

Review

Sun injury on apple fruit: Physiological, biochemical and molecular advances, and future challenges^{*}Luis Morales-Quintana^a, Jessica M. Waite^d, Lee Kalcsits^d, Carolina A. Torres^d, Patricio Ramos^{b,c,*}^a Multidisciplinary Agroindustry Research Laboratory, Instituto de Ciencias Biomédicas, Universidad Autónoma de Chile, Talca, Chile^b Instituto de Ciencias Biológicas, Universidad de Talca, Talca, Chile^c Núcleo Científico Multidisciplinario-DI, Universidad de Talca, Talca, Chile^d Tree Fruit Research and Extension Center, Department of Horticulture, Washington State University, Wenatchee, WA, United States

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ABSTRACT

Climate change negatively influences many human activities and one of the most affected is agriculture. In the apple industry, water availability, elevated temperatures and altered phenology will transform fruit production in traditional growing regions. Extended periods of intense solar radiation and high temperatures during the growing season cause problems in fruit quality increasing losses and reducing sustainability and profitability. Photooxidative and heat stress stimulate sunburn development on apple fruit in the field growing under increasingly stressful conditions. In particular, apples growing in semi-arid conditions are frequently exposed to high solar irradiance and elevated temperature during the growing season that promote the development of sun-related skin disorders. Furthermore, regions that have traditionally not faced sunburn pressure may begin to experience losses in this area. Apple cultivars differ in their susceptibility to sun damage, which is evidenced, in part, by the timing of symptom development and severity. Some studies attribute genotypic variation to physiological and morphological differences while others do to antioxidant-related metabolic differences between them. Here, we discuss the physiological and molecular progress and gaps in knowledge of sunburn damage and the development of sunburn resistance in apple fruit. This information will help develop stronger sunburn mitigation strategies and enhance breeding efforts to address challenges associated with sunburn in apple production.

1. Introduction

In apples (*Malus domestica* Borkh), stressful conditions such as high irradiance, elevated temperatures, and low relative humidity stimulate the development of physiological disorders including sunburn (Schrader et al., 2001, 2003) and watercore (Ferguson et al., 1999). Climate change will affect global agricultural production and specifically for apple, longer periods of extreme solar radiation and high temperatures during the growing season can reduce fruit quality and increase losses. Sun injury or sunburn symptoms range from white patches to dark brown regions developing on the fruit, depending on cultivar and environmental conditions. Affected fruits can show other anomalies in their skin as lenticel marking and postharvest sunscald (Hernandez et al., 2014). Also, fruit can be more prone to pathogen attack in the affected area (Racskó et al., 2005). These sun-related disorders can strongly affect fruit quality and, as a consequence,

decrease market value (Brown, 2009).

Natural defense mechanisms provide some degree of fruit protection, and cultural practices have also been used to reduce sun injury. Physiochemical properties such as the thickness of the epicuticular layer, the composition of waxes and pubescence (Wünsche et al., 2004a), accumulation of antioxidant compounds and photoprotective pigments (Felicetti and Schrader, 2009) can all affect the susceptibility to sunburn. Horticultural strategies such as the application of Kaolin-based film to reflect the solar radiation on fruit surface (Gindaba and Wand, 2005; Glenn et al., 2002; Wünsche et al., 2004b) and shade nets on top of the trees in orchards to prevent the excessive radiation (Gindaba and Wand, 2005; Iglesias and Alegre, 2006) can be used to prevent sunburn. Nevertheless, the generation of sun-related physiological disorders in fruit is a complex and understudied process. This problem requires further research into the environmental and physiological processes that occur prior to and during sun injury development

^{*} Main message: The development of resilient apple cultivars resistant to sunburn requires a better understanding of the physiological, biochemical and molecular controls regulating sunburn development in apple.

^{*} Corresponding author: 2 Norte 685, Talca, Chile.

E-mail address: pramos@utalca.cl (P. Ramos).

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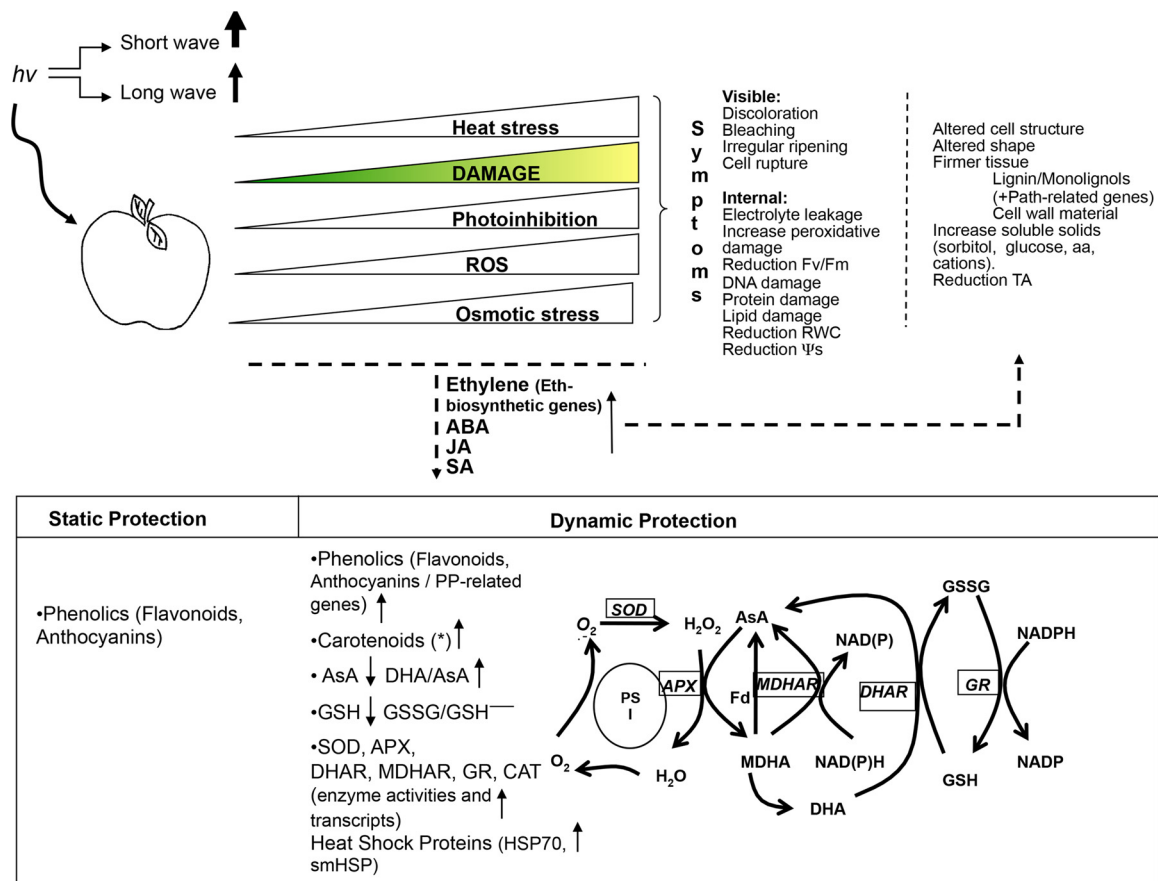


Fig. 1. Environmental, physiological and biochemical factors involved in sun injury development on apple and other fleshy fruits. As sun injury develops on sun-exposed fruit, photooxidative, thermal and osmotic stress drive phenotypic changes not only on fruit surface but also underneath deep into the cortex tissue. Visually, fruit peels start discoloring due to chlorophyll degradation and later different levels of bronzing (enzymatic browning) occurs sometimes followed by thermal damage and cell rupture. During this process cells engage dynamic defense mechanisms signaled by ROS and stress-related phytohormones leading to enhanced antioxidant metabolism and thermal dissipation mechanisms, as well as osmoprotectants synthesis and accumulation. Some species, such as apples, within minutes upregulate the phenylpropanoid pathway leading to flavonoids accumulation, as well as anthocyanins and monolignols in a lesser extent, providing static protection acting as solar screen.

and more importantly, biochemical changes that may contribute to resistance to environmental conditions that cause sun-related disorders in fruit.

2. Characterization of sunburn development in fruit on the tree

Sun injury in fruit is caused by photo-oxidative stress in chlorophyll-containing tissue when exposed to intense solar irradiation and elevated temperatures during the growing season (Naschitz et al., 2015; Rabinowitch et al., 1974, 1983; Torres et al., 2006). Excess light energy can overwhelm the light absorption capacity of fruit. When light-energy absorbed by the tissue exceeds its photosynthetic capacity, reactive-oxygen-species (ROS) can form causing photo-oxidation that can result in the manifestation of sunburn symptoms (Ma and Cheng, 2003, 2004; Torres et al., 2006) (Fig. 1).

Sun injury symptoms vary upon cultivar and environmental conditions from light to dark brown areas and necrosis with or without tissue bleaching (Felicetti and Schrader, 2008). Schrader et al. (2001) found that sunburn symptoms on apples developed when, in addition to high light, fruit reached a threshold temperature that they called minimal Fruit Surface Temperature (FST). Higher the temperature, the less time required to induce damage of different degrees. Fruit Surface Temperature threshold varied with cultivar, where ‘Cameo’ and ‘Honeycrisp’ showed the lowest threshold (46 °C) and ‘Cripps Pink’ the highest (49 °C) (Schrader et al., 2008). Tissue bleaching caused by chlorophyll photooxidation can be more important in de-acclimated fruit.

et al. (2008) found that this type of damage, which they called photooxidative sunburn (PS), can appear at FST below 31 °C under one day of high irradiance. While PS is known to develop from sudden exposure to high light conditions, the threshold for shading and sun exposure is still relatively unknown. The adoption of netting systems (Mupambi et al., 2019) with varying shade factors (Mupambi et al., 2018a,b) and with the capacity to be rapidly deployed and retracted may increase the risk of photooxidative sunburn events. To prevent these issues, a better understanding of the impacts of adaptation of fruit to light is required including thresholds limits for where reductions in light reduce induced acclimation responses.

3. Additional factors affecting sunburn development

Several orchard-related factors also contribute to sunburn development, such as cultivar and rootstock, row orientation, tree structure, and horticultural practices that affect fruit exposure to direct sunlight (Parchomchuk and Meheriuk, 1996). High-density plantings with smaller trees are more susceptible to sunburn injury because of greater fruit exposure than in traditional lower density plantings with larger trees (Parchomchuk and Meheriuk, 1996). Dwarfing rootstocks limit vegetative vigor and increase light penetration into the canopy increasing susceptibility to sun-related damage (Middleton et al., 2002; Racsó et al., 2005; Gonda et al., 2006; Racsó et al., 2009). Row orientation is also an important factor affecting sunburn incidence in orchards where north-south orientations have higher sunburn incidence

Table 1
Apple peel relative lightness of colors (L^*) (mean \pm SE) and hue angle (h°) (mean \pm SE).

	Sunburn	Shaded side of sunburned	Healthy sun exposed side	Shaded side of healthy
L				
'Golden Delicious'	53.0 \pm 1.2 a	61.5 \pm 0.4 b	61.9 \pm 0.8 b	61.6 \pm 0.3 b
'Braeburn'	57.4 \pm 1.0 a	59.9 \pm 0.4 b	59.6 \pm 0.6 b	58.7 \pm 0.5 ab
h°				
'Golden Delicious'	73.5 \pm 1.4 a	106.2 \pm 0.2 c	100.4 \pm 1.1 b	106.0 \pm 0.5 c
'Braeburn'	75.5 \pm 2.1 a	105.6 \pm 0.2 c	101.4 \pm 0.9 b	105.7 \pm 0.2 c

Table adapted from Zupan et al., 2014.

on the west side while east-west orientations have higher incidence on the south side of the trees (Barber and Sharpe, 1971). Orientation is particularly important during the critical afternoon period when sunburn pressure is greater (Barber and Sharpe, 1971). Mineral nutrition can also have direct or indirect effects on sunburn development (Racskó and Schrader, 2012). Racskó et al. (2006) reported a negative correlation between the amounts of nitrogen applied and sunburn susceptibility of apples where enhanced vigor can provide protection for fruit from sunburn. However, over application of nitrogen is not a reliable tool for sunburn control because of negative effects on fruit quality and storability. Cultural practices that can be used to limit fruit sunburn development include evaporative cooling (Gindaba and Wand, 2005), protective sprays (Racskó and Schrader, 2012) and netting (Kalcits et al., 2017; Mupambi et al., 2018a,b; Mupambi et al., 2019). However, these strategies are not completely effective in controlling sunburn and can have negative consequences or significant costs associated with these practices that limit adoption or effectiveness. It is critical that, moving forward, new cultivars that are being developed need to be more tolerant to high temperatures during fruit development.

Some cultivars are more susceptible to sunburn than others in the same edaphoclimatic conditions (Meyer, 1932; Moore and Rogers, 1943). Studies conducted in several world regions have shown that 'Granny Smith' and 'Jonagold' are highly susceptible to sunburn (Racskó et al., 2005; 2011; Sibbett et al., 1991; Van den Ende, 1999); 'Fuji', 'Golden Delicious', 'Braeburn', 'Boskoop', and 'Delicious' are moderately sensitive (Carbó et al., 2005; Racskó et al., 2005), whereas 'Cripps Pink', 'Idared', and 'Topaz' as the less susceptible (Van den Ende, 1999; Gindaba and Wand, 2005; Racskó et al., 2005, 2011; Lebe and Schulte, 2008). As indicated by Racskó and Schrader (2012), early-ripen cultivars (e.g., 'Gala') display strong sunburn damage some years, but not other years. In addition, a study conducted in several apple cultivars showed no differences in fruit peel photosystem efficiency under heat stress at 50, 95 and 150 days after full bloom (Hengari et al., 2014a, b). Furthermore, in fruit exposed to UV-B light, PSII photochemical efficiency ratio decreased in green varieties but remained stable in red varieties, supporting the protective role of anthocyanins against high light conditions (Hengari et al., 2014a, b). In the last two decades, the transition from three-dimensional trees to simplified two-dimensional structures with dwarfing rootstocks has increased sunburn risk (Hampson et al., 2002). These changes coupled with a recent history of elevated summer temperatures has led to the presence of sunburn in regions that traditionally have not had issues with this disorder (Reig et al., 2019). It will be important that new cultivars developed are less susceptible to sunburn. However, to achieve these goals, a better understanding of the underlying physiology conferring resistance to sunburn in apple fruit needs to be developed.

4. Biochemical response mechanisms of apple fruit to sunlight and radiation

Apple fruit exposed to excessive solar radiation switch on a complex defense program that prevents molecular damage and minimizes tissue injury. The stimulation of this defense system can induce morphological changes, pigmentation, and finally, the development of sunburn

symptoms and alteration of fruit quality. When the excitation energy from sunlight exceeds the fruit's capacity to absorb light, thermal dissipation, or scavenging of free radicals by antioxidants, photooxidative damage can develop (Bertamini et al., 2004; Torres et al., 2006). Damage to the photosynthetic apparatus occurs by the denaturation of photosystem II proteins, the photosynthetic electron transfer system, and Calvin cycle enzymes (Cheng et al., 2008; Smillie, 1992). Biochemical defense mechanisms to combat this damage can include antioxidant metabolites, such as ascorbic acid (AsA) and glutathione (GSH), and antioxidant enzymes such as ascorbate peroxidase (APX), dehydroascorbate reductase (DHAR), monodehydroascorbate reductase (MDHAR), glutathione reductase (GR), catalase (CAT) and superoxide dismutase (SOD) (Cheng et al., 2008; Torres et al., 2006). The concentrations of phenolic compounds important for defense are also induced by stress (Felicetti and Schrader, 2008). During the development of sunburn, chlorophyll and carotenoid concentrations decrease, and xanthophyll concentrations increase (Cheng et al., 2008; Torres et al., 2006). Recently, a comprehensive analysis of several antioxidant metabolites, enzyme activity, and their respective transcript abundance was assessed in apple fruit showing severity of sun-injury symptoms in the tree and after several days of cold storage (Hernandez et al., 2014). In this study, it was reported that 'Granny Smith' apple fruit tissue presenting symptoms of sunburn had minimal concentrations of antioxidant metabolites (AsA or GSH) or antioxidant enzymes (APX, DHAR, MDHAR, GR, CAT) to cope with oxidative postharvest stress. Zupan et al. (2014) assessed phenolic composition and peroxidase activity in the peel of sun-exposed fruit for 'Braeburn' and 'Golden Delicious' apple. Here, they reported strong phenolic compounds and peroxidase activity in response to photooxidative stress, which could be related with the peel color of apple (Table 1). Interestingly, genotypic differences among apple cultivars in the accumulation of heat shock proteins (HSP) in the peel of apple under high temperature in the field has been reported (Fig. 2) (Ritenour et al., 2001). HSPs are molecular chaperones that provide tolerance to high temperatures, avoiding denaturation and aggregation of target proteins and helping protein refolding. These differences among cultivars may correspond to some degree of sunburn resistance.

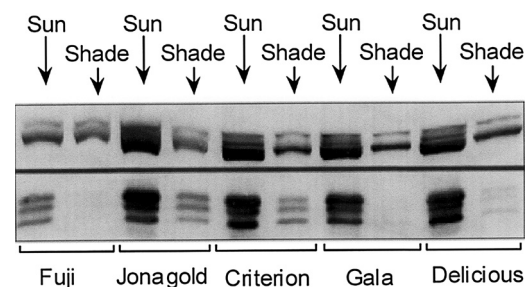


Fig. 2. Immunoblot of protein from apple peel of different cultivars exposed and non-exposed to direct sun light in field. Blot was tested with antibodies against human HSP70 and HSP 18.1. Image adapted from Ritenour et al. (2001).

5. Molecular mechanisms involved in sunburn development responses

The activity of enzymes involved in sorbitol and glucose metabolism were reported to be significantly different between sun-exposed and shaded apple tissue (Li et al., 2013). This study also reported changes in flavonoid and anthocyanin biosynthesis-related enzymes in addition to intermediary metabolites during sunburn development in apple fruit (Li et al., 2013). Identifying the main components of the transcriptional network will be critical for identifying the genetic differences underlying the physiological differences in sunburn susceptibility among apple cultivars, and would inform the development of new cultivars with enhanced resistance to sunburn.

It is well known that members of the MYB transcription factor (TF) family are involved in transcriptional regulation of the phenylpropanoid pathway in plants, including flavonoid and lignin biosynthesis (Dubos et al., 2010). Knowledge about the regulatory specificity of MYB TFs and their interactions with other factors which control flavonoid biosynthesis is important for understanding the genetic pathways activated by each TF. In *Arabidopsis thaliana*, accumulation of anthocyanins and their precursors have been suggested to be stress-dependent, and probably mediated by stress-specific TFs (Kovinich et al., 2014). In apple, the TF MdMYB10, and its allelic genes, MdMYB1 and MdMYBA have been reported to control apple red color development through the transcriptional regulation of structural genes in the anthocyanin biosynthetic pathway (Ban et al., 2007; Espley et al., 2007; Espley et al., 2009; Wang et al., 2011). Apple skin patterning has also been associated with differential expression of MYB10. Both 'Honeycrisp' and 'Royal Gala' had higher mRNA levels of *MdMYB10* and biosynthetic genes *MdCHS*, *MdCHI*, *MdF3H*, *MdDFR1*, *MdLDOX*, and *MdUFGT* in red stripes compared to green stripes (Telias et al., 2011).

Despite the economic importance and extensive understanding of the environmental conditions leading to sunburn development, the genes and their associated molecular pathways associated with sunburn development in apple are still poorly described. However, recently studies have started to describe the molecular changes associated with sunburn development in fruit. For example, Feng et al. (2013) exposed fruit to full sun by turning fruit 180° about one week before harvest to determine the expression of key genes involved in anthocyanin synthesis in response to sunlight exposure, and their relationships with the levels of anthocyanins and other phenolic compounds. The sun-exposed peel had higher expression levels of *MdMYB10*, and seven structural genes in anthocyanin synthesis (*MdPAL*, *MdCHS*, *MdCHI*, *MdF3H*, *MdDFR1*, *MdLDOX*, and *MdUFGT*), and higher levels of anthocyanins and flavonols compounds compared to the shaded peel for two different cultivars: 'Fortune' (red peel) and 'Mutsu' (yellow/green peel) (Feng et al., 2013). Interestingly, when the shaded peel for the fruit was exposed to full sun for both cultivars, significant up-regulation of the expression of *MdMYB10* and all seven structural genes was reported. Consequently, this led to higher levels of anthocyanins, flavonols, and total phenolics than in either the shaded peel or sun-exposed peel of control fruit (Feng et al., 2013).

Lignin accumulation occurs not only in trees and model plants, but also in fleshy fruit as loquat (*Eriobotrya japonica* Lindl.) (Cai et al., 2006) and mangosteen (*Garcinia mangostana* L.) (Kamdee et al., 2014). For fruit, accumulation is induced by elevated temperatures and mechanical stress (Kamdee et al., 2014; Xu et al., 2014). In strawberry, cultivar-specific differences in lignin accumulation were reported (Ring et al., 2013). MYB TFs have been linked to flesh lignification. In loquat fruit, two MYB transcription factors were reported to regulate loquat flesh lignification, with activation by EjMYB1 and repression by EjMYB2 (Xu et al., 2014). Recently, Wang et al. (2016) demonstrated that EjMYB8 is also able to transcriptionally regulate the lignification of loquat fruit after temperature-induced stress conditions.

6. Hormones and damage in apples exposed to solar radiation

Plants are phenotypically plastic in response to environmental stimuli. Most commonly described responses include growth and development through the action of phytohormones (Wolters and Jürgens, 2009). Based on these generalized descriptions, Torres et al. (2013) suggested that photooxidative stress responses in apple fruit could be modulated by ethylene, which has recently been in apple (Torres et al., 2017). Additionally, auxin (indole-3-acetic acid, IAA), abscisic acid (ABA), jasmonic acid (JA), salicylic acid (SA) profiles were assessed when apples were exposed to either photooxidative or heat stress (Torres et al., 2017). For this study, IAA was not directly related to the development of sun injury symptoms. However, IAA strongly decreased in sun-exposed tissue in addition to a general decrease during fruit development. ABA, JA, SA and ethylene concentrations have been reported to increase significantly in fruit with moderate damage (Torres et al., 2017). With the exception of ethylene, concentrations of these important phytohormones were unchanged for fruit exposed to solar irradiation (Torres et al., 2017). In Japan, the foliar application of S-ABA, the biologically active form of ABA ([5-(1-hydroxy-2,6,6-trimethyl-4-oxo-2-cyclohexen-1-yl)-3-methyl-2,4-pentadienoic acid]) resulted in a reduction of sunburn incidence in 'Tsugaru', 'Sensyu', 'Yataka' and 'Fuji' apples cultivars by up to 30% (Iamsub et al., 2008; Iamsub et al., 2009). In contrast, Mupambi et al. (2018a,b) reported that foliar applications of S-ABA were ineffective for reducing sunburn in apple in South Africa. Overall, the inconsistent association of specific phytohormones during the development of sunburn symptoms suggests that fruit peel responses to high light and temperature involve complex pathways and interactions that need to be described in greater detail.

7. Fruit acclimation to heat and light stress: physiological and molecular changes

As previously discussed, tolerance to the harmful effects of excess light and heat varies among different apple cultivars (Gindaba and Wand, 2005; Racskó et al., 2005, 2011). This tolerance may, in part, be due to an enhanced ability to acclimate to environmental stimuli. Many different plant species have been reported to develop memory to stress. This memory provides the platform for acclimation to stress and thus protection against future potentially damage-inducing environmental conditions. These types of responses have not been described in apple. For other species, such as alpine blueberry (*Vaccinium gaultherioides*), exposure to controlled heat events simulating long-term moderate heat waves (30 °C for 7 days) led to significant reductions in heat-induced lethality in leaves that were re-heated to determine tolerance (Karadar et al., 2018). The authors additionally reported that growth under low light improved heat-hardening in these plants. Studies in both model systems and crop plants have uncovered molecular and physiological events involved in temperature memory and acquired thermotolerance (Friedrich et al., 2019; Katano et al., 2018; Yeh et al., 2012). Similar to the study in alpine blueberry, many of these experiments involve a "priming" stimulus with a sub-lethal temperature, followed by a rest and a retreatment with higher temperatures. Upon retreatment, a variety of traits have been measured to assess the acquisition of heat tolerance, including seedling viability, membrane integrity and electrolyte leakage, chlorophyll accumulation in leaves, organ growth, photosynthetic efficiency, and fruit ripening and grain filling (Yeh et al., 2012). Despite the variety of traits and developmental stages studied, these investigations have revealed some common responses and genetic pathways.

Proteins in the Heat Shock Factor (HSF) family, as well as several small Heat Shock Proteins (HSPs), have been implicated in acquired thermotolerance. Experiments in *Arabidopsis* were able to show mechanistic insight into the requirement of two HSPs, HSA2 and HSA32, for long term acquired tolerance (Charng et al., 2006; Lämke et al., 2016). Additionally, a feedback loop between HSA32 and HSP101 was

found to improve heat acclimation in rice (Lin et al., 2014). HSF1 was shown to be important for acquired thermotolerance, both in plant viability and in fruit ripening in tomato (Mishra et al., 2002), as well as seedling viability in Arabidopsis (Yoshida et al., 2011). Many of these HSF and HSP members have additionally been described as key players in ROS signaling and regulation (Katano et al., 2018). Chromatin-based and epigenetic responses have also been identified as central to stress memory and adaptation (Friedrich et al., 2019; Lämke and Bäurle, 2017). A recent study in potato demonstrated a light-dependent acquired thermotolerance response, highlighting expression differences in chromatin-remodeling genes and HSPs, as well as genes involved in hormone pathways, cell-wall modification, protein turnover, and photosynthesis between acclimated and non-acclimated plants (Trapero-Mozos et al., 2018).

Also of potential interest is the phenomenon of cross-priming, where a sub-lethal stimulus with one type of stress (i.e. cold, drought, salt, or heat) leads to improved tolerance to another stress. For example, reports of cold treatment leading to increased heat tolerance have been described in grape, and heat treatments have been used to decrease chilling injury in tomato (Wan et al., 2009; Zhang et al., 2013). Similarly, priming plants with chemicals has been used as a way to harden plants to future abiotic stresses (reviewed in (Savvides et al., 2016)). A proposed hypothesis to explain that abiotic stresses, as well as these chemical priming agents, all induce similar physiological and molecular changes, such as induction of stress-related genes and antioxidants, and protein modifications. To develop the potential of chemical priming agents or the use of cross priming mechanisms in sunburn risk

assessment in apple will require substantial research into understanding the conditions that induce stress protection mechanisms (Fig. 3).

In addition to the molecular and physiological components discussed here, many more genes identified in Arabidopsis appear to be involved with temperature memory and acquired heat tolerance. These genes may help guide the study of acclimation in crop systems through the identification of gene orthologs in these crop species. Moving forward, research into the molecular mechanisms underlying acclimation to sunburn-inducing stresses in apple, as well as sunburn development, will help elucidate how fruit acclimate to high heat and light throughout the growing season and inform management strategies to avoid solar injury.

8. New strategies for early detection of sun damages on apples

Lack of genetic information regarding the molecular mechanism commanding photooxidative and heat stress during sun damage on apple fruit highlights the importance to develop investigative frameworks to better understand their regulation. Progress in this arena can be in breeding programs that are currently in regions that experience sunburn pressure and areas that are forecast to be impacted by future climate change. To support this, several studies have been conducted to identify and characterize TFs involved in resistance or tolerance to different abiotic stresses, with successful results in several crop systems (Gürel et al., 2016). Molecular manipulation of TFs has the potential to be more effective than modification of an individual gene involved in a specific stress response, due to the ability to modulate expression of

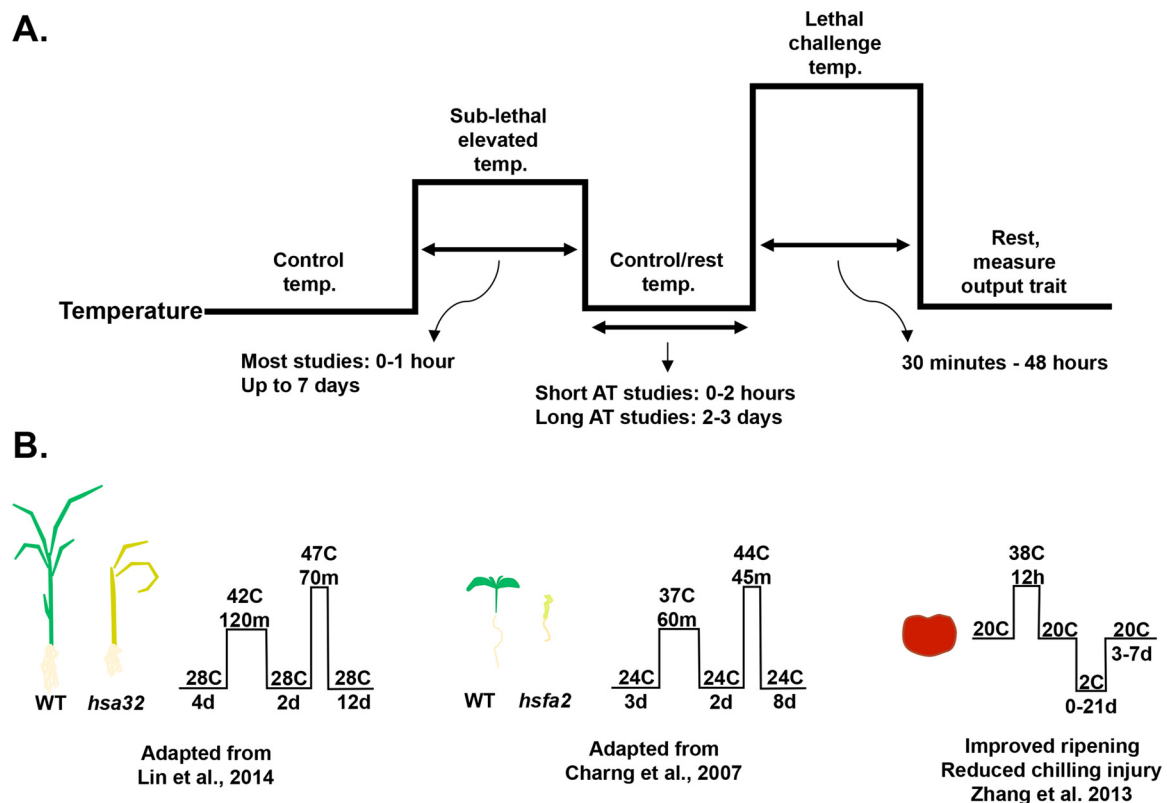


Fig. 3. Variable temperature regimes are used to investigate the molecular players and mechanisms underlying acclimation and thermotolerance. A) Acclimation and acquired thermotolerance studies often involve raising the temperature to an elevated, but sub-lethal temperature to induce plant defenses and stress memory. Most studies to date have used a 30–60 minute stimulus, however some studies have elevated temperatures up to 7 days. This will be followed by a rest at the control temperature. Studies investigating short-term acquired thermotolerance will have a short rest of a couple hours. Long-term thermotolerance studies will allow a 2–3 day rest. Following the rest, plants are then challenged with an otherwise lethal heat shock stimulus, usually 30–90 minutes, but some studies have lengthened this time to 48 h. Variable rest times are then followed by measurement of the output trait. B) Several examples of characterization of genes involved in acquired thermotolerance, as well as studies into cross-priming effects. Both HSA32 and HSA2 are involved in long-term acquired thermotolerance and plant mutants lacking their expression are unable to acclimate to heat stress. In tomato, a hot-air stimulus was able to improve ripening and reduce chilling injury in cold-stressed tomato fruit.

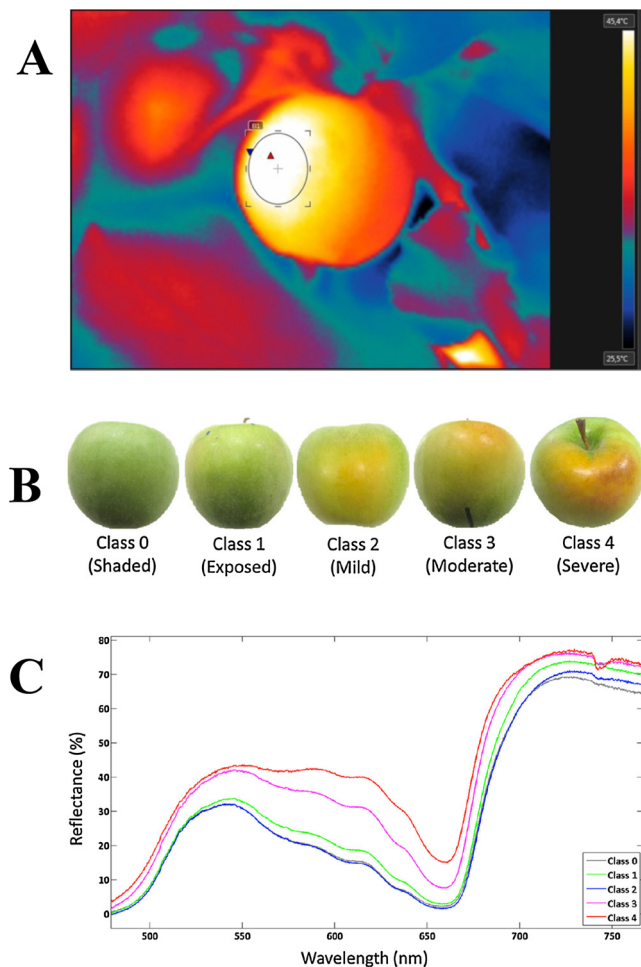


Fig. 4. A) Thermal of infrared image used to calculate the crop water stress index (CWSI), an early predictor of sun damage on apple surface. B) Classification of sun-injured fruits to calculate damage in peel by Vis/NIR spectra. C) Vis/NIR spectra of fruit from different sun exposure categories (classes 0–4). Images adapted from Torres et al. (2016a, 2016b).

several downstream-genes involved in metabolic pathways associated with stress tolerance in plants (Khong et al., 2008; Nakashima et al., 2012).

Torres et al. (2013) performed a study analyzing sun-exposed versus non-exposed tissues of apples and reported that osmotic stress is also generated under photooxidative and heat stress in the field, evidenced by lower water content and increase sugars as sorbitol and glucose in sun-exposed tissue. Recently, a crop water stress index (CWSI) was also proposed as an early indicator of sun-damage in fruit without visible symptoms (Fig. 4) (Torres et al., 2016b). Through thermal images, the occurrence of sunburn symptoms in Fuji was predicted to be earlier than in Royal Gala apples. These responses highlight cultivar-specific responses to sun-related stress. In addition to CWSI analysis, Vis/NIR fingerprint analysis of fruit surfaces with different sun-exposure was also able to predict sun damage in Granny Smith apples (Fig. 3) (Torres et al., 2016a). Both technologies could be useful for early identification of molecular events commanding physiological responses involved in sunburn, prior to the development of visual symptoms.

9. Genomic information and new transcriptomic challenges to support future breeding strategies

Understanding the molecular basis that control the responses of apple fruit exposed to excessive sunlight or temperature, which cause sunburn damage, is imperative for the development of new cultivars

that are better suited to hot and dry environments around the world. Identifying the underlying physiology imparting sunburn resistance in the orchard will also help in the creation of new protective products or decision aid systems that can help reduce losses for susceptible cultivars. The full apple genome that is available today (Velasco et al., 2010) provides opportunities to identify key genetic and molecular mechanisms contributing to sunburn in apple. Specifically, the analyses of promoter regions of differentially expressed genes between susceptible and tolerant cultivars in order to identify common *Cis*-regulatory elements will be helpful to distinguish TFs from RNAseq data, which could be critical for regulating the molecular response that occurs prior to physiological disorder development. With this information, molecular markers could help design new cultivars in breeding programs targeted to apple production in semi-arid growing conditions such as those found in Chile, WA state-USA, South Africa, Argentina, Australia and Israel, among others.

Declaration of Competing Interest

The authors declare no competing financial interests.

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