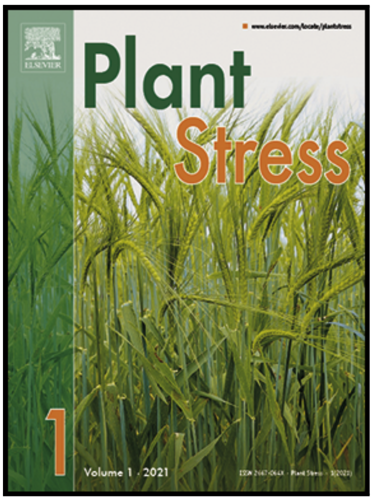

Physiological, Biochemical and Molecular Regulatory Mechanisms of Kiwifruit Responses to Heat Stress: A Review and Future Perspectives

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Highlights

- Highlights the effects of heat stress on different stages of kiwifruit plant development
- Offers an overview of key elements mechanisms induced by heat stress on kiwifruit
- Summarizes the available strategies to handle global warming effects on kiwifruit
- Presents future research directions for breeding development of HSR cultivars

Physiological, Biochemical and Molecular Regulatory Mechanisms of Kiwifruit Responses to Heat Stress: A Review and Future Perspectives

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Abstract

As a globally traded fruit, kiwifruit (*Actinidia* spp.) cultivation has expanded rapidly in recent decades. However, temperature rises induced by climate change are increasingly threatening plant production, with prolonged heat exposure causing irreversible physiological damage and significant yield losses. This review summarises the physiological, biochemical and molecular responses of kiwifruit to heat stress (HS), and possible actions to enhance crop resilience to heating, both now and in the future. We have compiled information on the effects of HS exposure on kiwifruit plants at different developmental stages, as well as on hybridisation and grafting as potential methods of increasing heat stress resistance (HSR). We also explore the methods and mechanisms underlying HSR in kiwifruit as well as the available information on cultivar development. Finally, we discuss some prospects for counteracting the effects of HS on kiwifruit production. To achieve HSR, a mix of strategies based on zoning, orchard management, intra- and interspecific hybridization and cultivar development must be understood in depth.

Keywords: heat stress, global warming, heat damage, kiwifruit breeding, hybridization

1. Introduction

The global climate is changing, and rising temperatures are one of the major challenges. Summer is hotter, winter is less cold, and erratic seasonal events have become the norm. The adverse effects of global warming and heat stress (HS) in plants have been described (Thompson, 2010; Zhao *et al*., 2021). These include phenological shifts, stamen development inhibition, flower deformation and drop, reduced fruit yield, physiological malfunction and plant death (Gornall *et al*., 2010; Zhao *et al*., 2021; Wang *et al*., 2024). Over the years, HS exerts considerable pressure on crop plants, and consequently on the food supply and economy.

Climate models have predicted an unprecedented temperature increase 3.3 - 5.7 °C by the end of the century if the emissions of greenhouse gases continue reaching high levels, putting the survival and validity of many species at risk (IPCC, 2023; Saleem *et al*., 2025). Furthermore, global surface temperature has risen 1.09 °C from 2011 to 2020 (IPCC, 2023), which far exceeds the rate of historical geological warming. This rapid increase has already been observed in China's kiwifruit producing regions, where summer temperatures exceeding 40°C for over 10 days have been recorded (Tang *et al*., 2014). Besides, a heat wave event lasting 74 days was recorded in 2024 (Zhou *et al*., 2025).

The major kiwifruit-producing province of Shaanxi has warned that high temperatures pose a threat to kiwifruit cultivation, especially in the south, leading to explore potential habitat suitability for the crop (Ma *et al*., 2021; Niu *et al* 2025). Since kiwifruit plants get stressed with temperatures above 30°C (David et al., 2020), the disastrous effects of heat on plant physiology led to impediments in fruit production and quality, ultimately resulting in death due to irreversible cellular damage (Figure 1) (Antunes and Sfakiotakis, 2000; Li *et al*., 2022; Ma *et al*., 2021; Man *et al*., 2015).

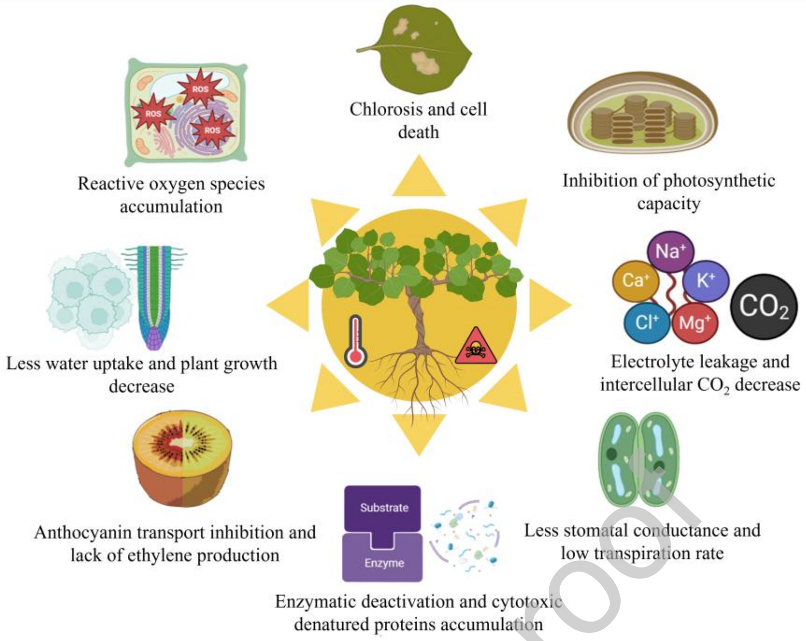

Figure 1. Major effects of heat stress reported on kiwifruit plants, malfunction, and deterioration until plant general collapse.

The valuable kiwifruit industry is experiencing substantial yield losses worldwide due to high temperatures (Shen *et al.*, 2023). In recent years, scientists have played a significant role in raising awareness of the effects of HS on kiwifruit and the survival mechanisms that plants activate in such conditions (Liang *et al.*, 2018; Shen *et al.*, 2023; Yuan *et al.*, 2024). However, the important economic significance of kiwifruit, coupled with its recent domestication status (Ferguson and Huang, 2007), provides an opportunity for a well-documented approach to preparing for future climatic scenarios. Understanding this plant genus's evolution and survival mechanisms provides new insights into kiwifruit's heat stress resistance (HSR). Attention could focus on the genetic diversity of the genus *Actinidia* and the wild germplasm available in China and surrounding areas (Ferguson, 2013; Huang, 2016).

Therefore, researchers are interested not only in innovations in planting systems, but also in biotechnological approaches to developing HSR cultivars.

The development of kiwifruit cultivars has been mainly focused on commercial traits such as appearance, flavour, yield and disease resistance, particularly to bacterial canker (*Pseudomonas syringae* pv. *actinidiae*) (Kisaki *et al*., 2018; Olsson *et al*., 2018; Zhang *et al*., 2024). However, the characteristics of HSR on these cultivars are largely unclear. It is now known that heat tolerance in fruit trees can be enhanced through short sublethal heat exposure or prolonged exposure to mild HS (Zhao *et al*., 2021). To safeguard cell integrity, plants undergo osmotic regulation, stress gene expression, and antioxidant defence (Wang *et al*., 2024). A strong positive correlation has been found between the upregulation of heat shock transcription factors (*Hsfs*), the accumulation of heat shock proteins (Hsps), and HSR in plants (von Koskull-Döring et al., 2007). *Hsfs* is a family of transcriptional factors that play a critical role in plant responses to stress, particularly HS, these transcription factors regulate the expression of Hsps, which serve as chaperones that stabilise heat-inactivated proteins and facilitate their refolding (Jha et al., 2014).

Some studies have been conducted to understand HSR mechanisms in kiwifruit using cultivars and mutants, as well as physiological and molecular variations and the overexpression of HS associated genes. These studies have shown satisfactory results for further research and application to HSR cultivar development (Huo *et al*., 2023; Liang *et al*., 2018; Shen *et al*., 2023, 2019). In light of the increasing demand for kiwifruit in the global market and the threat that heat poses to production, the purpose of this review is to summarise recent progress of HS in kiwifruit and to provide a theoretical basis for further research on orchards management and the breeding of heat-resistant varieties.

2. Physiological responses induced by HS in kiwifruit

High temperature alters physiological activities in plants, hindering the entire reproductive process and having a significant effect on yield (Figure 2) (Zinn *et al*., 2010). The negative effects of HS include high reactive oxygen species (ROS) generation, enzyme deactivation, reduced leaf stomatal conductance, chlorosis, electrolyte leakage, impaired cell enlargement, increased ethylene production, reduced water uptake, disrupted transformation of carbohydrates, and diminished photosynthetic activity (Hassan *et al*., 2022; Ntanos *et al*., 2022; Yuan *et al*., 2024) (Figure 1). The physiological responses induced by HS in kiwifruit were summarized as follows:

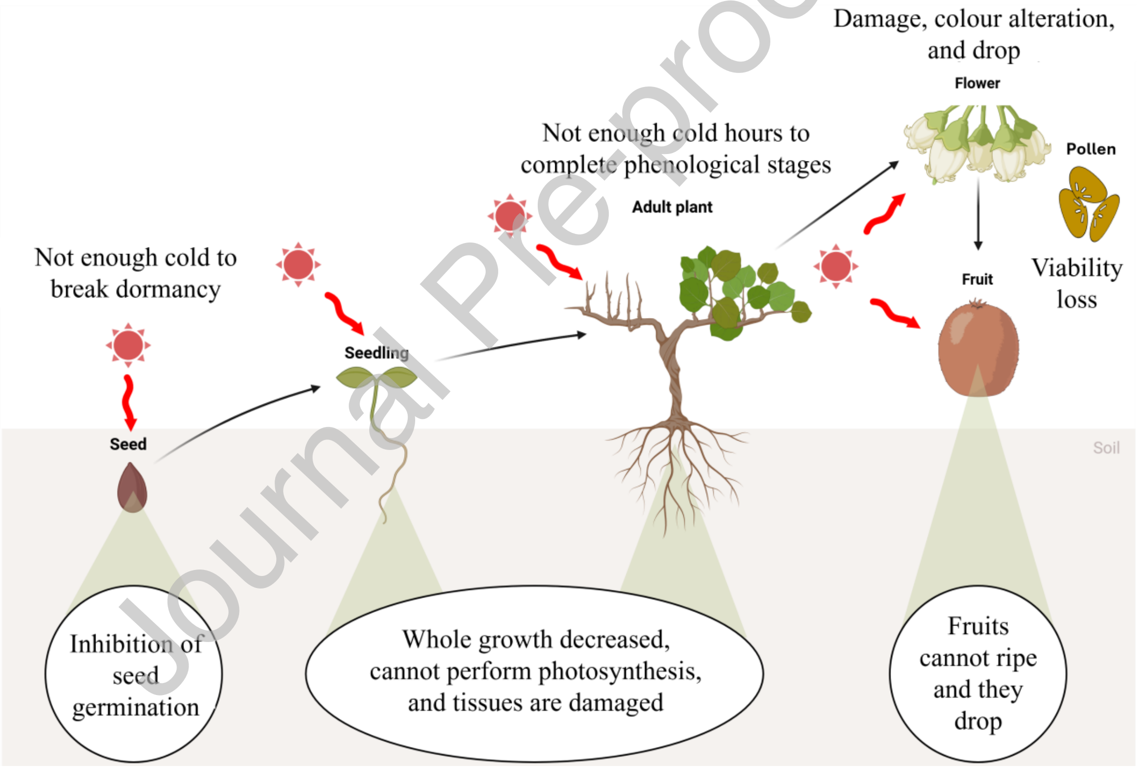

Figure 2. Kiwifruit plant growth stages and environmental heating consequences.

2.1. Effects of HS on seeds

Seeds are extremely sensitive to environmental cues. During development, seeds are far more vulnerable to HS than vegetative tissue (Chebrolu *et al*., 2016). Seed filling is vital for all crops and is hindered by HS, which suppresses seed maturation by inhibiting the synthesis of fundamental components such as starch and proteins (Sehgal *et al.*, 2018). In addition, it is known that seeds deteriorate in low humidity and high temperature conditions (Krishnan *et al.*, 2004). Kiwifruit seeds are affected by HS, and it has been demonstrated that germination is affected at 30°C (Çelik *et al.*, 2006). Particularly, the germination of *A. chinensis var. chinensis* was reported completely inhibited at 35°C (Reina-García *et al.*, 2025). Hence, considerations over germination protocols and seed storage must consider the optimal temperature to keep quality and reach high germination in kiwifruit seeds.

Mechanisms related to seed desiccation and longevity in Arabidopsis thaliana, a model plant, have shown that Abscisic Acid Insensitive 3 (*ABI3*), a key regulator of seed development, germination, and abiotic stress responses, induces the expression of *HsfA9* (Kotak *et al.*, 2007b). *HsfA9* may cooperate with *HsfA4*, activating the Dehydration Responsive Element-Binding Protein 2 (*DREB2*). This member of the *DREB* transcription factor family, plays a critical role in the plant's response to water scarcity, and it is also involved in responses to other abiotic stresses, including HS (Almoguera *et al.*, 2009; Tejedor-Cano *et al.*, 2014). Through its action, *DREB2* upregulates the synthesis of *Hsps*, which are crucial for protecting cellular integrity during stress. Notably, this pathway has been observed in seeds of *Helianthus annuus* (sunflower), where the coordinated action of these transcription factors enhances seed HS tolerance (Almoguera *et al.*, 2009; Tejedor-Cano *et al.*, 2014).

The previous described pathway leads to resistance against heat, desiccation, and improves longevity in seeds. *Hsps* must be acting to protect seed storage proteins (SPPs) from degradation. SPPs are a primary source of energy stored during seed development, and they are also related to translation and energy metabolism (glycolytic and tricarboxylic acid cycle pathways), and vitamin E synthesis (Nguyen *et al*., 2015). Thanks to these mechanism seeds can keep longevity counteracting ROS accumulation due to HS and unfavourable humidity conditions (Nguyen *et al*., 2015). Transcriptional machinery under HS has not yet been studied in kiwifruit seeds. However, *HsfA4* and *HsfA9* homologous have been detected in other tissues both usually down regulated, only *HsfA4d* has shown up regulation in flowers, leaves and roots. Analyzing these transcriptional factors in relation to *DREB2* in kiwifruit seeds under HS may be a good starting point to comprehend seed longevity and differences among cultivars in relation to germination rates and seed viability (Tu *et al*., 2023).

Auxins are a class of phytohormones involved in regulating various aspects of plant development. They accumulate in seeds during development, playing a critical role in growth and differentiation. In Pisum sativum (pea), it has been observed that under HS, the upregulation of tryptophan aminotransferase (*TAR*) genes increases the levels of auxins, including 4-chloroindole-3-acetic acid (4-CI-IAA), indole-3-acetic acid (IAA), and various auxin conjugates. *TAR* genes encode enzymes that catalyse the first step in the biosynthesis of IAA, specifically the conversion of tryptophan to indole-3-pyruvate (*IPyA*), a key precursor of IAA (Tejedor-Cano *et al*., 2014; Kaur *et al*., 2021).

The auxins produced in association with abscisic acid (ABA) and sufficient bioactive gibberellic acid (GA), protects the seed formation, preventing abortion and continuing growth and development (Kaur *et al*., 2021). Another particular function is that exhibit by auxin responsive protein (IAA27), acting as a repressor of *HsfA9*, playing a role in Hsps synthesis regulation, thus the participation of auxins has been proposed as important regulators for the transcriptional activation of seed longevity (Tejedor-Cano *et al*., 2014; Kaur *et al*., 2021). A study conducted on *A. arguta* (kiwiberry) detected higher amount of auxins in fruit´s inner tissues possibly related to seed development (Sorce *et al*., 2017). Nevertheless, the direct participation of auxins and HS in seeds of kiwifruit species remains unclear.

2.2. Effects of HS on seedlings

The seedling stage is a critical developmental phase that can be drastically affected by HS throughout ROS accumulation. Oxidative processes can cause severe cellular damage, resulting in impaired protein polymerisation, reduced membrane transport function and thermal instability (Liang *et al*., 2018; Wang *et al*., 2024). Seedlings exposed to HS show low photosynthetic rates, reduced protein and carbohydrates contents and short production of chlorophyll (Khanzada *et al*., 2024; Wang *et al*., 2024). Meanwhile, antioxidant levels increase under HS, as observed in kiwifruit seedlings, initiating the ROS scavenging (Liang *et al*., 2018).

Two candidate genes have been revealed in wheat seedlings under HS (Fu *et al*., 2024), one of them *TaWRKY74-B* a member of *WRKY* family (Gupta *et al*., 2019), and the other one *TaSnRK3.15-B* a member of the sucrose non-fermenting related protein kinase family (*SnRK*), also reported up regulated under abiotic stress, including cold and heat (Jiang *et al*., 2022). *WRKYs* has been analysed phylogenetically and functionally, there is a conserved molecular function and participation in biological processes across species (Gupta *et al*., 2019), indicating the strategical importance of these genes in plants performance under stress. *CaWRKY40* participates in the response of *Capsicum annuum* (chili pepper) to high temperatures (Liu *et al*., 2021), in a similar way *SlWRKY3* have been reported expressed in *Solanum lycopersicum* (tomato) (Ying Wang *et al*., 2024).

Even though *WRKYs* appear decisive in HS response, in kiwifruit they haven’t appeared as prominent mechanism in mutant HSR plants (Yuan *et al*., 2024). In addition, the expression profiles of *AcWRKY* genes in response to abiotic stress have been conducted but high temperature was not included (Jing and Liu, 2018). Thus, candidate genes from the WRKY family under HS remain to be discussed in kiwifruit. Conversely, *SnRK* genes, a family of kinases that participates in metabolic balance under stress, have been reported expressed in kiwifruit, specifically, *AcSnRK2.4* is a candidate gene down regulated during HS. Interestingly, when this gene is overexpressed, it appears to enhance the HS response machinery, elevating SPAD values (chlorophyl content expressed as photosynthetic capacity) and decreasing malondialdehyde (MDA), electrolyte leakage, and ROS, as well as implications in photosynthesis regulation, increasing chlorophyll fluorescence parameters (Wang *et al*., 2025). However, further analysis is needed to understand the upstream and downstream regulations involved in such outcomes.

2.3. Effect of HS on bud break

Cold hours, which refer to the accumulation of chilling temperatures in winter, are vital for breaking dormancy and ensuring synchronized bud development in spring. When kiwifruit plants do not receive enough cold hours, it can result in delayed or premature bud break, often out of sync with the natural seasonal progression (Rajan *et al*., 2024). However, HS during late winter or early spring can exacerbate these issues, further complicating the normal development process (David *et al*., 2020). Insufficient cold hours can delay the completion of dormancy, causing buds to remain dormant longer than usual. If there is HS in an early period, it can cause premature bud break or an incomplete dormancy release. This can lead to vulnerability to late frosts, as the buds may be vulnerable before they have fully adapted to the spring conditions (David *et al*., 2020).

HS in early spring, triggered by higher-than-usual temperatures (especially during periods of insufficient cold hours), can further damage developing buds. When buds break prematurely, they are exposed to risks like frost damage, reduced photosynthesis, and stunted growth (Pichakum *et al*., 2018; David *et al*., 2020). HS, when it occurs too early, can accelerate phenological processes (such as bud break and flowering), but the buds may not be fully developed or ready for the increased metabolic demands. This results in abnormal development, where the plant's normal spring growth cycle is disrupted (Pichakum *et al*., 2018). Chilling and HS together can create a phenomenon of "false spring", where the plant's phenological stages are advanced too early, only to be followed by a return to colder temperatures or even frost. This mismatch in timing can cause flower drop, poor and fruit set. The regular bud break dormancy break should be occurring in spring when the temperatures can keep steady warm for a proper flower development, however as it occurs in vegetative bud break therequirement of chilling hours and growing season can vary between species, and cultivars (Zhao *et al*., 2017; Sultonov, 2023)

2.4. Effects of HS on flowers

Moderate temperature promotes timely flowering, whereas extreme events can cause early or late blooming, leading to disruption of pollination due to asynchrony (Qian *et al*., 2025). Flowers undergo size and colour reduction, and some genes like Flowering Locus T (*FT*), and Chalcone synthase (*CHS*) can be stimulated, promoting changes in flowering time and pigmentation. For instance, in long-day spring flowers such as *Arabidopsis thaliana,* high temperatures accelerate flowering induction. In contrast, high temperatures delay the induction of short-day autumn flowers, such as chrysanthemums. High temperatures can also reduce flower size and cause paler petals. For example, flowers such as chrysanthemum, rose, and eustoma may experience faded colour (Hegde *et al*., 2020; Qian *et al*., 2025; Wu *et al*., 2024). Warmer temperatures in winter may have significant effects on wild populations and direct effect on kiwifruit yield, since cold is an important mechanism for stimulating flowering and fruit set (Tait *et al*., 2018). Nevertheless, the situation regarding kiwifruit flowers remains unclear. However, it has been demonstrated that if plants suffer HS during the accumulation of starch in fruits, this affects flowering time and number, reducing yield in the subsequent harvest season (Richardson *et al*., 2004).

In addition, HS decreases the anthocyanin accumulation in *A. eriantha* petals (typically red coloured) (Yang *et al*., 2017). Chalcone isomerase-like (*CHIL*) proteins, classified as type IV CHI proteins, have roles in the cell that remain largely undefined. However, it was noticed that while *A. eriantha* lose colour by downregulation of *AcCHIL*, the yellow petals of *A chrysantha* don’t exhibit significant changes in the expression of this gene under HS conditions (Yang *et al*., 2017). The difference in *A. eriantha* could be seen as a potential mechanism for protecting flowers from heat damage.

Petal colour may influence the flower´s temperature regulation. Darker-coloured petals, for instance, tend to absorb more heat, potentially raising the flower´s temperature. In contrast, lighter coloured petals might reflect more sunlight and absorb less heat, keeping the flower cooler. By changing their petal colour, plants might be able to modulate the flower internal temperature and protect the reproductive tissue from overheating during extreme heating conditions (Hegde *et al*., 2020). Heat causing anthocyanin degradation and petal fading is a relatively limited studied field, but it appears to be a common process occurring in flowers from different species (Zhao *et al*., 2025).

It has been mentioned that in *A. thaliana* the flowering time is regulated by the expression of pseudo-response regulator 7 (*PRR7*), a type of protein related to the regulation of circadian rhythms and development, that upstream regulated by *HsfB2b* after heat stimulation. Furthermore, the ovule development is regulated by *HsfB2a*, which can be suppressed by lncRNA regulated by *HsfA1* (Bakery *et al*., 2024). Under HS conditions is reasonably to think that this suppression is a way to save energy for fundamental processes implicated in plant survival, perhaps after a failure in buffering flower temperature, indicating the umbral between protecting flowers and abort them. Pyruvate decarboxylase (*PDC*) genes are also implicated in responses against abiotic stress facilitating the obtention of energy in hypoxic conditions (Ismond *et al*., 2003), which is vital when HS affects the gas exchange and the consumption of oxygen overpassed. *AdPDC2* was identified in kiwifruit as an important upregulated gene under HS in reproductive organs, which overexpressed in mutant Arabidopsis was able to increase HSR in seedlings (Luo *et al*., 2017), indicating the importance of the activation of metabolic pathways linked to ethanolic fermentation as a source of energy for survival.

2.5. Effects of HS on pollen

Pollen is a valuable resource for fruit production and depends on the correct development of flowers. HS is associated with the inhibition of stamen development and significantly affect the growth of the long and short filaments of stamens (Wang *et al*., 2024). Studies on various plant species have revealed that HS substantially reduces pollen germination, tube elongation, and viability (Kumar *et al*., 2015; Pereira *et al*., 2014; Sever *et al*., 2012). Fruit size and seed production in kiwifruit depend on pollination and pollen viability, consequently pollen degradation could be a key abiotic factor limiting plant productivity. However, results on the effects of HS on *A. eriantha* pollen have shown that pollen germination and pollen tube growth are highly variable among different genotypes, which also respond differently to HS (Seyrek *et al*., 2016). Thus, screening pollen genotypes based on HSR performance could be a way to screen heat-resistant genotypes in kiwifruit.

Pollen development is protected by HS induced genes, this mechanism is highly conserved, and the male gametophytes is highly sensitive to high temperature (Bakery *et al*., 2024). *Hsfs* have been identified in sunflowers with different functions. For instance, *HsfA5* is involved in pollen development by controlling nucleolar functions. The activation of *HsfA1* during the early stages of pollen development is important for the induction of E3 ligase (*HEI10*) that is associated with meiotic crossovers and the induction of *HsfA2*, which leads to the upregulation of HSR genes for Hsps synthesis in the absence of stress, seemingly as an acclimation mechanism. The function of *HsfA1* can be repressed by plant heat shock factor binding proteins (*HSBP*), the latter inhibit the formation of *Hsf* oligomers (Bakery *et al*., 2024).

A. thaliana Hsfa5 mutants show malfunction in male gametophyte development, indicating the importance of this gene for the proper development of this reproductive tissue and pollen maturation under HS (Reňák *et al*., 2014). In kiwifruit plants, two homologs of *Hsfa5* have been identified: *AcHsfA5a* and *AcHsfA5b*. Under elevated temperature conditions, the expression of *AcHsfA5b* increases in various tissues, including both reproductive and vegetative tissues, with the exception of roots. However, the specific function of *AcHsfA5b* remains unknown but clearly participating in the above ground response to HS (Tu *et al*., 2023).

2.6. Effects of HS on fruits

Prolonged periods of HS (25-35°C) affect fruit set and are linked directly with pollen release and anther tissue damage. Suppression of fruit can also result from ovule sterility, the viability of which is reduced by HS (Kawasaki, 2015). Even if plants do not suffer HS during flowering and pollen development, the fruit phase is still critical as HS affects fruit formation and quality before harvest. Sun scald is common affection worldwide, during periods of strong sun irradiance and high temperature it can cause an average of 5.6% of damage to kiwifruit production and in poor managed orchard the rate can increase up to 45% (Huang, 2016).

High temperatures cause suppression of colour development, ethylene biosynthesis, and fruit softening, while respiration rate is increased and taste is worsened. (Antunes and Sfakiotakis, 2000; Huang, 2016; Man *et al*., 2015). Colour expression is the result of anthocyanin accumulation in vacuoles in the inner pericarp; the vacuolization is affected by high temperature, reducing anthocyanic vacuolar inclusion (AVI)-like structures (Man *et al*., 2015). Some *MYB*, a family of transcription factors that play crucial roles in regulating biological process in plants such as growth, development, response to stresses, and secondary metabolism, have shown a key role in anthocyanin metabolism under HS. For example, when the temperature is over 25°C *AcMYB1* promotes downregulation on anthocyanin biosynthesis in kiwifruit, congruent with results on Malus × domestica with the participation of *MYB10* (Lin-Wang *et al*., 2011).

Likewise, temperature above 38°C inhibits enzymatic activity related to ethylene biosynthesis and may affect the cell-wall degrading enzymes preventing fruit softening (Antunes and Sfakiotakis, 2000). In addition, nutritional quality and taste are also affected. During the cell expansion/starch accumulation phase of fruit growth, carbon is partitioned less efficiently to the fruit. This results in low levels of sugar, starch and vitamin C, as well as increased fruit acidity (Richardson *et al*., 2004). After harvest, HS during storage disrupts ripening stimulating ethylene production and rapid weight loss (Yin *et al*., 2012). This implies that avoid heat exposure extend shelf life.

Ethylene response factors (*ERFs*) are a large family of genes with many implications in plants, including different types of stress (Bleecker and Kende, 2000). The mechanism that initiates *ERF* transcription involves the activation of the mitogen-activated protein kinase (MAPK) signalling pathway, crucial in cell response to external stimuli, which can be triggered either by ethylene binding to its receptors or by a direct effect of stress on *WRKY*, *MYB*, and possibly *Hsf* transcription factors (Thirugnanasambantham *et al*., 2015).

Under HS pressure, *ERF*, *Hsfs* and ABA increase and are considered responsible to maintain the response during the HS period, this mechanism induces accumulation of Hsps (Carbonell-Bejerano *et al*., 2013). Since *ERFs* can be activated depending on ethylene and in an independent manner, it is a critical mechanism operating in fruit protection under HS, first activated under mild stress when the ethylene increases but acting independently when the 38°C umbral is overpassed (Yin *et al*., 2012). In kiwifruit some members like *AdERF7, AdERF9, AdERF10* are particularly responsive under HS postharvest treatments, however the information related to specific functions is unknown, but it is clear that participation of ERFs can be specific as some members acts only in specific stress conditions. For example, *AdERF4* and *AdERF6* shows an increase in high CO_2 (both with a 4-fold change mRNA abundance), and *AdERF3, 8, 12, 13* and *14* increase (more than 2-fold) at low temperatures (Yin *et al*., 2012).

2.7. Effects of HS on leaves

Leaves are the organs in where photosynthesis occurs to ensure plant survival. Since leaves are usually over 10-18 °C above the air temperature, during the hottest days of the year 50°C can be easily reached accompanied by devastating tissue damage, affecting physiology, biochemistry, and molecular pathways, with a detrimental effect on the photosynthetic rate (Docherty *et al*., 2023; Guan *et al*., 2022; Li *et al*., 2022). Furthermore, leaf scorch and wilting can occur due to high solar irradiance, accelerating leaf senescence (Ntanos *et al*., 2022). Kiwifruit is particularly susceptible to this kind of damage due to its large leaf area. In kiwifruit crop lands, heat stress often impedes the normal growth of leaves, resulting in inhibited plant growth, reduced yield and deteriorating fruit quality (Huo *et al*., 2023; Li *et al*., 2022; Xia *et al*., 2021).

Leaf senescence under HS is initially thought to be a result of ethylene accumulation and chlorophyl degradation(Tan *et al*., 2023). Ethylene, a phytohormone, accumulates as stress signals and one of its effects is the breakdown chlorophyll, which leads to leaf yellowing and aging. However, the process is more complex when considering the additional environmental factor of light. As temperature increases, there are also changes in light environment. Which in turn influence the regulation of phytochrome-interacting factors (*PIF4* and *PIF5*) by other signalling molecules, such as early flowering 3 (*ELF3*) and phytochrome B (*PhyB*). The latter is a light receptor that helps plants sense light conditions, while ELF3 is involved in plant´s circadian rhythm and responses to light and temperature. The accumulation of *PIFs*, key intermediaries between light signals and plants development, in response to environmental cues leads to the activation of ethylene and ABA signalling pathways, causing the activation of OSA1-related expressed protein 1 (*ORE1*), a master regulator primarily linked to plant stress tolerance and growth. Consequently, the activation of *ORE1* accelerates senescence (Kim *et al*., 2020).

In shoot tissues on warm conditions *PIFs* regulation have implications in the auxin synthesis participating in thermo-morphogenesis, conformational changes in tissues due to light perception and temperature rising act as precursors of this pathway (Sato *et al*., 2024). This indicates that changes in the stimuli input and tissue specificity can trigger different responses, making *PIFs* able to participate in both senescence and growth promotion.

2.8. Biochemical responses induced by HS conserved in plants

HS promotes ROS accumulation generating a cytotoxic environment within the cells. To protect cellular structure and homeostasis against these toxic oxygen intermediates, plant cells and their organelles, such as chloroplasts, mitochondria and peroxisomes employ antioxidant defence systems. These systems comprise a series of enzymatic and non-enzymatic agents that work together to mitigate damage during periods of harm (Cao *et al.*, 2023; Fujita and Hasanuzzaman, 2022).

Accumulation of ROS is a key process for the activation of transcription factors including the master regulator *HsfA1* and stress related proteins as important as Hsps. Ros rapidly triggers antioxidant defence by multiple mechanisms, including retrograde signalling, transcriptional control, post-transcriptional regulation, posttranslational redox modifications or phosphorylation, and protein–protein interactions (Dvořák *et al.*, 2021). In relation to ROS accumulation, changes in redox state within the cells activates nucleoredoxin 1 (NRX1) and thioredoxin, which target several important antioxidant enzymes, including Catalases 1, 2, and 3, Glutathione s-transferase (GST), APX1, Glutaredoxin family protein, Methionine sulfoxide reductase (MSR), Glutathione peroxidase 6, MDHAR6, among others (Kneeshaw *et al.*, 2017). ROS accumulation is also responsible for increasing Ca+ influx which also initiates the calcium dependant pathway for antioxidant synthesis (Dvořák *et al.*, 2021). The involvement of antioxidants in kiwifruit's HSR has been reported (Liang *et al.*, 2018; Yuan *et al.*, 2024). Their activity is described in the following subsections, based on general findings in plants.

2.8.1. Superoxide dismutase (SOD)

SODs are metalloenzymes that are abundant in all aerobic organisms. They are important for plant stress tolerance and provide the first line of defence against the toxic effects of elevated levels of ROS. The SODs remove $O_2^{\cdot -}$ by catalysing its dismutation: one $O_2^{\cdot -}$ is being reduced to H_2O_2, while another is oxidized to O_2 (Gill and Tuteja, 2010). This decreases the risk of OH formation via the metal-catalysed Haber–Weiss reaction (Mittler, 2002). All forms of SOD are nuclear-encoded and targeted to their respective subcellular compartments by an amino terminal targeting sequence. The upregulation of SODs is critical for plant survival under environmental stress, as it is reported in mulberry (Harinasut *et al.*, 2003).

2.8.2. Catalase (CAT)

CATs are enzymes with the potential to directly dismutate H_2O_2 into H_2O and O_2 and are indispensable for ROS detoxification under stressed conditions. CAT has one of the highest turnover rates of all enzymes: one molecule of CAT can convert over 6 million molecules of H_2O_2 into H_2O and O_2 per minute (Gill and Tuteja, 2010). It is also important in removing H_2O_2 generated in peroxisomes by oxidases involved in β-oxidation of fatty acids, photorespiration, and purine catabolism (Garg and Manchanda, 2009; Gill and Tuteja, 2010).

2.8.3. Peroxidases (POD)

POD are a group of enzymes involved in physiological phenomena, such as biotic and abiotic stress responses, growth, and senescence. They participate in the scavenging of H_2O_2 from the cytosol and chloroplasts, the detoxification of reactive oxygen species during oxidative stress, and cellular metabolic processes (Kalsoom *et al.*, 2015). Among them, ascorbate peroxidase (APX) is thought to play the most essential role in the scavenging of ROS and the protection of cells in higher plants. APX participates in the scavenging of H_2O_2 in the water-water and Vitamin C-Glutathione cycles, utilising vitamin C as the electron donor. The APX family contains at least five different isoforms, including thylakoid (tAPX), glyoxisome membrane forms (gmAPX), chloroplast stromal soluble forms (sAPX), and cytosolic forms (cAPX). APX has a higher affinity for H_2O_2 than CAT, suggesting that it may play a more crucial role in managing ROS during abiotic stress (Gill and Tuteja, 2010).

2.8.4. Glutathione reductase (GR)

GR is a flavo-protein oxidoreductase with enzymatic activity on the Vitamin C-Glutathione cycle and plays an essential role in defence system against ROS by sustaining the reduced status of Glutathione. It is primarily found in chloroplasts, although small quantities of the enzyme can be detected in mitochondria and the cytosol (Gill and Tuteja, 2010). GR catalyses the reduction of glutathione, a molecule involved in many metabolic regulatory and antioxidant processes in plants. GR catalyses NADPH dependent reaction of the disulphide bond in oxidized glutathione, which is important for maintaining the glutathione pool (Rao and Reddy, 2008).

2.8.5. Monodehydroascorbate reductase (MDHAR) and Dehydroascorbate reductase (DHAR)

MDHAR is a flavin adenine dinucleotide (FAD) enzyme, which is present in chloroplasts and cytosol as isozyme forms. Accompanying APX, MDHAR is also located in peroxisomes and mitochondria, scavenging H_2O_2 (del Río *et al*., 2002). During enzyme-FAD reduction, a charge transfer complex is formed, where the reduced enzyme donates electrons to MDHA, producing two molecules of Vitamin C via a semiquinone form [E-FAD-NADP(P)$^+$] (Gill and Tuteja, 2010). DHAR regenerates Vitamin C from the oxidized state and regulates the cellular Vitamin C redox state which is crucial for tolerance to various abiotic stresses linked to the production of ROS, including HS (Gill and Tuteja, 2010).

2.8.6. Ascorbic acid (Vitamin C)

Vitamin C is the most abundant, powerful, and water-soluble antioxidant, preventing or minimizing the damage caused by ROS in plants (Smirnoff, 2005). It’s ubiquitous in all plant tissues, generally higher in photosynthetic cells and meristems. Vitaminc C concentration is highest in mature leaves with fully developed chloroplast and highest chlorophyll. It has been reported that vitamin C mostly remain available in reduced form in leaves and chloroplast under normal physiological conditions (Smirnoff, 2000). Near 40% of the total Vitamin C is found in chloroplasts, with stromal concentrations as high as 50 mM have been reported (Foyer and Noctor, 2005). Vitamin C is considered the most powerful ROS scavenger because of its ability to donate electrons in several enzymatic and non-enzymatic reactions. It can protect membranes by directly scavenging O_2 and OH (Gill and Tuteja, 2010).

2.8.7. Glutathione (GSH)

GSH is a crucial metabolite in plants which is considered as the most important intracellular defence against ROS induced oxidative damage. It occurs abundantly in reduced form in plant tissues and is localized in all cell compartments, such as the cytosol, the endoplasmic reticulum, vacuole, mitochondria, chloroplasts, peroxisomes as well as in apoplast (Gill and Tuteja, 2010). GSH is required to maintain the normal reduced state of cells and counteract the inhibitory effects of ROS induced oxidative stress (Meyer, 2008). It is a potential scavenger of $^1O_2$, H_2O_2 and the most dangerous ROS, such as OH. Additionally, GSH plays a key role in the antioxidant defence system by regenerating another potential water-soluble antioxidant, such as Vitamin C, via the Vitamin C-GSH cycle (Gill and Tuteja, 2010).

2.8.8. Flavonoids

Flavonoids are metabolites that are typically stored in plant vacuoles in the form of glycosides. However, they can also be found as exudates on leaves and other above-ground plant parts (Gill and Tuteja, 2010). Flavonoids and other phenolic compounds enable plants to absorb UV light, increasing their tolerance to high UV irradiation (Clé *et al.*, 2008). These compounds are among the most bioactive plant secondary metabolites often outperforming well-known antioxidants, such as Vitamin C and a-tocopherol. Flavonoids, in particular, act as ROS scavengers, neutralizing free radicals before they can cause damage to the cells. When a flavonoid molecule encounters a free radical, it donates an electron or a hydrogen atom to the radical. This process stabilizes the free radical by neutralizing its reactivity, preventing oxidative damage (Løvdal *et al*., 2010).

2.8.9. Proline (Pro)

Proline is an important amino acid that is considered to be a potent non-enzymatic antioxidant and a potential inhibitor of apoptosis (Gill and Tuteja, 2010). Free Pro has been proposed to act as an osmoprotectant, protein stabilizer, metal chelator, inhibitor of lipid peroxidation, and OH and $^1O_2$ scavenger. Consequently, it is an effective suppressor of ROS formed under abiotic stress conditions in all plants (Ashraf and Foolad, 2007; Trovato *et al*., 2008).

3. Molecular mechanisms induced by HS in kiwifruit plants

In fruit plants, the biomolecules described in the following subsections act as the main regulatory mechanisms under HS (Wang *et al*., 2024). Different elements have been studied in kiwifruit, providing insight into the molecular basis of HSR. However, our knowledge is still in its infancy, with full pathways and functional characterisations of specific elements yet to be depicted (Figure 3). While physiological responses provide macroscopic responses of HS, molecular mechanisms reveal the intricate regulatory networks underlying kiwifruit's thermal adaptation.

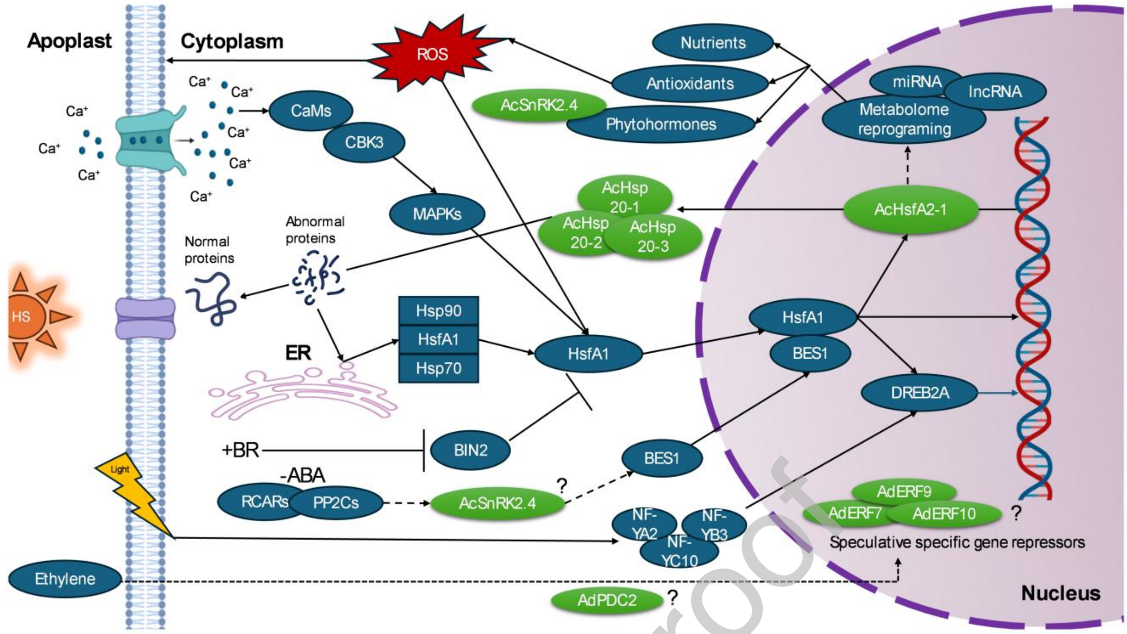

Figure 3. Suggested mechanisms involved in heat stress resistance enhancing on kiwifruit. Purple ovals indicate HS specific elements identified in kiwifruit; questions mark refers to unknown element participation within the regulation process. Dashed lines indicate indirect regulation.

Hsfs are master pieces in Heat stress response, but they are not alone. Different stimuli activate *HsfA1* (master regulator of heat stress response, responsible for translocating the signal to the nucleus), Conformational changes in the membrane due to HS and ROS (molecules generated by stress that serve as response triggering signal) accumulation leads to Ca+ influx, activating the calcium dependant signalling of MAPKs (key components of signal transduction, transmitting stress signals from the membrane to the nucleus) with further activation of *HsfA1*, similarly ROS directly triggers the same response. Protein damage is perceived in the endoplasmic reticulum (ER), calling for the release of *HsfA1* from the Hsp90/70 (members of heat shock proteins, usually associated with prevention of protein aggregation under stress condition) repression complex. The translocation of *HsfA1* can be prevented via *BIN2* (a negative regulator of brassinosteroid that prevents growth and development in plants) which can also be inhibited by accumulation of brassinosteroid (BR) (Dündar *et al*., 2024). Inside the nucleus *HsfA1* can form a module with BRIl-EMS-suppressor 1 (*BES1*) known for its participation in growth and stress response, enriching the induction of Hsps. *BES1* translocation from cytoplasm to the nucleus is mediated by ABA signalling pathway where *AcSnRK2.4* (a type of Sucrose non fermenting kinase from the group 2 that are associated with ABA signalling pathway in stress response) could be an important downstream element for the activation of downstream ABA regulated transcription factors. The HS response is further enriched in the nucleus via *DREB2A* (member of *DREB* family largely associated with stress response to drought and heat) which is targeted by the nuclear factor trimer *YA2*, *YB3*, and *YC10* giving the specificity for HS, although they are primarily conceived as plant development regulators as members of *YABBY* family, here their participation is stimulated by heating and light changes perception involving them in *DREB2* Pathway (Sato *et al*., 2024). The HSR mechanism in the nucleus follows the activation of *AcHsfA2-1* by *HsfA1*, which as a member of *HsfA2* is critical triggering metabolome reprograming to keep cellular energetic balance, sustain the response mechanism and counteract ROS accumulation. ROS metabolism is also regulated by miRNA and lncRNA. On the other hand, *AcHsfA2-1* is involved in synthesis of Hsp20s implicated in protein refolding.

3.1. Heat shock proteins (Hsps)

Short-term and long-term HS events in plants promote the downregulation of genes related to non-stress and preserve ATP resources for the upregulation of genes related to stress and the synthesis of proteins involved in heat stress response (Wang *et al*., 2024). When the cell membrane receptors in plants are stimulated by heat and ROS starts to accumulate, the signalling cascade involving Ca^{2+} ion, calmodulins, protein kinases, calcinarum B-like protein (CBL) and CBL-interacting (CBLI) proteins is triggered.

The calcium dependent mechanism activates transduction molecules, such as Ca-dependent protein kinases (CDPKs) and MAPKs, which in turn activate transcriptional regulators associated to the HS response, including *Hsfs*, *WRKY*, *DREB*, *MYB*, multiprotein binding factor 1c (*MBF1c*), NAM-ATAF1/2-CUC2 (*NAC*), basic leucin zipper (*bZIP*), and basic-helix-loop-helix (*bHLH*) (Haider *et al*., 2021; Saini *et al*., 2022). Among the transcriptional mechanism, *Hsfs* pathway plays a leading role on HSR in plants, activating the genes to synthetise Hsps (Kotak *et al*., 2007a). These proteins prevent the denaturalization of functional and structural proteins under HS conditions, thereby maintaining cellular homeostasis under heat stress (Jha *et al*., 2014; Wang *et al*., 2018).

According to their molecular weight, Hsps are classified into five types: Hsp100, Hsp90, Hsp70, Hsp60 and sHsps. All of these are characterised as chaperones in signal transduction under HS and have unique roles (Al-Whaibi, 2011). The Hsp100 class is responsible for recycling non-functional aggregated proteins; the Hsp90 class is important for immune responses; the Hsp70 class is involved in responses to temperature stress; Hsp60 assists with protein folding and aggregation after transport in chloroplasts and mitochondria; and sHsps are chaperones that do not require ATP and participate in HSR (Huang and Xu, 2008; Wang *et al*., 2004).

The amount and type of Hsps expressed by plants varies greatly, and higher plants are characterised by the presence of at least 20 types of sHsps. However, one species could contain up to 40 types of these sHsps (Al-Whaibi, 2011). In kiwifruit, the *Hsf* family has phylogenetic relationship between species, domains and motifs conserved, with most of the family members responsive to HS (Tu *et al*., 2023). In particular, the transcription factor *AcHsfA2-1* has been identified as the most strongly induced mechanism during HS, promoting Hsp20 activities (Shen *et al*., 2023). This is consistent with results obtained for *A. thaliana*, in which 13 of the 21 Hsp20 genes were expressed under HS, followed by eight Hsp70 genes, seven Hsp90 genes and eight Hsp100 genes (Swindell *et al*., 2007). Hsp20s comprise the most prominent family of sHsps in plants. The current molecular weights range from 15 to 22 kDa, and the proteins are intimately associated with temperature stress in plants. They are expressed in cytoplasm, mitochondria, and endoplasmic reticulum, conferring HSR in plant cells (Waters, 2013).

3.2. Messenger RNA (mRNA)

High temperatures increase the mRNA expression of Hsps, *DREBs*, encoding expansin protein (AsEXP1), the galactitol synthetase gene, and genes encoding antioxidant enzymes (Huang and Xu, 2008; Wang *et al*., 2024). *DREBs* are important plant transcription factors that regulate the expression of various stress induced genes, thereby controlling ABA synthesis. They interact with the DRE/CRT cis structure of promoter regions of various stress responsive genes (Lata and Prasad, 2011). As downstream genes in the heat shock response, *DREBs* trigger *Hsfs* and induce the expression of other HS related genes to enhance HSR in fruit trees (Díaz-Martín *et al*., 2005; Sakuma *et al*., 2006). The subgroup *DREB2* is particularly responsive to heat and drought (Sakuma *et al*., 2006), and one of its members, the ethylene response factor 3 of *A. deliciosa* (*AdERF3*), is expressed under HS conditions along the other members, playing a role in modulating fruit ripening under abiotic stress (Yin *et al*., 2012).

3.3. Micro RNA (miRNA)

In plants, miRNAs are involved in various metabolic and signalling pathways, primarily by suppressing the expression of target genes. A determined miRNA can target multiple genes, and the target genes differs depending on the plant subjected to HS (Ding *et al*., 2020). miRNAs identify target genes through base complementary pairing principles. Depending on the degree of complementation with target genes, miRNAs guide the RNA-induced silencing complex (RISC), which is a restriction endonuclease targeting Small interfering RNA (siRNA) to mediate the downregulation of gene expression by inhibiting target gene cleavage and translation, which are two transcriptional regulatory mechanisms (Wang *et al*., 2024).

Genes encoding for TF are important targets for miRNA. The , *MYB*, *WRKY*, auxin response factor (*ARF*) and squamosa promoter-binding protein-like (*SPL)* families of transcription factors are upregulated by miRNAs in fruit trees under HS (Khraiwesh *et al*., 2012; Wang *et al*., 2024). Kiwifruit mutants with enhanced HSR exhibit upregulation of the transcription factors related with growth and development such as *MYB5*, *MYB38*, *ERF1A*, MADS-box transcription factor 23 (*MADS23*) and GRAS transcription factor 13 (*GRAS13*) upon HS exposure (Yuan *et al*., 2024). When plants are exposed to HS, the responses regulation involves, miR160, miR167, miR390, and miR393 participating in the auxin metabolic pathway (Khraiwesh *et al*., 2012).

miR159 contributes to the metabolic pathway of gibberellic acid (GA_3), treatment with this phytohormone has demonstrated increased activity of SOD and CAT, non-enzymatic antioxidants and osmoprotectants (Zhang *et al*., 2023). Furthermore, exogenous application in tomato has demonstrated thermotolerance induction by enhancing physiological response and growth with increased levels of proline, nitrogen, phosphorus and potassium (Guo *et al*., 2022). On the other hand, miR319 is involved in the metabolic pathway of jasmonic acid (JA) (Ding *et al*., 2020), this phytohormone applied to *A. thaliana* has demonstrated the activation of *DREB2A*, activating thermotolerance (Wang *et al*., 2023). In addition, JA can improve the antioxidant content by modulating the phenolic compound content (Rehman *et al*., 2023).

3.4. Long noncoding RNA (lncRNA)

The abundance of lncRNAs in plant cells is significant, with four main functions: signalling, decoying, guiding, and scaffolding. These functions actively maintain and regulate the cellular environment and gene expression (Ji *et al*., 2021; Quan *et al*., 2015; Zhang *et al*., 2018). For instance, in *Populus simonii* a total of 204 HS responsive lncRNAs that are potentially RNA scaffolds or interferers of RNA pathways were identified through sequencing (Song *et al*., 2020). Since long term HS is detrimental to cellular physiology, cells need to disable the HS response to recover from a high-temperature environment (Wang *et al*., 2024). LncRNAs, which are generated in response to HS, downregulate HS response genes by interacting directly with the Hsf1 family during the recovery process following HS exposure (Ji *et al*., 2021).

Several lncRNAs have now been identified in kiwifruit fruits that participate in the synthesis of diverse metabolites, including antioxidants and nutrients (Tang *et al*., 2016). These pathways are also linked to the HS response (Yuan *et al*., 2024), but the regulation of these pathways by lncRNAs in kiwifruit plants under HS remains to be studied. Omics technologies have been applied to elucidate genetics, physiology, and metabolism in kiwifruit, enabling assisted breeding strategies. However, there is a lack of information regarding HSR. Most of the studies are focused on fruit quality traits such as colour, size, and ripening, as well as, pathogen resistance, while abiotic stress damage is scarcely considered (Nazir *et al*., 2024), with just few studies on chilling injury and freezing tolerance using proteomic and metabolomic approaches (Sun *et al*., 2021; Yajing Wang *et al*., 2024; Zhang *et al*., 2021).

3.5. Omics approach comprehending HS in Kiwifruit

Omics studies have shed light on the molecular basis of HSR in kiwifruit, providing deeper insights into the HS mechanisms in kiwifruit (Table 1). Genome wide identification has permitted the identification of core genes such as *Hsf* and *SnRK* families revealing their roles in HSR (Tu *et al*., 2023; Wang *et al*., 2025). Transcriptomics in combination with physiological analyses have revealed regulatory networks including and upregulation of key transcripts encoding for HS response elements, bringing connectivity between damage minimization, Hsps synthesis and metabolite synthesis (Shen *et al*., 2023; Yuan *et al*., 2024). Today there are no proteomic, metabolomic or multiomic studies targeting kiwifruit under HS, and those are opportunity areas that can provide more comprehensive and integrative understanding of the molecular mechanisms underlying HSR in kiwifruit.

3.6. Gene identification, overexpression and pathway analysis under HS in kiwifruit

Some particularities have been revealed in kiwifruit under HS conditions. A total of 36 and 48 *Hsfs* were identified in the diploid kiwifruits *A. chinensis* and *A. eriantha.* RT-qPCR and dual-luciferase reporter assay revealed that most of *Hsf*s, especially *AcHsfA2a*, are expressed under high-temperature conditions (Tu *et al*., 2023). Plants overexpressing *AcHsfA2-1* can tolerate heat shock temperatures over 45°C for at least 2 hours (Shen *et al*., 2023). HS can also promote overexpression of *PDC* in kiwifruit. *AdPDC1* and *AdPDC2* have been proven to be involved in HSR, specifically in reproductive organs (Luo *et al*., 2017). Similarly, ethylene response factors (ERF) have been proven to be involved in HS responses in *A. chinensis* var. *deliciosa* fruits. *AdERF* genes, *AdERF3, 4, 7, 9, 10, 11, 12, 13* and *14* genes are upregulated during heat exposure (Yin *et al*., 2012). Thanks to RT-qPCR, knockout, transgenic, and sequencing technologies, now is clear that different genes participate in the HSR response, with different implications and allocations within the plant.

Over the past two decades, many HSR plant varieties have been developed through transgenic breeding as genes related to resistance have been identified (Anwar and Kim, 2020; Janni *et al*., 2020; Ku and Ha, 2020). The latest findings have permitted a bigger overlook of pathways that kiwifruit plants undergo HS. Antioxidant genes, Hsps, cuticle layer compounds biosynthesis, starch and sucrose metabolism, autophagy, flavonoid biosynthesis, phenylpropanoid biosynthesis, MAPK signalling pathway, arginine and proline metabolism, and ABC transporters, are prominent upregulated elements in mutant plants with enhanced HSR than wild types (Yuan *et al*., 2024). These findings reveal the complexity of HSR mechanism, and future research should explore each route in detail.

4. Summary of strategies for counteracting the HS now and in the future

4.1. Developing HSR through hybridisation and grafting in kiwifruit

In fact, the hybridisation of many *Actinidia* species has been proven under experimental conditions, and hybridisation among wild taxa has been inferred through molecular approaches (Table 2). HSR could be conferred through heterosis, whereby a hybrid exhibits superior performance for a trait compared to its parents (Huang *et al*., 2016). This offers an important opportunity for kiwifruit crop breeding. However, few hybrid cultivars have been assessed under HS conditions. Nevertheless, interspecific hybrids such as the Jinyan and Sanuki kiwicco cultivars both demonstrate high HSR (Kataoka *et al*., 2022; Zhong *et al*., 2012). The success of the Jinyan suggests that we need to pay attention to the evaluation of heat-tolerant kiwifruit species in the genus *Actinidia*, and to assess their breeding potential as hybrid parents. Obtaining hybrid HSR cultivars allows the mechanisms conferring resistance to offspring to be studied and important sources of germplasm for grafting trials to be acquired.

Grafting provides an opportunity to improve kiwifruit plants and impart unique characteristics. Seeds from wild plants and cultivated varieties are a valuable resource for propagating rootstock with high variability for the scion (Akbaş *et al*., 2014; David *et al*., 2020), allowing the incorporation of abiotic resistance into the grafted plant. Distinct species of kiwifruit have been evaluated as potential germplasm for grafting. Genotypes of *A. macrosperma* and *A. valvata* are promising materials that could accelerate the process of water logging and drought tolerance in kiwifruit breeding (Bai *et al*., 2022; Zhong *et al*., 2018). Moreover, rootstocks can modulate the physiological response to stress conditions, potentiating the antistress machinery that in some extend is conserved to counteract different stressors, including HS (Bai *et al*., 2022). In view of this, grafting can be one of the ways for kiwifruit scions to acquire HSR, but the prerequisite is to obtain excellent heat-tolerant rootstock varieties.

4.2. Exogenous substance for HSR promotion in kiwifruit

The application of exogenous substances has been shown to trigger HS. For example, exogenous melatonin has been shown to protect against oxidative damage by reducing H_2O_2 levels in kiwifruit seedlings. It enhances the activity of SOD, CAT, GR, APX and POD, and increases vitamin C levels via MDHAR and DHAR (Liang *et al*., 2018). Similarly, exogenous γ-aminobutyric acid (GABA) enhances heat tolerance by upregulating Hsp70 expression and protecting the photosynthetic system in seedlings. Furthermore, it also enhances SOD, GSH, POD activities for ROS scavenging (Huo *et al*., 2023).

Application of osmoprotectant Glycine betaine (BlueStim), spray application of Calcium carbonate (PureShade), and spray application of antioxidant (SunProtect) demonstrated mitigation properties for HS. The first protects photosynthetic activity by raising stomatal conductance, preserving the RuBisCo enzyme activity, and conserving the ultrastructure of chloroplasts, The second reduces leaf temperature during the hottest days of summer by acting as a reflective protection layer. The third promotes the synthesis of endogenous antioxidants (Ntanos *et al*., 2022).

4.3. Other considerations at present scenario

Molecular strategies have enabled the editing and acceleration of the traditional selection process, which takes several years. In this context, special attention is given to marker-assisted selection, which is considered a vital tool for improving climate resilience (Hazarika *et al*., 2022; Nazir *et al*., 2024). HSR genes evaluated in different plants (Table 3) have paved the way for the development of genotypes that can withstand the effects of rising temperatures.

In kiwifruit plants, many genes involved in HS signalling pathways, plant hormone signal transduction, and transcriptional regulation have been revealed, making HSR a mixture of multiple mechanisms (Yuan *et al*., 2024). Nevertheless, the mechanism involved in kiwifruit HSR is starting to be understood (Figure 4), and the application of omics approaches would greatly enhance our understanding of the phenomenon. Currently, transgenic mutants are the main subjects of study to understand mechanisms and functions. Thanks to CRISPR/Cas9, understanding gene functions has become quick and precise. Gene editing is now being applied to major crop species, which makes us better prepared to face future challenges (Iqbal *et al*., 2020).

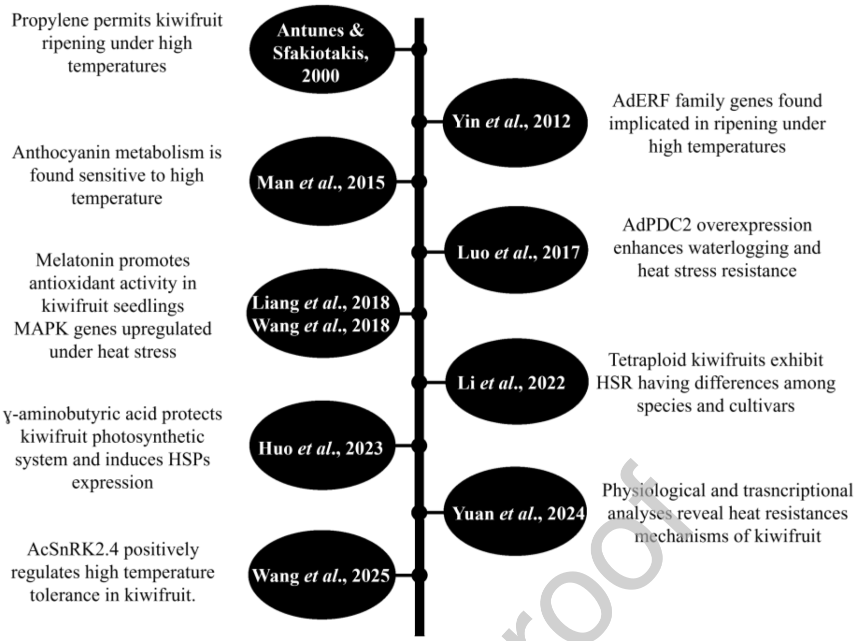

Figure 4. Timeline of the research progresses on kiwifruit heat stress resistance

In the context of climate change and rising temperatures, more attention is being paid to the consequences of heat stress for plants. Usually, elevated temperatures are accompanied by extended periods of drought. This combination can be deadly for kiwifruit plants: with inadequate irrigation and reduced water in the vascular system, the leaves are unable to withstand the warming, and the damage spreads rapidly throughout the canopy. Therefore, irrigation schemes are essential for cooling vegetal tissues and protecting plants from photosynthetic disruption (Rajan *et al*., 2024). Proper orchard management that understands the potential effects of rising temperatures is essential to prevent irreparable damage, death and economic losses (Table S1).

To learn more about kiwifruit evolution and resistance mechanisms against stressors, conservation measures should be promoted. Wild germplasm still has secrets awaiting to be explored. However, changes to niche suitability caused by human intervention endanger natural populations. Efforts to protect wild kiwifruit germplasm resources and mitigate damage would give us time before losing information linked to species extinction. Kiwifruit with all its associated species and cultivars have shown differences in HSR. Thus, adaptability solutions come along diversity. In addition, the benefits of understanding adaptability strategies can benefit countries that trying to cultivate kiwifruit in tropical latitudes, where the heat can be even more challenging. For example, kiwifruit plants in Mexico have demonstrated sufficient plasticity to acclimate to tropical conditions and produce fruit (Cruz-Castillo *et al*., 2022).

5. Prospects

In the long term, breeding HSR cultivars is the most efficient way to solve HS complications for kiwifruit. The genetic characteristics of HSR cultivars should be assessed in order to accelerate the breeding process. The most important way is to rely on the rich species resources and genetic diversity of kiwifruit to select and breed heat-tolerant germplasm. Interspecific and intraspecific hybridisation breeding using existing superior varieties is an effective method of obtaining heat-tolerant offspring. Meanwhile, using exogenous substances and effectively and reasonably managing orchards are also effective methods of alleviating HS. Combining new generation molecular technologies with tissue culture strategies may be a way to quickly improve kiwifruit HSR. In summary, evaluating and screening heat-tolerant species and wild resources, applying interspecific and intraspecific hybridisation, using modern molecular markers and gene editing technologies, applying exogenous substances, and managing orchards effectively all play a significant role in the future breeding of heat-tolerant kiwifruit varieties and kiwifruit production.

Despite the advancements in understanding the mechanisms of HSR in kiwifruit, several research gaps remain. There is a lack of comprehensive studies that integrate multiple stress factors. For example, *DREB2A* is a crosstalk point between drought and HS (Sato *et* *al*., 2024). Hence, considering a wider range of stress factors would be a more effective way to comprehend real scenarios that kiwifruit plants are facing and how is the molecular network affected. In addition, the transcriptomic advances have offered many HS responsive genes with not clear interactions elucidated, particularly is not clear how the metabolic reprograming, energy efficiency preservation, phytohormone regulation and ROS metabolism occurs after the activation of Hsfs. Future research should focus on the previous gaps and keep combining traditional strategies and new technologies to counteract HS emergency.

Given the increasing global temperatures and the vulnerability of kiwifruit to HS, breeding for heat tolerance is a critical area of research. Omics approaches provide essential tools for identifying genetic markers associated with heat tolerance. By using genomic, transcriptomic, proteomic, and metabolomic data, breeders can identify heat-resistant traits and incorporate them into new cultivars. With the sequencing of the kiwifruit genome, genomic selection can be employed to select for heat-resistant traits. Marker-assisted breeding can be used to incorporate these traits into elite cultivars. CRISPR/Cas9 and other gene-editing technologies offer the potential to directly modify genes involved in heat stress response, such as HSPs, antioxidant enzymes, and heat shock transcription factors. The identification of heat-resistance markers through omics studies can facilitate marker-assisted breeding, enabling the development of heat-tolerant kiwifruit varieties in a shorter time frame.

The integration of multifactorial aspects would provide a comprehensive understanding of HS responses in kiwifruit. Hereby, several areas remain to be explored:

- Systems Biology: Integrating genomics, transcriptomics, proteomics, and metabolomics into a systems biology approach could reveal more holistic insights into heat stress tolerance.

- Epigenetics: The role of epigenetic modifications in heat stress tolerance needs further investigation. Epigenetic changes might provide a mechanism for long-term adaptation to heat.

- Environmental Interactions: Understanding how kiwifruit interacts with its environment under heat stress (e.g., soil composition, water availability) is crucial for developing robust heat-resistant cultivars.

- Microbiome Interactions: The plant microbiome can influence heat tolerance (Ali *et al*., 2018; Aly *et al*., 2011; Shekhawat *et al*., 2021). Understanding how beneficial microbes contribute to heat resistance in kiwifruit could open new avenues for improving stress tolerance.

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CRediT authorship contribution statement

Edgar Manuel Bovio-Zenteno: Writing – original draft, Visualization. **Tianjiao Jia:** Investigation, Validation. **Mian Faisal Nazir:** Formal analysis. **Longyu Dai:** Data curation. **Jie Xu:** Formal analysis. **Yafang Zhao:** Investigation. **Shuaiyu Zou:** Conceptualization, Resources, Writing – review & editing. **Hongwen Huang:** Resources, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Table 1. Omics studies conducted in kiwifruit under HS

Applied methods	**Key traits under study**	**Key pathways**	**Genes/Markers identified**	**Authors**
Genome wide identification, structural and functional characterization	Hsf gene family high temperature response	Mechanisms of HS response	Hsfs, especially AcHsfA2a	(Tu *et al.*, 2023)
Transcriptome analysis	Heat tolerance when AcHsfA2-1 is overexpressed	Post-translational modification, protein turnover, chaperones, transcription and signal transduction mechanisms.	AcHsp20–1, AcHsp20–2 and AcHsp20–3, E3 ubiquitin-protein ligase, DnaJ subfamily B member like, Chaperone Member-like, CCR4-associated factor 1-like, Bax inhibitor-like, BAG domain-containing protein, Zinc metallopeptidase EGY3, Uncharacterized protein.	(Shen *et al.*, 2023)
Transcriptome and physiological analysis	Heat tolerance	Genes related to stress-response, phytohormone signaling, and transcriptional regulatory pathways	AOX, GPX, GST, POD, Hsps, LAR, CCoAOMT, CHI, VSR, CAD, CSE, PAL, PR1, PYL4, ARF, BAK1, SRK2, MADS, MYB, bZIP, ERF, TCP, bHLH	(Yuan *et al.*, 2024)
Genome wide identification and functional characterization	HS response	SnRK gene family mechanism of HS response	SnRKs, especially AcSnRK2.4	(Wang *et al.*, 2025)

Table 2. Summary of documented hybrids and parental origin from artificial crosses and some inferred from nature.

Hybrid name	Parental species ploidy [a]	Condition	Reference
A. chinensis x A. callosa	*A. chinensis (2x) x A. callosa (2x)*	Artificial	(Hirsch *et al*., 2001)
A. chinensis x A. eriantha	*A. chinensis (2x) x A. eriantha (2x)*	Artificial	
A. eriantha x A. callosa	*A. eriantha (2x) x A. callosa (2x)*	Artificial	
A. eriantha x A. chinensis	*A. eriantha (2x) x A. chinensis (2x)*	Artificial	
A. eriantha x A. lanceolata	*A. eriantha (2x) x A. lanceolata (2x)*	Artificial	
A. eriantha x A. polygama	*A. eriantha (2x) x A. polygama (2x)*	Artificial	
A. hemsleyana x A. chinensis	*A. hemsleyana (2x) x A. chinensis (2x)*	Artificial	
A. hemsleyana x A. eriantha	*A. hemsleyana (2x) x eriantha (2x)*	Artificial	
A. kolomikta x A. chinensis	*A. kolomikta (2x) x chinensis (2x)*	Artificial	
A. chrysantha x A. arguta	*A. chrysantha (4x) x A. arguta (4x)*	Artificial	
A. chrysanta x A, valvata	*A. chrysanta (4x) x A, valvata (4x)*	Artificial	
A, arguta issai x A. deliciosa	*A, arguta issai (6x) x A. deliciosa (6x)*	Artificial	
A. arguta x A. melanandra	*A. arguta (4x) x A. melanandra (4x)*	Artificial	(Beatson *et al*., 2007)
A. arguta x A. valvata	*A. arguta (4x) x A. valvata (4x)*	Artificial	
A. arguta x A. deliciosa	*A. arguta (N.A.) x A. deliciosa (N.A.)*	Artificial	
A. arguta x A. polígama	*A. arguta (N.A.) x A. polígama (N.A.)*	Artificial	
A. arguta-deliciosa x A. purpurea	*A. arguta-deliciosa x A. purpurea*	Artificial	
A. arguta-deliciosa x A. chinensis	*A. arguta-deliciosa (N.A.) x A. chinensis (N.A.)*	Artificial	
A. arguta-deliciosa x A. melanandra	*A. arguta-deliciosa (N.A.) x A. melanandra (N.A.)*	Artificial	
A. purpurea x A. chinensis	*A. purpurea (N.A.) x A. chinensis (N.A.)*	Artificial	
A. chinensis x A. arguta	*A. chinensis (N.A.) x A. arguta (N.A.)*	Artificial	

A. chinensis x A. purpurea	*A. chinensis (N.A.) x A. purpurea (N.A.)*	Artificial	
A. chinensis x A. macrosperma	*A. chinensis (4x) x A. macrosperma (4x)*	Artificial	
A. chinensis x A. melanandra	*A. chinensis (4x) x A. melanandra (4x)*	Artificial	
A. chinensis x A. arguta-melanandra	*A. chinensis (N.A.) x A. arguta-melanandra (N.A.)*	Artificial	
A. macrosperma x A. melanandra	*A. macrosperma (N.A.) x A. melanandra (N.A.)*	Artificial	
Cultivar Jinyan	*A. eriantha (N.A) x A. chinensis (N.A.)*	Artificial E.I H.R.	(Zhong *et al.*, 2012)
A. fulvicoma var. *fulvicoma*	*A. cylindrica (2x) x A. eriantha (2x)*	Wild Inferred	(Liu *et al.*, 2017)
A. cylindrica var. *reticulata*	*A. cylindrica (2x) x A. eriantha (2x)*	Wild Inferred	
A. hubeiensis	*A. chinensis (2x) x A. callosa (2x)*	Wild Inferred	
A. lijiangensis	*A. chinensis (2x) x A. callosa (2x)*	Wild Inferred	
A. callosa var. *strigillosa*	*A. chinensis (4x) x A. callosa (4x)*	Wild Inferred	
A. indochinensis	*A. callosa (2x) x A. chinensis (2x)*	Wild Inferred	
A. zhejiangensis	*A. eriantha (2x) x A. rufa (2x)*	Wild Inferred	
A. valvata	*A. Kolomikta (4x) x A. polygama (4x)*	Wild Inferred	
A. chinensis var. *deliciosa*-5	*A. arguta (6x) x A. chinensis (6x)*	Wild Inferred	
MTH	*A. eriantha (2x) x A. chinensis (2x)*	Artificial	
Sanuki kiwicco	*A. rufa (N.A.) x A. chinensis* var. *chinensis (2x)*	Artificial E.I. H.R.	(Kataoka *et al.*, 2022)

[a] Female parent is written first, N.A. Not available data, E.I. Economic importance, H.R. Heat resistant

Table 3. Modification strategies applied to provide heat resistance in major crop plants and kiwifruit.

Plant species	**Gene**	**Function**	**Modification**	**Reference**
Oryza sativa (Rice)	OsTMS5	Transcription factor	Clean transgene insertion	(Zhou *et al*., 2016)
Solanum lycopersicum (Tomatoe)	SlHyPRP1	Proline-rich protein synthesis	Functional domains deletion	(Klap *et al*., 2017; Tran *et al*., 2023; Yu *et al*., 2019)
	SlMAPK3	Protein kinase	Knock out	
	SIAGL6	MADS-Box transcription factor	Knock out	
Zea mayz (Maize)	ZmTMS5	Transcription factor	Knock out	(Li *et al*., 2017)
Lactuca sativa (Lettuce)	LsNCED4	Enzyme for abscisic acid biosynthesis	Knock out	(Bertier *et al*., 2018)
Actinidia chinensis (Kiwifruit)	AdPDC2	Pyruvate decarboxylase synthesis	Over-expression transgenic	(Luo *et al*., 2017; Shen *et al*., 2023)
	AcHsfA2-1	Transcription factor	Over-expression transgenic	

Declaration of Interest Statement

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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