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TEMPERATURE CRITICAL THRESHOLD FOR YIELD IN CHILI PEPPER (*CAPSICUM ANNUUM* L.)

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SUMMARY

Chili (*Capsicum annuum* L.) is a horticultural plant susceptible to high-temperature stress. This research studied how agronomic and physiological characteristics of chili decline due to high temperature and determined the threshold value of temperature decreasing 50% of its yield. The experiment layout followed a randomized design, consisting of five temperature stress levels (in the growth chamber), namely, 31°C (daily temperature as a control), 33°C, 35°C, 37°C, and 39°C, with an exposure duration of 10 h. The temperature stress started when the plant reached the flowering phase. The plant parameters observed included agronomic and physiological characteristics. The study results showed that high-temperature decreased production significantly with the decline in all agronomic and physiological traits. The threshold temperature at 32.86°C has reduced the production of chili plants by 50% compared with the control. The study found that an increase in temperature of 2°C for 10 h in the flowering phase reduces chili production by 68.78%, and temperature stress at a maximum of 39°C for 10 h during flowering reduces chili production up to 87.52%. Hence, based on the study results, future research on chili should focus on developing varieties that are adaptive to high temperatures.

Keywords: Chili pepper (*Capsicum annuum* L.), heat stress, pollen viability, stomatal damage, flowering stage, yield

Key findings: Chili (*Capsicum annuum* L.) is very sensitive to heat stress; an increase in temperature of less than 2°C (32.86°C) compared with daily temperature (31°C) for 10 h (equivalent to two days of exposure) reduced production by 50%.

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INTRODUCTION

The global temperature increase continues, and extreme weather can persist significantly by 2050 (IPCC, 2022). Environmental temperature is vital to plant growth, affecting all phases—from germination to vegetative and ripening (Rosmaina 2021; dos-Santos *et al.,* 2022). At extreme temperatures, which cause damage to the cellular organization, cell damage or cell death of the plant can occur within minutes (Lobell *et al.,* 2011), expressed

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through changes in morphology, physiology, and crop production (Hussain *et al.,* 2019; Raza *et al.,* 2019). Some studies reported that an increase in temperature of 1°C–2°C decreases plant productivity, at 3.2% in rice (Jin and Zhu, 2020) and 7%–10.5% in wheat (Lu *et al.,* 2019). However, there are no reports of decreased production levels in chili (*Capsicum annuum* L.) caused by extreme temperature increases.

One of the efforts to adapt to increased temperature impacts in the agriculture sector is to use a variety of heat-tolerant plants (dos-Santos *et al.*, 2022). To date, a heat-tolerant chili variety is yet to exist. Therefore, developing plant varieties that maintain healthy growth under high-temperature stress is vital. Plant breeding programs for heat-tolerant plants are essential to produce plants adaptive to high temperatures (Yeh *et al.*, 2016; Rosmaina *et al.*, 2019; Gurung *et al.*, 2020; Sahid *et al.*, 2020). As initial steps, an investigation of the plant's agronomic and physiological characteristics' response to high-temperature stress needs executing. The critical temperature, which reduces yield by 50% needs to be determined. Knowing the critical temperature value helps determine the safe level of plant yield at 50% of the actual yield that can saved from damage. The critical temperature value can also be the basis for selection, where straightforward, inexpensive, and quick selection criteria are required.

Research on tolerance to heat stress is still rare, especially in chili pepper, because setting up and maintaining a stable temperature during the experiment is difficult. Generally, the temperature fluctuates, affecting factors in the research setup related to temperature and, thus, challenging. It is essential to do it in controlled conditions (growth chamber). No studies reported how severe the level of damage or degradation of the agronomic and physiological traits of chili plants existed due to high-temperature stress. On the other hand, the threshold temperature for high-temperature stress testing is unknown. Chili crops are sensitive to high-temperature stress, mainly during flowering and seed formation phases (Pagamas and Nawata, 2008). This research aims to study how severe the damage to agronomic and physiological characteristics of curly red chili pepper appears at high temperatures and determine the threshold value of temperature that decreases 50% of its yield. Study results hope to help determine the selection of indicators to identify pathways tolerant of high temperatures.

MATERIAL AND METHODS

Material and growth condition

The study conducted experiments at the Genetic and Plant Breeding Laboratory, Universitas Islam Negeri Sultan Syarif Kasim, Riau, Indonesia. The ambient temperature was 31°C–32°C, and relative humidity was 75%–85%. The plant material, curly pepper 'Kopay' variety, was used. Seed sowing happened in the nursery, followed by seedling transfer into a polybag (10 kg) containing topsoil and the compost ratio at 3:1 after 30 days. Researchers fertilized with NPK fertilization at two grams/polybag. The plant maintenance followed the standard high-yielding cultivation approach (Maharijaya and Syukur, 2014).

High-temperature stress

The experiment set up a randomized design with five temperature stress levels: 31°C (control), 33°C, 35°C, 37°C, and 39°C. Each treatment got replicated in four polybags. From the seedling to flowering stages (approximately 60 days old), the curly chili pepper was grown under natural conditions. One week after the flowering plant, the plants were moved into the *Growth Chamber* (*Alab Tech model LGC-5101*) to subject the plants to the temperature stresses mentioned above, with a 10 h exposure duration. Meanwhile, the plant control remained in natural conditions. After treatments, all the plants were returned to and maintained in natural conditions, followed by the conventional high-yielding cultivation approach (Maharijaya and Syukur, 2014).

Data recording

The parameters observed included the number of flowers, the total of flower abortion, fruit set (%), number of fruits, fruit weight, fruit length, fruit diameter and number of seeds, pollen viability, stomatal, and chlorophyll content. Pollen viability testing was carried out using acetocarmine staining (Yankova-Tsvetkova *et al.*, 2013). Pollen was harvested from blooming flowers in the morning from treated plants, taking three flowers from each plant. The pollen, placed on a glass object, received two to three drops of 0.75% acetocarmine, then allowed to stand for 10 min and finally observed under a microscope. The stomatal copy was captured using nail polish (Miller and Ashby, 1968) and then viewed under a microscope. The viewing of pollen viability and stomatal observations used the Nikon Eclipse

50i microscope (Nikon, Japan). The images were captured using the camera Nikon DS-Fi1 and were analyzed using NIS-Element software. The measurement of chlorophyll content used Arnon's (1949) method.

Statistical analysis

Analysis of variance computations used SAS software version 9.1. Testing the significant difference of means among treatments used Duncan multiple range test at the $P < 0.05$.

RESULTS AND DISCUSSION

Flowers set and abortion

The temperature stresses caused a significant difference in the number of flowers set and the percentage of flower abortion. For example, at 39°C temperature, the plants only produced an average of 33 flowers per plant, significantly different from the control plants, which had an average of 120 flowers per plant, a decrease of up to 72.50% (Figure 1a).

The temperature stresses increased flower abortions in the first and second weeks after treatment, ranging from 8.66% to 66.73% and 4.22% to 62.04%, respectively (Figure 1b). However, in the third week, the flower abortion was not significantly different compared with the control. Therefore, the plants are presumed to have begun recovery. The highest value of flower abortion was observed at 37°C and 35°C in the first and second weeks after treatment, respectively. In other words, an increase in flower abortion occurred as many as 2.28–14.70 times in the first week and 4.38–7.70 times in the second week.The study results confirmed that the flowering phase in chili pepper was susceptible to high temperatures. Plants experienced failure in reproduction due to flowers failing to develop, becoming abnormal, or losing pollen and anther production. Tall flower abortion due to high-temperature stress was closely related to balancing the hormonal of auxin and ethylene (Goren, 2010). Furthermore, Liu *et al*. (2013) explained that flower abortion in high temperatures correlated with increases in ethylene, ACC, and ABA and decreases in IAA, cytokinin, and polyamine.

Fruit set and fruit harvest

Heat stress significantly reduced the fruit set and the number of fruits. The lowest fruit set was observed at 39°C (23.03%), followed by 37°C (26.09%) and 35°C (30.18%), whereas the control plants produced 88.47% fruit set. These show that temperature stress reduces the fruit set by 59.69%–73.79%. The decrease in fruit set impacts the number of fruits harvested. Under heat stress of 33°C–39°C with an exposure time of 10 h resulted only in 64-27 fruit/plant, whereas control (31°C) produced 160 fruit/plant showing a decrease of 59.69%–83.03% (Figure 1c). Several researchers have reported declining fruit sets due to high-temperature stress (Erickson and Markhart, 2002; Yamazaki and Hosokawa, 2019; Kumar *et al.*, 2020). The decrease in fruit sets varies greatly depending on temperature and duration of exposure, even with the 'wonder' variety (relatively tolerant), which only produced 10%–55% of fruit sets (Kaur *et al*, 2016). Based on the facts above, the response of the fruit set to temperature stress correlates strongly to the genotype, duration of exposure, and the given temperature level. The fruit set is associated with the number of fruits per plant. With high-temperature stress, a study reported reductions in the number of fruit in tomatoes (Meco *et al.,* 2019; Panthee *et al.,* 2018) and rice (Yaliang *et al.,* 2019). The low number of fruit produced due to temperature stress is closely related to the fruit set. Heat stress causes severe damage to spikelets, disrupts cytokinin synthesis, causes peroxide accumulation, decreases sugar levels, and damages cell construction (Das *et al*., 2014; Rieu *et al*., 2017; Zhang *et al*., 2018; Wu *et al*., 2020).

Fruit weight, length, diameter, and number of seeds

Heat stress notably reduced fruit weight, fruit length, fruit stem length, fruit diameter, and the number of formed seeds. Fruit weight decreased to 28.03% of control when subjected to 37°C temperature with 10 h of exposure. Fruit length decreased to 16.24% at 39°C compared with control (Figure 1d). In addition to reducing fruit length, fruit weight,

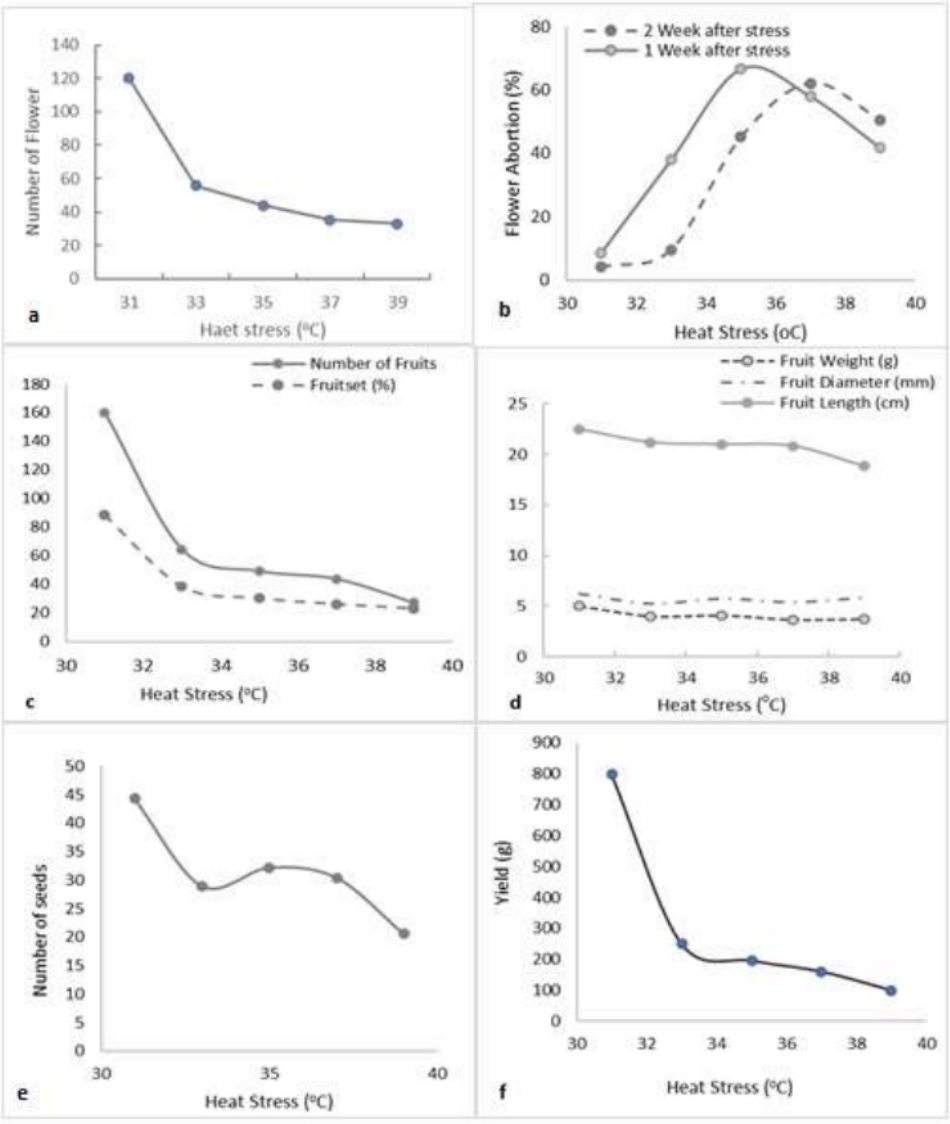

Figure 1. Response of chili pepper under heat stress: a) the number of flowers, b) percentage of flower abortion, c) the number of fruits harvested and the percentage of fruit set, d) fruit weight, diameter, and length decrease, e) the number of seeds, f) yield due to heat stress.

and fruit diameter, temperature stress also significantly reduced the number of regular seeds formed. In control plants, the number of healthy seeds produced was around 44.29 seeds/plant, whereas in stressed plants (39°C), only 20.55 healthy seeds were produced or decreased by 53.60% (Figure 1e). Generally, the seeds become abnormal, i.e., blackened, empty, and lumpy. These reveal that heat stress hurts not only production but also seed availability. A decrease in the number of seeds, fruit length, and fruit diameter due to temperature stress was also reported by Thuy and Kenji (2015), Kumar *et al*. (2020), and Kaur *et al*. (2016). The percentage decrease due to temperature stress

is influenced strongly by the temperature level, duration of exposure, and the genotype used, so it is crucial to study the effect or level of damage due to temperature stress on each plant and the genotype for improvement. In soybeans, a study reported a diversity of responses between genotypes to increasing temperature during seed filling. It shows the potential for soybean heat tolerance improvement through breeding and underscores the importance of identifying efficient selection strategies for the tolerant plant (Ortiz *et al*., 2022).

Fruit yield per plant

Fruit weight per plant decreased significantly. The control plants (daily temperature of 31°C) produced 779.02 g of fruit weight/plant at the fourth week of harvest. In comparison, plants exposed at 33°C (2°C higher than control) were only able to produce an average of 249.47 g of fruit weight/plant, and fruit weight/plant continued to decrease to 87.52% or 99.74 g per plant at stress temperature of 39°C (Figure 1f). Zhao *et al*. (2017) reported a decrease in production in some plants due to high-temperature stress of 6% in wheat, 3.2% in rice, 3.1% in soybean, and 7.4% in corn. Furthermore, Lobell *et al*. (2011) explained that each increase of 1°C caused a decrease in the production of up to 8.3% in corn. The decline in yield was closely related to the reduction of several agronomic characteristics, such as, the number of flowers formed, the number of flowers aborted, the percentage of fruit set, the number of fruit harvested, fruit weight, fruit length, and fruit diameters. This study saw that an increase in temperature of 2°C from the daily temperature reduced all these agronomic characteristics and ultimately impacted the weight of fruits per plant (yield).

Physiological response

Pollen viability

High-temperature stress significantly decreased pollen viability. Pollen viability ranged from 53.52% to 78.90% or decreased by 13.74%–41.49% compared with the control plants. The highest decrease in pollen viability occurred at 39°C, namely, 53.52%, or a reduction of 41.19% from the control plant, which had pollen viability of 91.47% (Figure 2a). Reduced pollen viability relates closely to the ability of pollen to germinate and causes failure in fruit formation. The pollens exposed to high temperatures underwent morphological changes such as shrinking, clustering, empty, and clumping (Figure 3b-c), and the characteristic of unviable pollen shows an inability to absorb dyes (Figure 3c). In contrast to pollen on control plants, pollen did not clot but spread perfectly and can absorb stain well (Figure 3c). High-temperature stress causes the inhibition of the development of stem cells (mother cells), and the decomposition of the tapetum becomes abnormal (Ullah *et al*., 2022; Giorno *et al*., 2013). Furthermore, Begcy *et al*. (2019) explained that the most critical stage of heat stress in pollen development is the tetrad stagewhich is tapetum degraded, decreased starch content, and reduced enzymatic activity. It affects the metabolic pathway, causes a low ability to absorb dyes, and produces deformed and sterile pollen. The amount of reduction in pollen viability is influenced strongly by the genotype and temperature. Several researchers reported a decrease in pollen viability due to high-temperature stress, i.e., a temperature of 40°C–45°C for 1-2 h of exposure, caused a decline of 61.7%–79.9% pollen viability (Arnaoudova *et al*., 2020), ranged from 6.74% to 46.35% (Kumar *et al*., 2020), and 70% (Zhang *et al*., 2018) in rice.

High-temperature stress inhibited the transportation of sugar to pollen, causing insufficient or unavailable nutrients, thus, reducing pollen activity (Endo *et al.,* 2009), although morphologically, pollen appeared still normal. Pollen viability and development filament are highly dependent on the accumulation of metabolite content. During the reproductive phase, photosynthate is transferred to the pollen sac and stored as starch granules (De-strom and Geelen, 2014). In high-temperature stress, fructokinase activity in pollen lowers sharply, and pollen germination is only 35% (Karni and Aloni, 2002). Fructokinase is an enzyme that plays a role in glucose starch to sugars needed in pollen development. This starch is a source of food reserves in pollen. Ullah *et al*. (2022) stated that high-temperature stress reduced the viability of pollen and the amount of pollen that formed. Heat stress decreased starch content and enzyme activities by 30% and 60%, respectively. It is associated with a reduced pollen germination ability (Begcy *et al.,* 2019). Temperature above 35°C inhibited anther development, resulting in less pollen and imperfect fertilization (Jagadish *et al.,* 2010).

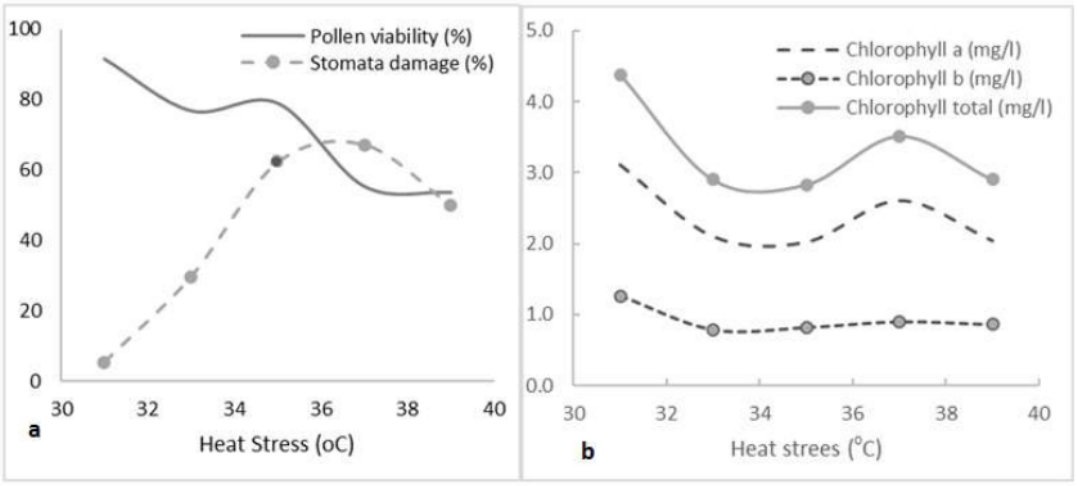

Figure 2. a) Percentage of pollen viability and stomata damage (%) under heat stress, b) Chlorophyll content of chili pepper under heat stress.

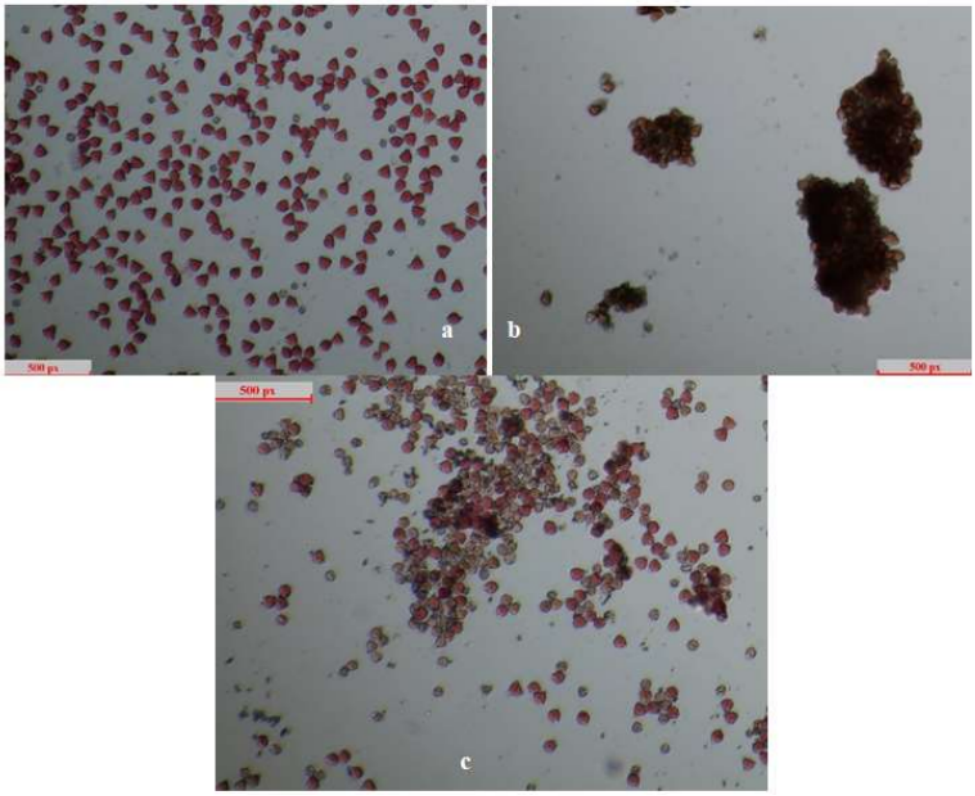

Figure 3. Pollen exposed to high temperature: (a) pollen in control plants, (b) pollen agglomerate and pile up, and (c) viable pollen (absorb dyes) and unviable pollen (unable to absorb stains).

Stomatal damage

High-temperature stress significantly increased the percentage of stomata damage up to 67.14% at 37°C. In addition, some stomatal damage shapes were damage to guard cells, broken stomata, and wrinkled stomatal (Figure 4a-c). Stomatal plays a vital role in the diffusion of CO_2 gases from the air into leaf cells and regulates the transpiration and temperature of the leaf cell. The results of this study indicate that high temperature not only causes larger stomatal openings but also damages the photosynthetic organelles. Stomata will open continually to cool the leaf cells at high temperatures if sufficient water protects photosynthetic organelles (Schymanski *et al*., 2013). It means wider stomata opening causes lower water use efficiency. Also, stomata play an essential role in the absorption of CO_2 and regulate water loss, significantly affecting the growth and yield of plants. Therefore, the stomata's response and their organelles are essential for determining plant resistance to high temperatures.

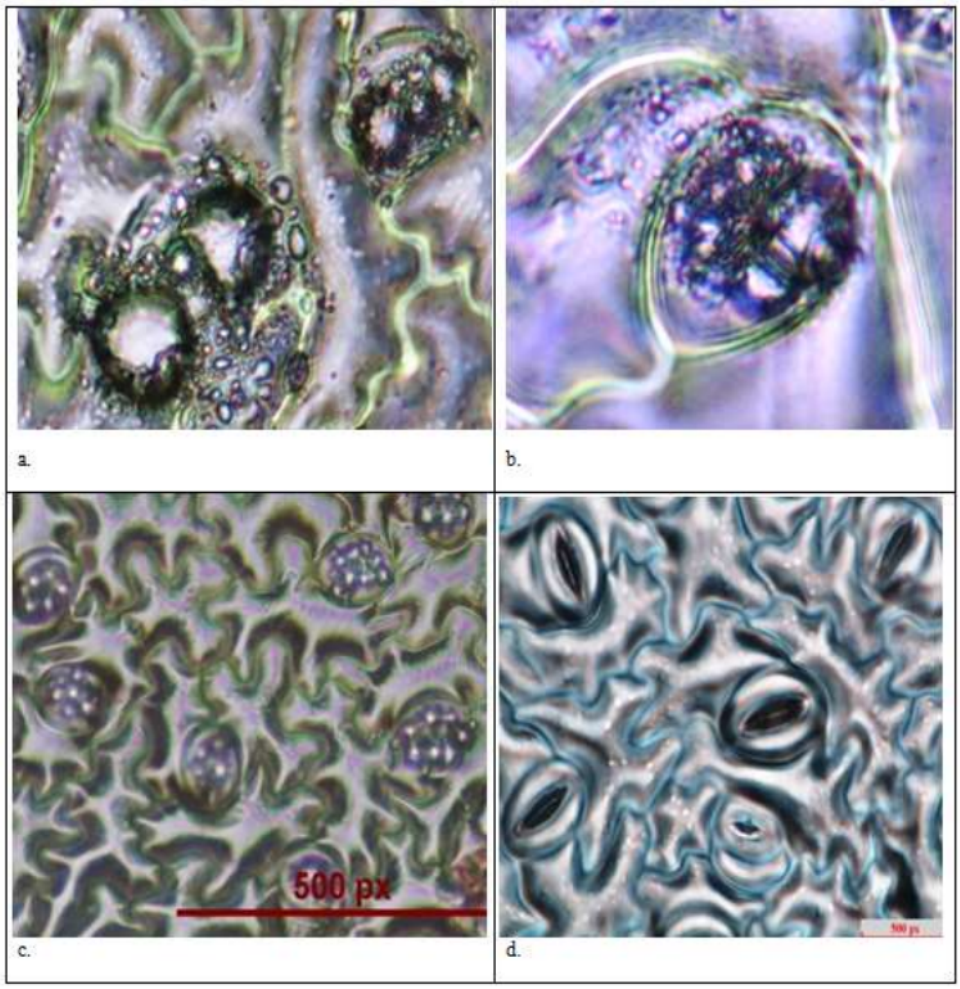

Figure 4. The shapes of stomatal damage due to high temperature: [a] stomatal broken, [b] guard cells damaged, [c] larger stomata opening, and [d] stomata in control plants.

Chlorophyll contents

Heat stress significantly reduced the chlorophyll a, b, and total chlorophyll content. The average value of total chlorophyll decreased to around 16.35%–35.25%. The highest reduction in chlorophyll occurred at 35 °C, at 35.25%. In comparison, the decrease in the average value of chlorophyll b was 8.57%–37.30%. The decline in chlorophyll b content was more significant than the percentage reduction in chlorophyll a, at 16.25%–35.36% (Figure 2b). The amount of reduction in chlorophyll is significantly affected by temperature. The decrease in chlorophyll a and b causes a reduction in total chlorophyll content. The chlorophyll can be used to evaluate the damage to the photosynthetic structure, which can be used as an indicator of plant tolerance to high-temperature stress (Ristic *et al.,* 2007). The decrease in chlorophyll content was higher than those that Kumar *et al*. (2020) reported, in which the average ranged from 2.61% to 8.40%.

Furthermore, Ghai *et al*. (2016) reported a decrease in chlorophyll content in high-temperature stress due to a reduction of photosynthetic pigments. In wheat, Ristic *et al*. (2007) reported a decline in chlorophyll content of up to 70% in specific genotypes with stress for 16 days at 36 °C. Still, some genotypes did not experience a decrease in chlorophyll content due to heat stress. It indicates that the changes in chlorophyll content can show high-temperature tolerant in plant selection. The reduction in chlorophyll content occurs because of damage to the thylakoid membrane, structure and function of the chloroplast, structural damage from pigment-protein complexes, and activity in PS2 (Hu *et al.,* 2020; Murkowski, 2001). These caused the disturbance of chlorophyll biosynthesis (Gupta *et al.,* 2013), thus, impacting a decreasing photosynthetic activity due to inhibition of the electron transfer of some enzymatic activity required by photosynthesis and the accumulation of reactive oxygen species (ROS), which causes damage to the thylakoid structure (Demirel *et al.,* 2020; Ram *et al.,* 2017; Hu *et al.,* 2020).

Temperature critical threshold for yield

High temperatures caused a decrease in growth and production. High-temperature stress of 33°C–39°C with a duration of 10 h exposure significantly decreased production to 68.78%–87.52% compared with the control plants. The higher the temperature, the more the decrease in yield. Based on this data, the critical point of production in chili plants can be estimated, assuming an increase in temperature only occurs within 10 h or equivalent to two days of exposure. The chili crop experienced a 50% decrease in yield at 32.86°C compared to daily temperature (ambient temperature) (Figure 5). The results showed that chili is very sensitive to an increase in temperature; an increase in temperature of less than 2°C for 10 h has reduced production by 50%. In rice, plants reported a decreased fertility spikelet that occurred significantly at 38°C for three days of exposure. A report stated the temperature threshold in rice plants was 35°C with a maximum exposure time of three days (Yaliang *et al.,* 2019). It was also suspected to be influenced by the genotype used. Temperature stress causes an imbalance of sources and sinks, which ultimately affects growth and yields economically. A study also said this to be related to decreased photosynthesis rate and assimilation mobilization between plant tissues (Fahad *et al.,* 2017). The higher the temperature given, the lower the weight of the crop produced.

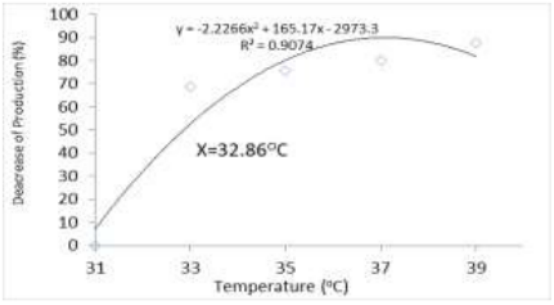

Figure 5. The critical temperature for 50% of production loss.

CONCLUSIONS

High-temperature stress decreased production significantly by reducing the number of flowers, percentage of fruit set, number of fruits harvested, fruit weight, fruit length, fruit diameter, number of seeds, and chlorophyll content, and increasing flower abortion and damage to photosynthetic organelles, in this case, the stomata. The temperature threshold at 32.86°C reduced the production of chili plants by 50% compared with the control, with 10 h of exposure time. The selection of indicators to identify pathways tolerant of high temperatures can be made at a temperature of 32.82°C or the equivalent of 33°C with an exposure time of 10 h.

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