Adv. Hort. Sci., 2026 40(2): 219-234
DOI: 10.36253/ahsc-19221
https://oaj.fupress.net/index.php/ahs

Review paper

AHS
Advances in Horticultural Science

Heat and light induced physiological disorders in apples: Sunburn, mechanisms, and management strategies

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Citation:
İKİNCİ A., 2026 - *Heat and light induced physiological disorders in apples: Sunburn, mechanisms, and management strategies.* - Adv. Hort. Sci., 40(2): 219-234

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Data Availability Statement:
All relevant data are within the paper and its Supporting Information files.

Competing Interests:
The authors declare no conflict of interests.

Received for publication 20 November 2025
Accepted for publication 28 January 2026

Key words: Climate change, fruit surface temperature, heat stress, oxidative stress, photoselective net, sunburn.

Abstract: Global climate change has intensified heat and light stress in apple (*Malus domestica* Borkh.) orchards, markedly increasing the incidence of sunburn and related physiological disorders. Sunburn represents a complex stress response triggered when fruit surface temperature (FST) exceeds critical thresholds, leading to oxidative imbalance and structural damage. This review provides an integrated synthesis of sunburn typology - sunburn browning, sunburn necrosis, and photo-oxidative sunburn - and explores underlying cellular and biochemical mechanisms, including reactive oxygen species (ROS) accumulation, membrane peroxidation, and pigment degradation. Evidence indicates that FST values between 46-52°C are decisive in the onset of photo-oxidative injury and necrotic lesions, compromising fruit integrity and storage potential. Secondary disorders such as watercore, lenticel breakdown, and bitter pit are discussed as consequential outcomes of thermal stress. Mitigation strategies are critically evaluated, highlighting the efficacy of photoselective nets, kaolin-based particle films, and evaporative cooling, which collectively reduce sunburn incidence by up to 60%. Emerging technologies, including sensor-based early warning systems and precision agriculture tools, offer novel perspectives for proactive management. Conclusively, sustaining fruit quality under increasingly variable climatic conditions requires a multidimensional approach that integrates microclimate regulation with physiological optimization.

1. Introduction

Apple (*Malus domestica* Borkh.) is one of the most widely cultivated fruit species worldwide, occupying more than 4.6 million hectares with an annual production exceeding 97 million tons, and it represents a crop of high nutritional and economic importance (FAO, 2023). Despite continuous improvements in orchard management and cultivar development, the increasing frequency and intensity of heat and radiation events associated with climate change have markedly

AHS - Firenze University Press
ISSN 1592-1573 (on line) - 0394-6169 (print)

intensified the incidence of sunburn and related physiological disorders in apple production systems. In regions characterized by Mediterranean-type climates, FST frequently reaches 45-52°C during summer, a threshold range that substantially elevates sunburn risk and severity (Schrader *et al.*, 2003; Reig *et al.*, 2020). This damage is not limited to visual peel injury but also predisposes fruit to secondary storage disorders such as sunburn necrosis, Fuji stain, and lenticel breakdown.

Sunburn is fundamentally the result of the combined action of thermal stress and photo-oxidative damage. When FST rises approximately 10-15°C above ambient air temperature, cellular membranes destabilize, proteins denature, and reactive oxygen species (ROS) accumulate, triggering oxidative imbalance within peel tissues (Morales-Quintana *et al.*, 2020). Concomitant degradation of photosynthetic and photoprotective pigments - including chlorophylls, carotenoids, and anthocyanins - further weakens photoprotection and leads to irreversible color loss (Olivares-Soto and Bastías, 2020). Based on physiological injury patterns, sunburn is classified into three major forms: sunburn browning (SB), sunburn necrosis (SN), and photo-oxidative sunburn (PS), which develop at increasing combinations of radiation load and thermal stress (Racsko and Schrader, 2012).

Field studies conducted across multiple seasons in neotropical orchards have demonstrated that FST is the primary operational variable integrating incoming radiation, air temperature, and orchard water status in determining sunburn onset and progression. Under photoselective netting systems, FST distributions shift downward and become more homogeneous compared with non-netted canopies, thereby reducing the occurrence of extreme thermal events (Severino *et al.*, 2021). Notably, sunburn progression has been shown to correlate more strongly with soil water balance (SWB) than with daily maximum air temperature, highlighting irrigation and water relations as critical co-determinants of risk alongside thermal load (Severino *et al.*, 2020).

The microclimate surrounding individual fruits is further shaped by canopy structure, fruit position, exposure duration, air humidity, wind velocity, and plant water status (Kalcsits *et al.*, 2017). Water stress, in particular, reduces epidermal thickness and increases thermal conductivity of the peel, thereby enhancing cellular susceptibility to heat injury (Yaqoobi *et al.*, 2024). These interacting factors explain why substantial variability in sunburn severity is commonly observed even within the same orchard block.

Recent advances in sensing technologies now permit more precise quantification of sunburn risk at both the tree and harvest scales. Sensor-based diagnostics, including visible-near-infrared reflectance indices such as the Plant Senescence Reflectance Index (PSRI) and whole-fruit hyperspectral imaging (HSI), provide reliable tools for assessing sun exposure, pigment transitions, and early sunburn development, thereby complementing FST-based management approaches (Severino *et al.*, 2020; Mogollón *et al.*, 2024). At the biochemical level, cultivar-specific δ-absorbance signatures and associated heat-stress metabolites scale with browning severity, strengthening mechanistic links between thermal load, pigment degradation, and oxidative status (Ross *et al.*, 2023). Moreover, rootstock-dependent differences in damage-free yield under sustained heat stress underscore the importance of genotype × microclimate × water relations interactions in determining orchard resilience (Xu *et al.*, 2022).

Collectively, these findings establish sunburn as a complex physiological disorder driven by tightly coupled environmental, biochemical, and genetic processes. Effective mitigation therefore requires an integrated strategy that combines microclimate modification, physiological monitoring, and targeted orchard management. In addition, recent molecular evidence indicates that transcriptional control of the procyanidin pathway (e.g., MdGATA15/MdMYBR9 →MdANR) contributes to peel resilience under combined heat-light stress, providing a mechanistic bridge from gene regulation to field-level tolerance (Feng *et al.*, 2025; Fu *et al.*, 2025). This review synthesizes current knowledge on the mechanisms of sunburn development, its cellular and biochemical consequences, associated postharvest disorders, and modern mitigation strategies, with the objective of guiding the development of more resilient apple production systems under a warming climate.

2. Types and Mechanisms of Sunburn

Definition and formation process of sunburn

Sunburn in apples is defined as a physiological disorder that occurs in epidermal and subepidermal

cells as a result of direct exposure of the fruit surface to solar radiation. This disorder arises from the synergistic effect of heat and radiation and is generally characterized by symptoms such as discoloration of the fruit surface, tissue degradation, skin cracking, and necrosis. The severity of sunburn is evaluated as a result of the interaction between environmental factors (air temperature, solar radiation, relative humidity, wind speed) and the physiological characteristics of the fruit (water content, pigment composition, epidermal thickness).
According to Schrader *et al.* (2003) and Racsko and Schrader (2012), sunburn occurs when FST exceeds 45°C and is classified into three different forms (Fig. 1): Sunburn Browning (SB), Sunburn Necrosis (SN), and Photo-oxidative Sunburn (PS).

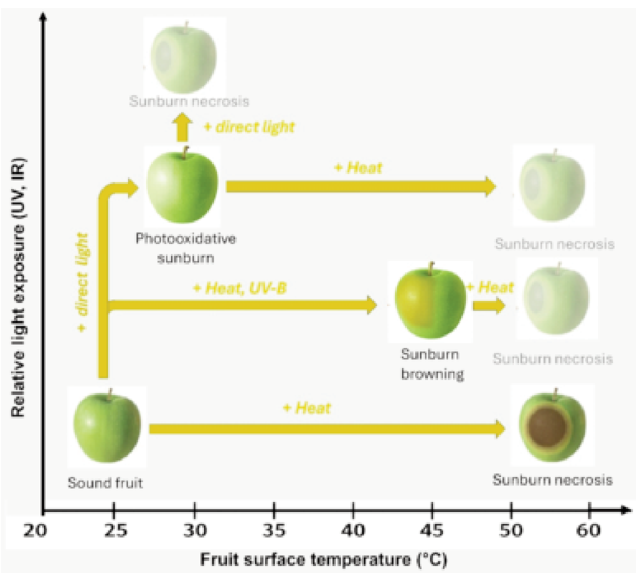

Fig. 1 - Conditions for the development of three sunburn types in apple fruit. Sunburn necrosis (SN), Sunburn browning (SB), and Photo-oxidative sunburn (PS). SN results from thermal cell death at fruit surface temperatures (FST) near 52°C. SB occurs under combined exposure to high temperature (45-49°C) and UV-B radiation without cell mortality. PS develops under visible light when non-acclimated, shade-grown fruit are suddenly exposed to sunlight and can occur at FST below 31°C. SB and PS may progress to SN with increasing FST or prolonged solar exposure. Excessive heat and UV-B are prerequisites for SB and SN; SB and SN do not revert to PS. (Adapted from Racsko and Schrader, 2012).

Sunburn browning (SB)

Sunburn browning is defined as the most common form of sunburn in apples and is induced by both an increase in FST and exposure to UV-B radiation (Racsko and Schrader, 2012). SB generally occurs under conditions where FST remains in the range of 46-49°C for approximately 60 minutes accompanied by UV-B radiation (Schrader *et al.*, 2003). At the onset of this form, cell death was not observed; however, yellowing, bronzing, and browning were reported in the epidermal tissue as a result of chlorophyll degradation and phenolic oxidation (Felicetti and Schrader, 2009 a, b). Pigment analyses revealed a decrease in anthocyanin and chlorophyll concentrations, while phenolic compounds accumulated; this was interpreted as an indicator of oxidative stress response (Morales-Quintana *et al.*, 2020). Moving beyond visual symptoms, recent studies on 'Buckeye Gala' apples provide a more detailed quantitative picture. It has been observed that as sunburn browning (SB) becomes more severe, the fruit develops a thicker cuticle and the sun-exposed side becomes notably firmer. On a metabolic level, while anthocyanin levels in the peel drop, there is a significant buildup of tartaric esters and total phenolics in the flesh underneath (Ross *et al.*, 2023). Researchers are now using specific measurements like skin absorbance ($\delta A_{670-720}$) to better track how fruit reacts to long-lasting heat waves (Ross *et al.*, 2023). Additionally, in regions with neotropical climates, monitoring tools such as chlorophyll fluorescence and reflectance indices have become essential for detecting the early stages of this damage (Severino *et al.*, 2020). The incidence of SB was reported to be higher under conditions dominated by hot and dry winds, especially in fruits located on the southwest side of the tree. Microscopic examinations revealed shrinkage in epidermal cells, cuticular cracks, and stomatal deformations (Reig *et al.*, 2020). Differences in susceptibility among cultivars were observed; 'Honeycrisp' and 'Cameo' were found to be more sensitive, while 'Pink Lady®' was more tolerant (Schmidt, 2018). Among management strategies, photoselective nets and kaolin applications were found to significantly reduce the incidence of SB (Kalcsits *et al.*, 2017; Reig *et al.*, 2020).

On peak heat-stress days, the use of 50% black shading nets has been shown to eliminate FST values exceeding approximately 46°C, significantly reduce within-canopy thermal variability, and shift harvest distributions toward the mild-damage category. Nevertheless, these thermal advantages should be carefully weighed against associated capital expenditures (CAPEX), including net infrastructure, support systems, and installation costs, as well as operating expenditures (OPEX), such as seasonal handling and maintenance, cleaning and re-application, water and energy consumption, and labor training requirements. Moreover, potential impacts on fruit coloration and market quality should be explicitly considered when implementing shading technologies in commercial orchard systems (Severino *et al.*, 2021).

Sunburn necrosis (SN)

Sunburn necrosis is the most severe form of sunburn in apples and is entirely heat-induced, not requiring UV radiation. It has been determined that when FST temporarily exceeds approximately 52°C, plasma membranes in epidermal and subepidermal cells deteriorate and irreversible cell death occurs (Schrader *et al.,* 2003; Racsko and Schrader, 2012). In this case, dark brown to black necrotic spots form on the fruit surface, and tissue collapse and skin cracking are observed due to the release of lysosomal enzymes (Glenn *et al.,* 2002). Sunburn necrosis generally occurs more frequently in regions dominated by hot and dry winds, especially in fruits located on the southwest side of the tree. At the cellular level, increased activities of phenolic oxidase and peroxidase, elevated lipid peroxidation, and increased membrane permeability leading to ion leakage have been identified; this accelerates water loss and causes wrinkling of the skin (Reig *et al.,* 2020; Morales-Quintana *et al.,* 2020). Microscopic examinations revealed epidermal shrinkage, cuticular cracks, and stomatal deformations. The incidence of SN increases under conditions of high air temperature and low humidity, and FST can be 10–15°C higher than air temperature (Schrader *et al.,* 2003). Photoselective nets and evaporative cooling applications were found to reduce FST by 2-4°C and significantly decrease SN risk (Kalcsits *et al.,* 2017; Reig *et al.,* 2020).

Photo-oxidative sunburn (PS)

Photo-oxidative Sunburn (PS) has been reported to occur when fruits that have developed in shade are suddenly exposed to full sunlight, particularly to high levels of photosynthetically active radiation (PAR) (Racsko and Schrader, 2012). This type of damage can occur even at low fruit surface temperatures (30-40°C) and is characterized by pale, bleached spots on the surface, with severity ranging from mild photo-oxidative lesions to advanced necrosis as illustrated in figure 2. The incidence of PS is higher in fruits exposed after branch breakage, thinning, summer pruning, or postharvest exposure. Mechanistically, high photon flux density suppresses Photosystem II (PSII) in chloroplasts, resulting in increased accumulation of reactive oxygen species (ROS) (Felicetti and Schrader, 2009a). ROS accumulation leads to lipid peroxidation, protein denaturation, and nucleic acid damage, forming the basis of photo-oxidative stress. Furthermore, low anthocyanin and flavonoid contents play an important role in the development of PS; the deficiency of these pigments reduces photoprotective capacity and intensifies oxidative damage (Morales-Quintana *et al.,* 2020). Microscopic examinations revealed shrinkage in epidermal cells, cuticular cracks, and stomatal deformations (Reig *et al.,* 2020).

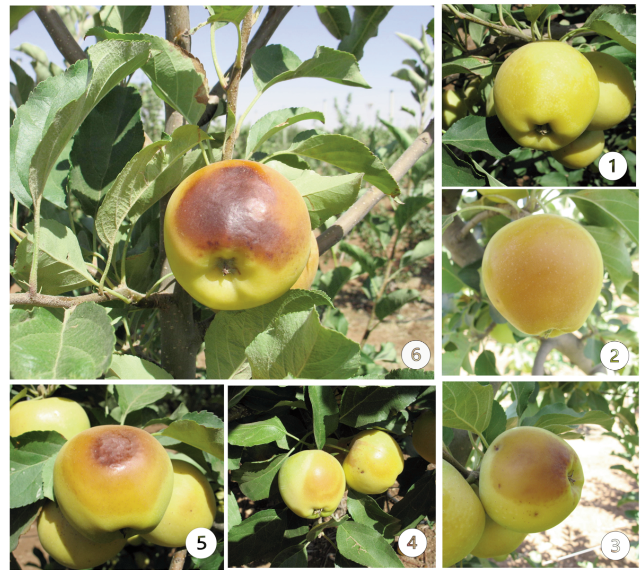

Fig. 2 - Types and severity levels of sunburn in apples: (1) Photo-oxidative sunburn; (2-4) Sunburn browning progressing from mild to severe; (5-6) Sunburn necrosis.

In shade-grown fruit suddenly exposed, visible-NIR skin spectroscopy and δ-absorbance changes provide early optical markers of PS severity; low anthocyanin/flavonoid content reduces photoprotection, consistent with cultivar-resolved metabolite patterns (Ross *et al.*, 2023).

Factors affecting sunburn

It has been determined that both environmental and plant-related factors play a role in the occurrence of sunburn. Among environmental factors, temperature, solar radiation intensity, wind speed, relative humidity, and water stress are reported as the most important (Racsko and Schrader, 2012). Plant-related factors are associated with fruit position on the tree, peel structure, color pigments, cuticular thickness, and antioxidant capacity. In trees with open canopy structure and sparse pruning, fruit surfaces are exposed to more sunlight, thus increasing sunburn incidence (Felicetti and Schrader, 2009 b). Fruit surface color is also an important factor; dark-colored fruits (e.g., 'Fuji') absorb more radiation, thereby increasing FST (Felicetti and Schrader, 2008; Torres *et al.,* 2013). The interaction of these factors is considered the main mechanism determining the incidence and severity of sunburn. Recent multi-season field observations further demonstrate that sunburn dynamics are more closely associated with shortwave radiation balance (SWB) than with maximum air temperature (Tmax), exhibiting moderate to strong interannual coupling (-0.37 to -0.70, depending on season). Moreover, these analyses indicate that rootstock-dependent differences in canopy vigor and plant water relations play a critical role in modulating damage-free yield under prolonged heat stress conditions (Severino *et al.*, 2020; Xu *et al.*, 2022).

Fruit surface temperature (FST) and threshold

FST has been defined as the most critical parameter in sunburn formation. Schrader *et al.* (2003) reported that sunburn in apples begins at 46°C and that necrotic lesions develop at temperatures above 52°C. Factors determining FST include ambient temperature, radiation intensity, wind speed, fruit angle, and surface albedo.

Especially under conditions of low wind speed and low air humidity, the fruit surface cannot provide convective cooling, and heat accumulation increases rapidly. This situation causes large temperature differences even under microclimatic conditions. Glenn *et al.* (2002) reported that kaolin particle films increased solar reflectance on the fruit surface, reduced FST by an average of 4-5°C, and decreased sunburn incidence by 40%.

The biophysical basis of sunburn is the disruption of oxidative balance at the cellular level due to heat and light stress. The development process is shaped by pigment degradation, membrane damage, ROS accumulation, and changes in enzymatic activity. Management of FST is possible through both microclimate adjustments and the use of photoselective materials.

Recent side-by-side field trials further support the central role of FST management, demonstrating that shading net systems markedly reduce the proportion of fruit experiencing injurious thermal exposure (e.g., 0% of observations exceeding 46°C under 50% black netting, compared with 35-43% in non-netted or particle-film-treated plots). In contrast, particle film applications exhibited season-dependent effectiveness and practical limitations, including reduced coverage persistence and the need for removal during packing operations, particularly under humid summer conditions (Severino *et al.*, 2021).

Therefore, effective control of sunburn requires integrated use of practices that reduce fruit surface temperature, increase reflectance, and balance plant physiology (e.g., kaolin, netting systems, evaporative cooling).

3. Molecular and Physiological Mechanisms of Sunburn

Sunburn in apples is a multilayered stress response that occurs at the cellular and molecular level due to the simultaneous effect of heat and radiation. The increase of FST up to 50°C disrupts the stability of cell membranes, leading to oxidative imbalance, metabolic dysfunction, and structural deformation. This process is shaped by the interaction of interconnected biochemical pathways, including excessive production of reactive oxygen species (ROS), weakening of the antioxidant defense system, pigment degradation, activation of heat shock proteins, and impairment of cuticle-cell wall integrity (Racsko and Schrader, 2012; Morales-Quintana *et al.*, 2020).

Recent advances in quantitative spectroscopy have further strengthened this mechanistic framework by demonstrating that the severity of browning is closely associated with characteristic shifts in δ absorbance and the accumulation of heat-stress-related metabolites, thereby providing a functional diagnostic link between thermal load, pigment dynamics, and cellular ROS status (Ross *et al.*, 2023).

Moreover, recent molecular findings suggest that the fruit's ability to defend itself depends heavily on how it regulates the flavonoid and procyanidin (PA) biosynthetic pathways. Specifically, the accumulation of PAs and chlorogenic acid acts as a natural protective barrier against heat and light stress, a process largely controlled by the key regulatory gene MdANR (Feng *et al.*, 2025).

Oxidative stress and cellular damage process

High light and temperature conditions disrupt the electron transport systems in organelles such as chloroplasts, mitochondria, and peroxisomes, causing excessive ROS formation (Schrader *et al.*, 2003). Reactive molecules such as superoxide anion (O_2^-), hydrogen peroxide (H_2O_2), and hydroxyl radical (OH·) interact with membrane lipids, proteins, and nucleic acids, weakening cellular integrity (Torres *et al.*, 2013; Morales-Quintana *et al.*, 2020).

In this process, the increase in malondialdehyde (MDA) accumulation indicates that membrane permeability has deteriorated and ion leakage has begun. Mitochondrial dysfunction leads to disruptions in energy production, causing the collapse of cellular metabolism (Yaqoobi *et al.*, 2024). ROS accumulation also plays a role in cellular signaling, altering the activity of stress response genes. Thus, sunburn transforms from a local tissue reaction into a systemic stress response throughout the fruit (Willsea *et al.*, 2023).

These organelle level effects align with field scale observations where shortwave radiation balance (SWB) modulates the pace of sunburn progression more than Tmax, underscoring water relations as a central axis for risk reduction (Severino *et al.*, 2020).

Weakening of the antioxidant defense system

Plants have developed an advanced antioxidant defense system to limit the harmful effects of ROS. However, under sunburn conditions, the efficiency of this system decreases. Significant reductions are observed in the activities of superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), and glutathione reductase (GR), while the activities of phenylalanine ammonia-lyase (PAL) and polyphenol oxidase (PPO) increase (Ranjan *et al.,* 2024).

This enzymatic imbalance accelerates the oxidation of phenolic compounds, causing browning of the peel and reduction in tissue firmness. The weakening of oxidative defense facilitates ROS accumulation, leading to further damage to membrane lipids, increased water loss, and disruption of ion balance. This cascade of events constitutes the fundamental biochemical processes determining the progression of sunburn.

In parallel with these enzymatic changes, the activation of procyanidin (PA) biosynthetic pathways provides an additional biochemical buffering mechanism. Enhanced PA accumulation contributes to improved ROS scavenging capacity and stabilization of cellular membranes, thereby functionally complementing the classical enzymatic antioxidant network under sunburn stress conditions (Feng *et al.*, 2025; Fu *et al.*, 2025).

Pigment degradation and photo-oxidative damage

The color changes observed in sunburn result from the degradation of photosynthetic and photoprotective pigments. High temperature and radiation cause the breakdown of chlorophyll, oxidation of carotenoids, and suppression of anthocyanin synthesis (Olivares-Soto and Bastías, 2020). These events have been associated with inhibition of electron transport in Photosystem II (PSII) (Racsko and Schrader, 2012).

In cultivars such as 'Fuji' and 'Gala', a decrease in the expression of genes responsible for anthocyanin synthesis, such as *chalcone synthase (CHS)* and *UDP-glucose:flavonoid 3-O-glucosyltransferase (UFGT)*, has been detected (Willsea *et al.,* 2023). Pigment loss not only causes color changes but also reduces the fruit's capacity to reflect light energy and prevent photo-oxidative damage, as illustrated by sunburn symptoms on the red cultivar 'Mondial Gala' in figure 3.

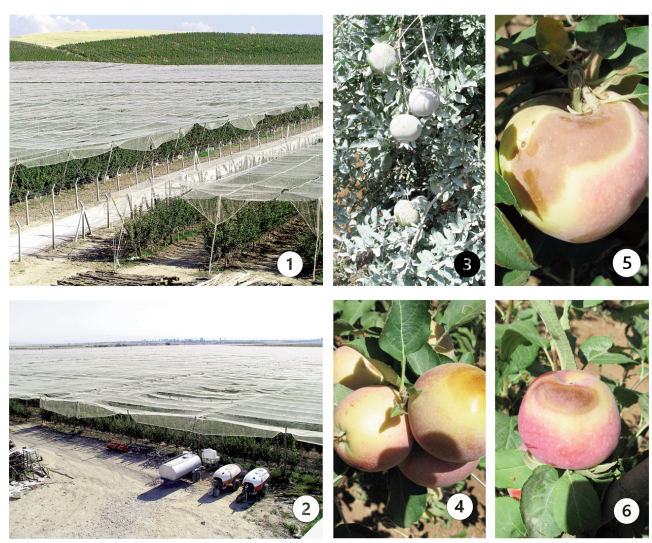

Fig. 3 - Sunburn management and damage types in fruit crops: (1-2) Shade nets used in apple orchards to prevent sunburn, hail, and bird damage; (3) Kaolin application in pomegranate to reduce sunburn; (4-6) Different sunburn types on 'Mondial Gala' apple cultivar.

In parallel with these pigment-related changes, cultivar-specific δ absorbance patterns show a clear relationship with pigment loss and the severity of browning, allowing reliable on-tree assessment of sunburn intensity and supporting the design of targeted mitigation strategies (Ross *et al.*, 2023).

Heat shock proteins and cellular protection mechanisms

Excessive heat disrupts the natural structure of proteins in the cell, causing loss of function. In response, the plant synthesizes heat shock proteins (HSPs) as a protective mechanism. Particularly, families such as HSP70, HSP90, and small HSPs (sHSPs) support protein stability by enabling the refolding of denatured proteins (Morales-Quintana *et al.,* 2020; Ranjan *et al.,* 2024). These proteins also contribute to maintaining membrane integrity by regulating lipid composition.

However, when FST exceeds 52°C, the protective effect of HSPs becomes insufficient, resulting in protein aggregation, cytoplasmic precipitation, and irreversible cellular damage (Schrader *et al.,* 2003). This stage represents the critical threshold at which sunburn physiologically progresses to the irreversible necrotic phase.

Consistent with field observations, the protective capacity of HSP-mediated responses collapses once FST exceeds approximately 52°C. Under these conditions, no durable external chemical interventions have yet been shown to sufficiently enhance HSP expression or antioxidant gene activity to extend this intrinsic tolerance limit, thereby underscoring the importance of genetic and molecular approaches for improving heat resilience in apple fruit (Morales-Quintana *et al.*, 2020; Severino *et al.*, 2021).

Gene expression and epigenetic regulation

Sunburn causes profound changes not only in cellular metabolism but also in gene regulation. Transcriptome analyses show that under high-temperature conditions, the expression of antioxidant genes (APX1, CAT1) decreases, while the activity of ethylene-responsive factor (ERF) genes increases (Morales-Quintana *et al.*, 2020).

Additionally, epigenetic regulation mediated by microRNAs (miRNAs) is also effective in this process. Changes in the levels of miRNAs such as miR398, miR156, and miR172 have been reported to influence the functional control of SOD and HSP genes (Ranjan *et al.*, 2024). Although these regulations support short-term adaptation, they cannot provide complete protection under prolonged sunburn stress.

Recent functional studies have provided deeper insight into this regulatory network. It has been demonstrated that the transcription factor MdGATA15 directly activates the MdANR promoter, thereby enhancing procyanidin biosynthesis and mitigating photo-thermal damage under combined high light and temperature stress; both overexpression and transient expression assays have confirmed reduced visible sunburn symptoms and increased accumulation of PA-associated metabolites (Fu *et al.*, 2025). In parallel, MdMYBR9 has been shown to directly upregulate MdANR, conferring anti-sunburn responses in both fruit peel and callus tissues. Dual-luciferase reporter assays, yeast one-hybrid analysis, and electrophoretic mobility shift assays collectively verify promoter binding and transcriptional activation, positioning the MdMYBR9-MdANR-PA regulatory module as a central adaptive mechanism in apple fruit under thermal stress (Feng *et al.*, 2025).

Changes in cell wall and cuticle structure

Sunburn causes significant structural changes in the cuticle and cell wall, which are the primary defense barriers of the fruit peel. High temperature reduces the proportion of wax components in the cuticle, increasing permeability; this accelerates water loss and oxidative damage (Olivares-Soto and Bastías, 2020). In addition, the observed increase in the activity of pectin methylesterase (PME) and polygalacturonase (PG) enzymes leads to the breakdown of pectin chains and a reduction in cell wall strength (Ranjan *et al.,* 2024).

These structural deteriorations make the fruit more susceptible to oxidative stress and penetration by secondary fungal pathogens (e.g., *Alternaria alternata*, *Botrytis cinerea*) (Racsko and Schrader, 2012; Morales-Quintana *et al.,* 2020). Therefore, these impairments in the cell wall and cuticle are considered the morphological reflections of the physiological collapse observed in the advanced stages of sunburn (Racsko and Schrader, 2012).

Recent evidence further indicates that time-sensitive nutritional management interacts closely with cell wall and cuticle dynamics. In particular, mid-May foliar applications of $CaCl_2$ (1%) combined with boron (2 g L^{-1}) have been shown to significantly reduce sunburn incidence while improving fruit firmness and size. In contrast, similar treatments applied in mid-June exhibit limited effectiveness, highlighting a narrow phenological window during which calcium-mediated stabilization of cell wall and cuticle structures can be achieved (Khadivi and Hosseini, 2024).

4. Associated Physiological Disorders

Although sunburn in apples appears to be a superficial problem primarily observed in the epidermis, it actually triggers a multidimensional stress response that deeply affects the physiological balance of the fruit, often accompanied by disorders such as lenticel breakdown, bitter pit, and watercore (Fig. 4). High temperature and intense light exposure increase epidermal permeability, accelerate ROS accumulation, and weaken cell membrane stability, making the fruit more susceptible to various secondary disorders. Therefore, in orchards where sunburn occurs, the likelihood of secondary disorders such as sunburn necrosis, Fuji stain, bitter pit, watercore, and lenticel blotch pit, which significantly reduce quality increases. Indeed, Racsko and Schrader (2012) and Reig *et al.* (2020) reported that the incidence of secondary disorders associated with sunburn can reach up to 30%. This indicates that sunburn is not limited to damage on the peel but initiates a chain reaction that threatens the metabolic integrity of fruit tissue.

Fig. 4 - Heat- and light-related physiological disorders in apples: (1) Lenticel breakdown in ‘Honeycrisp’ apple [adapted from Lora and Farcuh, 2025]; (2) Bitter pit; (3) Moderate lenticel breakdown in ‘Gala’ apple [adapted from Lora and Farcuh, 2025]; (4) Internal browning; (5) Lenticel blotch pit [adapted from Dar, 2024]; (6) Watercore.

Thermal regulation through fruit surface cooling and canopy shading contributes not only to the mitigation of external sunburn symptoms but also to the maintenance of internal physiological homeostasis. By constraining fruit temperature within non-injurious limits, these practices preserve vascular functionality and stabilize the translocation of calcium and carbohydrates. Such stabilization reduces the risk of localized mineral deficiencies and carbohydrate imbalances that predispose fruit to secondary disorders, including bitter pit and watercore.

Secondary disorders associated with sunburn

In fruits affected by sunburn, structural weakness is observed in cell membranes, cuticle, and epidermal tissue; this increases the impact of oxidative stress and paves the way for the emergence of secondary damage. Increased epidermal permeability accelerates water loss, disrupts ion balance, and makes tissues more vulnerable to storage stress, especially due to the oxidation of phenolic compounds. Reig *et al.* (2020) reported that the incidence of post-storage disorders significantly increased in fruits exhibiting SN-type sunburn and that the occurrence of skin scald reached high levels. Racsko and Schrader (2012) stated that fruits with sunburn showed significant increases in both postharvest respiration rate and oxidative stress indicators. These findings confirm that sunburn acts as an “initiating physiopathological trigger” for secondary disorders.

Sunburn scald

Sunburn scald is an important oxidative stress disorder that occurs during cold storage in fruits exposed to sunburn. It is particularly evident in cultivars such as ‘Golden Delicious’, ‘Granny Smith’, and ‘Honeycrisp’. During sunburn, various terpenoid compounds, especially α-farnesene, accumulate in epidermal tissues. Under storage conditions, these compounds undergo oxidative polymerization, converting into conjugated trienol hydroperoxides, and these reactions cause dark brown to black discoloration of the peel (Morales-Quintana *et al.*, 2020). Reig *et al.* (2020) reported that the scald rate in fruits with SN-type sunburn could reach up to 70%, while in shaded fruits this rate remained around only

15%. These findings reveal that sunburn plays a critical role in the development of scald after storage.

Recent postharvest studies indicate that HSI enables the early identification of fruit lots with elevated scald risk at harvest, allowing susceptible fruit to be diverted from long-term storage and thereby reducing the overall incidence of storage-related losses (Mogollón *et al.*, 2024). In parallel, the application of selected plant essential oils, including thyme and lavender, has been reported to suppress postharvest decay and contribute to the maintenance of quality in heat-stressed fruit during storage (Al-Hassanavi *et al.*, 2023).

Preventing sunburn scald requires avoiding sudden changes in storage temperature, reducing oxidative stress, and limiting α-farnesene oxidation. In this context, diphenylamine applications, ethylene inhibitors such as 1-MCP, and controlled atmosphere conditions are recommended as effective strategies to reduce the risk of scald.

Fuji stain

Fuji stain is a disorder observed particularly in the ‘Fuji’ cultivar and is characterized by irregular brown spots on the peel. Its development is mainly determined by high FST, low relative humidity, and intense light exposure (Torres *et al.,* 2013). On sun-exposed surfaces, FST exceeding 45°C, increased epidermal water loss, and the formation of microcracks disrupt pigment stability; suppression of anthocyanin synthesis and increased phenolic oxidase activity result in rough spots on the peel.

Glenn *et al.* (2002) demonstrated that kaolin application could reduce the incidence of Fuji stain by up to 50%, and this effect was associated with both heat reduction and UV reflection. In addition, integrated microclimate management involving photoselective net systems, evaporative cooling, and antioxidant support is recommended to limit the development of this disorder. The severity of Fuji stain has been reported to increase particularly during periods when FST rises rapidly within a short time; therefore, controlling temperature fluctuations is of critical importance.

Bitter pit

Bitter pit is an important physiological disorder associated with calcium (Ca^{2+}) deficiency and appears as localized necrotic depressions on the peel surface. The higher incidence of bitter pit in fruits affected by sunburn indicates that sunburn negatively affects Ca^{2+} transport (Racsko and Schrader, 2012). Increased transpiration, epidermal water loss, and disruption of membrane integrity adversely affect xylem flow, reducing calcium (Ca^{2+}) uptake. Ca^{2+} deficiency significantly weakens membrane stability and accelerates electrolyte leakage. De Freitas *et al.* (2015) showed that Ca^{2+} deficiency severely compromises cell membrane stability and is a key determinant in bitter pit formation.

Preventing bitter pit involves foliar calcium applications (e.g., $CaCl_2$), implementing balanced irrigation programs, and reducing excessive fruit load. Additionally, reducing heat stress, which negatively affects calcium transport, can indirectly prevent the increased risk of bitter pit caused by sunburn.

Watercore

Watercore is a disorder that creates a transparent, water-soaked appearance in the fruit flesh and develops before harvest, especially during hot and sunny periods. Its formation is closely related to imbalances in sorbitol transport and sugar metabolism. Liu *et al.* (2022) reported that under high-temperature conditions, the transfer of sorbitol from phloem to xylem was disrupted, resulting in fluid accumulation in intercellular spaces.

The disorder progresses through local increases in osmotic pressure, rapid conversion of starch to sugar, and deterioration of cell membrane permeability. Chen *et al.* (2024) reported that the incidence of watercore increased up to 35% after a heatwave and that this increase was directly associated with a 4-5°C rise in FST. The development of watercore has been reported to be more intense in late-maturing cultivars such as ‘Fuji’ and ‘Ambrosia™’ (Morales-Quintana *et al.,* 2020; Reig *et al.,* 2020).

In advanced stages, watercore can turn into more serious physiological disorders such as internal browning and core breakdown. Additionally, imbalances in Ca, K, and Mg increase the risk of watercore; particularly excess K and Mg create an antagonistic effect by inhibiting Ca transport (Uçgun *et al.,* 2014). Therefore, microclimate regulation, balanced irrigation, and early harvest practices in sensitive cultivars are recommended during hot periods.

Lenticel blotch pit

Lenticel blotch pit is a disorder characterized by small, brown, and superficial depressions on the peel and has a higher incidence especially in orchards where sunburn is common. Schrader *et al.* (2003; 2011) reported that lenticels on surfaces directly exposed to sunlight dry out and become clogged, which disrupts gas exchange and makes epidermal cells more susceptible to oxidative stress. High relative humidity, low air circulation, and peel softening due to moisture can increase the severity of the disorder (Lora and Farcuh, 2025).

Nutrient imbalances are also important determinants. Dar (2024) reported that local calcium deficiency increased the incidence of lenticel blotch pit in 'Fuji' apples. Additionally, Blakey (2018) stated that excess K and Mg inhibited Ca uptake, weakening peel tissue. In cultivars with high susceptibility such as 'Gala', 'Fuji', 'Honeycrisp', 'Braeburn', 'Ambrosia', and 'Golden Delicious', the large lenticel structure and thin epidermis lead to more frequent occurrence of this disorder (Lora and Farcuh, 2025).

5. Management Strategies (Physical, Chemical, Cultural)

Physical management strategies

Shading and photoselective net systems. Shading and photoselective net systems are among the most effective methods for reducing sunburn in apple orchards. Glenn and Puterka (2010) reported that photoselective nets providing 20% shading reduced FST by an average of 4-5°C and decreased sunburn incidence by 40-60%. Photoselective nets (Fig. 3) not only reduce light intensity but also optimize photosynthetically active radiation (PAR) through wavelength selectivity. Shahak *et al.* (2009) compared the effects of nets of different colors and found that white nets reduced FST the most, while red nets had less impact on fruit color development. These findings indicate that net color is critical for both temperature control and color formation. Shading systems also help balance the microclimate by reducing wind speed and evaporation; however, excessive shading may limit photosynthetic activity, so net density should be determined at an optimum level. In conclusion, shading and photoselective nets provide an effective solution against sunburn, but they should be applied considering cultivar-specific light requirements and net characteristics.

Across multiple seasons, the use of black nets with 50% shading was shown to substantially narrow FST distributions and eliminate peak-day readings exceeding 46°C, thereby shifting harvest outcomes toward lower sunburn severity classes. Nevertheless, the agronomic benefits of this thermal regulation must be carefully balanced against capital and operational costs (CAPEX/OPEX), ongoing maintenance requirements, and potential impacts on fruit coloration, underscoring the importance of site-specific calibration of shading systems (Severino *et al.*, 2021).

Evaporative cooling systems. Evaporative cooling (EC) is considered one of the most effective active methods for controlling sunburn, especially in hot and dry climates. In these systems, both ambient temperature and FST are reduced through the evaporation of water sprayed onto the fruit surface. Schrader *et al.* (2003) reported that overhead irrigation reduced FST by an average of 8–10°C on hot days and significantly decreased sunburn incidence. Felicetti and Schrader (2008) stated that EC could reduce FST by 3-7°C. Goodwin (2017) reported in a study conducted under Australian conditions that EC could lower FST by as much as 15-20°C. Reig *et al.* (2020) revealed that the system reduced FST from 47°C to 42°C and decreased necrotic sunburn by 70%. These findings show that EC provides critical protection during extreme heat periods.

Evaporative cooling not only provides thermal protection but also improves uniform color development and peel quality. However, water quality and spraying frequency should be carefully managed; excessive humidity may trigger the development of fungal diseases (Racsko and Schrader, 2012). Therefore, modern applications prefer pulsing irrigation (e.g., 15 minutes on - 15 minutes off cycles), and irrigation is initiated when FST approaches the damage threshold, usually when air temperature exceeds 32°C (Goodwin, 2017). In new-generation systems, micro-sprinkler nozzles and automatic humidity sensors are used to increase energy and water efficiency. Furthermore, combining EC with lipophilic film coatings (Raynox™) has been reported as one of the most successful management strategies, reducing sunburn incidence by up to 95% (Schrader *et al.,* 2011; Schmidt, 2018).

Today, EC systems are integrated with precision agriculture technologies to become more efficient. Sensor-based early warning systems monitor FST and meteorological data, ensuring that evaporative cooling is automatically triggered at the right time (Wittich, 2021; Ranjan *et al.,* 2024). Additionally, when used together with photoselective nets and reflective film coatings, synergistic protection targeting both light and heat stress is achieved (Afonso *et al.,* 2025).

Integration of EC with HSI- and PSRI-based early warning systems has been shown to improve cooling precision and water-use efficiency, while structured pulsing regimes further reduce disease pressure; however, successful adoption depends on proper sensor calibration, operator training, and local water resource constraints (Severino *et al.*, 2020; Mogollón *et al.*, 2024).

These integrated approaches are among the modern strategies recommended to achieve the lowest risk level against sunburn.

Chemical management strategies

Particle film coatings (Kaolin, Surround WP). Kaolin ($Al_2Si_2O_5(OH)_4$)-based particle films form a thin white layer on the fruit surface, reflecting part of the sunlight and reducing FST Glenn *et al.* (2002) reported that FST decreased by an average of 4-6°C in apples treated with kaolin and that sunburn incidence dropped by up to 60%. Similarly, Glenn *et al.* (2002) stated that kaolin-based films reduced FST by 4-5°C and decreased sunburn by 40-60%. This effect is mainly due to kaolin's high reflectance capacity, which removes part of the solar radiation (Fig. 3).

Kaolin applications not only provide thermal protection but also create a physical barrier against pests and reduce water loss from the fruit surface (Fig. 3). Olivares-Soto and Bastías (2020) reported that kaolin application in 'Fuji' and 'Gala' cultivars reduced FST by an average of 4.8°C, limited ROS accumulation, and increased antioxidant enzyme activities (SOD, CAT, APX). These findings reveal that kaolin also plays an important role in reducing oxidative stress. Application usually begins when fruit diameter reaches 3-4 cm and is repeated at intervals of 3-4 weeks.

Some studies have reported that kaolin application may cause slight fading in fruit color but positively affects storage quality (Reig *et al.,* 2020). Schmidt (2018) emphasized that commercial formulations (Surround® WP, ScreenDuo®) could reduce UV-B absorption by up to 40%, but they create limitations such as washing requirements and color changes from a marketing perspective. Additionally, Schrader *et al.* (2011) revealed that lipophilic film coatings (RAYNOX™) provide protection by reflecting UV-B radiation and, when combined with evaporative cooling, can reduce sunburn by up to 95%. In new-generation formulations, mixtures of kaolin, calcite, and silica have been used to increase both reflectance and water retention capacity.

In conclusion, kaolin and particle film applications offer an effective strategy against sunburn by reducing both thermal load and oxidative stress; however, application intensity, cultivar-specific color requirements, and postharvest cleaning costs should be considered.

Under humid neotropical summer conditions, repeated applications, limited coverage persistence, and removal requirements during packing can constrain long-term effectiveness. Comparative field trials have further reported inferior sunburn control relative to netting systems in certain seasons, highlighting important practical limitations and cost-related trade-offs associated with particle film use (Severino *et al.*, 2021).

Oil-based coatings (RAYNOX™, Vapor Gard). Oil-based film coatings (e.g., RAYNOX™, Vapor Gard) provide protection by reflecting UV-B radiation and, when combined with evaporative cooling, have been reported as one of the most effective methods for preventing sunburn. Schrader *et al.* (2003) revealed that this combination could reduce sunburn incidence by up to 95%.

Schmidt (2018) emphasized that lipophilic film coatings offer marketing advantages but that application costs and the risk of color changes should be considered. In conclusion, chemical management strategies alone are not sufficient; when integrated with physical methods such as photoselective nets and evaporative cooling, they provide the most effective protection against sunburn.

Anti-transpirants and other film coating materials. Among chemical protectants used against sunburn, anti-transpirants and film coating materials play an important role. These substances form a semi-permeable layer on the fruit surface, reducing evaporation and preventing excessive increases in FST. Anti-transpirants are compounds that limit water loss by reducing permeability on leaf and fruit surfaces. For example, products such as di-1-p-menthene (Vapor Gard®) and pinolene (Nu-Film 17®) form a thin layer that reflects light on the surface, preventing excessive increases in FST (Felicetti and

Schrader, 2009 b). However, depending on application intensity, changes in fruit color and reductions in respiration rate may occur. Racsko and Schrader (2012) stated that these substances could sometimes increase FST instead of reducing it; therefore, they should only be used under high humidity conditions and for temporary protection. Additionally, coatings containing calcium carbonate ($CaCO_3$) have been reported to not only reduce FST but also enhance peel mechanical strength through improved calcium availability. Beyond $CaCO_3$-based formulations, recent studies further indicate that combined mineral nutrition exerts synergistic protective effects against sunburn. In particular, foliar application of 1% calcium together with 2 g L^{-1} boron in mid-May was shown to be highly effective in reducing SB incidence in 'Golden Delicious' apples. This early-season nutritional intervention not only mitigates heat-related injury but also improves key quality attributes, including fruit firmness and total soluble solids, underscoring that nutrient-based preventive strategies are most effective when implemented during the initial stages of fruit development (Khadivi and Hosseini, 2024).

Antioxidants and plant activators. Antioxidant applications are an important strategy for reducing oxidative stress associated with sunburn. Antioxidants such as ascorbate, α-tocopherol, glutathione, and phenolic compounds protect cell membrane integrity by increasing the capacity to scavenge reactive oxygen species (ROS) and alleviate the effects of sunburn. Morales-Quintana *et al.* (2020) reported that applications based on ascorbic acid and tocopherol provided internal physiological protection and reduced oxidative stress levels. The effect of these compounds becomes evident particularly when applied during fruit development and before storage. However, such applications should be carefully dosed based on leaf analyses; otherwise, there is a risk of growth retardation.

Signal molecules known as plant activators, such as salicylic acid, jasmonic acid, and brassinosteroids, increase stress tolerance by stimulating cellular defense systems. Ranjan *et al.* (2024) stated that these compounds triggered the expression of heat shock proteins (HSPs) and antioxidant genes against sunburn. This mechanism strengthens the plant's adaptation capacity under photo-oxidative stress conditions. Furthermore, it has been reported that the application of these activators strengthens the antioxidant defense system on the fruit surface and reduces ROS accumulation (Olivares-Soto and Bastías, 2020).

Recent studies have shown that the combined use of antioxidant supplements and plant activators creates a synergistic effect. Afonso *et al.* (2025) reported that this combination could reduce sunburn incidence by 40-70% and preserve fruit quality. These findings reveal that chemical management strategies should focus not only on surface protection but also on strengthening plant physiology.

Although plant activators can transiently induce antioxidant and HSP-related defense pathways, no durable upregulation sufficient to extend HSP-based tolerance beyond the critical threshold of FST ≥52°C has been demonstrated under field conditions. This limitation highlights the need to prioritize genetic and molecular strategies for achieving sustained improvements in heat tolerance (Morales-Quintana *et al.*, 2020).

Preventive mineral nutrition (Ca-B). Preventive mineral nutrition has recently emerged as an important complementary strategy for mitigating sunburn through the stabilization of cell wall and membrane structures. In this context, foliar application of calcium chloride ($CaCl_2$, 1%) in combination with boron (2 g L^{-1}), when applied in mid-May - coinciding with the transition from cell division to the onset of fruit enlargement - has been shown to significantly reduce sunburn incidence while improving key quality attributes such as fruit firmness and size. In contrast, identical treatments applied in mid-June were found to be largely ineffective, demonstrating the existence of a narrow phenological window during which calcium-mediated structural reinforcement of cell walls and membranes can be achieved. These findings emphasize that the efficacy of mineral-based preventive strategies depends not only on nutrient composition but also on precise timing relative to fruit developmental stage (Khadivi and Hosseini, 2024).

Cultural management strategies

Irrigation Management. Balanced irrigation is one of the most critical cultural factors that reduce the incidence of sunburn. In water-stressed fruits, epidermal thickness decreases, which increases thermal conductivity and raises fruit surface temperature, thereby increasing the risk of sunburn. Regular and controlled irrigation helps maintain stable FST and preserve cellular turgor (Kalcsits *et al.,* 2017).

For optimum water management, soil moisture sensors, tensiometers, or plant-based water potential measurement systems can be used. However, excessive irrigation may cause cuticular thinning and the formation of microcracks on the fruit surface, creating a predisposition to fungal infections. Therefore, irrigation programs should be dynamically planned considering evapotranspiration data and climatic conditions.

Pruning and canopy management. Canopy structure is one of the main factors determining the degree of direct exposure of the fruit surface to sunlight. Excessive thinning pruning that reduces leaf density too much causes fruits to lose protective shade and increases the risk of sunburn. Balanced pruning maintains the leaf-to-fruit ratio, optimizes light distribution, and sustains photosynthetic efficiency.

During fruit thinning, fruits on sun-exposed parts should be protected, and care should be taken not to excessively open the leaf cover. The timing of pruning is also critically important; late pruning performed in summer can increase the risk of photo-oxidative stress and sunburn in fruits suddenly exposed (Racsko and Schrader, 2012). In modern applications, canopy architecture can be optimized using light simulation models.

Cultivar selection and harvest time. The susceptibility of cultivars to sunburn varies depending on peel pigment structure, epidermal thickness, and cuticular characteristics. Dark red cultivars (‘Fuji’, ‘Red Delicious’) are more sensitive due to higher light absorption, whereas light-colored cultivars (‘Golden Delicious’) are more tolerant.

Determining the correct harvest time plays a critical role in reducing the effects of sunburn on quality. With delayed ripening, cuticular thickness increases, but surface pigments become more sensitive to oxidative stress. Therefore, the optimum harvest time for each cultivar should be determined considering both color development and sunburn risk (Serra *et al.,* 2020).

Beyond cultivar choice, increasing evidence indicates that rootstock selection plays a decisive role in determining damage-free yield under heat stress conditions. In ‘Ambrosia’ apples, rootstock-dependent differences in tree vigor and canopy architecture markedly influence the fruit microclimate. Trees grafted onto more resilient rootstocks (e.g., Geneva 935) have been shown to maintain higher yield efficiency and superior fruit quality following sustained heat events compared with more susceptible rootstocks, underscoring rootstock choice as a fundamental cultural strategy for climate-resilient apple production (Xu *et al.*, 2022).

Integrated approaches

A single method is not sufficient to prevent sunburn; physical, chemical, and cultural methods must be applied in an integrated manner. For example, the use of photoselective nets together with kaolin application can reduce FST by 6-8°C; when supported by irrigation and evaporative cooling strategies, sunburn incidence can be reduced by up to 70% (Glenn *et al.*, 2002; Afonso *et al.*, 2025).

Today, sensor systems supported by artificial intelligence enable real-time monitoring of fruit surface temperature, radiation intensity, and humidity, optimizing the timing of preventive measures. Thus, both yield and quality losses are minimized. Integrated approaches stand out as a critical strategy for sustainable production.

However, the adoption of integrated management strategies must be carefully evaluated in terms of economic feasibility, operational complexity, and long-term sustainability. Capital and operational expenditures (CAPEX/OPEX), system maintenance requirements, and potential trade-offs related to fruit coloration should be critically assessed under site-specific conditions to ensure durable field performance (Severino *et al.*, 2021).

A pragmatic risk-management framework further supports tiered triage at harvest: visibly sunburned fruit are removed at intake, HSI-classified high-risk lots are redirected to early markets, and low-risk fruit are reserved for long-term storage. This approach integrates microclimate control (netting and evaporative cooling), time-sensitive mineral nutrition (Ca-B), and sensor-guided decision support, thereby optimizing both risk reduction and resource efficiency (Mogollón *et al.*, 2024; Khadivi and Hosseini, 2024).

6. Conclusion and Future Perspectives

Rising temperatures and increasing radiation intensity associated with global climate change are driving more frequent and severe sunburn and heat-light-induced physiological disorders in apple production. This stress is not merely a superficial quality defect but profoundly disrupts fruit metabolism, storage potential, and commercial value.

At the physiological level, sunburn develops when critical thresholds of FST are exceeded, triggering oxidative imbalance characterized by excessive reactive oxygen species (ROS) accumulation, pigment degradation, membrane peroxidation, and weakening of the antioxidant defense system. The three major forms of sunburn - sunburn browning, sunburn necrosis, and photo-oxidative sunburn - manifest across a gradient of thermal and radiative stress, reflecting distinct but interconnected injury pathways.

Recent advances demonstrate that precise monitoring and management of FST are central to effective sunburn control. Sensor-based measurement platforms, artificial intelligence–supported modeling, and early-warning systems now provide producers with the ability to anticipate risk and deploy interventions with greater temporal precision. When physical (photoselective nets, kaolin, evaporative cooling), chemical (anti-transpirants, antioxidants), and cultural practices (balanced irrigation, canopy management, cultivar and rootstock selection) are integrated, substantial reductions in sunburn incidence can be achieved, although performance remains strongly dependent on local climate and cultivar-specific responses.

Looking forward, the limits of current physical and chemical interventions are increasingly defined by the intrinsic biological tolerance of the fruit. Extending cellular tolerance beyond critical thermal thresholds (e.g., FST≥52°C) will likely require advances in genetic and molecular strategies. Identification of sunburn-tolerant genotypes and the targeted use of genes associated with heat shock proteins, antioxidant systems, and photoprotective pigments represent promising directions for breeding climate-resilient cultivars.

In parallel, the continued expansion of precision agriculture will enable real-time integration of FST sensing, radiation and humidity monitoring, on-tree spectral diagnostics, and at-harvest hyperspectral triage. Future research should resolve genotype × environment × management interactions by coupling these sensing platforms with cultivar/rootstock variability and by systematically evaluating time-critical nutritional windows (e.g., early-season Ca-B applications) across diverse climatic regions. Such efforts must also explicitly quantify trade-offs between thermal protection, color development, postharvest performance, and phytosanitary outcomes.

In conclusion, sustainable mitigation of sunburn and its associated physiological disorders requires a holistic production framework that unites plant physiology, microclimate regulation, genetic improvement, and advanced agricultural technologies. The success of future apple production systems will depend on their capacity to translate this integrated knowledge into resilient, climate-adaptive management strategies that preserve both yield and fruit quality.

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