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High temperature in potato: plant responses and adaptive cultivation strategies to increase production

Abstract. Climate change, with global temperatures rising by 1.09°C from 1850–1900 to 2011–2020, threatens potato production, a critical staple crop, by exceeding the optimal temperature range of 15–20°C. This review synthesizes over 45 peer-reviewed studies published between 2015 and 2025 from Google Scholar and ScienceDirect to evaluate the physiological, morphological, and tuber quality responses of potatoes to high temperatures and to identify adaptive cultivation strategies for sustainable production. High temperatures reduce photosynthetic efficiency through chlorophyll degradation and stomatal closure, increase respiration, and divert photosynthates to vegetative growth, leading to 18–32% yield losses globally by the 2050s. Heat-tolerant varieties, such as Atlantic (11.47 tons/ha), Merbabu-17 (11.04 tons/ha), and Granola (3.61 tons/ha), maintain productivity in medium-altitude lands. Plant growth regulators (PGRs), including BAP, melatonin, and paclobutrazol, enhance tuber yield by regulating hormonal balance and antioxidant activity. Drip irrigation and mulching (e.g., straw, wheat, plastic films) improve water use efficiency and buffer soil temperature. These integrated strategies of heat-tolerant varieties, PGRs, irrigation, and mulching offer practical solutions to mitigate heat stress and ensure sustainable potato production under changing climate conditions.

Keywords: High temperature · Heat-tolerant varieties · Plant growth regulator · Irrigation · Mulch

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Introduction

Potatoes (*Solanum tuberosum* L.) are horticultural crops with the tuber as their economic organ. Based on data Statistics Indonesia (2023), potato production increased by 6.2% from 1.28 million tons in 2020 to 1.36 million tons in 2021), yet it fails to meet the annual demand of 6.16 million tons, driven by rising consumption of processed products like French fries and chips (Yulinarti et al., 2021; Asmara et al., 2022). Potato consumption in Indonesia grew by 2.79% from 2016 to 2020 (Agricultural Data and Information System Center, 2021). Optimal potato growth requires highland environments (>1,000 masl), 9–10 hours of daily irradiation, 1,500 mm/year rainfall, and temperatures of 20–25°C during vegetative growth and 15–20°C during tuber formation (Setiadi, 2009; Diwa et al., 2015; Rykaczewska, 2016; Struik, 2007).

Rising global temperatures due to climate change are altering the morphological and physiological responses of potato plants, significantly affecting productivity (Hancock et al., 2014; Jagadish et al., 2021). The Intergovernmental Panel on Climate Change (IPCC) noted that the 2011-2020 global average temperature was 1.09 ºC higher than the period 1850-1900. Exposure to high temperatures disrupts plant metabolism processes that divert growth mechanisms into plant protection to survive in abiotic stress conditions (Cramer et al., 2011). In potato plants, signals that trigger tuber formation are inhibited, respiration increases, and photosynthate accumulation is diverted to shoot growth due to high temperature (Hamdani et al., 2021; Muthoni & Kabira, 2015; Ningsih et al., 2021). As a result, there is a reduction in yield due to extreme environmental conditions. It can also lower starch content (Mubarok et al., 2022), similar to reduced oil content in high-temperature rapeseed (Qaseem et al., 2019). Potato yield losses due to high temperature are predicted to reach 18-32% by the 2050s (Hijmans, 2003).

This review examines the global impact of high temperatures on potato crop, with a particular focus on focusing on physiological, morphological, and tuber quality responses, and also explores adaptive cultivation practices such as the use of selected heat-tolerant cultivars, plant growth regulators, drip irrigation, and mulching to support sustainable potato cultivation under climate change. Literature selection criteria included scientific journals published in the 2015–2025 timeframe obtained through ScienceDirect and Google Scholar.

Morpho-physiological Response of Potato Plants to High Temperature

Photosynthesis is an important process in plants to produce energy. Temperatures that exceed the optimum range of potato plants cause changes in plant growth and development. Stomata are the place of CO_2 exchange, the release of water vapor during transpiration, and the place where the photosynthesis process takes place (Lawson & Matthews, 2020). High temperatures (>25°C) disrupt potato physiology and morphology, affecting photosynthesis, respiration, and tuber development (Hancock et al., 2014). Most studies indicate that Rubisco activity declines above 30°C, particularly in cultivars like Desiree and Russet Burbank, due to degradation of Rubisco activase enzymes (Wang et al., 2018; Perdomo et al., 2017). Stomatal closure, triggered by increased abscisic acid (ABA) levels, reduces CO_2 uptake and photosynthetic rates (Thakur et al., 2019; Urban et al., 2017). Chlorophyll degradation further limits light absorption, with studies on cultivars like Atlantic showing up to 20% reductions in chlorophyll content at 35°C (Hamdani et al., 2020; Singh et al., 2020). High temperatures also cause leaf metabolic dysfunction by damaging thylakoid membranes, disrupting electron transport, and inactivating oxygen-producing enzymes, leading to oxidative stress (Djanaguiraman et al., 2018). High temperature increases water transpiration through stomata, disrupting plant water status and reducing growth potential (Matthews et al., 2018; Urban et al., 2017).

Morphologically, high temperatures increase gibberellin levels, promoting canopy growth (stems, branches, leaves) at the expense of tuberization (Ohtaka et al., 2020). This leads to taller plants, increased leaf area, and shading, which reduces photosynthetic efficiency (Nunes et al., 2019). Studies on Granola and Kennebec cultivars report a 15–25% reduction in tuber number and weight at temperatures above 25°C due to reduced photosynthate translocation to stolons (Ramadhani et al., 2024; Zhang et al., 2021) Soil temperature is critical during tuberization (15–20°C optimal), as higher temperatures (e.g., 25–

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30°C in Inceptisols, common in tropical potato fields) reduce soil water availability and porosity, particularly in clay-rich soils with low organic matter, inhibiting tuber formation (Hamdani et al., 2019; Khan et al., 2015). For example, 35% of digested carbon is lost to respiration at high temperatures, reducing assimilate availability for tubers (Muthoni & Kabira, 2015). High temperature-induced stress not only leads to yellowing leaves due to chlorophyll degradation (Hancock et al., 2014) but also reduces stomatal conductance and chlorophyll content, as reported in potato, rice, and wheat (Djanaguiraman et al., 2018; Hamdani et al., 2020; Vinitha et al., 2020; Singh et al., 2020; Yuan et al., 2021). Gibberellin, a hormone responsible for cell division and elongation, especially in shoot apices and stolons, also increases with temperature (Latifa & Indriyatmoko, 2022; Nuraini et al., 2016). During the vegetative phase, gibberellin promotes canopy development (stem elongation, branching, and leaf area expansion), thus increasing the relative growth rate (Sardoei et al., 2024). It also supports stolon elongation, enhancing potential tuber formation sites (Meng et al., 2024).

In the source-sink relationship, leaves act as sources producing sucrose via photosynthesis, while stolons act as sinks for storage (Golovko & Tabalenkova, 2019). However, increased canopy growth caused by high gibberellin levels and elevated temperatures can disturb the source-sink balance (Meng et al., 2024; Ohtaka et al., 2020; Rademacher, 2015). During the vegetative phase, the hormone gibberellin plays an important role in promoting canopy through stem elongation and increasing the number of branches, leaves, and leaf area, but its excess disrupts carbon allocation to tubers, leading to fewer fewer and smaller tubers (Sardoei et al., 2024; Durand et al., 2018; Ludewig & Sonnewald, 2016). These findings are supported by several studies reporting reductions in both the number and weight of tubers under high temperature conditions (Ramadhani et al., 2024; Zhang et al., 2024; Mubarok et al., 2022; Singh et al., 2020). This reduction is attributed to the fact that stolons are meristem tissues, and elevated endogenous levels under heat stress promote continuous stolon elongation, which limits assimilate allocation for tuber enlargement (Hamdani et al., 2016; Mariana & Hamdani, 2016; Nuraini et al., 2016). Based on Nuraini et al. (2016), the reduction in tuber mass due to uninhibited gibberellin activity is approximately 21% compared to p3 (30 mL L^{-1} paclobutrazol).

Potato Quality Response to High Temperature

High temperatures have a direct effect on potato tuber quality by altering photosynthate allocation and disrupting metabolic processes, which leads to changes in physical and chemical composition (Jagadish et al., 2021). Elevated temperatures increase reducing sugar levels (e.g., glucose, fructose) in tubers, leading to browning during processing (e.g., potato chips) due to the Maillard reaction (Kusandriani, 2016; Ahmed et al., 2018). For example, cultivars like Eramosa show increased reducing sugars at 30°C, reducing marketability (Zhang et al., 2021). High temperatures also elevate solanine levels a toxic glycoalkaloid in tuber exposed to direct sunlight or soil temperatures above 25°C, causing bitterness and health risks like nausea and diarrhea, and potentially exceeding the 200 mg/kg safety threshold adopted by several countries, although the FAO/WHO Joint Expert Committee (JECFA) has reported natural levels ranging from 20–100 mg/kg and concluded that no specific safe intake level could be established due to limited toxicological data (Karaca & Erbaş, 2024; Schrenk et al., 2020). Additionally, heat stress induces irregular tuber shapes, skin cracking, and pre-harvest sprouting, reducing commercial value (Momčilović, 2019; Muhie, 2022; PengBo et al., 2019). Several studies have shown that planting potatoes in high temperature environments results in small tuber weights (Dewi et al., 2024; Hamdani et al., 2019, 2024; Hernawati et al., 2022; Mariana & Hamdani, 2016). The growth rate of tubers decreases due to high temperature because of the reduction of starch content in tuber (Mubarok et al., 2022; Ramadhani et al., 2024). According to Muhie (2022), heat stress can induce sprouting before harvest, which reduces tuber quality.

According to Mori et al. (2015), high soil temperatures cause discoloration in sweet potatoes to brown due to decay. Based on research by Momčilović (2019) that heat stress produces irregular tuber shape by disrupting dilation and elongation in the tuber enlargement phase, which constricts the tuber base. Heat reduces the soil water supply, causing low starch content due to breakdown into sucrose, which leads to increased sugar content, revealing translucent tubers and jelly-like texture changes that reduce tuber quality and tuber resistance from bacterial and fungal attack (Momčilović, 2019; Muthoni & Shimelis, 2020).

In addition, high temperatures cause the potato skin to crack. This is due to the skin cell layer developing during tuberization due to the continuous expansion of the potato (Molteberg, 2017). High temperature reduces the resistance of potato plants infected with Potato virus Y, which can lead to a decrease in yield quantity and quality (Choi et al., 2017; Makarova et al., 2018). Thus, there is a need for adaptive potato cultivation practices to deal with temperature changes to increase and maintain sustainable production.

Adaptive Cultivation Practices: Election of Superior Varieties

Heat-tolerant potato varieties are critical for maintaining productivity under high temperatures. Varieties like Atlantic, Merbabu-17, and Granola exhibit tolerance due to enhanced stomatal efficiency, reduced chlorophyll degradation, and stable tuberization at temperatures above 25°C (Djuariah et al., 2016; Firdausy et al., 2024). For instance, Atlantic maintains yields of 11.47 tons/ha in medium-altitude lands by sustaining photosynthetic rates, while Granola's tolerance stems from efficient photosynthate translocation (Prabaningrum et al., 2015). Thus, planting with superior varieties contributes to the sustainability of production under climate change conditions. High temperature tolerant potato varieties are presented in Table 1.

Adaptive Cultivation Practices: Plant Growth Regulator under Heat Stress

Plant Growth Regulators (PGRs) are natural or synthetic compounds that influence physiological processes at low concentrations (Emilda, 2020). High temperatures elevate ABA, gibberellin, and ethylene levels, which disrupt normal tuber development by promoting excessive vegetative growth and inhibiting assimilate partitioning to the tuber, inducing stomatal closure, and reducing photosynthesis (Thakur et al., 2019). Stomatal closure restricts CO_2 uptake, limiting photosynthetic activity (Lawson & Matthews, 2020). In contrast, PGRs like BAP (cytokinin) promote stomatal opening by stimulating guard cell turgor and improving photosynthetic efficiency (Pal et al., 2016). Retardants like paclobutrazol, chlorocholine chloride, and prohexadione-Ca inhibit gibberellin synthesis, redirecting assimilates from canopy growth to tuberization (Hamdani et al., 2016). Additionally, high temperatures elevate methylglyoxal levels, a toxic compound that induces ROS in plants and reduces chlorophyll, thereby inhibiting photosynthesis and plant growth (El-Yazied et al., 2022; Takagi et al., 2016). In response, exogenous melatonin application enhances antioxidant enzymes such as superoxide dismutase (SOD), catalase (CAT), guaiacol peroxidase (G-POX), and ascorbate peroxidase (APX), preserving cell membranes, promoting chlorophyll synthesis, supporting photosynthetic activity, and delaying senescence (El-Yazied et al., 2022; Jahan et al., 2021; Youssef et al., 2021; Arnao & Hernández-Ruiz, 2018). Melatonin improves potato yield under heat stress by inhibiting ABA transport from root to shoot and maintaining soil water availability, stimulating root growth, and supporting photosynthetic efficiency by increasing chlorophyll content, which can delay plant senescence (Arnao & Hernández-Ruiz, 2018; Ibrahim et al., 2020; El-Yazied et al., 2022). Several studies have shown that melatonin application can increase photo-synthetic efficiency with increased chlorophyll content in tomato (Jahan et al., 2021), wheat (Buttar et al., 2020), and kiwi (Liang et al., 2018).

Numerous studies confirm the effectiveness of PGRs in improving potato growth and yield under heat stress. For instance, BAP (40 ppm) applied at 40 and 60 DAP significantly increased tuber weight, number, chlorophyll content, and harvest index (Abouelsaad & Brengi, 2022). Melatonin (23.23 ppm and 50 ppm) applied from 42 to 70 DAP enhanced leaf water status, reduced ABA, improved antioxidant enzyme activity, and increased yield (El-Yazied et al., 2022; Amelia et al., 2023). Paclobutrazol (100 ppm) applied at 30–40 DAP improved harvest quantity and quality by up to 108%, enhancing stolon formation and chlorophyll levels (Hamdani et al., 2024). Similarly, chlorocholine chloride (2000 ppm) and prohexadione-Ca (50–100 ppm) suppressed excessive shoot growth and solanine synthesis, while improving tuber yield and quality (Tak et al., 2024; Ramadhani et al., 2024). These empirical results highlight the significant role of PGRs in mitigating heat stress in potato cultivation. Table 2 presents a summary of the major PGRs and their physiological effects under elevated temperature conditions.

Table 1. High temperature tolerant potato varieties

Varieties	Location	Effect	Tolerance Mechanism	Reference
Granola	Medium land	Yield 3.61 tons/ha; tuber dry weight 62.45 g; growth rate 0.87 g/plant/day	Efficient photosynthate translocation	(Prabaningrum et al., 2015; Rogi et al., 2016)
Atlantic	Medium land	Yield up to 11.47 tons/ha	High stomatal efficiency	(Djuariah et al., 2016)
Merbabu-17	Medium land	Yield reached 11.04 tons/ha	Reduced chlorophyll degradation	(Firdausy et al., 2024)

Table 2. Effect of different types of PGRSs on potato plants

Hormone	Concentration	Time Application	Effect	Reference
BAP	40 ppm	40 and 60 DAP	Increase leaf chlorophyll, tuber weight and number of tubers, harvest index, mineral, protein, and ascorbic acid content of potato tubers	(Abouelsaad & Brengi, 2022)
Melatonin	23.23 ppm*	42, 49, 56, 63, and 70 DAP	Reduce ABA levels and increase leaf chlorophyll, leaf water status, antioxidant enzyme activity, and yield	(El-Yazied et al., 2022)
	50 ppm		Produce the highest weight and harvest index	(Amelia et al., 2023)
Paclobutrazol	100 ppm	30 DAP	Increase harvest quality and quantity by up to 108% in high temperature	(Hamdani et al., 2016)
		30 and 40 DAP	Suppress plant height and biomass, increase stomatal conductance, chlorophyll, number of stolon, percentage of stolon, forming tubers, number and weight of tuber per plant	(Hamdani et al., 2024; Ramadhani et al., 2024)
		40, 50, and 60 DAP	Increase tuber growth rate, number and weight of tubers per plant	(Mubarok et al., 2024)
Chlorocholine-chloride	2000 ppm	25 and 45 DAP	Suppress plant height and secondary metabolite solanine and increase leaf chlorophyll content, tuber weight, yield, starch content	(Tak et al., 2024)
Prohexadione-Ca	50 ppm	40 DAP	Increase chlorophyll content, stomatal conductance, number, and weight of tubers	(Hernawati et al., 2022)
	100 ppm	-	Increase chlorophyll content index, number and weight of tubers per plant	(Ramadhani et al., 2024)

Note: *: Convertion mM to ppm; DAP: Days After Planting

Growth retardants are specialized PGRs that inhibit gibberellin biosynthesis, thereby reducing excessive vegetative growth (Chen et al., 2020; Hamdani et al., 2016). By limiting gibberellin levels, these retardants redirect assimilates from canopy development to tuber formation, enhancing yield (Desta & Amare, 2021; Ramadhani et al., 2024; Tak et al., 2024). The mechanism of paclobutrazol inhibition in gibberellin synthesis is to inhibit the activity of ent-kaurene oxidase, which plays a role in catalyzing ent-kaurene into ent-kaurenoic acid (Kumar et al., 2023; Tesfahun, 2018). Chlorocholine chloride inhibits the early biosynthesis of gibberellins by blocking the conversion of GGPP (geranylgeranyl pyrophosphate) to ent-kaurene (Khella, 2018). Prohexadione-Ca interferes with the late-stage conversion of GA20 to GA1 by altering the related oxidase enzyme (Pal & Johal, 2019). Beyond gibberellin suppression, retardants enhance heat stress tolerance by stimulating antioxidant enzyme activity (Azmi et al., 2022; Kamran et al., 2020; Liu et al., 2022; Skłodowska et al., 2021). In addition, retardant application can improve water use efficiency, making it suitable for dry climate areas (Bhattarai, 2017; Mabvongwe et al., 2016; Teixeira et al., 2021).

Adaptive Cultivation Practices: Irrigation and Mulch Application

High temperature reduces soil water availability during the tuberization phase, decreasing the number and weight due to potato shallow root systems (Li et al., 2016; Aliche et al., 2018; Joshi et al., 2016). The use of irrigation and mulch can be used as a practice for potato cultivation under heat stress conditions (Table 3). Application of irrigation can increase the efficiency of water use in the soil, so that plant growth and development are not hampered (Biswas et al., 2015). Among irrigation methods, drip irrigation appears most effective under heat stress, as it directly targets the root zone and improves tuber weight by 15–20%, and supports quality traits like vitamin C content and yield, unlike furrow irrigation, which despite saving water, performs poorly in heavy soils (clay-rich inceptisols) and sprinkler irrigation less suitable in water-limited regions due its high water demand (Dianawati et al., 2019; Wang et al., 2020; Yang et al., 2019).

Table 3. Effect of different types of irrigation and mulch on potato plants

Type	Treatment	Effect	Reference
Drip irrigation	Water volume 300 ml/polybag and frequency 5 times	Increase primary and secondary stolon growth, number, weight, and harvest index	(Dianawati et al., 2019)
	-	Increases soil moisture content, suppresses canopy growth, and increases yields	(Zhou et al., 2018)
Alternate furrow irrigation)	Frequency of application 4 times	Increases harvest index, saves water use by 35% and increases water productivity by 50% suitable for use in dry environments	(Kumer et al., 2019)
Sprinkler irrigation	10 mm water volume	increases yield, reduces soil N_2O emissions, and saves water	(Yang et al., 2019)
Straw mulch	-	Reduces maximum soil temperature, increases yields by 30–40%, and produces safe food without herbicides	(Adamchuk et al., 2016)
Wheat mulch	-	Reduced soil temperature by 1–2 °C and increased soil moisture by 42%, water use efficiency, and crop yields	(Goel et al., 2020)
Wheat + straw mulch	Dose of 4.5 tons/ha	Increased tuber yield by 19.5%, ready to sell tubers (> 40 mm) by 21.2%, water use efficiency, soil water availability, number of tuber, and retained soil moisture	(Král et al., 2019)
Silver black mulch	-	Increased leaf area index, plant growth rate, harvest index, and tuber weight of G1 and G3 seedlings	(Jella et al., 2017)
	-	Increases number of tuber per plot, tuber weight per sample, and tuber weight per plot	(Ismadi et al., 2021)
Plastic film mulch	-	Increased yield and nitrogen use efficiency	(Wang et al., 2019)
White/black plastic mulch	-	Retained leaf nutrients and yield increased by 38.7%.	(Ruíz-machuca et al., 2015)

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Mulch is a soil surface cover made from either organic material, such as decomposed plant parts that contribute nutrients to the soil, or inorganic material, such as plastic (Yetnawati & Hasnelly, 2021; Irianti et al., 2017). In terms of mulch, organic mulches (e.g., straw, wheat) are more beneficial in hot climates due to their cooling and water retention capacity, whereas inorganic mulches (e.g., silver-black plastic) enhance light reflection but are less effective in water retention (Goel et al., 2020; Ruíz-Machuca et al., 2015; Nurbaiti et al., 2017). By lowering soil temperature, mulch creates favorable conditions for stolon initiation, thereby increasing potato yield (Banerjee et al., 2016; Chen et al., 2019; Dash et al., 2018). Both types of mulch suppress weed growth, enhance water use efficiency by lowering evaporation, improving soil structure, and reducing competition for nutrients, water, and growing space (Irianti et al., 2017; Li et al., 2018; Wang et al., 2019). Lack of water in the soil causes reduced sugar in the potato due to increased levels of ROS that damage cells (Muttucumaru et al., 2015; Nasir & Toth, 2022; Dvořák et al., 2015). Therefore, combining drip irrigation with organic mulch appears to be the most effective strategy to sustain potato growth and yield under heat stress by improving water efficiency and maintaining soil quality.

Future Implications

Future research should investigate the synergistic effects of multiple PGRs, particularly the combined application of melatonin, BAP, and gibberellin inhibitors under varying heat stress intensities. Field-based validation is also crucial to determine optimal dosages, application timing, and cost-effectiveness. Moreover, molecular studies exploring gene expression linked to ROS scavenging and ABA transport in response to PGRs can deepen the understanding of their regulatory mechanisms. In addition, integrating heat-tolerant varieties with PGRs and precision irrigation in field trials remains underexplored and should be prioritized to assess their combined effectiveness.

Conclusion

High temperatures (>25°C) reduce potato yield and quality by impairing photosynthesis, increasing respiration, and altering tuber chemistry, with global yield losses projected at 18–32% by the 2050s. This review, synthesizing 45 studies, highlights heat-tolerant varieties, PGRs, irrigation, and mulching as effective strategies to mitigate these impacts, particularly in tropical regions. Limitations include the lack of field-scale studies combining multiple practices and insufficient economic data on adoption feasibility. This review contributes a comprehensive framework for sustainable potato cultivation under heat stress, guiding future research and policy.

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