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Abscisic, gibberellic, and salicylic acids effects on germination indices of corn under salinity and drought stresses

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ABSTRACT

The expression of genes that control germination-related processes in corn (*Zea mays* L.) is influenced by environmental factors. Germination of seeds may be facilitated by hormonal priming. The purpose of this investigation was to quantify the effects of different germination temperatures [(5, 10, 15, 20, 25, 30, 35, and 40°C), NaCl-induced stress (0, −0.4, −0.8, and −1.2 MPa), and priming solutions (control, hydropriming, abscisic acid (ABA), gibberellic acid (GA), and salicylic acid (SA)] (Experiment 1). Effects of germination temperatures, PEG 6000-induced stress (0, −0.4, −0.8, and −1.2 MPa), and priming solutions were also evaluated separately (Experiment 2). In both cases, a completely randomized design with four replications was used. Increasing temperatures from 5 to 25°C gradually improved germination percentage and rate, whereas temperatures > 25°C decreased these indices. After imposing drought (PEG 6000-induced stress) or salinity (NaCl-induced stress) treatments, hormonal priming caused germination to occur at a lower base temperature, compared with the non-priming treatment. However, the effect of hormonal priming was dependent on temperature. At sub-optimal temperatures (< 25°C), the highest germination percentage and rate were recorded after GA priming. At above-optimal temperatures (> 25°C), ABA priming resulted in the highest germination percentage and rate. Moreover, hydrothermal time constant decreased in hormone-treated seeds. Based on coefficient of determination (R^2) and root mean square error (*RMSE*), a dent-like model predicted cardinal temperatures more accurately than a beta model did. Generally, GA-, SA-, and ABA-priming were recommended under sub-optimal, optimal, and above-optimal temperatures, respectively.

Introduction

Corn (*Zea mays* L.) is one of the most important crops grown in semi-arid climates (Thapa et al. 2018), where various abiotic stresses occur during the vegetative and reproductive stages (Jia et al. 2020). Despite the relative adaptation of corn to drought conditions (Potop 2011), temperature stress

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can negatively affect seedling emergence and establishment (Zahedifar and Zohrabi 2016).

Radicle protrusion, a biochemical process completely dependent on seed reserves, is more related to cell elongation than to cell division (Sánchez-Linares et al. 2012). Accelerated allocation of nutrients to the meristem makes it possible for the autotrophic seed to become a heterotrophic seedling (Soltani, Gholipoor, and Zeinali 2006). Further development of seedling tissues and gradual initiation of nutrient absorption are considered the beginning of seedling establishment (Müller et al. 2019; Tavakkol Afshari and Seyyedi 2020).

Besides food reserves, seed germination is directly controlled by environmental signals, especially temperature and water potential (Seyyedi, Tavakkol Afshari, and Daneshmandi 2018; Zerpa-Catanho et al. 2019). Restricting water absorption during germination can adversely affect germination percentage, rate, and uniformity (Yan 2015), which ultimately results in reduced seedling establishment (Liu et al. 2015; Xiong et al. 2018). The induction of oxidative stress is another consequence of water restriction, which can disrupt germination (Ahammed et al. 2018).

The successful establishment of normal seedlings, especially under adverse environmental conditions, is directly dependent on the balanced synthesis of plant hormones, such as abscisic acid (ABA), gibberellic acid (GA), and salicylic acid (SA) (Gharbi et al. 2018; Shatpathy et al. 2018). These phytohormones, considered anti-stress compounds, are endogenously synthesized in plants to activate the defense functions (Mohaddes Ardebili et al. 2019) and to mitigate lipid peroxidation (Nazari et al. 2020). However, intensifying environmental stresses may reduce the efficiency of defense mechanisms during cell division-related processes, such as protein synthesis, and eventually lead to germination failure or the emergence of abnormal seedlings (Seyyedi et al. 2015).

To alleviate the effects of environmental stresses on germination, exogenous application of plant hormones is considered one of the most widely used techniques (Eisvand et al. 2010; Hajiabbasi et al. 2020). Phytohormonal priming with ABA, GA (Mohaddes Ardebili et al. 2019), and SA (Nazari et al. 2020) can accelerate cell division and differentiation of the embryonic tissue by reducing ionic toxicity and stabilizing membrane integrity.

Modeling has been recognized as a useful technique to evaluate the effects of stressful conditions on seed germination and seedling establishment (Tatari et al. 2020). In this regard, the modeling patterns associated with the germination process are mainly analyzed on the basis of environmental parameters, especially temperature and water potential. For instance, the hydrothermal time model can accurately estimate seed germination patterns across suboptimal temperatures and reduced water potential (Alvarado and Bradford 2002).

Corn seed germination in response to phytohormones has not been precisely quantified, especially under stressful conditions. Therefore, the current study was aimed at assessing the germination indices in response to different temperatures and water potentials. Although drought and salinity can similarly affect water uptake in germination media, salinity stress may have more severe effects on seedling growth through ion accumulation (Llanes et al. 2016). Accordingly, similar water potentials resulting from salinity (Experiment 1) and drought (Experiment 2) stresses were studied to distinguish ion toxicity. In addition, seed germination in response to phytohormones was quantified under stressful conditions. Thermal and hydrothermal time concepts for predicting cardinal temperatures and finding the best hormonal treatments were also studied.

Materials and methods

Plant materials

The seeds of corn hybrid SC 704 were obtained from Khorasan Razavi Agricultural and Natural Resources Research Center, Mashhad, Iran. The seeds, produced in 2018, had a 1000-seed weight of 248.72 g, with an initial water content of 9.89% and germination of 98%.

Prior to initiating the tests, all equipment (including Petri dishes, filter papers, and Erlenmeyer flasks) was autoclaved under 1.2 bar pressure at 121°C for 20 min. Corn seeds were surface sterilized with 2.5% sodium hypochlorite for 60 s and rinsed several times with distilled water. The washed seeds were placed on an absorbent paper and kept under laboratory conditions (23–26°C) for 24 h. At this time, the moisture content of the seed lot, measured according to ISTA (2011), was equivalent to the initial content.

Experimental layout

Two separate experiments were conducted based on a factorial, completely randomized design with four replicates. The experiments were performed at Faculty of Agriculture, Ferdowsi University of Mashhad, Mashhad, Iran in 2019.

In the first experiment, eight different germination temperatures (5, 10, 15, 20, 25, 30, 35, and 40°C), four salinity levels (0, −0.4, −0.8, and −1.2 MPa), and five priming solutions (control, hydro-priming, GA, ABA, and SA) were applied. Similarly, effects of different germination temperatures (5, 10, 15, 20, 25, 30, 35, and 40°C), drought stress levels (0, −0.4, −0.8, and −1.2 MPa), and priming solutions (control, hydro-priming, GA, ABA, and SA) were evaluated in the second experiment.

Preparing solutions and performing seed priming

To perform seed priming, a solution concentration of 0.5 mM of each of GA, ABA, and SA was prepared. Seed weight to solution volume ratio was 1:5 (g/ml) (Farooq et al. 2008). Erlenmeyer flasks were sealed with aluminum foil and kept in an incubator at 20°C for 12 h. During the priming period, the solutions were slowly swirled several times to ensure proper aeration (Seyyedi et al. 2015). Similarly, distilled water was used for hydro-priming treatment. As previously stated, the primed seeds were washed with distilled water and kept under the laboratory conditions (23–26°C for 24 h).

Imposing drought and salinity stresses

Depending on the target germination temperatures, amount of sodium chloride (g/L) needed to induce salinity stress was calculated according to the Van't Hoff equation. Similarly, polyethylene glycol 6000 (PEG 6000) solutions (g/L) were prepared according to Michel and Kaufmann (1973) to set drought levels.

Germination-related traits

To perform the germination test, four replicates of 25 seeds per treatment were placed in 15-cm Petri dishes lined with Whatman filter paper. The seeds were germinated at 25°C in a germinator for 7 d (ISTA 2011). A seed was considered to have germinated when the radicle length was ≥ 2 mm.

Germination rate (GR) was calculated according to the following equation:

$$GR = \Sigma(n_1/t_1 + n_2/t_2 + \ldots n_i/t_i) \tag{1}$$

where n is the number of newly germinated seeds each day, and t is the number of days from the beginning of the germination test.

Cardinal temperatures

Cardinal temperatures were predicted by the regression relationship between temperature and germination rate. In this regard, X and Y axes were regarded as independent (temperature) and dependent (the required time to reach 50% germination) variables, respectively. Beta and dent-like models were used to determine cardinal temperatures. Determining the best model was based on root mean square error (RMSE, equation 2) and the coefficient of determination (R^2, Eq. 3):

$$RMSE = \sqrt{\left(\frac{1}{n}\right)(\text{Yobs} - \text{Ypred})^2} \qquad (2)$$

where Yobs = observed values, Ypred = predicted values, and n = the number of samples.

$$R^2 = SSR/SST \qquad (3)$$

where SSR = the sum of squares for regression and SST is the total sum of squares.

Hydrothermal time model

To predict the germination time under different temperatures and water potentials, four parameters are needed (Parmoon et al. 2015): base temperature (T_b), base water potential (ψ_b), hydrothermal time constant (θ_{HT}), and standard deviation (σ). These parameters can be estimated based on probit analysis (Alvarado and Bradford 2002), as follows:

$$Probit\ (g) = \ \{[(\psi - \theta_{HT})/(T - \ T_b)t_g] \ - \psi_b(50)\}/\sigma_{\psi_b}$$

where probit (g) is the germination in probit units, tg is the actual time to germination of fraction g, and σψb is standard deviation of base water potential.

Statistical analyses

All experimental data were subjected to analysis of variance using SAS 9.3 software (SAS 2011). Before analysis of variance, the normality of the data was assessed, using the Kolmogorov–Smirnov test and the Box-Cox transformation for data having zero values. The least significant difference (LSD, 5% level) was used to declare statistical differences between treatment means.

Results and discussion

Experiment 1

Variation attributable to temperature, salinity, and priming was significant for germination percentage and germination rate (Table 1). Also, the interaction between temperature and salinity, and that between temperature and priming were significant for the above-mentioned two traits (Table 1).

Table 1. Analyses of variance showing the effects of temperature, salinity, and priming on percentage germination and germination rate in corn.

Source of variation	df	Germination percentage	Germination rate (d^{-1})
Temperature (T)	7	120,236.8 **	26,644.0 **
Salinity (S)	3	32,833.76 **	255.6 **
Priming (P)	4	343.7 **	100.9 *
$T \times S$	21	3589.3 **	209.0 **
$T \times P$	28	182.4 *	191.8 **
$S \times P$	12	91.9 NS	1.9 NS
$T \times S \times P$	84	74.8 NS	1.1 NS
Error	480	26,644.0	0.7
CV (%)	-	14.29	17.72

*, ** Significant at $P \leq 0.05$ and $P \leq 0.01$, respectively. NS: Non-significant.

Table 2. Interaction effect of temperature and salinity on the percentage and rate of germination in corn.

Temperature (°C)	Salinity (MPa)	Germination percentage	Germination rate (d^{-1})
5	0.0	0.00	0.00
	−0.4	0.00	0.00
	−0.8	0.00	0.00
	−1.2	0.00	0.00
10	0.0	14.00	0.54
	−0.4	2.00	0.09
	−0.8	0.00	0.00
	−1.2	0.00	0.00
15	0.0	83.80	4.71
	−0.4	67.80	3.58
	−0.8	29.20	1.29
	−1.2	3.40	0.13
20	0.0	93.20	7.85
	−0.4	90.20	6.66
	−0.8	78.60	5.05
	−1.2	36.40	1.91
25	0.0	97.60	11.42
	−0.4	95.20	10.51
	−0.8	91.20	8.80
	−1.2	67.60	5.33
30	0.0	94.60	9.03
	−0.4	92.60	8.99
	−0.8	83.20	8.51
	−1.2	58.60	5.33
35	0.0	91.20	6.59
	−0.4	79.80	7.75
	−0.8	67.60	7.01
	−1.2	46.40	4.86
40	0.0	0.00	0.00
	−0.4	0.00	0.00
	−0.8	0.00	0.00
	−1.2	0.00	0.00
LSD (0.05)		4.629	0.531

Increasing temperatures from 5 to 25°C gradually improved germination percentage and rate, whereas higher temperatures (> 25°C) decreased these

indices (Table 2). The best result was obtained with the application of 0.0 Mpa salinity level at 25°C.

At each level of salinity stress, the germination process completely failed at 5 and 40°C. Therefore, it seems that in the presence or absence of salinity stress, germination at 25°C occurs optimally. However, as the temperature decreases or increases from the optimum, temperature changes may have more negative effects on germination percentage and rate.

In the range of 10 to 35°C, increasing salinity stress significantly reduced germination percentage and rate. The highest germination percentage (97.60%) and rate (11.42 d^{-1}) were obtained when the salt-untreated seeds were stored at 25°C (Table 2). At the same temperature, applying −1.2 Mpa salinity level reduced these indices by 30.7 and 53.3%, respectively (Table 2). Although corn is known to be a relatively adaptable plant to stressful conditions (Boyacıoğlu and Uyanöz 2014), the results indicated the relative sensitivity of corn to salinity stress, especially during the early stages of growth.

In the temperature range of 10 to 35°C, the lowest percentage and rate of germination were observed in non-primed seeds (Table 3). Under these conditions, hormonal treatments had a positive effect on germination parameters; however, the effect of hormonal priming was dependent on temperature (Table 3). At sub-optimal temperatures (< 25°C), the highest germination percentage and rate were recorded after GA priming. At 25°C, the highest values were obtained with SA priming. Moreover, at above-optimal temperatures (> 25°C), ABA priming produced the best results (Table 3).

The hormone-based defense responses are rapidly induced in stress-exposed seedlings because germination and early establishment are the most sensitive stages to salinity (Shatpathy et al. 2018). The interactions between temperature and priming suggested that a certain hormone was induced in the plant depending on temperature, which might stimulate various defense mechanisms against salinity stress.

The determination of cardinal temperatures under different osmotic potentials was performed by beta and dent-like functions (Table 4). From the results, cardinal temperatures were predicted more accurately by the dent-like model (R^2: 0.97, *RMSE*: 0.26) than by the beta model (R^2: 0.93, *RMSE*: 0.43) (Table 4). Under normal conditions (without salinity stress), non-primed seeds showed the base temperature (T_b) of 9.51°C using dent-like function. Also, estimates of lower limit of optimum temperature (T_{o1}), upper limit of optimum temperature (T_{o2}), and ceiling temperature (T_c) were 24.12, 35.10, and 44.62°C, respectively (Table 4). Concurrent with the increase in salinity stress, base temperature (T_b value) significantly increased (Table 4). For example, when unprimed seeds were tested by the dent-like model, a change in salinity level from zero to −1.2 MPa increased T_b up to 14.99°C. This could be attributed to the disruption of biochemical signals that induce mobilization of reserves and germination metabolism at lower

Table 3. Interaction effects of temperature and priming on the percentage and rate of germination in corn.

Temperature (°C)	Priming	Germination percentage	Germination rate (d^{-1})
5	Control (no priming)	0.00	0.00
	Hydropriming	0.00	0.00
	Abscisic acid	0.00	0.00
	Gibberellic acid	0.00	0.00
	Salicylic acid	0.00	0.00
10	Control (no priming)	0.00	0.02
	Hydropriming	4.25	0.14
	Abscisic acid	4.25	0.17
	Gibberellic acid	8.00	0.29
	Salicylic acid	3.50	0.17
15	Control (no priming)	44.00	2.20
	Hydropriming	45.50	2.49
	Abscisic acid	46.25	2.37
	Gibberellic acid	47.75	2.63
	Salicylic acid	46.75	2.46
20	Control (no priming)	67.50	4.61
	Hydropriming	75.50	5.38
	Abscisic acid	75.75	5.35
	Gibberellic acid	79.00	5.88
	Salicylic acid	75.25	5.59
25	Control (no priming)	85.50	8.57
	Hydropriming	88.25	9.24
	Abscisic acid	87.25	9.23
	Gibberellic acid	88.75	8.62
	Salicylic acid	89.75	9.41
30	Control (no priming)	79.25	8.14
	Hydropriming	81.25	7.73
	Abscisic acid	87.50	8.53
	Gibberellic acid	82.75	7.68
	Salicylic acid	80.50	7.76
35	Control (no priming)	70.75	7.20
	Hydropriming	71.00	6.44
	Abscisic acid	76.50	6.92
	Gibberellic acid	72.75	6.37
	Salicylic acid	65.25	5.83
40	Control (no priming)	0.00	0.00
	Hydropriming	0.00	0.00
	Abscisic acid	0.00	0.00
	Gibberellic acid	0.00	0.00
	Salicylic acid	0.00	0.00
LSD (0.05)		5.176	0.594

temperatures (T_b). In fact, following the reduced water potential and impaired seed vigor, the higher T_b might be required to initiate the germination process.

Although T_b in non-primed seeds increased considerably with increasing salinity levels, priming treatments, especially hormonal priming, attenuated the increase in T_b (Table 4). For instance, after imposing -0.4 MPa salinity on non-primed seed, T_b, predicted by dent-like model, was 10.41°C. In contrast, with the application of ABA and GA, T_b was 9.90 and 8.51°C, respectively (Table 4). On average, cardinal temperatures for control, ABA,

Table 4. The estimated parameters based on regression models affected by salinity and priming. Values were estimated based on 50% germination of corn seed.

Salinity (MPa)	Priming	Function	T_b [a]	T_o [b]	T_{o1} [c]	T_{o2} [d]	T_c [e]	R^2 [f]	RMSE [g]
			span Cardinal temperatures (°C)						
0	Control (no priming)	Beta	9.99	34.99	-	-	42.75	0.97	0.23
		Dent-like	9.51	-	24.12	35.10	44.62	0.99	0.24
	Hydropriming	Beta	4.78	30.36	-	-	44.47	0.96	0.95
		Dent-like	8.97	-	28.08	35.05	40.02	0.99	0.16
	Abscisic acid	Beta	3.84	35.08	-	-	44.96	0.94	0.71
		Dent-like	9.23	-	31.20	35.63	44.95	0.99	0.34
	Gibberellic acid	Beta	4.17	35.06	-	-	44.98	0.97	0.43
		Dent-like	8.26	-	28.16	38.50	45.06	0.99	0.26
	Salicylic acid	Beta	4.20	35.15	-	-	44.99	0.94	0.66
		Dent-like	9.37	-	27.58	35.30	44.47	0.98	0.43
−0.4	Control (no priming)	Beta	11.51	34.09	-	-	43.17	0.98	0.28
		Dent-like	10.41	-	25.26	34.97	44.60	0.99	0.23
	Hydropriming	Beta	10.03	30.16	-	-	44.97	0.97	0.52
		Dent-like	10.47	-	28.63	33.84	41.91	0.98	0.24
	Abscisic acid	Beta	10.06	30.23	-	-	44.99	0.95	0.66
		Dent-like	9.90	-	28.40	32.45	41.53	0.99	0.26
	Gibberellic acid	Beta	4.34	35.06	-	-	44.99	0.85	0.76
		Dent-like	8.51	-	31.55	35.13	44.93	0.88	0.52
	Salicylic acid	Beta	10.07	30.32	-	-	44.98	0.97	0.22
		Dent-like	9.86	-	25.01	35.00	44.95	0.98	0.45
−0.8	Control (no priming)	Beta	13.87	30.12	-	-	36.23	0.97	0.20
		Dent-like	13.72	-	26.96	33.95	43.96	0.98	0.21
	Hydropriming	Beta	10.07	30.05	-	-	44.98	0.94	0.27
		Dent-like	13.11	-	34.58	34.91	44.98	0.98	0.18
	Abscisic acid	Beta	10.48	34.85	-	-	45.01	0.97	0.20
		Dent-like	12.6	-	26.52	34.74	43.63	0.99	0.13
	Gibberellic acid	Beta	11.49	34.96	-	-	44.92	0.96	0.31
		Dent-like	13.23	-	24.44	34.15	44.09	0.98	0.19
	Salicylic acid	Beta	11.31	34.93	-	-	44.93	0.94	0.38
		Dent-like	13.55	-	23.67	33.57	45.11	0.97	0.24
−1.2	Control (no priming)	Beta	15.10	30.02	-	-	44.99	0.89	0.24
		Dent-like	14.99	-	25.01	34.97	44.98	0.93	0.23
	Hydropriming	Beta	10.29	35.06	-	-	44.96	0.88	0.51
		Dent-like	14.47	-	28.86	35.81	42.03	0.92	0.43
	Abscisic acid	Beta	15.00	30.32	-	-	44.99	0.94	0.23
		Dent-like	16.90	-	26.47	34.41	44.67	0.99	0.10
	Gibberellic acid	Beta	10.06	30.08	-	-	44.96	0.88	0.44
		Dent-like	14.42	-	28.01	33.87	43.59	0.94	0.23
	Salicylic acid	Beta	10.13	30.17	-	-	44.96	0.82	0.36
		Dent-like	15.74	-	31.51	33.62	45.32	0.97	0.14
Average									
0			7.23	34.13	27.83	35.92	44.13	0.97	0.44
−0.4			9.52	31.97	27.77	34.28	44.10	0.95	0.41
−0.8			12.34	32.98	27.23	34.26	43.78	0.97	0.23
−1.2			13.71	31.13	27.97	34.54	44.55	0.92	0.29
	Control (no priming)		12.39	32.31	25.34	34.75	43.16	0.96	0.23
	Hydropriming		10.27	31.41	30.04	34.90	43.54	0.95	0.41
	Abscisic acid		11.00	32.62	28.15	34.31	44.34	0.97	0.33
	Gibberellic acid		9.31	33.79	28.04	35.41	44.69	0.93	0.39
	Salicylic acid		10.53	32.64	26.94	34.37	44.96	0.95	0.36
		Beta	9.54	32.55	-	-	44.31	0.93	0.43
		Dent-like	11.86	-	27.70	34.75	43.97	0.97	0.26

aBase temperature.
bOptimum temperature.

cLower limit of optimum temperature.
dUpper limit of optimum temperature.
eCeiling (maximum) temperature.
fCoefficient of determination.
gRoot mean square error.

GA, and SA treatments were found to be 12.39, 11.0, 9.31, and 10.53°C, respectively (Table 4). During the hormonal priming, the accumulation of secondary metabolites might improve germination function against salinity stress by balancing mobilization of reserves and regulating osmotic potential. As a result, the onset of germination mechanisms can be induced at a lower temperature (T_b).

Experiment 2

The interaction between temperature and drought as well as that between drought and priming had a significant effect on germination percentage and rate (Table 5). According to Figure 1, increased drought stress caused a significant decrease in germination percentage and rate. For example, at 20° C, imposing drought stress with −1.2 MPa reduced germination percentage more than six-fold (15.40%) compared with non-stress conditions (97.60%) (Figure 1). Hormonal priming alleviated these effects; for example, at the most severe drought level (−1.2 MPa), GA priming improved germination percentage and germination rate by 51.45% and 58.90%, respectively, over the non-primed seeds (Figure 2). For ABA priming, the respective values for the two traits were 29.24% and 41.10% (Figure 2). Similar to the salinity response, hormonal priming might accelerate cell division and differentiation by regulating osmotic balance and improving water uptake. These processes can mitigate the negative effects of drought stress on germination parameters.

When control, hydropriming, and SA treatments were applied under non-drought conditions, the dent-like function calculated cardinal temperatures more accurately than the beta function did (Table 6). Similar results were

Table 5. Analyses of variance showing the effects of temperature, drought, and priming on the percentage and rate of germination in corn.

Source of variation	df	Germination percentage	Germination rate (d^{-1})
Temperature (T)	7	104,285.9 **	1164.9 **
Drought (D)	3	76,499.5 **	10,989.0 **
Priming (P)	4	421. **	110.8 **
T × D	21	6914.6 **	104.1 **
T × P	28	64.0 NS	1.7 NS
D × P	12	184.1 *	128.1 **
T × D × P	84	93.3 NS	0.7 NS
Error	480	16,340.00	189.6
CV (%)		12.87	15.5

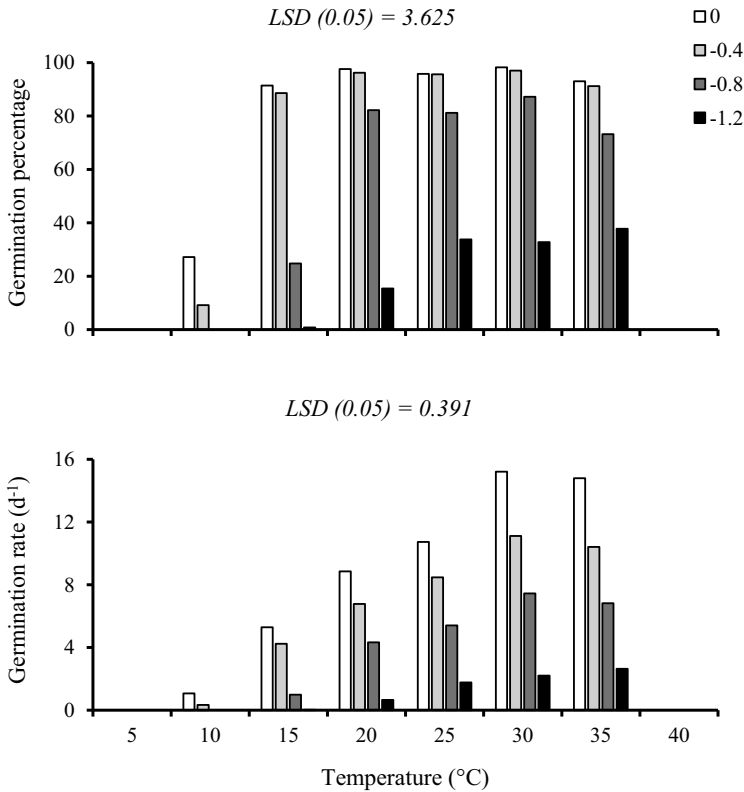*, **Significant at $P \leq 0.05$ and $P \leq 0.01$, respectively. NS: Non-significant.

Figure 1. Interaction effects of temperature and drought on the percentage and rate of germination in corn.

also observed in response to −0.4, −0.8, and −1.2 Mpa salinity levels (Table 6). As stated for salinity stress, hormone treatments were instrumental in alleviating the effects of drought stress on cardinal temperature. For instance, following −1.2 Mpa drought stress, T_b in un-primed treatment was 18.94°C with the dent-like model (Table 6); whereas with the application of ABA, GA, and SA treatments, the predicted T_b value was 14.98, 17.74 and 14.93°C, respectively (Table 6).

The ABA, GA, and SA priming reduced the negative effects of drought stress, compared with the control treatment, by increasing germination rate and decreasing T_b. Following a decrease in T_b, the physiological mechanisms associated with stress tolerance are likely to be activated more effectively. In this regard, increasing T_b along with reducing seed vigor has been reported (Soltani, Gholipoor, and Zeinali 2006). This justifies the exogenous application of plant hormones as an effective method.
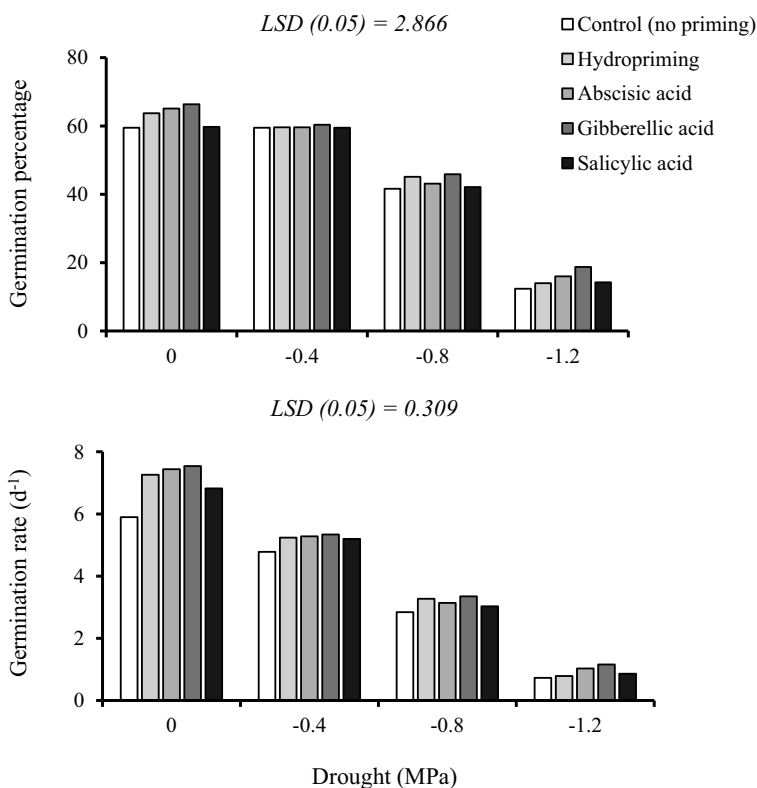
Figure 2. Interaction effects of drought and priming on the percentage and rate of germination in corn.

Hydrothermal time model

Based on hydrothermal time model, R^2 was 90% for the control treatment. For hydropriming, ABA, GA, and SA, R^2 was 99%, 96%, 98%, and 97%, respectively (Table 7). Similarly, T_b, affected by control, hydropriming, ABA, GA, and SA treatments, was 8.41, 7.83, 8.02, 5.62, and 8.01°C, respectively (Table 7).

After applying hormonal treatments, a considerable decrease in θ_{HT} was observed, compared with the control treatment (Table 7). These results suggested that hormonal priming increased germination rate. The lowest values of T_b and θ_{HT} were obtained with the application of GA and ABA priming, respectively (Table 7).

In general, the high R^2 and low *RMSE* represent enhanced accuracy of model output (Parmoon et al. 2015). When priming treatments were applied, hydrothermal time analysis accurately predicted the effects of temperature and water potential on germination capacity.

The considerable decrease in θ_{HT}, which is parallel to the increased germination rate, indicated the positive effects of hormonal priming on cell

Table 6. The estimated parameters based on regression models affected by drought and priming. Values were estimated based on 50% germination of corn seed.

Drought (MPa)	Priming	Function	T_b [a]	T_o [b]	T_{o1} [c]	T_{o2} [d]	T_c [e]	R^2 [f]	RMSE [g]
0	Control (no priming)	Beta	9.99	34.99	-	-	42.75	0.99	0.17
		Dent-like	9.04	-	26.16	35.23	44.44	0.99	0.15
	Hydropriming	Beta	4.88	30.05	-	-	44.92	0.94	0.89
		Dent-like	8.15	-	31.36	33.76	41.90	0.99	0.17
	Abscisic acid	Beta	4.88	30.16	-	-	44.79	0.92	0.86
		Dent-like	7.69	-	31.77	34.47	44.99	0.98	0.25
	Gibberellic acid	Beta	4.52	35.27	-	-	45.00	0.97	0.35
		Dent-like	6.43	-	31.32	34.77	45.00	0.99	0.18
	Salicylic acid	Beta	4.79	30.69	-	-	44.44	0.94	0.80
		Dent-like	8.75	-	31.15	33.79	41.81	0.99	0.18
−0.4	Control (no priming)	Beta	10.12	30.14	-	-	44.91	0.98	0.29
		Dent-like	8.05	-	29.49	35.00	44.40	0.98	0.22
	Hydropriming	Beta	4.87	30.25	-	-	44.99	0.94	0.54
		Dent-like	8.71	-	28.21	34.83	43.77	0.98	0.22
	Abscisic acid	Beta	3.73	35.06	-	-	44.97	0.95	0.32
		Dent-like	8.65	-	27.52	34.57	44.99	0.99	0.10
	Gibberellic acid	Beta	4.12	35.11	-	-	44.98	0.96	0.41
		Dent-like	7.52	-	31.19	34.05	41.16	0.99	0.14
	Salicylic acid	Beta	7.02	35.13	-	-	44.97	0.95	0.36
		Dent-like	8.44	-	30.39	34.67	44.99	0.99	0.12
−0.8	Control (no priming)	Beta	10.10	35.44	-	-	45.00	0.97	0.17
		Dent-like	11.94	-	27.45	35.03	42.62	0.98	0.17
	Hydropriming	Beta	9.99	31.11	-	-	44.98	0.80	0.60
		Dent-like	10.62	-	28.82	35.40	43.09	0.98	0.19
	Abscisic acid	Beta	10.48	35.57	-	-	44.97	0.95	0.21
		Dent-like	12.97	-	26.88	35.02	42.97	0.96	0.19
	Gibberellic acid	Beta	10.13	34.83	-	-	45.00	0.97	0.17
		Dent-like	11.62	-	29.40	34.46	42.89	0.95	0.13
	Salicylic acid	Beta	10.02	30.09	-	-	44.97	0.72	0.70
		Dent-like	10.30	-	30.01	35.62	45.15	0.76	0.55
−1.2	Control (no priming)	Beta	14.99	35.01	-	-	43.73	0.72	0.33
		Dent-like	18.94	-	26.45	35.24	44.50	0.73	0.32
	Hydropriming	Beta	15.02	30.35	-	-	44.99	0.90	0.09
		Dent-like	19.97	-	20.08	32.36	41.46	0.93	0.07
	Abscisic acid	Beta	15.06	35.48	-	-	44.99	0.95	0.11
		Dent-like	14.98	-	32.12	35.50	43.62	0.95	0.10
	Gibberellic acid	Beta	15.10	35.21	-	-	44.99	0.97	0.76
		Dent-like	17.74	-	27.03	35.47	44.79	0.98	0.05
	Salicylic acid	Beta	15.12	34.96	-	-	45.03	0.88	0.18
		Dent-like	14.93	-	30.14	33.32	44.48	0.90	0.12
Average									
0			6.91	32.23	30.35	34.40	44.00	0.97	0.40
−0.4			7.12	33.14	29.36	34.62	44.41	0.97	0.27
−0.8			10.82	33.41	28.51	35.11	44.16	0.90	0.31
−1.2			16.19	34.20	27.16	34.38	44.26	0.89	0.21
	Control (no priming)		11.65	33.90	27.39	35.13	44.04	0.92	0.23
	Hydropriming		10.28	30.44	27.12	34.09	43.76	0.93	0.35
	Abscisic acid		9.81	34.07	29.57	34.89	44.54	0.96	0.27
	Gibberellic acid		9.65	35.11	29.74	34.69	44.23	0.97	0.27
	Salicylic acid		9.92	32.72	30.42	34.35	44.48	0.89	0.38
		Beta	9.25	33.25	-	-	44.77	0.92	0.42
		Dent-like	11.27	-	28.85	34.63	43.65	0.95	0.18

aBase temperature.
bOptimum temperature.

cLower limit of optimum temperature.
dUpper limit of optimum temperature.
eCeiling (maximum) temperature.
fCoefficient of determination.
gRoot mean square error.

Table 7. The estimated parameters in hydrothermal time model to predict germination response under priming treatments.

Priming treatments	T (℃)	θ_{HT} (Mpa ℃ d) [a]	ψb (Mpa) [b]	$\sigma\psi b$ (MPa) [c]	T_b (℃) [d]	T_o (℃) [e]	R^2 [f]
Control (no priming)	10–35	1076.27	−1.50	0.25	7.65	26.10	0.90
Hydropriming	10–35	990.12	−1.41	0.26	7.83	31.94	0.99
Abscisic acid	10–35	865.04	−1.48	0.22	7.41	33.27	0.86
Gibberellic acid	10–35	864.28	−1.48	0.27	5.62	32.32	0.98
Salicylic acid	10–35	917.15	−1.44	0.28	8.01	32.69	0.97

aHydrothermal time constant.
bBase water potential.
cStandard deviation of base water potential.
dBase temperature.
eOptimum temperature.
fCoefficient of determination.

differentiation and germination metabolism. As reported by Patanè et al. (2016), a decrease in θ_{HT} significantly improved seed tolerance to drought stress. These changes are likely to cause a decrease in T_b, especially during drought and salinity stresses. A decreased T_b means the effects of hormonal priming on corn germination, especially under stressful conditions, were positive.

Conclusion

Our results indicated that drought and salinity stresses had a significant negative effect on germination percentage and germination rate in corn. However, hormonal priming treatments attenuated these detrimental effects on the germination process. A significant decrease in T_b following the application of ABA, GA, and SA can justify the positive effects of hormonal priming. The interaction between temperature and priming being significant, the highest germination parameters were obtained with GA, SA, and ABA priming at sub-optimal (< 25°C), optimal (25°C), and above-optimal (> 25°C) temperatures, respectively. The positive effect of hormonal priming on T_b reduction, identified as a new finding in this study, can be further evaluated in future experiments.

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Compliance with ethical standards

The authors declare that they have no conflict of interest. This article does not contain any studies involving animals or human participants performed by any of the authors.

Disclosure statement

No potential conflict of interest was reported by the authors.

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