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Impact of heat stress on growth and physiological parameters of soybean varieties at the seedling stage

Hassan Bashir[1], *Samanhudi*[1,2,3], *Parjanto*[1,3], *Andriyana* Setyawati[3*], *Komariah*[4], *Masateru* Senge[5], *Muji* Rahayu[3], and *Tilmiidzah* Salma Fathin[1]

[1]Department of Agronomy, Faculty of Agriculture, Universitas Sebelas Maret (UNS), Jl. Ir. Sutami 36A, Kentingan, Surakarta, 57126, Central Java, Indonesia
[2]Center for Research and Development of Biotechnology and Biodiversity, Universitas Sebelas Maret (UNS), Jl. Ir. Sutami 36A, Kentingan, Surakarta, 57126, Central Java, Indonesia
[3]Department of Agrotechnology, Faculty of Agriculture, Universitas Sebelas Maret (UNS), Jl. Ir. Sutami 36A, Kentingan, Surakarta, 57126, Central Java, Indonesia
[4]Department of Soil Science, Faculty of Agriculture, Universitas Sebelas Maret (UNS), Jl. Ir. Sutami 36A, Kentingan, Surakarta, 57126, Central Java, Indonesia
[5]Union-Infrastructure Maintenance Laboratory, Gifu University. Japan

Abstract. Climate change-induced heat stress poses a significant threat to global soybean production. This study investigated the impact of heat stress on growth and physiological parameters of 18 Indonesian soybean varieties at the seedling stage. Treatments involved exposing two-week-old seedlings to temperatures 25, 30, 35, 40 and 45°C for four hours daily over four consecutive days. The parameters assessed were survival rate, root length, shoot length, total plant weight, and relative water content. Results revealed significant variability in heat stress tolerance among varieties. While all varieties showed optimal growth at 25°C, increasing temperatures from 25 to 30°C led to an increase in growth. A critical threshold was observed between 35 and 40°C, where most varieties experienced a sharp performance decline. Notably, varieties Demas 1, Gepak Kuning, and Agromulyo consistently outperformed others even at 45°C where all other couldn't survive, maintaining higher survival rates and better growth parameters even under severe stress conditions. This study provides valuable insights into soybean heat stress tolerance mechanisms and identifies promising genetic resources for breeding heat-resilient cultivars in Indonesia. Our findings contribute to the development of strategies to mitigate the impacts of climate change on soybean production, crucial for ensuring global food security in the face of rising temperatures.

1 Introduction

Climate change has emerged as one of the most pressing global challenges of the 21st century, with far-reaching impacts on agricultural systems worldwide [1,2]. Among the various

* Corresponding author: andriyanasetyawati@staff.uns.ac.id

manifestations of climate change, heat stress has become increasingly prevalent, posing significant threats to crop production and food security [3,4]. Soybean (*Glycine max* L. Merrill), a crucial legume crop and it stands as a cornerstone of global food security, serving as a critical source of protein and oil for human and animal consumption [5,6,7,8]. Its economic significance is undeniable, with soybean production exceeding 350 million metric tons annually, fueling diverse industries [9].

Global soybean production is projected to face substantial challenges due to rising temperatures and more frequent heat waves [10]. Heat stress can severely impact plant growth, development, and physiological processes, ultimately leading to reduced yield and quality [11]. Understanding the effects of heat stress on soybean at the seedling stage is crucial, as this early phase sets the foundation for the plant's overall performance and productivity [12,13].

The impact of heat stress on soybean seedlings is multifaceted, affecting various growth and physiological parameters. Heat stress can negatively affect root development, nutrient uptake, and water relations, further compromising the plant's ability to establish itself and withstand subsequent environmental challenges [14]. Moreover, high temperatures can disrupt photosynthetic processes, alter hormone balance, and induce oxidative stress, all of which contribute to impaired seedling growth and development [15].

The severity of heat stress impacts on soybean seedlings can vary significantly among different varieties, highlighting the importance of genetic diversity in developing climate-resilient cultivars [16]. Some soybean varieties may possess inherent mechanisms to better cope with heat stress, such as enhanced antioxidant systems, more efficient heat shock protein production, or improved membrane stability. Identifying and characterizing these heat-tolerant traits in soybean seedlings is essential for breeding programs aimed at developing varieties better adapted to future climate scenarios.

Therefore, improving soybean's resilience to heat stress can contribute to maintaining or enhancing its role in sustainable farming systems. As a legume crop, soybean plays a significant role in nitrogen fixation and soil improvement, making it an important component of sustainable agricultural practices [17,18,19]. Additionally, its high protein content makes it a vital commodity for both human food and animal feed, further solidifying its importance for global food security [20,21,22]. Enhancing its heat tolerance could help ensure the continued provision of these ecosystem services under changing climatic conditions.

This study on the impact of heat stress on soybean seedlings addresses critical aspects of climate change research relevant to agriculture and food security. The findings of this research will not only advance our understanding of plant responses to heat stress but also support the development of adaptive strategies to ensure sustainable soybean production in the face of global climate change. Furthermore, this research will contribute to the broader field of climate adaptation in agriculture by providing insights into the physiological basis of heat stress tolerance in soybean. Such knowledge is essential for breeding programs and agricultural management practices aimed at enhancing crop resilience to rising temperatures.

2 Materials and Methods

This study involved 18 soybean varieties from Indonesia (Table 1). The method by Kaur et al., [23] and Rai et al., [24] was followed in this experiment. Cocopeat was used as the growing medium, filled into plastic cups. The experimental work was conducted in a controlled laboratory environment with initial growth conditions set at 25°C. The experimental design employed a nested arrangement of treatments, with five levels of heat stress (T1-T5): 25 (control), 30, 35, 40, and 45°C. Each treatment combination was replicated three times to enhance the reliability of the results.

Sowing involved placing four soybean seeds per cup. The seedlings were grown under control conditions (25°C) until two weeks. Subsequently, heat stress treatments were applied for four hours per day over four consecutive days. Following the heat stress treatment, all plants were returned to control conditions (25°C) for one week to allow for recovery. Data collection focused on assessing heat stress tolerance through various parameters measured after the recovery period. These parameters included survival rate (percentage of seedlings surviving the heat stress treatment), root length (cm), shoot length (cm), total plant weight (g), and relative water content (%). The data obtained were analyzed using analysis of variance (ANOVA) at a level of 5% using IBM SPSS Statistics 27 software.

Table 1. List of soybean varieties evaluated in the study

V1	Deja 1	V7	Devon 2	V13	Detap 1
V2	Deja 2	V8	Dering 1	V14	Derap 1
V3	Demas 1	V9	Dering 2	V15	Dega 1
V4	Dena 1	V10	Dering 3	V16	Gepak Kuning
V5	Dena 2	V11	Denasa 1	V17	Agromulyo
V6	Devon 1	V12	Denasa 2	V18	Grobogan

3 Results and Discussion

3.1. Descriptive Analysis for Traits Under Different Treatments

In the present study, descriptive analysis were computed (table 2). The descriptive analysis for five traits—Survival Rate (SR), Root Length (RL), Shoot Length (SL), Total Plant Weight (TPW) and Relative Water Content (RWC)—under five temperature treatments (25, 30, 35, 40, and 45°C) indicate significant impacts of temperature on soybean growth. At 25°C, soybean plants exhibited the highest SR (100%) and relatively high RL (11.04 cm), SL (16.85 cm), and TPW (1.52 g), suggesting optimal growth conditions. Increasing the temperature to 30°C resulted in the highest RL (13.86 cm) and SL (20.57 cm), with a slight decrease in SR (85.19%) and consistent high RWC (86.78%), indicating this temperature also supports good growth but introduces some stress. At 35°C, RL (12.05 cm) and SL (18.25 cm) were slightly reduced, and SR dropped to 67.59%, demonstrating moderate stress. More severe stress was observed at 40°C, where RL (8.10 cm), SL (12.97 cm), and TPW (0.95 g) significantly decreased, with SR falling to 44.91%. The most extreme temperature, 45°C, severely impacted all traits, with RL (11.22 cm) and SL (9.07 cm) notably lower, RWC (56.91%) substantially reduced, and SR (38.89%) markedly diminished, highlighting the adverse effects of high heat stress.

These findings align with previous studies that highlight the detrimental effects of heat stress on soybean physiology. Sarwar et al. [25] observed that heat stress significantly reduces root and shoot growth in soybean seedlings due to impaired cell elongation and division. Additionally, the decline in relative water content at higher temperatures observed in our study is consistent with findings by Hassan et al., [26], who reported that heat stress reduces water uptake and retention, likely due to disruptions in cellular water balance and membrane stability. The sharp decline in survival rates beyond 35°C is also in agreement with the findings of Sarwar et al. [25], who demonstrated that prolonged exposure to temperatures above 35°C critically affects soybean seedling survival and development. These results underscore the importance of identifying and breeding heat-tolerant soybean varieties for sustainable production under changing climatic conditions.

Table 2. Estimates of descriptive statistics of 18 different soybean varieties at different temperatures

Temperature	Traits	Mean	SE	SD	C.V.	Range
25	Survival Rate	100	0	0	0	100
	Root Length	11.04	0.31	2.27	20.54	7-16.1
	Shoot Length	16.85	0.24	1.74	10.34	14-20
	Total Plant Weight	1.52	0.03	0.21	13.51	1.08-1.89
	Relative Water Content	83.37	0.05	0.33	0.4	82.39-83.96
30	Survival Rate	85.19	2.6	19.13	22.46	50-100
	Root Length	13.86	0.53	3.93	28.33	7.7-22.6
	Shoot Length	20.57	0.43	3.19	15.5	15.7-30.3
	Total Plant Weight	1.71	0.03	0.24	14.3	1.2-2.16
	Relative Water Content	86.78	0.08	0.55	0.64	86-87.88
35	Survival Rate	67.59	2.35	17.26	25.53	25-100
	Root Length	12.05	0.49	3.56	29.57	5-19.2
	Shoot Length	18.25	0.38	2.76	15.14	12.8-23.8
	Total Plant Weight	1.52	0.03	0.21	13.54	1.08-1.89
	Relative Water Content	83.7	0.25	1.86	2.23	77.21-84.95
40	Survival Rate	44.91	2.59	19.05	42.41	25-100
	Root Length	8.1	0.32	2.38	29.44	2.4-11.9
	Shoot Length	12.97	0.32	2.37	18.29	8-17
	Total Plant Weight	0.95	0.02	0.14	14.79	0.6-1.22
	Relative Water Content	68	0.8	5.86	8.62	60-74.6
45	Survival Rate	38.89	4.39	13.18	33.88	25-50
	Root Length	11.22	0.22	0.65	5.81	10.4-12.4
	Shoot Length	9.07	0.28	0.85	9.33	8-10.2
	Total Plant Weight	0.95	0.04	0.12	12.65	0.81-1.2
	Relative Water Content	56.91	4.78	14.34	25.19	34.43-76.47

3.2. Survival Rate

The survival rate data reveals significant variability in heat stress tolerance among the tested soybean varieties, with clear trends of decreasing survival as temperature intensity increases from 25 to 45°C (Figure 1). All varieties showed 100% survival under 25°C temperature, likely representing optimal growing conditions. However, as stress levels increased, marked differences emerged. Under 30°C, survival rates ranged from 66.67% to 91.67%, with varieties V2, V3, V6, V8, V10, V12, V14, and V16 performing the best, maintaining 91.67% survival. The lowest survival rate at 30°C temperature was observed in V18 (66.67%). T3 conditions (35°C) exposed more pronounced variations, with survival rates ranging from 50% to 91.67%. Notably, V16 maintained its high performance with 91.67% survival, followed by V6 (83.33%). V11 showed the lowest survival rate at this temperature (50%). T4 conditions (40°C) demonstrated the widest response range (25% to 83.33%), highlighting significant differences in heat tolerance among varieties. V3 showed remarkable resilience, maintaining 83.33% survival, followed closely by V16 (75%). In contrast, V8, V10, V15, and V18 showed poor performance with only 25% survival rate.

Under the most severe T5 stress (45°C), most varieties failed to survive, with only four varieties showing any survival: V3 and V16 (both at 41.67%), V17 (33.33%), and V18 (41.67%). This severe drop in survival rates underscores the critical impact of extreme heat stress on soybean seedlings.

Notably, varieties V3 (Demas 1) and V16 (Gepak Kuning) consistently performed well across all stress levels, maintaining higher survival rates even under severe stress, followed closely by V17. These findings align with earlier research highlighting the heat tolerance of Demas 1 and Gepak Kuning, both of which have been noted for their superior physiological

responses to stress, including enhanced antioxidant activity and membrane stability [27,28,29]. Conversely, V18, despite showing poor performance under moderate to high stress conditions, unexpectedly maintained some survival under the most extreme condition, which could be attributed to its unique genetic makeup or epigenetic modifications, as observed in other soybean genotypes by Sarwar et al. [25].

This genetic variability in heat stress tolerance is crucial for breeding programs aimed at developing heat-tolerant cultivars [30]. The sharp decline in survival rates between T3 and T4 for many varieties suggests a possible threshold effect, where heat stress beyond a certain point leads to rapid loss of viability. Understanding these thresholds and the mechanisms behind the superior performance of varieties like V3 and V16 could provide valuable insights for improving soybean heat tolerance.

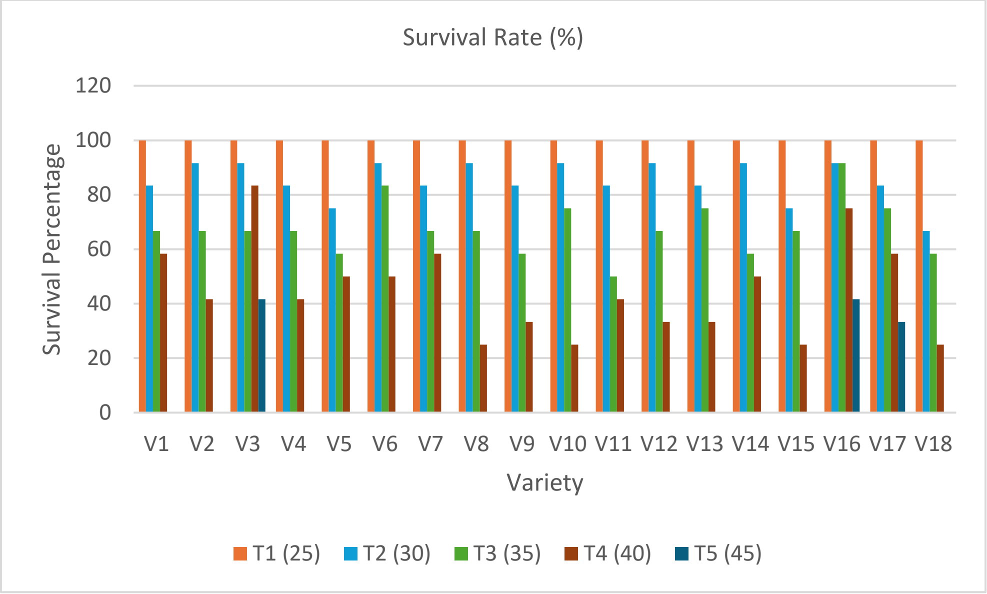

Figure 1. Survival rate of 18 soybean varieties under different temperature stress.

3.3. Root Length

The root length data shows significant variations among soybean varieties under different heat stress levels (T1-T5) (Figure 2). Like the shoot length data, root length generally increased from T1 to T2 for most varieties, indicating a mild stress-induced growth response. However, from T3 to T5, root length consistently decreased across all varieties. Varieties V3, V16, and V17 exhibited superior performance, maintaining longer root lengths even under higher stress. Notably, V17 had the highest root length under T2 (21.23 cm) and T3 (16.68 cm). V3 and V16 also maintained relatively high root lengths. In contrast, varieties V13 and V18 consistently showed shorter root lengths, indicating higher sensitivity to heat stress. Under T4 conditions, V13 and V18 had root lengths of 5.34 cm and 5.65 cm, respectively, much lower than the top performers.

The data shows a clear trend of decreasing root length with increasing heat stress, especially from T3 to T5, consistent with previous studies. This reduction is due to physiological responses like reduced cell division and elongation, altered hormone balances, and decreased water and nutrient uptake [10,31]. The superior performance of varieties V3, V16, and V17 under high temperatures aligns with findings by Salem et al. [32], who observed that heat-tolerant soybean varieties maintain better root development due to

enhanced cellular stability and water uptake efficiency. The initial increase in root length from T1 to T2 suggests a hormetic response, where mild stress promotes growth. This phenomenon, observed in various plants, has been attributed to adaptive mechanisms that help roots explore larger soil volumes for water and nutrients under mild stress conditions [33].

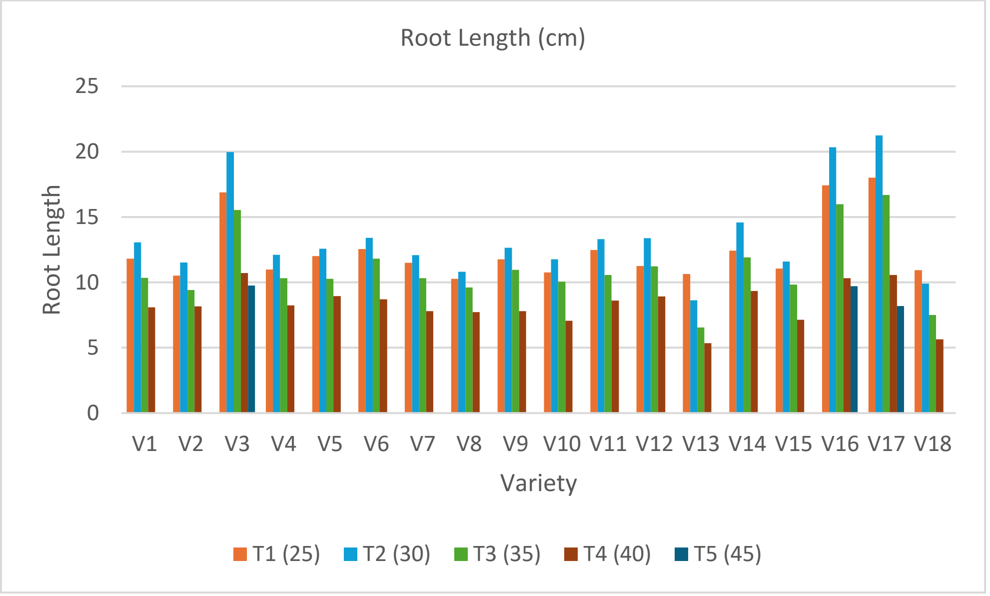

Figure 3. Root Length of 18 soybean varieties under different temperature stress.

3.4. Shoot Length

The shoot length data shows significant variations among soybean varieties under different heat stress levels (T1-T5) (Figure 3). Generally, shoot length increased from T1 to T2 for most varieties, suggesting a mild stress-induced growth response. However, as stress intensified from T3 to T5, all varieties exhibited a consistent decrease in shoot length. Varieties V3, V16, and V17 demonstrated enhanced tolerance and maintained shoot lengths even under higher stress conditions. Specifically, V17 showed the highest shoot length under T2 (24.63 cm) and T3 (21.5 cm). V3 and V16 also maintained relatively high shoot lengths across stress levels, indicating better heat stress tolerance, possibly due to more efficient photosynthetic processes or improved water relations. In contrast, varieties V13 and V18 consistently had the shortest shoot lengths, indicating higher sensitivity to heat stress, with V13 and V18 having shoot lengths of 8.95 cm and 8.55 cm under T4 conditions, respectively.

The data reveals a clear trend of decreasing shoot length with increasing heat stress, especially from T3 to T5, consistent with previous studies. Reduced cell elongation under high temperatures has been identified as a primary factor for reduced shoot growth, as shown by Salem et al. [32]. Heat stress disrupts hormonal balance, particularly auxins and gibberellins, which are critical for stem elongation. Varieties V3, V16, and V17, which maintained better shoot growth under stress, exhibit traits commonly associated with heat tolerance, such as higher photosynthetic rates and efficient water use. For instance, Djanaguiraman et al. [34] demonstrated that heat-tolerant soybean varieties sustain shoot elongation by maintaining cooler canopy temperatures and minimizing oxidative damage under high-temperature stress. The observed initial increase in shoot length from T1 to T2 aligns with the concept of a hormetic response, where mild stress promotes growth [33].

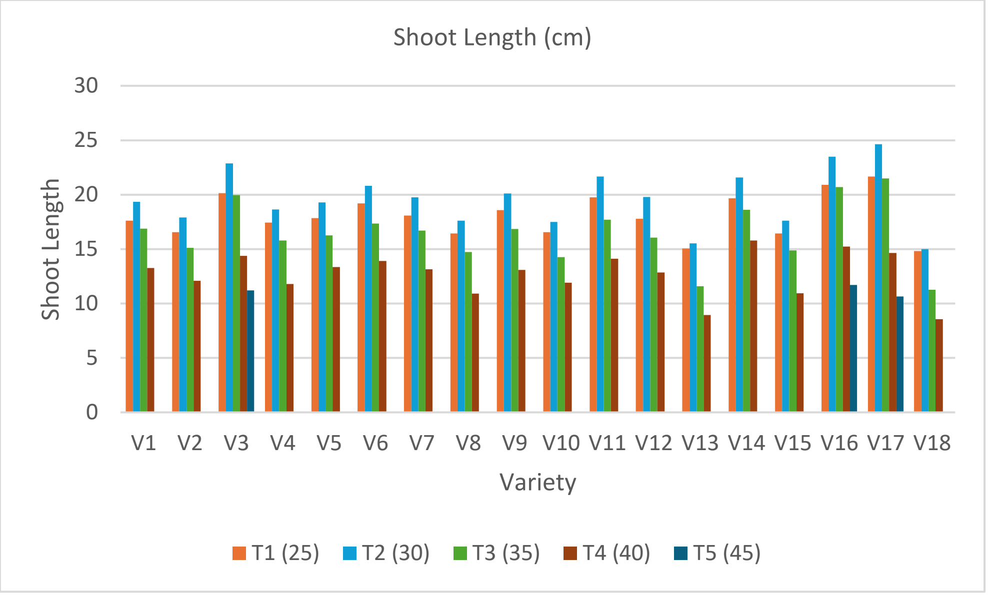

Figure 3. Shoot Length of 18 soybean varieties under different temperature stress.

3.5. Plant Weight

The plant weight data revealed significant variability among soybean varieties in response to different levels of heat stress (T1–T5) (Figure 4). Most varieties exhibited a slight increase in plant weight from T1 to T2, with V17 achieving the highest weight at 2.06 g under T2. This trend suggests that mild stress may have stimulated growth by activating adaptive mechanisms. However, as heat stress intensified from T3 to T5, plant weight consistently declined across all varieties. V16 and V17 demonstrated superior performance, maintaining higher weights even under severe stress conditions, with weights of 1.66 g and 1.52 g, respectively, under T3. In contrast, varieties V10 and V18 were the most sensitive, displaying the lowest weights across all stress levels. Under T4, their weights dropped to 0.685 g and 0.765 g, respectively, indicating a severe decline in biomass production.

The declining trend in plant weight under heat stress is consistent with previous studies. Salem et al. [32] attributed such reductions to disruptions in photosynthesis and increased respiration rates under elevated temperatures, which limit energy availability for biomass accumulation. The superior performance of V16 and V17 might be explained by their ability to maintain photosynthetic efficiency and allocate resources effectively under stress. Similar findings were reported by Djanaguiraman et al. [34], who observed that heat-tolerant soybean varieties exhibit enhanced photosynthetic activity and reduced oxidative damage, leading to improved biomass retention under heat stress. The remarkable performance of V16 and V17 highlights their potential as candidates for breeding programs aimed at enhancing resilience to heat stress. Further research focusing on their biochemical and molecular responses, particularly those related to photosynthesis and stress signaling pathways, could provide valuable insights for improving heat tolerance in soybean and other crops.

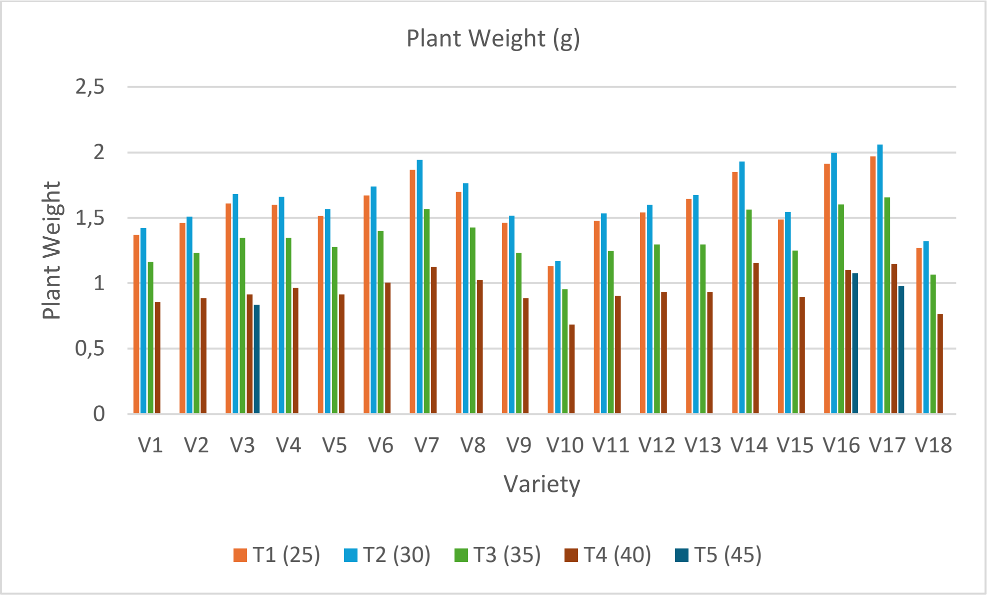

Figure 4. Plant Weight of 18 soybean varieties under different temperature stress.

3.6. Relative Water content

The relative water content (RWC) data revealed significant variations among soybean varieties under different heat stress levels (T1–T5) (Figure 5). Under T1 conditions, all varieties maintained high RWC values above 82%, indicating optimal water status. A slight increase in RWC from T1 to T2 (86.17% to 87.71%) was observed, suggesting an initial stress-induced water conservation mechanism or improved water uptake under mild stress. However, as heat stress intensified from T3 to T5, RWC consistently declined across all varieties, with varying rates of decrease reflecting differences in stress tolerance. Varieties V3, V4, V7, V8, and V16 performed best, maintaining RWC above 75% under T4, demonstrating effective water retention and uptake mechanisms. Conversely, V13 and V18 exhibited the steepest declines, with RWC values dropping to 68.28% and 64.73%, respectively, under T4.

The observed reductions in RWC under severe stress are consistent with the findings of Djanaguiraman et al. [34], who reported that heat stress disrupts water relations by impairing root water uptake and increasing transpiration rates. The ability of varieties like V3 and V16 to maintain higher RWC under T4 suggests superior cellular membrane stability and osmotic adjustment, traits also observed in heat-tolerant varieties in other studies [25,26,32]. In contrast, the rapid declines in RWC in V13 and V18 indicate higher sensitivity to heat stress, likely due to less efficient water retention mechanisms and greater vulnerability to oxidative damage. These findings highlight the critical role of water conservation in maintaining plant performance under heat stress. The superior performance of varieties V3, V4, V7, and V16 underlines their potential as key genetic resources for breeding programs targeting improved water use efficiency and heat tolerance [27,28,29].

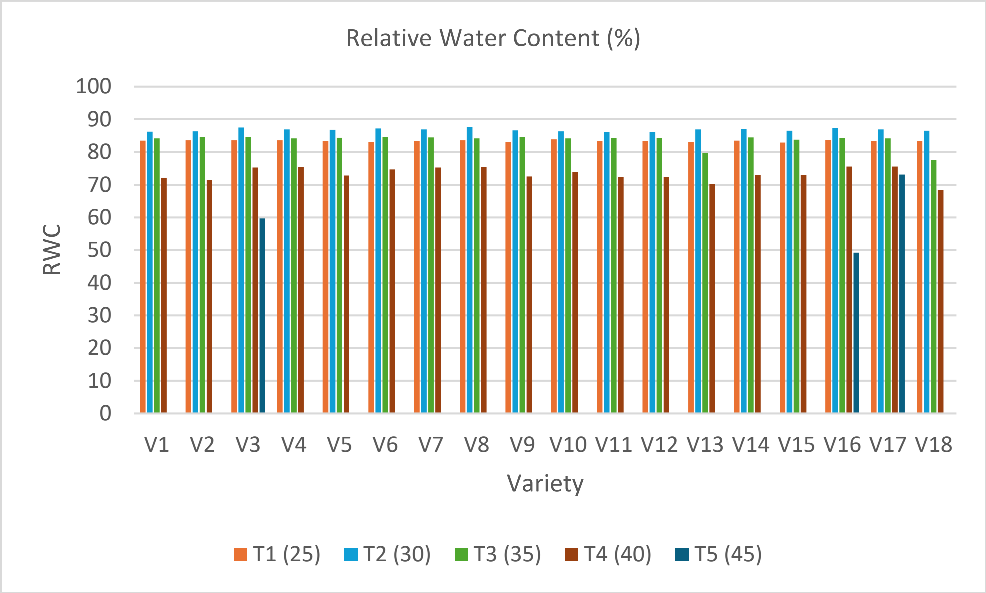

Figure 5. Relative Water Content of 18 soybean varieties under different temperature stress.

4 Conclusion

This study provides crucial insights into the heat stress tolerance of 18 soybean varieties at the seedling stage. Our findings reveal significant variability in response to increasing temperatures, with clear trends of declining performance across all measured parameters as heat stress intensified. Notably, varieties V3, V16, and V17 consistently demonstrated superior heat tolerance, maintaining higher survival rates, better growth parameters, and improved water relations even under severe stress conditions. These varieties offer promising genetic resources for breeding programs aimed at developing heat-resilient soybean cultivars. The observed threshold effect between 35°C and 45°C, where most varieties experienced a sharp decline in performance, highlights a critical temperature range for soybean heat stress tolerance. This information is valuable for predicting soybean responses to future climate scenarios and developing targeted management strategies. These findings contribute significantly to our knowledge of soybean physiology under heat stress and offer practical implications for agriculture in the face of climate change. Future research should explore the physiological and molecular mechanisms behind the superior performance of tolerant varieties and investigate their responses to combined stress conditions like heat and drought. Multi-environment trials and genomic studies could identify specific genes or markers associated with heat tolerance, facilitating more effective breeding strategies for sustainable soybean production in warming climates.

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