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Performance of GA_3 primed soybean seeds grown under different temperatures: effects on physiological and biochemical traits

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Abstract

Aim of study: To evaluate the effects of seed priming using gibberellic acid (GA_3) on the physiological and biochemical traits of soybean seeds, examining variations across different temperature environments.

Area of study: Ludhiana, Punjab, India.

Material and methods: Seed priming of soybean seeds with GA_3 at concentrations of 25, 50, 100 and 200 mg L^{-1} for 6 hours] at various temperatures (25, 30, 35 and 40 °C) on physiological and biochemical traits under *in vitro* conditions, carried out twice using a factorial complete randomized design, replicated four times.

Main results: The results revealed that seed priming with 100 mg L^{-1} GA_3 recorded higher germination percentage, total seedling length, speed of germination, seedling dry weight and vigour indices when grown at 30 °C than other seed priming treatments and temperatures. Seed treated with 100 mg L^{-1} GA_3 exhibited 21.8% and 11.0% higher speed of germination, 21.1% and 14.2% higher seedling vigour index I and 20.8 & 17.3% higher dehydrogenase activity over control and hydropriming, respectively. Priming seeds with 100 mg L^{-1} GA_3 led to a higher percentage of stained seeds and lowered electrical conductivity at various temperatures compared to other seed priming treatments.

Research highlights: The study suggests that priming soybean seeds with 100 mg L^{-1} GA_3 solution can enhance their physiological and biochemical parameters under high temperatures conditions, thus promoting quicker germination and uniform seedling emergence.

Keywords: Germination; gibberellic acid; seed priming; soybean; temperature.

Rendimiento de semillas de soja tratadas con GA_3 cultivadas a diferentes temperaturas: efectos en los caracteres fisiológicos y bioquímicos

Resumen

Objetivo del estudio: Evaluar los efectos del tratamiento (*priming*) de semillas utilizando ácido giberélico (GA_3 en los caracteres fisiológicos y bioquímicos de las semillas de soja, analizando las variaciones en diferentes ambientes de temperatura.

Área de estudio: Ludhiana, Punjab, India.

Materiales y métodos: El tratamiento de semillas de soja con GA_3 a concentraciones de 25, 50, 100 y 200 mg L^{-1} durante 6 horas a diferentes temperaturas (25, 30, 35 y 40 °C) para observar los caracteres fisiológicos y bioquímicos en condiciones *in vitro*. El experimento se repitió dos veces utilizando un diseño factorial completamente aleatorizado con cuatro repeticiones.

Resultados principales: Los resultados revelaron que el tratamiento de semillas con GA_3 a 100 mg L^{-1} registró el mayor porcentaje de germinación, longitud total de la plántula, velocidad de germinación, peso seco de plántula e índices de vigor cuando se cultivaron a 30 °C, en comparación con otros tratamientos de *priming* y temperaturas. Las semillas tratadas con 100 mg L^{-1} de GA_3 mostraron una velocidad de germinación 21.8% y 11.0% mayor, un índice de vigor de plántula I 21.1% y 14.2% mayor, y una actividad deshidrogenasa 20.8% y 17.3% mayor en comparación con el control y el tratamiento con agua, respectivamente. El tratamiento con 100 mg L^{-1} de GA_3 también resultó en un mayor porcentaje de semillas teñidas y menor conductividad eléctrica a diferentes temperaturas, en comparación con otros tratamientos.

Conclusiones: El estudio sugiere que el tratamiento de semillas de soja con una solución de GA_3 a 100 mg L^{-1} puede mejorar sus parámetros fisiológicos y bioquímicos en condiciones de alta temperatura, promoviendo así una germinación más rápida y una emergencia de plántulas más uniforme.

Palabras clave: Germinación; ácido giberélico; tratamiento de semillas; soja; temperatura.

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Introduction

Soybean [*Glycine max* (L.) Merrill] seeds, known for their rich nutritional composition including approximately 36-40% protein, 20-22% edible oil, and 34-37% carbohydrates alongside about 5% ash, as well as essential vitamins and minerals, hold significant importance in both human diet and animal feed (Chuwa et al., 2023). Consumption of soybean in diverse forms provides bioactive compounds that significantly reduce the risk of various cancers such as breast, prostate, bladder & liver, and along with offering protective effects against cardiovascular diseases, menopausal symptoms and elevated blood pressure (Kim, 2021). Soybean cultivation contributes to soil fertility by utilizing atmospheric nitrogen through biological nitrogen fixation and after harvesting, the nitrogen-rich soybean residues decompose into organic matter, replenishing nitrogen levels in the soil (Kebede et al., 2021). During 2022-23, soybean cultivation spanned approximately 133.7 million ha worldwide, yielding a total production of 348.8 million tonnes and achieving a productivity of 2,607 kg per ha. Specifically, in India during the same period, soybean production yielded 12.9 million tonnes, cultivated across 12.1 million ha, with a productivity of 1069 kg per ha. Brazil stands out as the global leading producer of soybean, trailed by the United States and Argentina. India occupies the fourth position in terms of cultivated area and the fifth position in production among the leading soybean-producing nations (FAOSTAT, 2024).

Seed germination is an important stage in the life cycle of soybean plant, profoundly impacting crop yield through its crucial role in ensuring uniform germination and subsequent seedling emergence (Panda and Mondal, 2020; Kumar et al., 2021). However, timely and uniform germination pose significant challenges under elevated temperatures in soybean production (Rhaman et al., 2020). These elevated temperatures have the potential to disrupt the physiological and biochemical processes crucial for seed germination and early seedling establishment, further influencing the subsequent stages of plant development (Hasanuzzaman et al., 2022). Globally, adverse environmental conditions such as drought and high temperatures have been found to decrease the productivity of soybean. Sowing soybean in conditions with high temperatures of 38.2 °C and 42.1 °C led to notable decrease in seed yield, with reductions of 41.1% and 63.2%, respectively (Jumrani and Bhatia, 2018). Adverse environmental conditions like elevated temperatures induce osmotic stress during seedling germination, disrupting cellular and physiological equilibrium and eventually leading to seedling mortality (Chaudhry et al., 2022).

Uniform and rapid seed germination is essential for ensuring the successful initiation of seedling growth. Seed priming has been successfully demonstrated to improve germination and emergence in many crops like groundnut (Beesanakoppa et al., 2020), chickpea (Choudhury & Bordolui, 2023), soybean (Lewandowska et al., 2020) and linseed (Ugile et al., 2020). This method involves subjecting seeds to a particular environment before germination, wherein they are partially hydrated to initiate germination processes without the emergence of the root (Aswathi et al., 2022). Seed priming is a cost-effective and efficient technique utilized to enhance plants' resilience against unfavorable temperatures (Biswas et al., 2023). This method involves regulating the moisture content of seeds to stimulate seed metabolism that leads to the breakdown of complex carbohydrates into more soluble forms, facilitating absorption by the developing embryo (Chakraborty & Dwivedi, 2021). Priming seeds encourages the synthesis of aquaporins, facilitating enhanced water passage across membranes, thus promoting tissue expansion and optimal germination potential. Furthermore, seed priming boosts the activity of xyloglucan endotranshydrolase, which initiates loosening of cell walls, enabling greater water absorption and hastening the germination process. During priming, late embryogenesis abundant proteins play a crucial role in maintaining cell shape and integrity, enabling plants to better endure challenges like drought stress (Marthandan et al., 2020). Moreover, priming enhances the germination percentage and reduces the time taken to germination under both optimum and unfavorable environmental conditions.

The utilization of plant growth hormones on the reproductive parts, specifically seeds, is a widely employed priming approach (Pawar and Laware, 2018). These hormones are crucial chemical compounds that facilitate cell growth and differentiation in actively developing areas, thereby influencing germination and overall plant growth (Ali and Baloch, 2020). In particular, gibberellic acid (GA_3) holds a significant role in seed germination, as it has been shown to enhance the germination in various crop species (Vishal & Kumar, 2018; Muniandi et al., 2018). It exerts its impact through enhancing the growth capacity of the embryo and by stimulating the production of hydrolytic enzymes. Gibberellic acid is crucial in facilitating the weakening

of the endosperm cap by being synthesized within the embryo and then transported to the aleurone layer, where it initiates the expression of α-amylase enzyme (Gupta & Chakrabarty, 2013). This α-amylase led to breakdown of starch into simpler sugars, thereby providing energy for the embryo's growth and development. Priming seeds with 225 mg L^{-1} GA_3 improved chickpea germination rate and reduced the time required for emergence (Mazed et al., 2015). Lentil seeds treated with 500 mg L^{-1} GA_3 exhibited significantly enhanced germination and subsequent plant growth (Reddy & Luikham, 2021). In soybean, seeds treated with 100 mg L^{-1} GA_3 for 2 hours demonstrated increased germination index, coefficient of velocity and vigour index (Jassal & Singh, 2018). Moreover, black gram seeds primed with 350 mg L^{-1} GA_3 showed higher germination, seedling length and seedling dry weight (Nedunchezhiyan et al., 2023).

High temperatures during the sowing season in June impede the germination by causing moisture loss. To address this concern, our study seeks to investigate effective methods to mitigate the negative effects of elevated temperatures on soybean germination and seedling growth. There is limited existing research concerning the effects of applying GA_3 to seeds on the physiological and biochemical traits during the germination of soybean under varying temperature conditions. Hence, the current investigation focuses on assessing the potential of utilizing hormonal priming with GA_3 to improve the germination rate and vigor of soybean seeds, especially under diverse temperature conditions. The objective is to offer a viable approach to address suboptimal crop establishment in environmentally challenged regions, thereby enhancing the soybean yield potential. With this objective, *in vitro* studies were designed to explore the impact of various seed priming techniques across different temperature regimes on the physiological and biochemical traits of soybean seeds.

Material and methods

Experimental design and details

The *in vitro* investigation was conducted at the Seed Physiology Laboratory, Office of Director (Seeds) at Punjab Agricultural University, Ludhiana, Punjab, India, during the years 2021-22. This study comprised of four different temperature levels (25 °C, 30 °C, 35 °C and 40 °C) alongside six seed priming treatments [control, hydropriming, seed priming with GA_3 at concentration of 25, 50, 100 and 200 mg L^{-1}]. The experiment was replicated twice and arranged in a factorial complete randomized design, with each treatment combination replicated four times.

Seed priming, experimental setup and germination assessment

The necessary amount of GA_3 was procured from Central Drug House Private Limited, located in New Delhi, India. In this experiment, the seeds of the variety 'Soybean Ludhiana (SL) 958' were used which are characterized by their shiny, light-yellow appearance with a black hilum and contains around 41.7% protein and 20.2% oil content. 'SL 958' is known for its resistance to yellow mosaic virus and soybean mosaic virus, it has maturity period of approximately 142 days and an average yield of 18.0 quintals ha^{-1}. The seeds were harvested at harvest maturity in the last week of October at the Pulses Research Farm, Department of Plant Breeding & Genetics, Punjab Agricultural University (PAU), Ludhiana, Punjab (30° 54′N, 75° 48′E, altitude 247 m). Following threshing and cleaning, the seeds were stored in gunny bags under optimal conditions to maintain their integrity and viability.

In each treatment, 400 seeds of variety 'SL 958' were primed for 6 hours at 25 °C by soaking them in GA_3 solution of different concentration (25 mg L^{-1}, 50 mg L^{-1}, 100 mg L^{-1} and 200 mg L^{-1}). Dry soybean seeds were used as control (non-primed). Following priming, the seeds were taken out and air-dried at room temperature until they reached their original weight. For each priming treatment, 100 seeds were placed between two moistened germination papers with a layer of butter paper underneath. This entire process was repeated four times for each treatment. The germination papers were then rolled up and placed vertically inside the incubator (CI- 10S, manufactured by Remi instruments limited) in the dark for 8 days, corresponding to their respective treatments. On the 8th day after germination (DAG), all relevant parameters were observed, measured and recorded (ISTA, 1999). Germination was determined by the emergence of a 2 mm radicle.

Determination of germination (%), total seedling length and seedling vigour indices

The germination (%) was determined through the following formula used by Onofri et al. (2019):

$$\text{Germination (\%)} = \frac{\text{Number of seeds germinated}}{\text{Total number of seeds}} \times 100$$

Ten representative seedlings, aged 8 days, were chosen from each replication. The length of the root (from root tip to base) and shoot (from shoot tip to base) were measured individually using a centimetre scale. The total length of each seedling was calculated by summing these measurements in centimetres. Subsequently, the selected seedlings were placed in individual paper bags and dried in a hot air oven at a temperature of 65±1 °C until reaching a constant weight. Once cooled, the dried

seedlings were weighed and the average weight of ten seedlings was expressed in grams. Seedling vigour index I and II were determined by using the formula given by Abdul-Baki and Anderson (1973):

Seedling vigour index I (SVI I) = Germination% × Mean seedling length (cm)

Seedling vigour index II (SVI II) = Germination% × Mean dry weight of ten seedlings (g)

Determination of speed of germination and electrical conductivity of seeds

To evaluate speed of germination, seeds were placed in Petri dishes containing moist filter paper. These dishes were subsequently incubated in a seed germinator in the absence of light for 8 days according to various treatments. The whole process (seeds weighing two grams per replicate) was replicated four times for each treatment. Daily observations were made, and the number of germinating seeds was recorded. The speed of germination (seed day^{-1}) was determined using the formula outlined by AOSA (1983):

Speed of germination = $\{ n1/d1 + n2/d2 + n3/d3 + - - - \}$

where, n= no. of seeds germinated; d= no. of days

The electrical conductivity (EC) of control and treated seeds was assessed following the guidelines outlined by ISTA (1999). Five grams seeds from each treatment were placed in quadruplicate into beakers containing 20 ml of distilled water. The beakers were incubated for 24 hours according to the treatments, after which the EC of the seed leachate was measured using a conductivity meter. Subsequently, the EC of the control (distilled water) was also assessed. EC was expressed in units of µS cm^{-1} g^{-1} through the formula:

$$EC = \frac{\text{Electrical conductivity}_t - \text{Electrical conductivity}_c}{\text{Weight of seeds}}$$

where, EC_t = Electrical conductivity of treatments

EC_c = Electrical conductivity of distilled water

Determination of dehydrogenase activity and percentage of stained seeds

The dehydrogenase activity of seeds was evaluated using the method outlined by Kittock & Law (1968). In beakers with distilled water, five grams seeds per replicate were replicated four times for each treatment and incubated overnight to initiate dehydrogenase activity and enable 2, 3, 5 triphenyl tetrazolium chloride (TTC) penetration. The following day, seeds were cut longitudinally, stained in 0.5% TTC solution for 4 hours, and then cleaned with water. Afterward, the seeds were crushed in 5 ml of acetone, centrifuged, and the supernatant was collected. The absorbance of the pink colour formed was measured using a spectrophotometer at 485 nm.

The percentage of stained seeds was assessed by seed staining with 0.5% TTC solution, following the procedure described by AOSA (2000). Seeds weighing five grams per replicate from each treatment were placed in quadruplicate in beakers containing distilled water. After overnight incubation at 25ºC, seeds were longitudinally cut and immersed in 0.5% TTC solution for 4 hours at 25ºC to allow for TTC penetration. Subsequently, seeds were removed, rinsed multiple times with water, and then examined to determine staining patterns. The seeds were represented as a percentage of stained (viable) seeds.

Statistical analysis

Data on all the observations of different treatments were analysed with analysis of variance (ANOVA) by utilizing a factorial completely randomized design, with four replications. The experiments were conducted twice, and the resulting data were pooled and subjected to statistical analysis using RStudio software (R, 2023). Statistical comparisons of means were performed using the Duncan multiple range test (DMRT) at a significance level of 0.05%. GraphPad Prism and Microsoft excel program were employed to generate heat maps and graphs.

Results

Germination percentage

The average germination percentage was significantly greater at 30 °C compared to 35 °C and 40 °C, but statistically similar to the average at 25 °C (Table 1). Seed priming led to a significant enhancement in germination percentage compared to the control, where seeds treated with GA_3 100 mg L^{-1} exhibited significantly higher germination percentage compared to control, hydropriming, and other GA_3 treatments. Priming with GA_3 100 mg L^{-1} resulted in 3.2 and 2.1 per cent points higher germination over control and hydropriming, respectively. The interaction between temperatures and seed priming led to significant impact, with the greater germination percentage observed at 30 °C when seeds were primed with GA_3 100 mg L^{-1}, but was statistically similar to hydropriming, GA_3 25, 50 & 200 mg L^{-1}, GA_3 50 & 100 mg L^{-1} at 25 °C and GA_3 100 mg L^{-1} at 35 °C.

Table 1. Influence of temperature and seed priming on germination percentage and total seedling length of soybean.

Temperature (ºC)	Seed priming						Mean
	Control	Hydropriming	GA_3 25 mg L^{-1}	GA_3 50 mg L^{-1}	GA_3 100 mg L^{-1}	GA_3 200 mg L^{-1}	
Germination (%)							
25	93.1±0.239cd^	94.1± 0.427bc	94.7±0.595bc	95.3±0.239abc	96.3±0.231ab	94.6±0.621bc	94.7±0.394AB^^
30	94.1±0.515bc	95.2±0.561abc	95.5±0.612abc	96.0±0.707abc	97.3±0.325a	95.4±0.660abc	95.6±0.564A
35	91.1±0.826d	93.3±0.531cd	93.8±0.561bcd	94.3±0.341bc	95.3±0.788abc	93.6±0.743bcd	93.5±0.629B
40	49.2±1.492e	47.1±2.023e	39.7±1.750f	41.2±1.199f	47.6±1.087e	40.2±0.782f	44.2±1.387C
Mean	81.9±0.768BC	82.4±0.885B	80.9±0.879C	81.7±0.621BC	84.1±0.607A	81.0±0.701C	
Total seedling length (cm)							
25	25.3±0.155efg	26.5±1.430def	26.9±0.504de	27.6±0.1.132de	28.9±1.543bcd	27.5±1.615de	27.1±1.021B
30	28.3±0.486cd	30.5±0.657bc	31.1±0.354b	34.1±0.417ab	35.4±0.698a	33.7±0.552ab	32.2±0.527A
35	20.0±0.715i	22.4±0.567h	22.6±0.497h	23.4±0.502gh	24.3±0.531fgh	23.1±0.256gh	22.6±0.511C
40	7.6±0.575j	8.2±0.745j	7.1±0.387j	7.6±0.299j	8.6±0.280j	7.7±0.552j	7.8±0.473D
Mean	20.3±0.482D	21.9±0.849C	22.0±0.435C	23.2±0.587B	24.3±0.763A	23.0±0.743B	

Data are represented as pooled mean (±SE), n=4. Means with same alphabets within a row are not significantly different from each other at $P \leq 0.05$ (DMRT). Lower case letters indicate the mean separation of interaction effects. Upper case letters indicate the mean separation of main effects.

Total seedling length

The total length of seedlings exhibited a significant increase at 30 °C compared to 25 °C, 35 °C and 40 °C, as indicated in Table 1. However, there was a notable decrease in total seedling length as temperatures surpassed 30 °C, with the shortest seedlings observed at 40 °C. An enhancement in total seedling length was observed across all seed priming treatments compared to control where seeds primed with GA_3 performed better than those hydroprimed. GA_3 100 mg L^{-1} showed significantly greater total seedling length compared to the control, hydropriming and GA_3 25, 50 and 200 mg L^{-1}. A significant interaction effect between temperatures and seed priming was observed, with the highest total seedling length recorded at 30 °C when seeds were primed with GA_3 100 mg L^{-1}, but remained statistically similar to GA_3 50 and 200 mg L^{-1}.

Dry weight of seedlings

The dry weight of seedlings exhibited a significant increase at 30 °C compared to 25 °C, 35 °C and 40 °C (Table 2). Beyond 30 °C, there was a notable decrease in dry weight, with the lowest dry weight recorded at 40 °C. Across all seed priming treatments, dry weight of seedlings was increased compared to the control. Specifically, seeds treated with GA_3 100 mg L^{-1} demonstrated significantly higher dry weight of seedlings compared to control, hydropriming and GA_3 25 mg L^{-1}, but was statistically comparable to the dry weight observed with GA_3 50 and 200 mg L^{-1}. The interaction effect between temperatures and seed priming did not yield significant effect.

Table 2. Influence of temperature and seed priming on dry weight of soybean seedlings and seedling vigour index II.

Temperature (ºC)	Seed priming						Mean
	Control	Hydropriming	GA_3 25 mg L^{-1}	GA_3 50 mg L^{-1}	GA_3 100 mg L^{-1}	GA_3 200 mg L^{-1}	
Dry weight of seedlings (g)							
25	0.80±0.009	0.81±0.009	0.82±0.017	0.84±0.025	0.86±0.018	0.83±0.009	0.83±0.014b
30	0.83±0.017	0.85±0.013	0.84±0.023	0.87±0.012	0.88±0.023	0.86±0.013	0.85±0.017a
35	0.72±0.023	0.74±0.020	0.75±0.017	0.78±0.009	0.79±0.008	0.77±0.009	0.76±0.014c
40	0.54±0.021	0.59±0.019	0.57±0.007	0.61±0.021	0.64±0.019	0.60±0.042	0.59±0.021d
Mean	0.72±0.017c	0.75±0.015bc	0.74±0.016bc	0.77±0.016ab	0.79±0.017a	0.76±0.018ab	
Seedling vigour index II							
25	7.46±0.063	7.63±0.098	7.83±0.174	8.02±0.225	8.30±0.183	7.85±0.101	7.85±0.140b
30	7.83±0.122	8.10±0.121	8.03±0.222	8.38±0.161	8.58±0.212	8.23±0.135	8.19±0.162a
35	6.61±0.263	6.96±0.166	7.03±0.186	7.36±0.089	7.54±0.110	7.23±0.070	7.12±0.147c
40	2.67±0.085	2.79±0.130	2.27±0.112	2.52±0.128	3.04±0.153	2.44±0.208	2.62±0.136d
Mean	6.14±0.133d	6.37±0.128bcd	6.29±0.173cd	6.57±0.150b	6.86±0.164a	6.44±0.128bc	

Data are represented as pooled mean (±SE), n=4. Means with same alphabets within a row are not significantly different from each other at $P \leq 0.05$ (DMRT). Lower case letters indicate the mean separation of main effects.

Seedling vigour index I and II

The seedling vigour index (I and II) exhibited a significant increase at 30 °C compared to 25 °C, 35 °C and 40 °C (Fig. 1a and Table 2). These indices decreased eventually as temperatures exceeded 30 °C, reaching their lowest values at 40 °C. Seed priming with GA_3 100 mg L^{-1} resulted in significantly higher vigour indices compared to other priming treatments. In particular, seed priming with GA_3 100 mg L^{-1} showed 21.1% and 14.2% increase in seedling vigour index I & 8.7% and 5.6% in seedling vigour index II as compared to control and hydropriming, respectively. An interaction effect between temperatures and seed priming was observed, with the highest seedling vigour index I recorded at 30 °C when seeds were primed with GA_3 100 mg L^{-1}, which remained statistically equivalent to GA_3 50 and 200 mg L^{-1}.

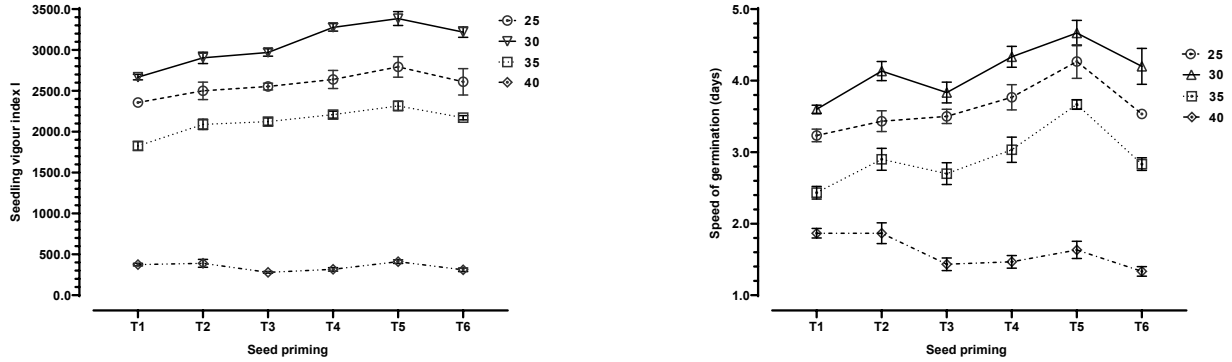

Figure 1. Seedling vigour index I (A) and speed of germination (B) under various temperatures and seed priming treatments. Seed priming treatments include control (T1), hydropriming (T2), GA_3 25 mg L^{-1} (T3), GA_3 50 mg L^{-1} (T4), GA_3 100 mg L^{-1} (T5) and GA_3 200 mg L^{-1} (T6). The values represent the pooled mean (±S.E.), which reflect the average values of each factor across four replicates, repeated twice.

Speed of germination

At 30 °C, the speed of germination was significantly faster compared to 25 °C, 35 °C and 40 °C (Fig. 1b), with a gradual decline in speed observed as temperatures increased beyond 30 °C, reaching the slowest germination rate at 40 °C. At 30 °C, speed of germination was 4.1 seeds day^{-1} that reduced to 1.6 seeds day^{-1} at 40 °C. Seed priming with GA_3 100 mg L^{-1} resulted in significantly faster germination compared to other priming treatments. Specifically, GA_3 100 mg L^{-1} showed a 21.8% and 11.0% increase in germination speed over control and hydropriming, respectively. An interaction effect between temperatures and seed priming was witnessed, indicating a higher germination speed at 30 °C when seeds were primed with GA_3 100 mg L^{-1}, but was statistically comparable to GA_3 50 & 200 mg L^{-1} and GA_3 100 mg L^{-1} at 25 °C.

Electrical conductivity

At 40 °C, the electrical conductivity (EC) of seeds demonstrated significant increase compared to 25 °C, 30 °C and 35 °C (Fig. 2a), showing a clear relationship between temperature elevation and higher EC levels. Hydroprimed seeds exhibited significantly higher EC levels compared to other seed priming treatments, while seeds primed with GA_3 100 mg L^{-1} displayed the lowest EC levels. Non-significant interaction was observed between temperatures and seed priming.

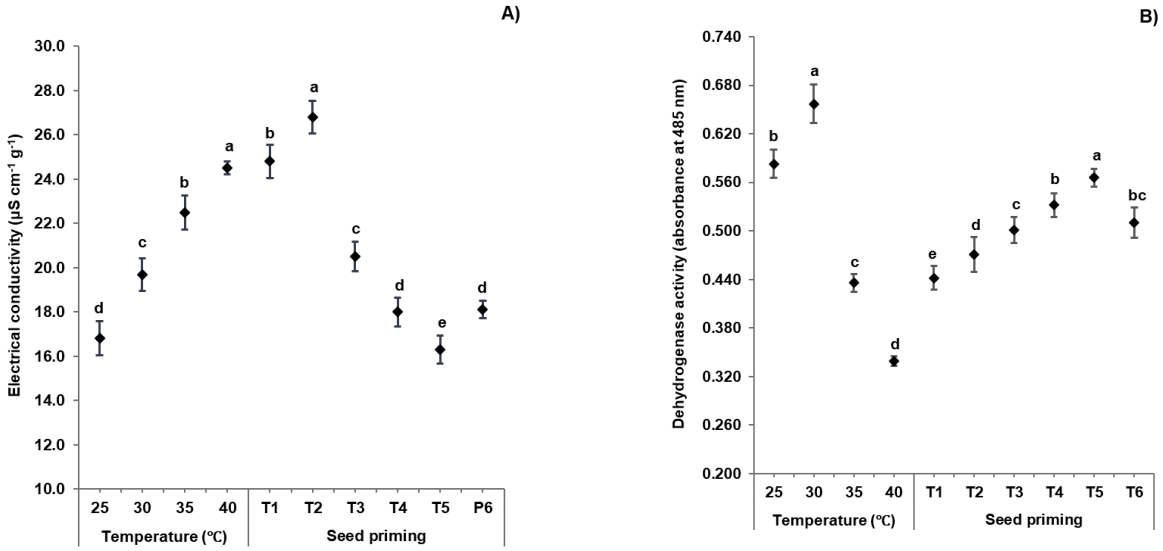

Figure 2. Electrical conductivity (A) and dehydrogenase activity (B) of seeds under various temperatures and seed priming treatments. Seed priming treatments include control (T1), hydropriming (T2), GA_3 25 mg L^{-1} (T3), GA_3 50 mg L^{-1} (T4), GA_3 100 mg L^{-1} (T5) and GA_3 200 mg L^{-1} (T6). The values represent the pooled mean (±S.E.), which reflect the average values of each factor across four replicates, repeated twice. Different letters represent significant differences between values from each other at $P \leq 0.05$ (DMRT).

Dehydrogenase activity

The enzymatic activity of dehydrogenase showed a significant increase at 30 °C compared to 25 °C, 35 °C and 40 °C (Fig. 2b). Priming seeds with GA_3 100 mg L^{-1} resulted in significantly higher dehydrogenase activity compared to control, hydropriming and GA_3 25, 50 & 200 mg L^{-1}. Seed priming with GA_3 100 mg L^{-1} exhibited 20.8 & 17.3% increase in dehydrogenase activity compared to control and hydropriming, respectively. The interaction effect between temperatures and seed priming were found to be non-significant.

Percentage of stained seeds

There was a significant increase in the percentage of stained seeds at 25 °C as compared to 30 °C, 35 °C and 40 °C (Fig. 3). Seeds treated with GA_3 100 mg L^{-1} exhibited significantly higher percentage of stained seeds compared to control, hydropriming and those treated with GA_3 25, 50 & 200 mg L^{-1}. There was non-significant interaction observed between temperatures and seed priming.

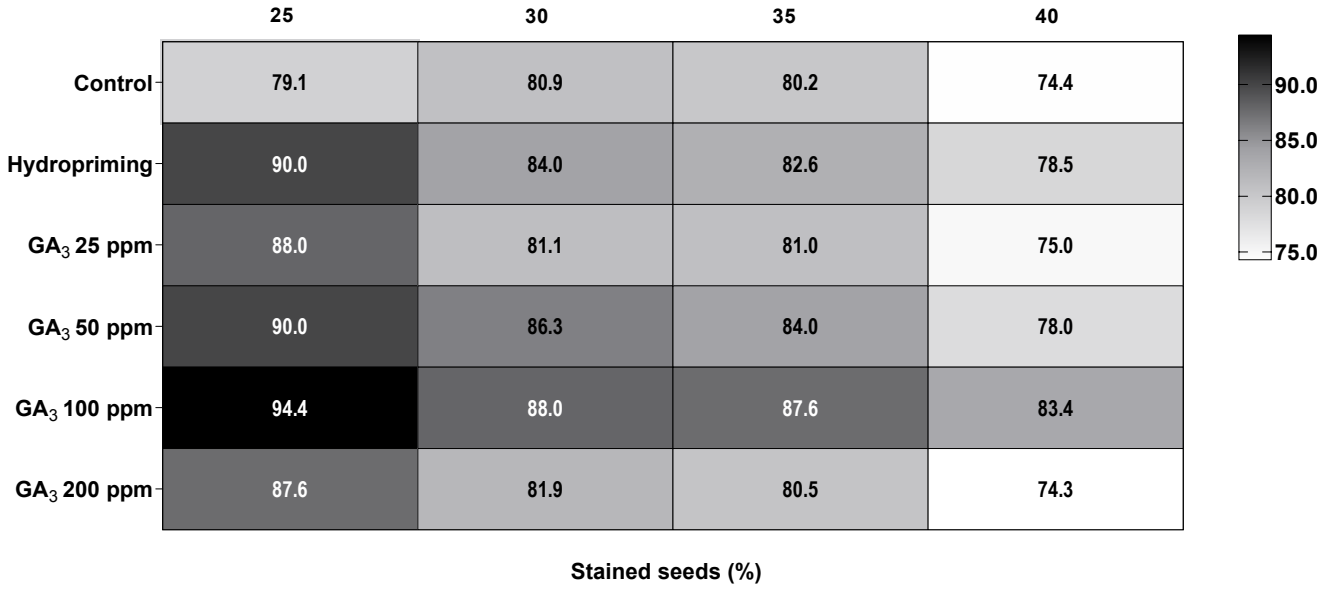

Figure 3. Heat map summarizing the effect of temperatures and seed priming on percentage of stained seeds. Results are visualized using a double gradient scale, with black indicating maximum (90.0) and light grey minimum values (75.0).

Discussion

The higher germination percentage observed at 30 °C could be attributed to the optimal temperature range for soybean seeds, accelerated metabolic activity, shortened germination time by facilitating enhanced water uptake which collectively created favourable conditions for enzymatic activity and rapid seedling emergence (Zhou et al., 2019). The decline in germination percentage with temperature exceeding 30 °C may be due to heat stress-induced damage to seed tissues and inhibition of enzymatic activity crucial for germination processes. Additionally, higher temperatures can aggravate water stress conditions, impeding water uptake by seeds and adversely affecting germination (Sehgal et al., 2018). Higher germination percentage in GA_3 100 mg L^{-1} primed seeds could be due to the activation of hydrolysis enzymes, particularly α-amylase, which catalyses the breakdown of starch into simpler sugars, providing essential energy for embryo development and expediting seed germination (Jassal & Singh, 2018). Similar results were also obtained by Toklu (2015), where GA_3 100 mg L^{-1} priming was found to enhance germination in lentil, potentially through increased cell division and hormonal balance.

Higher total seedling length observed at 30 °C could be due to the increased enzymatic activity, faster metabolic processes, increased cell division and elongation which contributed to enhancement in root and shoot length. Begum et al. (2022) similarly reported that temperatures ranging from 25-32 °C enhanced physiological processes, leading to increased cellular functions and overall seedling growth. Priming seeds with 100 mg L^{-1} GA_3 enhanced total seedling length by fostering enzymatic activity associated with cell wall elongation. and it might also trigger specific genes involved in growth regulation, leading to accelerated root and shoot development, consequently promoting overall seedling growth (Noor et al., 2017). Similar results were obtained by Khairul et al. (2015), who found that chickpea seed priming with 225 mg L^{-1} GA_3 led to improved emergence and seedling length. At 30 °C, seedlings exhibited their maximum dry weight, attributed to the optimum temperature enhancing the respiratory rate in seedlings, leading to higher energy consumption and accelerated growth rates (Alsajri et al., 2020a). The dry weight of seedlings was recorded higher in seed priming with 100 mg L^{-1} GA_3 which might be due to high seedling vigour and increased root & shoot length. Likewise, Shariatmadari et al. (2017) in chickpea observed that hormonal priming with 150 mg L^{-1} GA_3 increased dry weight of seedlings and plant vigour.

The speed of germination was notably faster at 30 °C likely due to the activation of specific enzymes and metabolic pathways within the optimal temperature range of 25-31 °C (Sita et al., 2017). This activation facilitates the rapid breakdown of stored reserves, leading to a faster softening and rupture of the seed coat. Adetunji et al. (2021) reported that exposure of seedlings to temperatures ranging from 37-43 °C resulted in oxidative stress, impairing seed viability and ultimately slowing down the germination process. Higher speed of germination obtained in seed priming with 100 mg L^{-1} GA_3 could be attributed to the involvement of gibberellins in breaking seed dormancy, leading to earlier and more uniform germination (Reed et al., 2022). Moreover, GA_3 seed priming may have enhanced seed water absorption and consequently initiates the germination at a faster pace (Gnawali & Subedi, 2021). Rehman et al. (2021) also corroborated that seed priming with 150 mg L^{-1} GA_3 accelerated radicle emergence with quicker and more synchronized soybean germination.

Assessing seedling vigour indices is crucial for observing initial growth and predicting the field performance of soybean seedlings. Higher seedling vigour index I and II observed at 30 °C might be due to the fact that seedling vigour index I, which considers germination percentage and total seedling length, and seedling vigour index II, which incorporates germination percentage and seedling dry weight, showed superior performance at this temperature. Consequently, these parameters contributed to enhanced seedling vigour indices under 30 °C. These findings are in conformity with Cirka et al. (2021), who reported that soybean seedlings exhibited increased vigour when grown within a temperature range of 20-28 ±2 °C. High temperatures reduced seedling vigour indices as a result of suboptimal germination, decreased seedling length and a decline in dry matter accumulation. Likewise, Alsajri et al. (2022b) also noticed diminished seedling vigour indices at high temperatures ranging between 33-38 ±2 °C in soybean. Similarly, higher seedling vigour indices observed with seed priming of 100 mg L^{-1} GA_3 might be due to the higher germination percentage, total seedling length and seedling dry weight associated with this treatment. Similar results were reported by Pradhan et al. (2022), who witnessed higher seed vigour indices with seed priming of 50 mg L^{-1} GA_3 in cowpea.

EC plays a vital role in detecting seed damage and assessing the effectiveness of seed treatments. Higher EC values observed at 40 °C might be due to the breakdown of cellular membranes in seeds, greater solute leakage and ion release leading to higher solute dissolution (Choudhury & Bordolui, 2023). Similarly, Kaur et al. (2023) reported that temperatures exceeding 35±3 °C increased the permeability of seed coat that facilitated the easier diffusion of ions and solutes into the solution, leading to elevated EC levels. Hydropriming led to a significant increase in EC values that might be due to softening of seed coat, cellular integrity loss which facilitated diffusion of ions and solutes from both the seed coat and embryonic tissues into the surrounding solution. These results align with those of Shukla et al. (2018), who observed elevated EC in mungbean seeds attributed to increased ion leaching from regions of higher concentration within the seed to regions of lower concentration in the surrounding water. Seeds primed with 100 mg L^{-1} GA_3 showed the lowest EC possibly due to less damage to the plasma membrane, increase in soluble proteins and improved protein binding within the membranes leading to enhanced membrane rigidity. These results are in conformity with findings of Lamichaney et al. (2018), who reported reduced EC in chickpea seeds primed with 50 mg L^{-1} GA_3 due to higher membrane intactness with minimal leakage of electrolytes.

Seed dehydrogenase activity serves as a valuable indicator for assessing seed viability, germination potential and metabolic status of cells. Higher dehydrogenase activity at 30 °C may be due to its correlation with the germination process, as ideal temperature for seed germination initiates metabolic functions (Huang et al., 2021), leading to enhanced DA in seeds. However, exposure of soybean seeds to temperatures beyond 35 °C resulted in the denaturation or inactivation of enzymes, particularly dehydrogenases and reducing their activity. These results align with findings of Mitra et al. (2021), who noticed decrease in dehydrogenase activity in pea seeds at high temperatures of 36-40 °C which could be due to disruption of enzymatic processes involved in metabolic pathways, influencing overall seed viability and subsequent germination. Seeds primed with 100 mg L^{-1} GA_3 recorded higher dehydrogenase activity likely due to enhanced synthesis and activation of enzymes crucial for seed metabolism. Likewise, MN et al. (2021) observed improved enzymatic activities associated with cellular respiration, leading to increased dehydrogenase enzyme activity in cowpea seeds treated with 100 mg L^{-1} GA_3 during priming.

The temperature of 25 °C optimally enhance metabolic activity and promote the conversion of TTC to formazan in viable cells, leading to a greater proportion of stained seeds without adverse effects on enzyme denaturation. These results align with the observations of Kari et al. (2022), who reported similar outcomes regarding positive impact of a temperature of 25 °C on seed viability and metabolic processes. However, 40 °C temperature negatively impacted the metabolic processes inside seeds that decreased the activity of dehydrogenase enzymes, hindering the conversion of TTC to formazan. Therefore, there was a reduction in staining intensity or even a total lack of staining. Likewise, Xing et al. (2023) reported the negative effect of high temperatures above 35 °C on the seed staining due to denaturing of enzymes and altering cellular processes in soybean. Priming seeds with 100 pm GA_3 might have increased the respiration rate and enzymatic activities within the embryo cells, causing an increase in DA and consequently improving the staining of seeds. These findings are in agreement with those of Kumar et al. (2014), which reported higher proportion of stained seeds through the priming of guar seeds with 50 mg L^{-1} of GA_3.

Conclusions

The study investigated the effectiveness of GA_3 seed priming in soybean to improve germination and crop establishment in environments with higher temperatures. The findings revealed that temperature of 30 ºC enhanced the germination percentage, speed of germination, total seedling length, dry weight of seedlings, seedling vigour indices and dehydrogenase activity. Among different seed priming treatments, seed priming with 100 mg L^{-1} GA_3 was the most effective treatment in improving the physiological and biochemical parameters of soybean. Treating seeds with 100 mg L^{-1} GA_3 demonstrated lower EC, higher percentage of stained seeds compared to other seed priming treatments at various temperatures.

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Statement about use of generative AI:

The author(s) confirm that no generative AI or AI-assisted technologies were used in the writing or content creation of this manuscript. The work was entirely prepared and reviewed by the author(s). The author(s) employed OpenAI. (2024), ChatGPT (April 2024 version) [Large language model] in order to translate the title, Abstract and Keywords form English to Spanish. Following their use, the author(s) assumed full responsibility for the publication's content and reviewed and edited it as necessary

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