avocado, Woolf et al., 1999b; apple, Wünsche et al., 2000). In ‘Braeburn’ apples, Tustin et al. (1993) observed higher soluble solids content (SSC), more advanced starch degradation, and higher internal ethylene concentration on fruit showing ‘marginal sunburn discolouration’. More severe and frequent sun exposure results in browning or blackening of the skin and tissue failure (Schroeder and Kay, 1961; Croft, 1995). Extreme levels of damage to skin tissue will result in complete inactivation of the photosynthetic system. Many years ago, it was recognised that tolerance to sunburn can be imparted by previous exposure (Brooks and Fisher, 1926a). However, this is an issue which still needs investigation, as are the observations that adjacent apple fruit, under the same exposure conditions, may differ in the extent of sunburn (Wünsche, pers comm).

An apple disorder sometimes associated with sun-exposure is watercore (Marlow and Loescher, 1984). Early work by Fisher et al. (1930) showed that artificially heating apple fruit on the tree could induce watercore, and fruit of a number of cultivars developed watercore in specific association with exposure to radiant heat, in many cases being associated with sunburn symptoms (Brooks and Fisher, 1926b). In cultivars such as ‘Cox’s Orange Pippin’, it can occur both as an evenly distributed core disorder and in the flesh closer to the skin in regions directly associated with high temperature and light exposure (Ferguson et al., 1999a Fig. 1D). A disorder with similarities to watercore is flesh translucence in pineapple, where the symptoms are water soaking and increased porosity (Paull and Reyes, 1996; Chen and Paull, 2000). Relatively high fruit temperatures early in the season may induce some tolerance to heat during later fruit growth; the disorder appears to be associated with heat stress in these later stages.

Stylar-end breakdown (SEB) is a common disorder of ‘Tahiti’ lime where juice vesicles rupture and juice invades the rind at the stylar end (Davenport and Campbell, 1977). Increasing temperatures result in higher incidence of SEB, and this disorder can be induced both in fruit exposed to the sun whether attached to the tree or detached (i.e. in a picking tray), and by using a postharvest hot water treatment (HWT) (Davenport and Campbell, 1977). Using the HWTs, temperatures as low as 35°C for 3 h resulted in a 20% increase in the disorder, and 50°C led to over 80% incidence.

3.2. *Effect of sun exposure on fruit quality characteristics*

A number of fruit properties influenced by exposure to high temperatures on the tree may have a considerable impact on quality during and after storage. There has been extensive work on the quality properties of grapes in relation to temperature, with high temperatures being associated with high sugar and low total acidity (Kliewer and Lider, 1968, 1970). Acidity can be halved by a 10°C rise (Coombe, 1987), and this is mostly expressed in malate, tartarate not being so affected by temperature (Kliewer and Lider, 1970; Lakso and Kliewer, 1975).

Other fruit contain higher sugar levels in tissues from exposed sides: 'sap' extracted from exposed sides of apple fruit had higher osmotic pressures (presumably sugar levels) than sap from shaded sides of the same fruit (Brooks and Fisher, 1926a), and more recently, Klein (unpublished data) found that exposed sides of apple fruit had higher soluble solids levels. In apples, this is also reflected in accumulation of high sorbitol levels in the watercore disorder. To some extent, similar

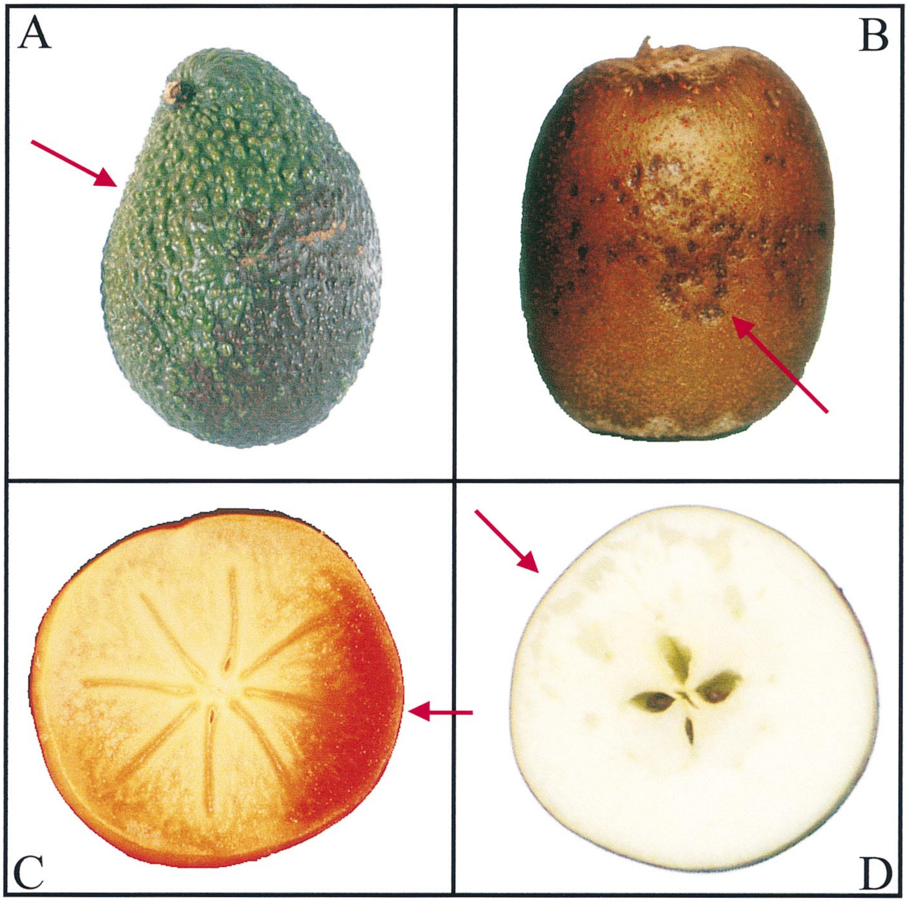

Fig. 1. Examples of fruit responses to sun-exposure (high fruit temperatures) on the tree. Arrows indicate exposed side of fruit: (A) skin chilling injury of 'Hass' avocado fruit following four weeks at 0°C, (B) skin pitting of 'Haywood' kiwifruit following 16 weeks storage at 0°C, (C) internal chilling injury (flesh gelling/softening) of 'Fuyu' persimmons following six weeks storage at 0°C and three days at 20°C and (D) watercore in 'Cox's Orange Pippin' apples three days after harvest (no storage).

metabolic differences might also account for the reported higher flesh firmness found on the blush (exposed) sides of 'Pacific Rose' (Opara and Tadesse, 2000) and 'McIntosh' (Studman et al., 1997) apple fruit. Greater firmness was also found on exposed sides of avocado fruit (Woolf et al., 1999b, 2000). Whether these differences are due to differing cell wall composition, cell number, or cell turgor properties is not known, and Opara et al. (1997) speculated that there may be differences in cell shape and structure between sun and shaded fruit.

In avocado, Woolf et al. (1999b) observed higher dry matter contents of sun fruit than shade fruit, and for sun fruit the exposed side of the fruit had higher dry matter content than the unexposed side. Dry matter is employed as a maturity index in avocado, and increasing maturity of avocado generally results in shorter time to ripening, yet exposed fruit with higher dry matter actually take longer to ripen (Woolf et al., 1999b, 2000). Thus, there may be a conflicting influence of sun exposure on dry matter and ripening which may relate to cell number/structure and carbohydrate economy, and/or effects on ripening processes such as ethylene production.

Other fruit components of importance in postharvest quality also differ according to light and heat exposure. Relatively small differences in calcium composition of avocado fruit were found from different quadrants of a tree, the fruit having differences in shelf-life (Whitney et al., 1990). However, segregating fruit on the basis of sun or shade position, showed that calcium, magnesium and potassium levels can be higher in exposed than in shaded fruit, and on the exposed sides of fruit in direct sunlight (Woolf et al., 1999b). This may be related to water flow; the differences in mineral levels across the fruit suggest that water flow may differ in the same way as the mineral distribution. Oil contents were also found to be higher on average in exposed fruit, with some fatty acids (e.g. palmitic) being higher and others (e.g. oleic) lower. This resulted in the monounsaturated to saturated fatty acid ratio being higher in shaded fruit (this generally being considered more 'healthy').

Skin properties are an important feature of postharvest quality and these properties are largely determined by preharvest development. The most pertinent properties are resistance to water loss in storage, and toughness as a textural feature. For example, the skin on exposed side of apple fruit is tougher (Ferguson et al., 1999b), and in citrus, differences in wax components (triterpenes and hydrocarbons), and wax platelet size have been observed with exposure (McDonald et al., 1993; Nordby and McDonald, 1995). Artificial inoculation of 'Fuerte' avocado skin with *Colletotricum gleosporioides* showed that the sun fruit were more resistant to decay development than shade fruit, but that the nonexposed side of the fruit was the most resistant (Woolf et al., 2000). This again suggests that sun exposure leads to differences in the skin, either in terms of morphology, or wax composition and structure. Other biochemical differences may occur, such as the antifungal diene levels which were found to be significantly different in the skin and flesh of sun and shade avocado fruit (Woolf et al., 2000). Higher levels of calcium might also be involved since exposed fruit have higher calcium contents (Woolf et al., 1999b).

4. Relationships between fruit temperatures and postharvest responses

4.1. Fruit ripening

While there are few data on the specific effects of high fruit temperatures and sun exposure on fruit ripening, a number of observations suggest that some of the variation commonly found in postharvest ripening of fruits may be associated with high temperature. In this, we are excluding the effects of differing fruit maturity in relation to position of fruit on the canopy. Maturity, in its horticultural sense, is a combination of properties such as firmness, skin colour and sugar contents, and is the result of the long-term developmental physiology of the fruit in relation to fruiting site on the tree and environmental influences such as light and temperature. One of the best examples of differential maturity is in the grapes on a bunch, where those exposed to direct sunlight ripen faster (higher sugars, lower acidity) than shaded berries (Kliewer and Lider, 1968).

Ripening responses to postharvest heat treatments are useful in suggesting possible preharvest heat effects on postharvest ripening. Fruit, which have undergone postharvest heating generally, ripen more slowly than non-heated fruits. Tomatoes ripened normally (colour development, ethylene and respiratory climacteric) after three days at temperatures above 36°C and three weeks at 2°C, although more slowly than freshly harvested fruit (Lurie and Klein, 1991). A similar slowing of ripening was found in heat-treated avocado fruit (Woolf et al., 1995; Woolf and Lay-Yee, 1997). The immediate effects of heat treatments have generally been to inhibit respiration and ethylene production, reduce protein synthesis, and increase protein breakdown (Eaks, 1978; Lurie and Klein, 1990, 1991; Ferguson et al., 1994). However, in apples, treatments of 38 and 40°C for 2–6 days did not have marked effects on respiration, although ethylene production was reduced (Liu, 1978; Porritt and Lidster, 1978). Both ethylene production and cell wall softening are directly inhibited in papaya and tomatoes by heat treatments (Chan et al., 1981; Picton and Grierson, 1988), although in vitro ACC oxidase activity showed some increased tolerance to 45°C when cucumber fruit were preconditioned at 32.5°C (Chan and Linse, 1989).

These data suggest that we might expect some effects on ripening if fruit have achieved high temperatures prior to harvest, and/or been exposed to high temperatures frequently during development. Using eating ripeness as a measure, Woolf et al. (1999b) found that exposed avocado fruit, which had achieved flesh temperatures of about 35°C before harvest, took about 1.5 days longer to ripen than fruit from shaded positions. This difference was also found when fruit were ethylene-treated, the exposed fruit being firmer and ripening more slowly. When ripening characteristics of a range of commercial avocado cultivars in Israel were examined, ‘Fuerte’, ‘Horshim’, ‘Pinkerton’ and ‘Hass’ (but not ‘Ettinger’) sun fruit ripened more slowly than shade fruit, i.e. were firmer at the same assessment time after harvest (Woolf et al., 2000). For ‘Fuerte’, ‘Horshim’ and ‘Hass’ fruit, the exposed side of sun fruit was also firmer than the unexposed side. The activity of polygalacturonase and cellulase was correlated with this greater firmness, but was not influenced by fruit type (i.e. sun vs shade). Thus, it appears that sun exposure generally delays ripening, but does not do this via its direct effect on cell wall degrading enzymes. It is more likely that some prior step in the ripening process is influenced. For example, it is likely that the ethylene biosynthetic pathway will be affected by heating (Chan and Linse, 1989).

4.2. Exposure-induced tolerance to low and high temperatures

Data showing effects of postharvest heat treatments on subsequent fruit quality at both low and high temperatures (Lurie, 1998) invites speculation on the effects of high fruit temperatures on the tree on postharvest tolerance. Indeed, this question has been raised in the past with apples (Brooks and Fisher, 1926a) and avocados (Schroeder, 1965).

With avocado fruit both in New Zealand and Israel, Woolf et al. (1999a, 2000) found significant tolerance to both high and low postharvest temperatures in fruit which had been growing in positions exposed to direct sunlight, and which had flesh temperatures routinely recording above 40°C. Sun exposure and subsequent storage at 0°C resulted in reduction in chilling injury on the exposed side of sun ‘Hass’ fruit, and generally less chilling injury on the sun fruit than shade fruit (also see Fig. 1A). Similar tolerance to high temperatures (50°C hot water treatments) was also observed. When these responses were examined in 5 avocado cultivars in Israel, the same patterns were observed in all cultivars except ‘Ettinger’ (Woolf et al., 2000). In both countries and all cultivars there was a high correlation of chilling injury with electrolyte leakage of skin tissue.

There are other indications in the literature that exposure may be associated with chilling tolerance. For instance, muskmelon fruit which exhibited solar yellowing (exposure to direct sunlight during fruit growth) were less susceptible to postharvest chilling injury (Lipton and Aharoni, 1979). This benefit was attributed to increased wax development on exposed sides of the fruit, although no measurements of this were made. There are also few available data on acquisition of heat tolerance on the tree. However, as early as 1926, Brooks and Fisher (1926a) showed that apple fruit under regular exposure to direct sunlight was more resistant to sunburn-like damage than fruit which had been shaded but was then exposed. In more recent work, Houck and Joel (1995) placed potted lemon trees in glasshouses under high (min 25–30°C, max 35–40°C) and low (min 5–10°C, max 20°C) temperature regimes for up to 4 weeks. They observed that high temperatures resulted in fruit with less damage when exposed to 55°C hot water treatments, and that damage decreased with longer exposure times.

4.3. Exposure-induced susceptibility to low and high temperature damage

Although preharvest exposure of fruit such as avocado may result in more postharvest chilling tolerance, there are fruits where exposure results in greater chilling sensitivity. Citrus such as grapefruit show chilling symptoms of skin pitting and discoloration. Chilling injury is greater in fruit taken from the exterior canopy, with direct sun exposure, than in fruit from the interior, shaded parts of the tree (Purvis, 1980). This difference is further reflected in greater chilling injury on exposed versus shaded sides of the same fruit (Purvis, 1984). These differences have been related to increased water loss from the exposed side of the fruit. In contrast to the increased tolerance to hot water temperatures by high growing temperatures, Houck and Joel (1995) observed that exposure to chilling temperatures (3 weeks at 2°C) resulted in more chilling injury for lemon fruit exposed to low temperature regimes, than high temperatures.

There are other instances of exposure-induced susceptibility to postharvest damage, although little has been published. Kiwifruit exposed to high sunlight may be more susceptible to a pitting disorder on the skin, which develops during low temperature storage (Fig. 1B; Thorp and Ferguson, unpublished data). Low temperature injury in persimmons is manifest as a gelling of the flesh (MacRae, 1987). This symptom often develops on the side of the fruit that has had direct sun exposure (Fig. 1C; Woolf and Thorp, unpublished data). However, chilling injury development is related to release of polyuronides from the cell walls and lack of subsequent degradation (Woolf et al., 1997a). Heat treatments at 47°C retarded this release (Woolf et al., 1997b). We can speculate that cell wall development in exposed sides of fruit may be different from that in shaded sides, and this may be reflected in the subsequent cell wall changes associated with the chilling injury.

5. Mechanisms

The universal response to high temperature is the induction of hsps. These have been shown to confer heat tolerance in animal and yeast cells, and the same processes may occur in plants. Hsp transcripts and proteins are up-regulated as a result of postharvest heat treatments of fruits such as papaya, tomatoes and avocados (Paull and Chen, 1990; Lurie and Klein, 1991; Lurie et al., 1993; Woolf et al., 1995 Sabehat et al., 1996), and in cultured cells of pear (Ferguson et al. 1994), and apple (Wang et al., 2000) fruit.

One of the most interesting results in the relationship of hsps to postharvest responses has been the finding that hsp transcripts remain elevated for considerable periods at low temperatures subsequent to heat treatments. Hsp mRNA has been found to remain up-regulated in fruit held at 2°C for some weeks after postharvest heat treatments (tomatoes, Lurie et al., 1993; avocados, Woolf et al., 1995). In cultured apple cells, hsp70 and low molecular weight hsp transcripts were maintained at elevated levels for four days at 1°C after 1 h at 38°C, whereas the levels returned to those in control cells within 24 h if the cells were held at 25°C (Wang et al., 2000). Sabehat et al. (1996) have shown the persistence of heat-induced hsps for 21 days at 2°C in tomato fruit. Recent data also show that hsps can be induced by low temperature alone (Li et al., 1999).

Involvement of hsps in the mechanisms of postharvest responses to high and low temperature is based on correlative evidence. Until expression of the genes can be modifed in these crops, we will be uncertain as to whether their role is critical. However, in model plants such as *Arabidopsis*, reducing expression of hsp101 by antisense does result in less capacity to acquire thermotolerance (Queitsch et al., 2000). If hsps were to have some role in field heat-induced postharvest responses, we would expect them to be part of the response of fruit on the tree to high temperatures, and that they might be maintained after harvest, depending on the postharvest conditions. Paull and Chen (1990) noted that new heat-associated polypeptides were present in fruit which had experienced high field temperatures. Up-regulation of both hsp70 and hsp17 mRNA, and new heat-induced proteins, were found in apple fruit under direct sunlight (Ferguson et al., 1998). A substantial cycling of hsp response was found, where hsp transcripts increased in the late afternoon and evening after fruit flesh temperatures reached >40°C. This high level was maintained until the morning when message rapidly declined before rising again the next afternoon. It is possible that the low night temperatures maintained message, much as found in low temperature storage after heat treatments (as described above).

A similar cycling was found with avocado fruit (Woolf et al., 1999a), where sun exposure led to diurnal cycling of low and high MW hsp gene expression and synthesis. Levels tended to be highest at 12 noon or 3 pm, and depending on the hsp, declined either during the evening, or by early morning (Woolf et al., 1999a). Although there were significant differences in terms of hsp gene expression and protein synthesis, the tolerance of the skin of ‘Hass’ fruit harvested at 8:00, 12:00, 15:00 and 20:00 h and then hot water-treated at 50°C was not significantly different among harvests (Woolf and Ferguson, unpublished data). These results correlate with the actual levels of hsps, where there were relatively few differences over a 24 h period, although there were higher levels of low molecular weight proteins in sun fruit (Woolf et al., 2000).

Whether or not persistence of hsp message and protein at low temperature is responsible for some of the chilling tolerance induced by heat treatments is yet to be determined. It is likely that hsps provide some protection from both heat- and cold-induced protein denaturation or dysfunction. However, there are a number of chilling symptoms, which may be related to other aspects of fruit physiology and morphology as developed on the tree. Many chilling injury symptoms are found on the skin, e.g. browning in avocados (Woolf, 1997) and pitting in citrus, mangoes and cucumbers (Purvis, 1980; McCollum et al., 1993; Wang and Qi, 1997). Wax thickness and composition are affected by exposure to both light and temperature, and these properties may determine postharvest low temperature responses, such as tolerance to chilling injury in citrus (Purvis, 1980, 1984). For example, triterpene ratios in grapefruit skin differed in fruit from exposed or shaded positions on the tree, and these differences were mirrored in shaded and exposed sides of the same fruit; triterpenes may react with sunlight and be associated with susceptibility of the fruit to postharvest chilling injury (Nordby and McDonald, 1995).

Evidence from postharvest heat treatments also highlights the importance of wax properties. Schirra et al. (1999) showed that even a heat treatment of only 37°C for 30 h caused partial melting of wax layers which sealed micro-wounds and cracks in cactus pear fruit. Hot water treatments, including brushing, of citrus resulted in a reduction in cracking, and possible melting of surface wax; this had a positive effect in reducing postharvest pathogen attack (Porat et al., 2000). Thus, heat effects on wax structure, as might occur in the field, may have postharvest benefits.

Where water loss is associated with chilling injury, cuticle thickness and properties will affect the low temperature response. Increased water loss at low temperatures have been associated with chilling injury (e.g. in citrus; Purvis, 1984). However, other aspects of water economy may be as influential in determining postharvest responses. For instance, it is probable that water transport and apoplastic sorbitol accumulation are closely linked in the apple disorder watercore (Marlow and Loescher, 1984), and the occurrence of exposure-related watercore symptoms (see Section 4.3) suggests that differences in carbohydrate transport and metabolism occur with exposure, and it is likely that these may be responsible for some of the postharvest responses. It would be interesting to discover the effects of differing carbohydrate levels, both in cells and in tissues, on responses to low temperature in stored fruit.

Browning is a characteristic response to heat damage and also a chilling injury symptom, both in the flesh and on the skin. This suggests a loss in compartmentation and membrane function in the cell with consequent phenol oxidation. Both postharvest heat treatments and exposure on the tree result in a reduction in this symptom (e.g. avocados; Woolf et al., 1995, 1999a). We do not have enough evidence to know whether such an effect of heat is direct or indirect. Oxidative enzymes such as polyphenol oxidase and peroxidase are relatively unaffected by high temperatures in in vitro studies (Vamos-Vigyazo, 1981), and thus thermal inactivation of browning enzymes is unlikely. Perhaps high temperature results in membranes which are more resistant to low temperature damage. In a study with cultured apple cells, Wang et al. (2000) showed that low temperature intolerant cells could be identified as those, which were undergoing necrosis and membrane damage. A 38°C 1 h treatment prior to chilling prevented this sub-population from appearing, suggesting protection from membrane damage.

Electrolyte leakage may give some hints as to the involvement of membrane permeability. Inaba and Crandall (1988) showed increased leakiness of tomato flesh with high temperatures, but this only occurred above 40–45°C. In avocado fruit, a slight increase in leakage was observed in skin disks from exposed sides of sun fruit (Woolf et al., 1999a). However, after storage at 0°C, less ion leakage was observed in skin tissue taken from exposed sides of fruit, concomitantly with less postharvest chilling injury (Woolf et al., 1999a, 2000). An effect of high preharvest fruit temperatures on membrane properties has also been suggested by Chen and Paull (2000), following experiments in which high temperatures in the latter stage of pineapple fruit development favoured the translucence symptom. Insofar as increased membrane leakage is a widespread chilling injury symptom, heat treatments can reduce it, both when applied before and after the chilling treatment (Saltveit, 2000). However, no unequivocal evidence for a protective heat effect on membranes or compartmentation has yet been provided. It is difficult to decide from most studies whether membrane damage is a primary or secondary response.

6. Horticulture implications

Perhaps the most important aspect of considering high fruit temperatures in the field is that the history of sun exposure or shading of a fruit may be a major source of variation in both at-harvest and postharvest quality. For instance, consideration of this may allow us to produce and work with a more consistent line of fruit. In work examining quality aspects, more emphasis should be put into considering and studying the possible effects of sun exposure. If possible, the effects of general sun exposure and/or high temperature should be separated by, for example, sampling fruit from different sides of the tree, or preferably from exposed and shaded locations on the same side of the tree.

Table 3 summarises some of the possible implications for horticulture practice of sun exposure on fruit and vegetables. These issues relate to production (e.g. managing fruiting position), harvesting (maturity indices and handling), grading (external and internal quality), storage responses (external and internal quality), and processing (e.g. dry matter and oils). There are also significant implications for sampling e.g. what part of the fruit to sample both pre- and postharvest for properties such as mineral contents, dry matter, soluble solids, etc. Increasing our understanding of these issues will ultimately lead to improvements in quality.

Future work in this area of research should consider examining the duration of time taken to induce the effects observed (is damage/tolerance induced by short- or long-term exposure?). Also, the possible effects of light (e.g. UV) and heat

Table 3
Possible implications for horticultural practices such as quality assessment, harvesting, handling and storage, arising from differences in fruit and vegetable properties associated with sun exposure and preharvest high temperatures

Properties affected by sun exposure or shade	Implications for horticultural practice
Skin colour	Variable colour at out-turn, mixed maturity, rejection outside grade standards at harvest (insufficient or excessive skin coloration)
Skin damage	Rejection due to poor external quality at harvest
Dry matter	Variability within a fruit associated with exposure will affect accuracy as a maturity or quality index
Soluble solids content	Variability within a fruit associated with exposure will affect accuracy as a maturity or quality index. Impact on poststorage taste acceptability
Fruit firmness	Improved storage potential if fruit are firmer (e.g. slower softening during storage)
Acidity	Impact on taste acceptability through varying acid levels and acid/sugar ratios
Mineral concentrations	Variable mineral contents within fruits may influence incidence of storage disorders, and low temperature responses
Rate of ripening	Variability due to exposure/shade may lead to differences in ripening rates of individual fruit; source of out-turn variability. Impact, for example, on duration of optimal ethylene treatments in ethylene-ripening programmes
Temperature tolerance	Exposure may lead to improved tolerance and subsequent quality where disinfesting heat treatments are used; postharvest low temperature tolerance may be dependent of fruit position on the tree or vine

should be separated, something which has important implications for management of tree architecture. Finally, it would be of great benefit to improve our understanding of the possible mechanisms involved in this range of heat effects.

Acknowledgements

We would like to thank Josh Klein and Robert Paull for unpublished data, and Katy Cox for assistance with literature searching.

References

Bergh, O., Franken, J., Van Zyl, E.J., Kloppers, F., Dempers, A., 1980. Sunburn on apples – preliminary results of an investigation conducted during the 1978/79 season. Decid. Fruit Grower 30, 8–22.

Bowen, J.H. 2000. Thermotolerance and the heat shock response in an apple cell culture. MSc Thesis, University of Auckland, New Zealand. pp. 138.

Brooks, C., Fisher, D.F., 1926a. Some high temperature effects in apples: contrasts in the two sides of an apple. J. Agri. Res. 23, 1–16.

Brooks, C., Fisher, D.F., 1926b. Water-core of apples. J. Agri. Res. 23, 223–260.

Chan, H.T., Linse, E., 1989. Conditioning cucumbers to increase heat resistance in the EFE system. J. Food Sci. 54, 1375–1376.

Chan, H.T., Tam, S.Y.T., Seo, S.T., 1981. Papaya polygalacturonase and its role in thermally injured ripening fruit. J. Food Sci. 46, 190–197.

Chen, N., Paull R.E., 2000. Fruit temperature and crown removal on the occurrence of pineapple fruit translucency. Sci. Hortic, in press.

Coombe, B.G., 1987. Influence of temperature on composition and quality of grapes. Acta Hortic. 206, 23–35.

Curtis, O.F., 1937. Vapor pressure gradients, water distribution in fruits, and so-called infra-red injury. Amer. J. Bot. 47, 705–710.

Curtis, O.F., Clark, A.K., 1938. The effect of a temperature gradient on the distribution of water in apples, tomatoes, oranges and potatoes. Proc. Amer. Soc. Hortic. Sci. 135, 160.

Croft, P.J., 1995. Field conditions associated with cranberry scald. HortScience 30, 627.

Davenport, T.L., Campbell, C.W., 1977. Stylar-end breakdown in 'Tahiti' lime: Aggravation effects of field heat and fruit maturity. J. Amer. Soc. Hort. Sci. 102, 484–486.

Eaks, I.L., 1978. Ripening, respiration and ethylene production of 'Hass' avocado fruit at 20 to 40°C. J. Amer. Soc. Hort. Sci. 103, 576–578.

Ferguson, I.B., Lurie, S., Bowen, J.H., 1994. Protein synthesis and breakdown during heat shock of cultured pear (Pyrus communis L.) cells. Plant Physiol. 104, 1429–1437.

Ferguson, I.B., Volz, R.K., Woolf, A.B., 1999a. Preharvest factors affecting physiological disorders of fruit. Postharvest Biol. Technol. 15, 255–262.

Ferguson, I.B., Snelgar, W., Bowen, J.H., Woolf, A.B., 1999b. Preharvest field heat and postharvest fruit response. Acta Hortic. 485, 149–154.

Ferguson, I.B., Snelgar, W., Lay-Yee, M., Watkins, C.B., Bowen, J.H., 1998. Heat shock response in apple fruit in the field. Aust. J. Plant. Physiol. 25, 155–163.

Fisher, D.F., Harley, C.P., Brooks, C., 1930. The influence of temperature on the development of watercore. Proc. Amer. Soc. Hort. Sci. 27, 276–280.

Hopp, R., 1947. Internal temperatures of plants. Proc. Amer. Soc. Hort. Sci. 50, 103–108.

Houck, L.G., Joel, F.J., 1995. Growth temperature influences postharvest tolerance of lemon to hot water, cold and methyl bromide. HortScience 30, 804 Abstract 354.

Inaba, M., Crandall, P.G., 1988. Electrolyte leakage as an indicator of high-temperature injury to harvested mature green tomatoes. J. Amer. Soc. Hort. Sci. 113, 96–99.

Kliewer, M.W., Lider, L.A., 1968. Influence of cluster exposure to the sun on the composition of Thompson seedless fruit. Amer. J. Enol. Viticul. 19, 175–184.

Kliewer, M.W., Lider, L.A., 1970. Effects of day temperature and light intensity on growth and composition of Vitis vinifera L. fruits. J. Amer. Soc. Hort. Sci. 95, 766–769.

Kliewer, M.W., Smart, R.E., 1989. Canopy manipulation for optimizing vine microclimate, crop yield and composition of grapes. In: Wright, C. (Ed.), Manipulation of Fruiting, vol. 1. Butterworths, London, pp. 275–291.

Kotzé, W.A.G., Carreira, J.A., Beukes, O., Redelinghuys, A.U., 1988. Effect of evaporative cooling on the growth yield and fruit quality of apples. Decid. Fruit Grower 38, 20–24.

Lakso, A.N., Kliewer, W.M., 1975. The influences of temperature on malic acid metabolism in grape berries I. Enzyme responses. Plant Physiol. 56, 370–372.

Lessler, M.A., 1947. Effect of a temperature gradient on distribution of water in apples. Bot. Gaz. 109, 90–94.

Li, Q.-B., Haskell, D.W., Guy, C.L., 1999. Coordinate and non-coordinate expression of the stress 70 family and other molecular chaperones at high and low temperatures in spinach and tomato. Plant Mol. Biol. 39, 21–34.

Lipton, W.J., Aharoni, Y., 1979. Chilling injury and ripening of ‘Honey Dew’ muskmelons stored at 2.5°C or 5°C after ethylene treatment at 20°C. J. Amer. Soc. Hort. Sci. 104, 327–330.

Liu, F.W., 1978. Modification of apple quality by high temperature. J. Amer. Soc. Hort. Sci. 103, 730–732.

Lurie, S., 1998. Postharvest heat treatments. Postharvest Biol. Technol. 14, 257–269.

Lurie, S., Klein, J.D., 1990. Heat treatment of ripening apples: Differential effects on physiology and biochemistry. Physiol. Plant 78, 181–186.

Lurie, S., Klein, J.D., 1991. Acquisition of low-temperature tolerance in tomatoes exposed to high-temperature stress. J. Amer. Soc. Hort. Sci. 116, 1007–1012.

Lurie, S., Klein, J.D., Watkins, C.B., Ross, G.S., Boss, P.K., Ferguson, I.B., 1993. Prestorage heat treatments of tomatoes prevent chilling injury and reversibly inhibit ripening. Acta Hort. 343, 283–285.

MacRae, E.A., 1987. Development of chilling injury in New Zealand grown ‘Fuyu’ persimmon during storage. NZ J. Exptl. Agric. 15, 333–344.

Maguire, K.M., Banks, N.H., Lang, A., 1999. Sources of variation in water vapour permeance of apple fruit. Postharvest Biol. Technol. 17, 11–17.

Marlow, G.C., Loescher, W.H., 1984. Watercore. Hortic. Rev. 6, 189–251.

McCollum, T.G., D’Aquino, S., McDonald, R.E., 1993. Heat treatment inhibits mango chilling injury. HortScience 28, 197–198.

McDonald, R.E., Nordby, H.E., McCollum, T.G., 1993. Epicuticular wax morphology and composition are related to grapefruit chilling injury. HortScience 28, 311–312.

Nordby, H.E., McDonald, R.E., 1995. Variations in chilling injury and epicuticular wax composition of white grapefruit with canopy position and fruit development during the season. J. Agric. Food Chem. 43, 1828–1833.

Opara, L.U., Tadesse, T., 2000. Fruit growth characteristics and chronological development of calyx-end splitting in Pacific Rose apples Fruit Var. J. in press.

Opara, L.U., Studman, C.J., Banks, N.H., 1997. Sunlight affects the incidence of internal-ring cracking and other physical attributes of ‘Gala’ apples. J. Tree Fruit Production 2, 45–52.

Queitsch, C., Hong, S.-W., Vierling, E., Lindquist, S., 2000. Heat shock protein 101 plays a crucial role in thermotolerance in Arabidopsis. Plant Cell 12, 479–492.

Palmer, J.W., 1989. Canopy manipulation for optimizing utilization of light. In: Wright, C. (Ed.), Manipulation of Fruiting, vol. 1. Butterworths, London, pp. 245–262.

Palmer, J.W., 1993. Recent developments on light and fruit tree canopies. Acta Hort. 349, 99–109.

Parchomchuk, P., Meheriuk, M., 1996. Orchard cooling with pulsed overtree irrigation to prevent solar injury and improve fruit quality of ‘Jonagold’ apples. HortScience 31, 802–804.

Paull, R.E., 1995. Preharvest factors and the heat sensitivity of field-grown ripening papaya fruit. Postharvest Biol. Technol. 6, 167–175.

Paull, R.E., Chen, N., 1990. Heat shock response in field-grown ripening papaya fruit. J. Amer. Soc. Hort. Sci. 115, 623–631.

Paull, R.E., Reyes, M.E.Q., 1996. Preharvest weather conditions and pineapple fruit translucency. Sci. Hortic. 66, 59–67.

Picton, S., Grierson, D., 1988. Inhibition of expression of tomato-ripening genes at high temperature. Plant Cell Environ. 11, 265–272.

Porat, R., Daus, A., Weiss, B., Cohen, L., Fallik, E., Droby, S., 2000. Reduction in postharvest decay in organic citrus fruit by a short hot water brushing treatment. Postharvest Biol. Technol. 18, 151–157.

Porritt, S.W., Lidster, P.D., 1978. The effect of pre-storage heating on ripening and senescence of apples during cold storage. J. Amer. Soc. Hort. Sci. 103, 584–587.

Purvis, A.C., 1980. Influence of canopy depth on susceptibility of March grapefruit to chilling injury. HortScience 15, 731–733.

Purvis, A.C., 1984. Importance of water loss in the chilling injury of grapefruit stored at low temperatures. Sci. Hortic. 23, 261–267.

Sabehat, A., Weiss, D., Lurie, S., 1996. The correlation between heat-shock protein accumulation and persistence and chilling tolerance in tomato fruit. Plant Physiol. 110, 531–537.

Saltveit, M.E., 2000. Chilling injury is reduced in cucumber and rice seedlings and in tomato pericarp discs by heat shocks applied after chilling. Postharvest Biol. Technol., in press.

Schirra, M., D'hallewin, G., Inglese, P., La Mantia, T., 1999. Epicuticular changes and storage potential of cactus pear (Opuntia ficus-indica Miller L.) fruit following gibberellic acid preharvest sprays and postharvest heat treatment. Postharvest Biol. Technol. 17, 79–88.

Schroeder, C.A., 1965. Temperature relationships in fruit tissues under extreme conditions. Proc. Amer. Soc. Hort. Sci. 87, 199–203.

Schroeder, C.A., Kay, E., 1961. Temperature conditions and tolerance of avocado fruit tissue. Calif. Avocado Soc. Yearbook. 45, 87–92.

Smart, R.E., Sinclair, T.R., 1976. Solar heating of grape berries and other spherical fruits. Agric. Meterol. 17, 241–259.

Studman, C.J., Brown, G.K., Timm, E.J., Schulte, N.L., Vreede, M.J., 1997. Bruising on blush and non-blush sides of apple-to-apple impacts. Trans. Amer. Soc. Agri. Eng. 40, 1655–1663.

Thorpe, M.R., 1974. Radiant heating of apples. J. Appl. Ecol. 11, 755–760.

Turrell, F.M., Perry, R.L., 1957. Specific heat and heat conductivity of citrus fruit. Proc. Amer. Soc. Hort. Sci. 70, 261–265.

Tustin, D.S., Watkins, C.B., Cashmore, W.M., Brookfield, P.L., 1993. Sources of variation in fruit quality of'Braeburn' apple at harvest and after storage. HortScience 28, 46 abstract.

Vamos-Vigyazo, L., 1981. Polyphenol oxidase and peroxidase in fruits and vegetables. CRC. Crit. Rev. Food Sci. Nutr. 6, 49–127.

Wang, C.Y., Qi, L., 1997. Modified atmosphere packaging alleviates chilling injury in cucumbers. Postharvest Biol. Technol. 10, 195–200.

Wang, C.Y., Bowen, J.H., Weir, I.E. Allan, A.C., Ferguson, I.B., 2000. Heat-induced protection against death of supension-cultured apple fruit cells exposed to low temperature. Plant Physiol, In press.

Whitney, G.W., Hofman, P.J., Wolstenholme, B.N., 1990. Effect of cultivar, tree vigour and fruit position on calcium accumulation in avocado fruits. Sci. Hortic. 44, 269–278.

Woolf, A.B., 1997. Reduction of chilling injury in stored 'Hass' avocado fruit by 38°C water treatments. HortScience 32, 1247–1251.

Woolf, A.B., Lay-Yee, M., 1997. Pretreatments at 38°C of 'Hass' avocado confer thermotolerance to 50°C hot water treatments. HortScience 32, 705–708.

Woolf, A.B., Bowen, J.H., Ferguson, I.B., 1999a. Preharvest exposure to the sun influences postharvest responses of 'Hass' avocado fruit. Postharvest Biol. Technol. 15, 143–153.

Woolf, A.B., MacRae, E.A., Spooner, K.J., Redgwell, R.J., 1997a. Changes to physical properties of the cell wall and polyuronides in response to heat treatment of 'Fuyu' persimmon which alleviate chilling injury. J. Amer. Soc. Hort. Sci. 122, 698–702.

Woolf, A.B., Wexler, A., Prusky, D., Kobiler, E., Lurie, S., 2000. Direct sunlight influences postharvest temperature responses and ripening of five avocado cultivars. J. Amer. Soc. Hort. Sci. 125, in press.

Woolf, A.B., Ferguson, I.B., Requejo-Tapia, L.C., Boyd, L., Laing, W.A., White, A., 1999b. 'Impact of sun exposure on harvest quality of 'Hass' avocado fruit. In: Proc. a IV World Avocado Congress, Uruapan, Mexico. Revista Chaingo Serie Horticultura. vol. 5, pp. 352–358.

Woolf, A.B., Watkins, C.B., Bowen, J.H., Lay-Yee, M., Maindonald, J.H., Ferguson, I.B., 1995. Reducing external chilling injury in stored 'Hass' avocados with dry heat treatments. J. Amer. Soc. Hort. Sci. 120, 1050–1056.

Woolf, A.B., Ball, S., Spooner, K.J., Lay-Yee, M., Ferguson, I.B., Watkins, C.B., Gunson, A., Forbes, S.K., 1997b. Reduction of chilling injury in the sweet persimmon 'Fuyu' during storage by dry air treatments. Postharvest Biol. Technol. 11, 155–164.

Wünsche, J.N., Greer, D.H., Lang, A., McGhie, T., Palmer, J.W., 2000. Sunburn – the cost of a high light environment. Acta Hortic, in press.