

PHYSIOLOGICAL, GROWTH AND YIELD RESPONSE OF POTATO (*Solanum Tuberosum* L.) TO HEAT STRESS

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ABSTRACT: Climate change adversely affects crop production as the associated rising temperatures damage its physiology and overall yield. Heat stress affects potato at various stages of growth, but sprout development and tuber initiation are the most sensitive to high temperatures. It also affects the photosynthesis (especially PII) activity, thereby limiting the production and partitioning of assimilates to the sink (tuber). The night temperature is more critical for potato tuber initiation and development. Tuber induction is best at 15°C, initiation at 22°C, and setting at 15°C. Yields are expected to decline by 18–32% in the 2050s due to the effects of global warming on potato cultivation. In addition, heat stress impacts quality resulting in physiological disorders. It also impairs the nutritive quality by boosting glycoalkoid levels in tubers, making the tuber bitter to consume. Therefore, strategies must be developed to combat the impact of heat stress. Priority strategic areas include the production of heat-tolerant potato genotypes by genetic engineering techniques such as screening, selection, and breeding as well as exogenous applications of osmoprotectants and agronomic methods.

KEYWORDS: Heat stress; Potato; Growth; Physiology; Yield; Quality

1. INTRODUCTION

Potato (*Solanum tuberosum* L.) is the world's most important vegetable crop, capable of ensuring food security in the face of mounting demand. With 381 million tons produced annually, it is the world's fourth most important food crop, after wheat (729 million tons), rice (741 million tons), and corn (741 million tons) (1037 million tons) (Ruan et al., 2021); but it ranked first among the non-cereal crops. Potato is a nutritious vegetable that is regarded as one of the most beneficial crops for reducing hunger, malnutrition, and poverty around the world because of its great productivity, as can be seen by its remarkably high harvesting index of over 75% (Wijesinha-Bettoni & Mouillé, 2019). Hence, potato has the potential to significantly contribute to human nutrition as an addition to other staple crops like rice and wheat (Campos & Ortiz, 2020).

For food security, understanding the effects of climate change on potato yield is

critical. Extreme heat and drought brought on by global climate change pose a significant threat to long-term crop production by reducing plant performance and output. Such a negative influence on agricultural productivity is projected to worsen in the future (Chourasia et al., 2021) due to increasing greenhouse gas emissions, which will lead to increased evapotranspiration and drought severity (Dahal et al., 2019).

When heat stress and moisture stress are combined, the result is massive losses in the agricultural industry (Mittler, 2006). According to reports, climate change is expected to reduce worldwide potato yields from 18 percent to 32 percent (Hijmans, 2003). For instance, in 2016, heat and drought reduced the potato crop in Ontario by 35–50% (Banks & VanOostrum, 2016). These great losses in potato yield are attributed to the impact of heat stress which is directly or indirectly related to physiological processes.

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Reviewing the effects of heat stress on physiological processes such as photosynthesis, dry matter accumulation and partitioning, tuberization (tuber initiation and development, tuber yield and quality), nutritive quality of tubers (composition and antioxidant property), and reproduction/breeding activities are the main objectives of this paper. Finally, methods to increase heat and moisture tolerance will be reviewed, and further steps will be suggested.

2. HEAT STRESS ON PHYSIOLOGY AND MORPHOLOGY

Due to the ever changing climate, there has been an increase in the CO₂ levels, resulting in an increase in global air temperature. Because of this, plants' physiological and morphological functions have been adversely affected. The next sections describe the effects on the two most important morphophysiological effects separately.

2.1 Photosynthesis

Heat stress has a deleterious impact on plant growth and development, including leaf photosynthesis. The most harmful consequence of heat stress on plants is the degradation of the plant's photosynthetic activity, with the light reaction's (PSII) and the dark reaction's RUBISCO activase enzymes being the most affected (Sun et al., 2017; Wang et al., 2018). The optimal temperature for full plant photosynthesis in a potato crop is 24°C (Fleisher & Timlin, 2006). Heat stress induces reversible photosynthesis reduction; higher heat stress causes irreversible damage to the photosynthetic machinery, resulting in greater plant growth suppression (Aldubai et al., 2022; Song et al., 2014).

Heat stress reduces the photosynthesis rate in heat tolerant and heat sensitive potato cultivars, according to (Aien et al., 2017). At high temperatures, these researchers also

saw a decrease in stomatal conductance. Chlorophyll is a key component of the photosynthesis process, which is influenced by high temperatures (Sadura et al., 2020; Yuan et al., 2021). The effect of heat stress on the level of chlorophyll in potatoes, on the other hand, is unpredictable. Previous research revealed that when temperatures were high, total chlorophyll decreased and the ratio of chlorophyll (a/b) increased (Aien et al., 2017; Hancock et al., 2014).

In potato plants, high temperatures have been shown to reduce whole-canopy photosynthesis (Obiero et al., 2020). Changes in leaf area, as well as the rate of net photosynthesis (Pn) per unit leaf area, are included in whole canopy measurements. Strong evidence is also that high temperatures affect potato leaf area development (Fleisher & Timlin, 2006). The reaction of Pn to high temperatures differed between younger and older leaves. The photosynthetic rate of older leaves was more likely to decrease, whereas the rate of younger leaves either increased or remained unchanged (Lemoine et al., 2013). The importance of these differences for overall plant carbon dynamics, and thus tuber growth, will be determined by the relative contributions of young and old leaves, as well as the impact of known changes in leaf area and canopy structure on light receipt by leaves of various ages (Obiero et al., 2020). A switch to high temperature increased the net photosynthesis of a young, fully grown leaf, which had previously declined. This was most likely due to stomatal reactions, and it raises the question of how important atmospheric humidity and leaf water status are in affecting potato sensitivity to high temperatures (Obiero et al., 2020). Strong visible light and heat are two abiotic stressors that can damage photosystem II. The most significant damage occurs

in the reaction center-binding D1 protein under both stressors. Phosphorylation and dephosphorylation of the D1 protein as well as the binding of the extrinsic PsbO protein to Photosystem II cause the most significant damage (Yamamoto et al., 2008). Since blocking this electron channel during anaerobiosis was found to dramatically increase the photoinactivation of PS I, it appears that heat-stress-induced PS I electron transport independent of PS II constitutes a protective mechanism in potato crops (Havaux, 1996).

2.1 Dry mater accumulation and photoassimilate partitioning

Potatoes have sink organs in the form of underground stolons, and source organs in the form of leaves (Golovko & Tabalenkova, 2019; Hastilestari et al., 2018). Sucrose in mesophyll cells initiates photosynthesis, which is carried to companion cells and the sink via sieve elements (Jensen et al., 2016). Temperature affects carbon transit to sink organs in the potato, and at high temperatures, less absorbed carbon is incorporated into the tubers. As a result, tuber yield is determined by the relative sink strength and assimilate translocation from leaves (Ludewig & Sonnewald, 2016). To enable continued growth and development, sucrose is unloaded and then degraded into hexoses by sucrose synthases (SuSy) (Hastilestari et al., 2018). SuSy overexpression in transgenic plants increases starch accumulation in tubers, implying that SuSy is involved in sink strength determination (Baroja-Fernández et al., 2009). Carbon accumulation at phloem unloading sites limits the carbon supply to tubers and weakens the sink during heat stress (Durand et al., 2018). Apart from sucrose, various phloem mobile compounds are synthesized in leaves and transferred to the sink to limit tuberization under favorable conditions (Abelenda et al., 2019).

For better knowledge and understanding of the source-sink regulation at elevated temperature, a tissue-specific heat exposure is administered to potato plant (Hastilestari et al., 2018). Photosynthesis and SP6A were influenced by below-ground heat stress, whereas tuberization was inhibited by above-ground heat stress. These findings show that tuberization under heat stress is regulated by bidirectional signaling between source and sink organs (Hastilestari et al., 2018).

Heat stress reduces tuber production, tuber dry matter, and net absorption rate considerably (Aien et al., 2017; Busse et al., 2019; Ferreira et al., 2014). Temperatures of 14°C to 22°C stimulate tuberization, boost dry matter partitioning, and inhibit haulm development (Rykaczewska, 2013). High temperature, on the other hand, increases dry matter partitioning to the haulm, shoot growth, root growth, and tuber yield reduction by reducing tuber size and quantity (Trapero-Mozos et al., 2018). It has been shown that rise in temperature leads to increased percentage of leaf dry matter and decreased percentage of tuber dry matter. They also saw a similar pattern in the dry weight of leaves and tubers (Hancock et al., 2014). During tuber initiation, high temperatures cause the respiration rate to increase, wasting up energy and lowering tuber set. High temperatures during bulking slow down tuber bulking, which results in yield losses. A high respiration rate mid-season or later may result in the development of a second set of tubers that never grow in size (Ewing, 1981; Finckh et al., 2006).

3 HEAT STRESS EFFECT ON TUBER FORMATION AND YIELD

3.1 Tuber initiation and development

The night temperature is critical for potato tuber initiation and development (Kim & Lee,

2019). Even if the daytime temperature is 30–35 °C, potatoes can produce a satisfactory yield if the nighttime temperature is below 18 °C. Even when the daytime temperature is 25–27°C, there is little tuberization when the nighttime temperature exceeds 22°C. It was also investigated that respiration can absorb 35% of the 14_c initially ingested during tuber formation, indicating a high efficiency of carbohydrate polymer storage in the form of starch. So, when it comes to heat tolerance in potatoes, the minimum night temperature is more important than the maximum day temperature (Muthoni & Kabira, 2015). Temperatures above the optimum significantly impact various physiological characteristics, including tuberization (Rykaczewska, 2013).

Tuber development begins with the suppression of longitudinal growth and the extension of radial growth. Tuberization in potatoes is a complex biochemical process involving numerous metabolic pathways and molecular and hormonal signaling (Dutt et al., 2017; Kondhare et al., 2020). Photoperiod (Zhou et al., 2017), growth hormones (Kolachevskaya et al., 2018), and night temperature all play a role in tuberization (Rykaczewska, 2015). Hence, potato tuber initiation and development is sensitive to high temperatures, and the asymmetric increase in day and night temperatures poses a difficulty.

Temperatures for tuber formation are lower: tuber induction is best at 15°C, initiation at 22°C, and setting at 15°C (Struik, 2007). As a result, the time when the heat-sensitive sink (i.e., tuber) develops is essential for potato yield and tuber size. In a recent independent experiment to investigate the effects of high temperature and higher CO₂, high temperature (35°C) significantly reduced tuber growth compared to normal temperature (25°C) at the tuber initiation

stage in both low (LowCO₂) and elevated (ElevCO₂) CO₂ settings. Tuber DMAR was reduced by 82 percent when temperatures were high and CO₂ levels were low (Chen & Setter, 2021).

3.2 Tuber Yield and Quality

Heat-stressed plants are partially immature, as a result of secondary growth. The size of a plant's assimilation region was determined by the duration of heat stress and the moisture content of the soil (Tang et al., 2018). Secondary tuberization is linked to secondary growth of the above-ground section of the plant in potatoes (Rykaczewska, 2017). High temperatures, regardless of water supply, cause second-growth in potato tubers, while dryness is not required to cause second-growth (Chang et al., 2018). Heat stress had a negative impact on potato tuber yield during the growing season. When heat stress influences plants in the II phase, the effect will be more pronounced. When the time of heat stress treatment on potato plants was delayed the negative effect on the yield of tubers became minimum (Rykaczewska, 2017).

High temperatures acting later in plant development had a detrimental impact on tuber physiological abnormalities (Figure 1), including deformations, sprouting, tubers sprouting in the soil before harvest, and tubers that were physiologically younger (immature). If potato plants are planted in warmer seasons, immature tubers frequently sprout during growth, a process known as "heat sprouts" or "heat sprouting." More than half of the tubers in the field have the potential to sprout. If potato tubers sprout before or shortly after harvest, the quality and utility of the potatoes is seriously harmed (Mikitzel, 2014; Stark et al., 2020).

One of the most major unpredictable factors affecting potato yields is high

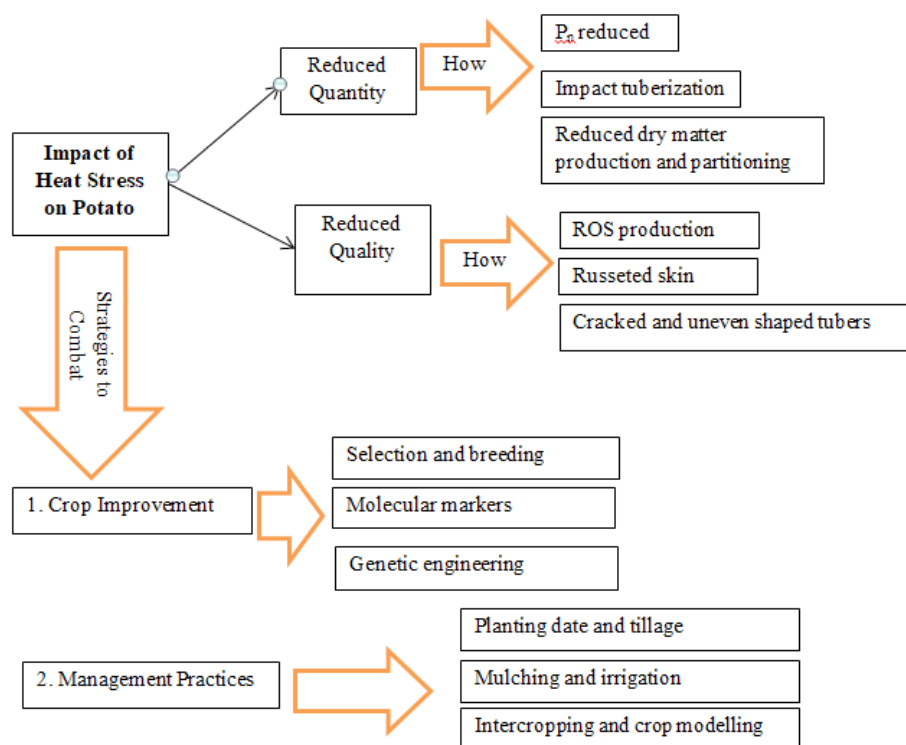


Figure 1. Impact of heat stress on potato and strategies to combat

temperature. Global yields are expected to decline by 18–32% in the 2050s due to the effects of global warming on potato cultivation (Hijmans, 2003). However, it should be noted that the ideal temperature for a potato crop varies depending on the plant's stage of development (Wohleb et al., 2014). Though temperatures between 14 and 22°C at night are ideal during the pre-stolon initiation stage, night temperatures should be around 17°C for proper tuber formation, as high temperatures promote vegetative growth and tuber production falls rapidly (B. Singh et al., 2020). There may not be any tuberization at 25°C and above, whereas potato plants can withstand up to 32°C without significant loss in total biomass production (A Singh et al., 2016).

The physiological impacts of high temperatures on the potato crop are numerous. Reduced early sprouting, unevenly

shaped tubers, increased number of small sized tubers, tuber cracking, bitter and toxic tuber formation, low-quality tubers with lower dry matter, secondary tuber formation, pre-harvest sprouting, irregular skin, necrosis, chlorophyll loss, reduced stem thickness, increased plant height, increased number of small sized leaves, increased concentration of reducing sugars, and increased disease susceptibility are just a few examples (George et al., 2017; B. Singh et al., 2020; Tang et al., 2018).

Furthermore, heat stress produced by excessive soil temperature causes interior brown patches and brown discolouration in the tuber. High soil temperatures produce tuber rot, which damages sprouts, and mulching can help to accelerate this process (Mori, 2015). High temperatures have been linked to increased skin/periderm cell layers, resulting in russeted or cracked tubers with

uneven skin. The greater thickness is related to phellogen's enhanced activity at high temperatures (Molteberg, 2017). Furthermore, the potato tuber moth (*Phthorimaea operculella* Zeller) grows more quickly at higher temperatures (Kroschel et al., 2013).

4. HEATS STRESS EFFECT ON NUTRITIONAL QUALITY

High temperatures alter potato tubers' nutritional profile and secondary metabolism by modifying the content of health-promoting components such as anthocyanin and carotenoids (Fogelman et al., 2019). Even a brief exposure to high temperatures during tuberization can increase the amount of reducing sugars in the tubers and increase stem end chip deformities (Busse et al., 2019). Heat stress also boosts glycoalkoid levels in tubers, making the tuber bitter to consume (Benavides et al., 2017; Uluwaduge et al., 2018). This issue is linked to greater amounts of glycoalkaloid in heat-tolerant potato types (Benavides et al., 2017).

Another independent study found that under high air temperatures, potatoes' total and tuber dry matter content falls significantly (Zhou et al., 2017). By inducing tuber diseases and affecting tuber processing and nutritional quality, high-temperature stress can adversely impair the overall and marketable output of potatoes (Momčilović, 2019).

5. STRATEGIES TO IMPROVE HEAT STRESS TOLERANCE

5.1 Selection and Breeding

Sessile plants are subjected to various climatic challenges, and they have developed various strategies to cope with temperature fluctuations in their environment (Pedroza-Garcia et al., 2022). To secure their survival, they respond to heat stress by undergoing

a complex series of adaptive modifications (Asthir, 2015). To prevent heat stress, plants use a variety of mechanisms, including leaf rotation, leaf rolling, early maturation, transpirational cooling, and changes in membrane lipid compositions (Sadok et al., 2021).

In a heat-stressed environment, the potato may experience oxidative damage. On the other hand, heat-resistant potato types have higher antioxidant enzyme activity to protect the cells. Rao et al., 2018, as cited in (B. Singh et al., 2020). Potato breeding for heat tolerance can be enhanced by a thorough understanding of the many processes governing ROS scavenging enzymes such as superoxide dismutase, ascorbate peroxidase, and catalase in response to heat stress, Rao et al., 2018 as cited in (B. Singh et al., 2020)

Heat tolerance is influenced by stress response expression. A substantial number of genes show differential expression following heat stress treatment in important food crops and model plants, according to previous research (Aldubai et al., 2022). Many heat responsive genes in potatoes have been found thus far using various methods. (Anupama Singh et al., 2015) used a microarray chip with 39,031 potato genes to find genes that cause tuberization at high temperatures in two different potato cultivars.

Many wild solanum species are resistant to abiotic stressors such high temperatures, frost, drought, salt, severe rains, and heavy metals (Imran et al., 2021). There are various wild heat-tolerant potato species that can be used in breeding programs to create heat-tolerant lines, including *S. kurtzianum* and *S. sogarandinum*, *S. chacoense*, *S. stoloniferum*, *S. demissum*, and *S. berthaultii* (Guedes et al., 2019). These wild species' genes can be employed to boost potato crops (Stokstad, 2019). Transfer of genes from other sexually

compatible wild species has been the most prevalent strategy used in the last century to generate abiotic stress tolerant variations (Stokstad, 2019). The majority of today's farmed potato cultivars are tetraploid, although some wild potato species can withstand extreme temperatures (Guedes et al., 2019). As a result, breeding with many wild species might be difficult due to ploidy differences (Bethke et al., 2017).

5.2 Management Strategies

In potato, genetic improvement alone is not enough to maximize crop production and productivity. Because current potato cultivars have a limited genetic background, they have poor abiotic stress tolerance (Tao et al., 2012). As a result, in order to cope with a variety of climatic challenges, it is required to modify present commercial cultivars in accordance with the requirements.

In order to successfully grow the potato crop under abiotic stress, better potato cropping systems are required. Superior genotypes, in combination with appropriate agronomic measures including planting date, soil management, tillage, mulching, irrigation, and intercropping, can help potatoes deal with abiotic challenges (Muthoni & Kabira, 2015; Resop et al., 2016). Farmers should modify the planting dates to increase potato yields in different climates (Franke et al., 2020).

Early sowing and increased usage of inorganic nitrogen can help prevent yield loss in potatoes (Bewket, 2018). Tillage can help with aeration, infiltration, and nutrient uptake in the soil. Soil moisture and temperature are directly related to potato yield and quality, which can be maintained by utilizing organic/biodegradable mulches (Bavougian & Read, 2018). One of the best approaches to reduce yield loss due to

heat stress is to vary the sowing season in response to climate change. Plants adapt to heat stress by changing stress proteins' expression, antioxidant defences, osmoprotectants, signaling pathways, and transcriptional regulation (Rasul et al., 2017; Xalxo et al., 2020).

6. FUTURE DIRECTIONS

Climate change is posing a threat to long-term potato production. With the creation of heat-tolerant potato types, this effect can be decreased. According to available information, photosynthesis, respiration, carbon partitioning, and hormonal signaling all affect tuber production during heat stress. Because potato tuberization is a complicated polygenic trait, using typical breeding approaches to fight heat stress is difficult. Furthermore, developing effective pure lines takes a long period in breeding programs. Scientists all across the world are working to not only expand potato production in tropical areas, but also to obtain a consistent tuber output under variable environmental conditions.

Apart from breeding, genetic engineering and genome editing techniques are now widely used to generate better crops in the future. Traditional and molecular breeding cycles, transgenic development, and genome editing procedures all require understanding of heat responsive genes.

Most existing cultivars' wild relatives are reservoirs of beneficial genes that could play a key role in crop improvement. The genus *Solanum* contains a number of wild species, the majority of which bear tubers and are widely scattered around the world. These have a wide variety of pest and disease resistance, as well as resistance to various abiotic stresses such as high temperatures, frost, drought, salt, heavy rains, heavy metals, and so on.

S. chacoense, *S. stoloniferum*, *S. demissum*, *S. berthaltii*, *S. kurtzianum*, and *S. soganandinum* are some of the heat-tolerant potato species that can be used in breeding programs to develop heat-tolerant lines. However, knowing the genes involved in tuberization at high temperatures isn't adequate because it's a multigenic characteristic. Understanding the specific molecular networking that occurs in response to heat stress would be a significant step forward.

7. CONCLUSION

Heat stress drastically lowered crop yields, and the impact of this stress is anticipated to grow in the future. Heat stress limits potato output since this crop is extremely sensitive to high temperatures, especially during tuber formation. Tuberisation in response to heat stress is a multigenic feature that is difficult to research and measure using traditional methods. With the use of advanced biotechnological methods, we hope to fully understand the mechanism of tuberculosis in the coming years.

However, using functional genomics, several possible candidate genes in potato have been found, opening up new possibilities for the production of heat-resistant variants. There is a pressing need to extend the database of heat stress-related genes in potatoes, as well as our understanding of how these genes express themselves in response to heat stress. In addition, well-known heat-tolerant genes from model plants can be inserted into the potato genome. To better understand the mechanism of heat tolerance by diverse genes, the novel genome editing tool CRISPR-Cas9 should be used in potato. Besides, better agronomic practices and meteorological analysis can aid in increasing potato production in high temperatures. In today's world, the best strategy to combat heat stress is to use a combination of methods.

Moreover, better agronomic practices and meteorological information can assist in increasing potato production at higher temperatures. In today's situation, combining traditional and new biotechnological procedures is the most effective strategy to prevent heat stress.

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