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The efficiency of prechilling and gibberellic acid (GA_3) for breaking thermodormancy in lettuce

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ABSTRACT: The study focused on increasing the germination of lettuce cultivars under high-temperature conditions by seed treatments. The seeds of lettuce cultivars Yedikule, Iceberg, Iri Kıvırcık, and BT Iri Kıvırcık with different leaf morphology were primed by different doses of gibberellic acid (GA_3) (0, 250, 500, and 1000 ppm) and preconditioned by chilling and heating. The seeds were germinated at optimal (20 °C) and high (35 °C) temperatures. The results showed that high temperature adversely influenced the germination percentage of lettuce cultivars. The mean germination percentage was 16.8% at 35 °C and 93.4% at 20 °C. Also, there was a significant difference among lettuce cultivars for germination at 35 °C. Iri Kıvırcık and BT Iri Kıvırcık showed a severe thermodormancy and hardly ever germinated at 35 °C. Prechilling and preheating promoted germination at 35 °C compared to unprimed seeds, but prechilling resulted in higher germination than preheating. GA_3 was found to be the most useful treatment for improving germination compared to the others. The germination percentage of Iceberg, Yedikule, and Iri Kıvırcık primed with GA_3 doses reached over 80%. The results suggested that the germination performance of lettuce cultivars suffering from thermodormancy or wherever climatic conditions with high temperatures should be promoted by the application of 500 ppm de GA_3.

Index terms: chilling, germination, gibberellic acid, hydration, *Lactuca sativa* L.

RESUMO: O estudo teve como foco aumentar a germinação de cultivares de alface sob condições de alta temperatura por meio de tratamentos de sementes. As sementes das cultivares de alface Yedikule, Iceberg, Iri Kıvırcık e BT Iri Kıvırcık com diferentes morfologias foliares foram submetidas a diferentes doses de ácido giberélico (GA_3) (0, 250, 500 e 1000 ppm) e pré-condicionadas por resfriamento e aquecimento. As sementes foram germinadas em temperaturas ótima (20 °C) e alta (35 °C). Os resultados mostraram que a alta temperatura influenciou negativamente a porcentagem de germinação das cultivares de alface. A porcentagem média de germinação foi de 16,8% a 35 °C e 93,4% a 20 °C. Além disso, houve diferença significativa entre as cultivares de alface para germinação a 35 °C. Iri Kıvırcık e BT Iri Kıvırcık apresentaram termodormência severa e quase nunca germinaram a 35 °C. O pré-resfriamento e o pré-aquecimento promoveram a germinação a 35 °C em comparação com as sementes não condicionadas, mas o pré-resfriamento resultou em maior germinação do que o pré-aquecimento. GA_3 foi considerado o tratamento mais útil para melhorar a germinação em comparação com os outros. A porcentagem de germinação de Iceberg, Yedikule e Iri Kıvırcık preparados com doses de GA_3 atingiu mais de 80%. Os resultados sugeriram que o desempenho germinativo de cultivares de alface que sofrem de termodormência ou onde condições climáticas com altas temperaturas devem ser promovido pela aplicação de 500 ppm de GA_3.

Termos de indexação: resfriamento, germinação, ácido giberélico, hidratação, *Lactuca sativa* L.

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INTRODUCTION

Lettuce (*Lactuca sativa* L.) is a cool-season crop consumed largely for its leaves. It grows in different forms, shapes, and colors throughout the world. It is one of the most important cash crops for farmers as it has short growing periods and can usually be grown year-round in a wide range of climatic conditions, including in greenhouses for seedling production and open fields with direct seeding (Duman, 2006).

Lettuce seeds are typically exposed to high temperatures whether they are grown as seedlings in a greenhouse or sown directly onto fields. Under such temperatures, lettuce seed germination is, to a large extent, inhibited; this is referred to as thermodormancy (Gonai et al., 2004). Therefore, thermodormancy is a main obstacle that limits germination rate and uniformity, resulting in irregular emergence and transplant development, especially in regions with high temperatures.

The most-suitable temperature for the growth of many lettuce cultivars ranges between 15 °C and 22 °C, and seeds have difficulty germinating in temperatures above 28 °C (Argyris et al., 2008). However, the responses of the various lettuce cultivars to high temperatures differ, and germination ability is determined by genetic factors (Argyris et al., 2005; Lafta and Mou, 2013). Previous research has determined that thermotolerant lettuce genotypes have a gene that controls an enzyme involved in the biosynthesis of abscisic acid (ABA) (Argyris et al., 2008; Huo et al., 2013; Yoong et al., 2016), and ethylene production in seeds of thermosensitive lettuce cultivars was found to increase at high temperatures (Nascimento et al., 2000). Yoshioka et al. (1998) and Gonai et al. (2004) indicated that high ABA content was responsible for the inhibition of germination at supraoptimal temperatures, and Yoong et al. (2016) determined that a gene, LsERF1, supported gibberellin biosynthesis and germination at high temperatures.

In addition to breeding research to overcome thermodormancy in lettuce seeds, a number of seed-priming methods have been evaluated. These methods are commonly used in many crop plants to induce germination and emergence potential under various abiotic stresses such as salinity, drought, and extreme temperatures (McDonald, 2000). Priming allows the seeds to increase enzyme and metabolic activity; consequently, germination is stimulated to a considerable extent (Nascimento et al., 2001). In lettuce, the beneficial effects of seed priming with various salt (KNO_3, K_3PO_4 and $CaCl_2$); solutions (Cantliffe et al., 1999; Duman, 2006; Jahangir et al., 2009); osmotic solutions (PEG) (Sung et al., 2008); low-temperature imbibition (Nascimento, 2003); growth regulators such as gibberellic acid (Gonai et al., 2004), ethylene, and cytokinin (Huang and Khan, 1992); and vitamin (Fodorpataki et al., 2019) and hydropriming (Mahmoudi et al., 2012) have been demonstrated.

In the present study, the responses of lettuce cultivars with different leaf morphologies to high temperature, germination recovery potential after high-temperature stress, and the effectiveness of preconditioning with chilling and heating were investigated. Furthermore, the study examined a suitable level of gibberellic acid inhibiting the biosynthesis of ABA, which is responsible for germination failure in lettuce seeds under supraoptimal conditions.

MATERIAL AND METHODS

The seeds of different leaf types of lettuce cultivars, namely Iceberg (Crisphead), Yedikule (Cos), Iri Kıvırcık (Bunching), and BT Iri Kıvırcık (Bunching), purchased from commercial seed suppliers were used. Preconditioning (chilling and heating), hydration, and gibberellic acid at different dosages were applied to seeds under the following conditions at the Seed Science and Technology Laboratory of the Department of Field Crops, Eskişehir Osmangazi University, Turkey.

Prechilling: Seeds of lettuce cultivars were placed on two layers of filter paper moistened with distilled water and incubated at 4 °C for 48 h.

Preheating: Seeds inserted between filter papers irrigated with distilled water were maintained at 35 °C for 48 h.

Gibberellic acid (GA_3): Seeds were soaked in solutions with GA_3 doses of 250, 500, and 1000 ppm at 10 °C for 24 h in darkness.

Hydration: Seeds were immersed in distilled water under the same conditions of GA_3 treatment.

At the end of the imbibition treatments, excessive surface water was removed with paper toweling, and seeds were allowed to dry at room-temperature (~24-26 °C) conditions. Non-primed seeds were used as the control. The primed and control seeds were maintained at room-temperature conditions for moisture stabilization.

Following these treatments, seeds were germinated under optimal (20 °C) and above-optimal temperature (35 °C) conditions to determine sensitivity to thermodormancy. In addition, to identify germination recovery capacity, non-germinated seeds at 35 °C were transferred to an incubator at 20 °C and counted for an additional 7 days.

Four replications of 50 seeds from the primed and control seeds were permitted to germinate between three layers of filter papers wetted with 21 mL of distilled water. After the filter peppers were rolled, they were placed in sealed plastic bags to avoid evaporation. The bags were transferred to incubators at 20 °C for the optimal condition and at 35 °C for high-temperature stress. The criterion for germination was a radicle protrusion of 2 mm. Germination speed was calculated by mean germination time (MGT) described by ISTA (2003) rules as:

$MGT = \Sigma Dn / \Sigma n$,

where: D is the number of newly germinated seeds each day, and n is the day number on which the count took place.

Germination index (GI) was computed by the formula described by Salehzade et al. (2009) with the following equation:

GI = Number of germinated seeds/days of first count +. . .+ Number of germinated seeds/days of the final count.

Statistical analysis: The treatments were distributed in a completely randomized block design with four replications in a factorial scheme and a total of 200 seeds for each treatment. Two-way interactions of cultivar × preconditioning (heating and chilling) and cultivar × GA_3 levels were separately computed by ANOVA using the JUMP 13.0 statistical package program. The differences among the means were compared using Tukey's test ($p < 0.05$).

RESULTS AND DISCUSSION

The significant main effect of temperature and cultivar, and temperature × cultivar interaction was determined for germination percentage, mean germination time, and germination index (Table 1). Germination percentage was statistically higher at 20 °C than at 35 °C, but it was significantly changed by the lettuce cultivars under optimal and high temperatures (Table 2). Iceberg and Yedikule showed higher germination percentages at 20 °C and 35 °C compared to the other cultivars; however, Iri Kıvırcık and BT Iri Kıvırcık hardly ever germinated at 35 °C. Mean germination time and germination index cannot be calculated at 35 °C because insufficient germination was obtained. Mean germination time was changed by cultivars, and the highest mean time to germination was recorded in BT Iri Kıvırcık. High temperature decreased germination rate and delayed mean germination time. The germination index was also diminished dramatically at 35 °C, while the lettuce cultivars were differently affected.

There were significant differences in germination percentage, mean germination time, and germination index of the lettuce cultivars at optimal and high temperatures (Table 2). This demonstrates that thermodormancy existed in the investigated lettuce cultivars. Iceberg and Yedikule had higher germination percentages than did Iri Kıvırcık and BT Iri Kıvırcık at 35 °C. These results are in accord with the findings of Lafta and Mou (2013), who found that the germination ability of lettuce genotypes within each leaf morphology except for bunching leaf was different at high temperatures. In addition, they reported that the threshold of thermodormancy temperature for each genotype was different. Souza et al. (2019) reported that seed quality parameters were changed by lettuce cultivars under organic management, while Gray (1975) reported that crisphead types of lettuce cultivars germinated better than butterhead types at 30 °C. However, transferring non-germinated seeds at 35 °C to the optimal temperature of 20 °C, increased germination percentages up to the levels at 20 °C. Similar findings were reported by Gonai et al. (2004), who reported that thermodormancy in lettuce varied according to cultivars and was controlled by genetic factors, while germination ability could be restored as soon as temperature was reduced. These results were supported by the findings of Yoshioka et al. (1998), who reported that germination of lettuce seeds was controlled by ABA content that was stable or increased under high temperatures. In addition, Gonai et al. (2004) demonstrated that the germination percentage of lettuce seeds at high temperature could be promoted by applying exogenous fluridone, which lowered the exogenous ABA content in seeds. The germination index showed a trend similar to that of germination percentage, and a higher germination index was obtained at low temperature and cultivars with high germination percentages.

The main effects of cultivar, preconditioning, and interactions on the germination performance of lettuce cultivars were found to be significant (Table 3). Higher germination percentages, germination indexes as well as shorter mean germination times were obtained at 20 °C. Due to insufficient germination in Iri Kıvırcık and BT Iri Kıvırcık at 35 °C, mean germination time and germination index could not be calculated. The germination percentages of Iri Kıvırcık and BT Iri Kıvırcık were reduced from 92.7% to 11.8%, from 89.7% to 3.5%, respectively, under supraoptimal temperatures. Compared to control seeds, prechilling caused a significant increase in germination percentage and germination index. As seen in Figure 1, the prechilling slightly enhanced germination of Iri Kıvırcık and BT Iri Kıvırcık at 35 °C. The highest germination rates among cultivars were obtained by prechilling under optimal and supraoptimal temperatures. The germination percentage of Iceberg reached 81% and 83% when seeds were preconditioned by prechilling and preheating; both were found to be effective for improving germination of these cultivars, but no significant improvement was observed in Iri-Kıvırcık and BT-Iri Kıvırcık. This means that the efficiency of these treatments depended on the cultivars. Similar results were obtained by Nascimento (2003), who demonstrated that seed imbibition at low temperature increased germination percentage of lettuce at 35 °C. In our study, lower temperatures and longer durations for prechilling were used since seeds of lettuce began to germinate one day after sowing at 20 °C. Our results argued that seeds should be prechilled at temperatures between +4 and +10 °C to regulate water imbibition and to obtain the chilling effect.

Those seeds primed by increasing gibberellic acid doses germinated better and faster than unprimed seeds under high-temperature conditions. The greatest mean germination rate was observed with 250 ppm GA_3, and the shortest germination duration was obtained with 500 ppm GA_3 (Table 4). Hydration stimulated germination percentages and resulted in greater germination in all cultivars compared to the control seeds. Moreover, the 250 ppm GA_3 dose

Table 1. Mean values and analysis of variance for germination traits of the lettuce cultivars under 20 °C and 35 °C.

Factors	Germination percentage (%)	Mean germination time (day)	Germination index
		Temperature	
20°C	93.4 a	1.58 a	36.4 a†
35°C	16.8 b	- b	- b
Cultivar			
Iceberg	63.3 a	1.28 d	43.3 a
Yedikule	63.3 a	1.37 c	40.7 a
Iri Kıvırcık	47.3 b	1.52 b	36.5 b
BT Iri Kıvırcık	46.5 b	2.17 a	25.0 c
Analysis of Variance			
Temperature (A)	**	**	**
Cultivar (B)	**	**	**
A×B	**	**	**

†: Means connected by the same letter(s) are not significantly different for each main effect within each column at $p < 0.05$. *, ** significant at 5% and 1%, respectively. -: Data could not be calculated due to insufficient germination.

Table 2. Interaction effects between lettuce cultivar and temperature in germination percentage and recovery germination percentage after high temperature stress.

Cultivars	Temperatures		Recovery percentage (%)
	20 °C	35 °C	
Germination percentage			
Iceberg	98.0 a	28.5 c†	92.0 a
Yedikule	94.0 ab	32.5 c	84.0 b
Iri Kıvırcık	92.5 ab	2.0 d	94.0 a
BT Iri Kıvırcık	89.0 b	4.0 d	76.0 b
Mean germination time (day)			
Iceberg	1.28 c	2.54 a	
Yedikule	1.37 c	1.49 c	
Iri Kıvırcık	1.52 c	- d	
BT Iri Kıvırcık	2.17 b	- d	
Germination index			
Iceberg	43.3 a	7.6 e	
Yedikule	40.7 a	11.3 d	
Iri Kıvırcık	36.5 b	- f	
BT Iri Kıvırcık	25.0 c	- f	

†: Means connected by the same letter(s) are not significantly different for each character at $p < 0.05$. -: Data could not be calculated due to insufficient germination.

Table 3. Mean values and analysis of variance for germination traits of the lettuce cultivars preconditioned by prechilling and preheating at 20 °C and 35 °C.

Factors	Germination percentage (%)		Mean germination time (day)		Germination index	
	20 °C	35 °C	20 °C	35 °C	20 °C	35 °C
Cultivar						
Iceberg	89.3 b	63.8 a	1.63 c	2.04 a	36.2 a	21.3 a†
Yedikule	89.1 b	49.2 b	1.80 b	1.47 b	33.7 b	18.9 b
Iri Kıvırcık	92.7 a	11.8 c	1.59 c	- c	35.4 ab	- c
BT Iri Kıvırcık	89.7 ab	3.5 d	1.97 a	- c	27.7 c	- c
Preconditioning						
Control	93.4 a	16.8 c	1.58 b	2.51 a	36.4 b	4.8 c
Prechilling	95.5 a	43.9 a	1.32 c	2.17 b	42.3 a	15.5 a
Preheating	81.8 b	35.6 b	2.34 a	2.46 a	21.0 c	9.9 b
Analysis of Variance						
Cultivar (A)	*		**		**	
Preconditioning (B)	**		**		**	
A×B	**		**		**	

†: Means connected by the same letter are not significantly different for each main effect within each column at $p < 0.05$. *, ** significant at 5% and 1%, respectively. -: Data could not be calculated due to insufficient germination.

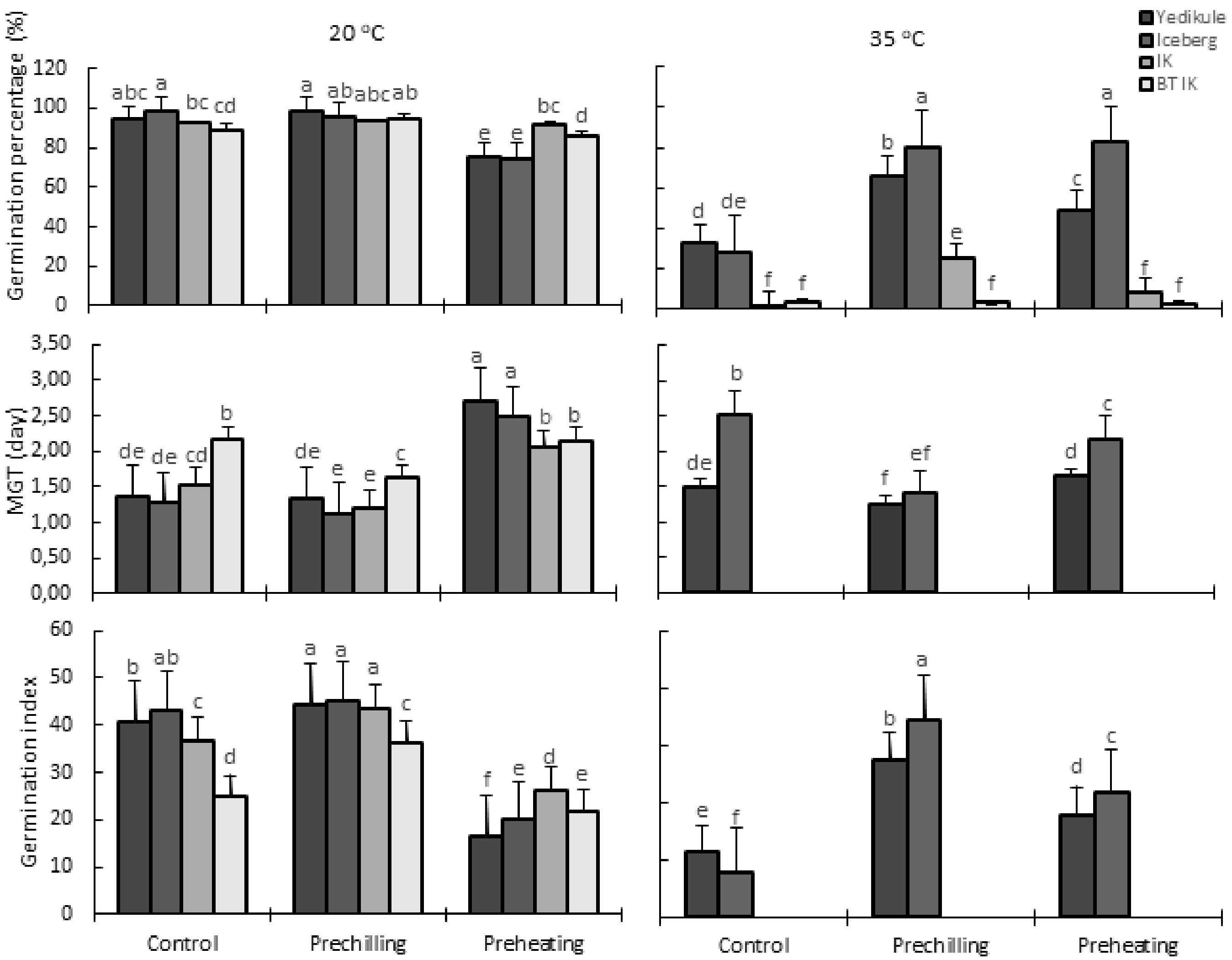

Figure 1. Interaction effects between lettuce cultivars and preconditioning (prechilling and preheating) on germination percentage, mean germination time, and germination index under optimal (20 °C) and high temperature (35 °C) conditions.

promoted germination of all the lettuce cultivars, and the superiority of gibberellic acid application is depicted in Figure 2. It is argued that high ABA concentration under supraoptimal temperatures restricted or inhibited germination of lettuce seeds, but the exogenous application of GA_3 changed the balance between ABA and GA, resulting in increased germination rates. Yoshioka et al. (1998) demonstrated that ABA content was stable in seeds germinated at 33 °C as amount as in dormant seeds, while it was reduced at 23 °C, or when the germination started. They indicated that delayed and inhibited germination resulted from ABA content. However, the results revealed that the exogenous application of GA_3 induced seed germination at 35 °C. This aligns with previous research findings of Gonai et al. (2004), who reported the helpful effects of 2 mM GA_3 along with fluridone, an inhibitor of ABA biosynthesis, rather than fluridone application alone for overcoming thermoinhibition in lettuce. However, Heydecker and Joshua (1977) reported that seed pretreatment with increasing GA_3 levels resulted in lower germination percentages than with kinetin at high temperatures. This may be due to differences in priming duration and temperature. They treated the seeds for 15 minutes at room temperature, while the seeds in the present study were primed for 24 h at 10 °C. Moreover, the lower priming temperatures were preferred for controlling water imbibition for seed treatments, and the seeds were prechilled along with GA_3 treatments, resulting in additional effects.

Table 4. Mean values and analysis of variance for germination traits of the lettuce cultivars primed with different doses of GA_3 under high temperature (35 °C) stress.

Factors	Germination percentage (%)	Mean germination time (day)	Germination index
Cultivars			
Iceberg	73.8 a	1.82 a	27.9 a†
Yedikule	65.0 b	1.71 a	23.9 b
Iri Kıvırcık	58.5 c	1.48 b	21.2 c
BT Iri Kıvırcık	21.2 d	- c	- d
GA_3			
Control	16.8 d	- c	4.7 d
Hydration	48.0 c	1.49 a	15.3 c
250 ppm GA_3	72.5 a	1.25 b	24.4 a
500 ppm GA_3	70.8 a	1.21 b	24.5 a
1000 ppm GA_3	65.1 b	1.29 b	22.2 b
Analysis of Variance			
Cultivar (A)	**	**	**
GA_3 (B)	**	**	**
A×B	**	**	**

†: Means connected by the same letter(s) are not significantly different for each main effect within each column at $p < 0.05$. *, ** significant at 5% and 1%, respectively. -: Data could not be calculated due to insufficient germination.

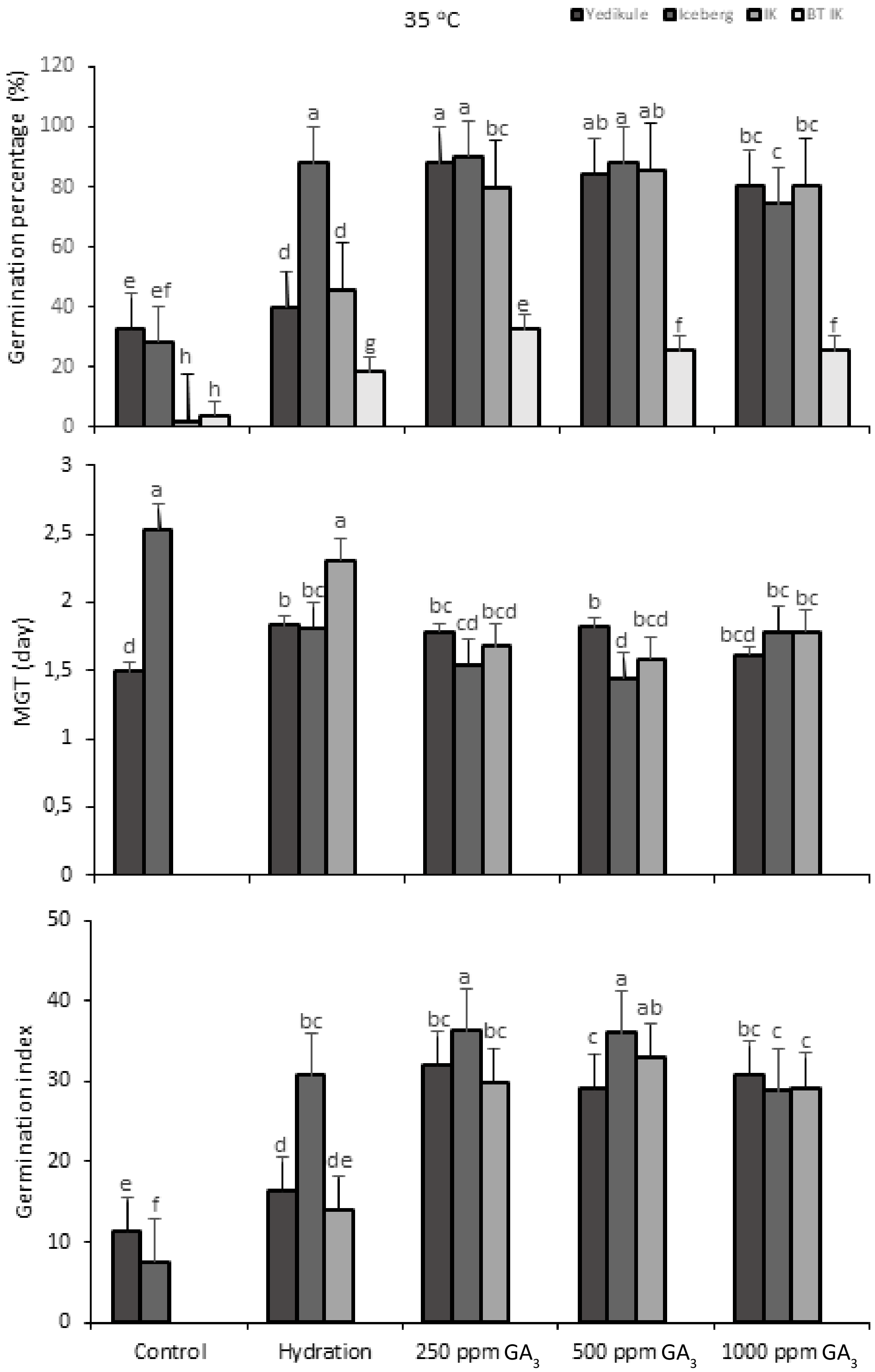

Figure 2. Interaction effects between lettuce cultivar and GA_3 doses on germination percentage, mean germination time, and germination index at 35 °C.

CONCLUSIONS

Seed treatments such as prechilling, preheating, and exogenous applications of different GA_3 doses were investigated to accelerate the process of breaking thermodormancy of lettuce seeds. In this study, Iri Kıvırıcık and BT Iri Kıvırcık with bunching leaves were identified as thermosensitive cultivars. Additionally, prechilling showed a promising performance, especially for sensitive cultivars to thermodormancy where it is necessary to prohibit the use of any chemical priming agents, such as in organic lettuce production. Similarly, hydration efficiently promoted the germination of lettuce cultivars, especially in Yedikule and Iceberg. The results revealed that GA_3 was the most powerful priming technique for promoting germination performance of the lettuce seeds and that they should be primed with 500 ppm GA_3 for circumventing germination failure under high-temperature stress.

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