Evaluation of Lettuce Genotypes for Seed Thermotolerance

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Abstract. Thermoinhibition of lettuce (*Lactuca sativa* L.) seed germination is a common problem associated with lettuce production. Depending on lettuce cultivars, seed germination may be inhibited when temperatures exceed 28 °C. The delay or inhibition of seed germination at high temperatures may reduce seedling emergence and stand establishment of lettuce in the field, leading to a reduction in economic yield. To identify heat-tolerant lettuce genotypes, lettuce varieties and germplasm accessions were screened for the ability to germinate under high-temperature stress. Twenty-four to 26 genotypes were selected from each lettuce types (crisphead, romaine, butterhead, loose leaf, and wild species) and their seeds were placed in petri dishes to test their ability to germinate at high temperatures (29 and 34 °C) as compared with controls at 24 °C. Some lettuce genotypes showed thermotolerance to 34 °C (less than 20% reduction in germination) such as Elizabeth, PI 342533, PI 358025, Florida Buttercrisp, Kordaat, Corsair, FL 50105, PRO 425, PI 278070, Noemie, Picarde, Gaillarde, *L. serriola* (PI 491112, UC96US23, PI 491147), *L. virosa* (PI 274378 D), *L. saligna* (PI 491159), and primitive (PI 187238 A, PI 289063 C). The germination rates were consistent with the germination percentage at the high temperatures. Seed germination in the field was very low and positively correlated with seed germination at 29 and 34 °C. The highest field germination percentages (greater than 40%) were observed in Belluro, Mantilia, Mid Queen, Headmaster, PRO 874, PRO 425, FL 50105, Corsair, Romaine SSC 1148, Romaine Romea, Green Forest, Grenadier, FL 43007, Squadron, Xena, Noemie, Green Wave, Picarde, and Red Giant. The results of this study indicated that lettuce genotypes differ greatly in their ability to germinate at high temperatures as determined by the percentages and the rates of germination. Our research indicates that thermoinsensitive varieties could be used to expand lettuce production seasons in warm and low land cost areas and reduce the need for seed priming, lowering the production costs. The information may also be useful for growers to better choose cultivars for warm environments and for lettuce breeders to improve the crop for adaptation to global warming and climate change.

Temperature is a major environmental factor that influences plant growth and development. Lettuce (*Lactuca sativa* L.) is a cool-season crop with optimum growth at an average temperature of 18 °C. Production of lettuce at higher temperature ranges results in yield and quality losses (Jenni, 2005; Jenni and Yan, 2009). At high temperatures, lettuce seed germination is inhibited (thermoinhibition) and the seeds became dormant, which is called thermodormancy (Gonai et al., 2004; Negm et al., 1972; Vidaver and Hsiao, 1975). It has been reported that seed germination at high temperatures is influenced by the environmental conditions, especially high temperatures, during seed development and maturation (Kozarewa et al., 2006; Sung et al., 1998, 2008). Poor seed germination and thermodormancy are major problems associated with lettuce production. Depending

on genotype, lettuce seed germination is inhibited at temperatures higher than 28 to 32 °C (Argyris et al., 2008a; Gray, 1975; Kozarewa et al., 2006; Thompson et al., 1979). This inhibition of seed germination at high temperatures causes a reduction in field emergence, stand establishment, and yield (Cantliffe et al., 1981; Valdes et al., 1985). Seed priming has been used to improve seed germination in vegetable crops grown under stress conditions. Germination rates and seedling emergence improved at high temperatures by seed priming in osmotic solutions (Bradford, 1986; Bradford and Somasco, 1994; Samfield et al., 1991). The alleviation of thermoinhibition in lettuce by priming may occur during imbibing the seeds at high temperature (Cantliffe et al., 1981; Valdes et al., 1985).

There are many factors that influence seed germination at high temperatures such as seed coverings and plant hormones. It has been reported that the endosperm layer of thermoinsensitive lettuce genotypes had lower resistance to a puncture test than that of the thermosensitive genotypes (Sung et al., 1998). This indicated that seed covering imposed restriction on seed germination at high temperature

(Ikuma and Thimann, 1963; Speer, 1974; Sung et al., 1998). Weakening of the endosperm layer before radicle emergence through enzymatic activity of endo- β -mannanase, a cell wall-bound enzyme, is essential for seed germination to occur at high temperatures (Nascimento et al., 2000). This suggested that seed priming overcomes the thermoinhibition in thermosensitive lettuce cultivars as a result of an increase in enzyme activity in the endosperm layer of the seed. The endosperm layer is considered the region that imposes physical resistance to seed germination at high temperature (Sung et al., 2008). The balance between embryo growth potential and the physical resistance to embryo growth exerted by the covering tissues is required for dormancy release and seed germination to occur (Kucera et al., 2005).

The plant hormones, gibberellic acid (GA), abscisic acid (ABA), and ethylene play a role in the regulation of seed germination in most plants. Seed germination is inhibited by ABA, which increases in thermodormant lettuce seeds (Argyris et al., 2008a). GA is involved in dormancy release or prevention by stimulating the activities of hydrolytic enzymes, which promote embryo growth (Khan, 1994). Ethylene may also play a role in extending the high temperature limit for lettuce seed germination by maintaining lower water potential in the embryonic region to allow growth and radicle emergence (Dutta and Bradford, 1994). Nascimento et al. (2000) observed a close relationship among lettuce seed germination, ethylene evolution, and the activity of endo- β -mannanase enzyme. Ethylene and cytokinin have been reported to be involved in alleviation of thermoinhibition in lettuce seeds (Huang and Khan, 1992; Khan and Prusinski, 1989).

The average temperature worldwide is predicted to increase over time, which impacts the agricultural production and food supplies (Karl and Trenberth, 2003; Wurr et al., 1996). This climate change and global warming may pose serious challenges to California agriculture, especially the leafy green industry. Adapting the leafy green industry to future climate conditions is important to meet the increasing demand for leafy vegetables as the population increases. The increasing need for leafy vegetables will put pressure on the leafy industry to expand the production to the low land cost and warmer areas of California. To expand lettuce production to warmer environments, lettuce germplasm and cultivars need to be evaluated to examine their tolerance to high-temperature stress. Lettuce seed germination is inhibited at high temperatures, which leads to a reduction in product quality and yield. Thus, thermoinhibition is a problem facing lettuce growers, which could be solved by selecting thermotolerant varieties that perform well under stressful conditions. The objective of this study was to screen lettuce germplasm and cultivars for resistance to thermoinhibition or thermodormancy to find lettuce germplasm that germinate well at high temperatures. We screened the lettuce collections at the U.S. Department of Agriculture (USDA) in

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Salinas, CA, for their tolerance to thermoinhibition or thermodormancy and identified the most thermotolerant genotypes from different lettuce types such as crisphead, butterhead, romaine, leaf type, and wild species.

Materials and Methods

Plant material. Five lettuce types were screened in this experiment to test their tolerance to thermoinhibition including crisphead, butterhead, romaine, loose leaf (green and red leaf), and wild species. Initially, we screened more than 3500 lettuce varieties and germplasm accessions for their ability to germinate at high temperature. Twenty-five to 26 genotypes from each lettuce type were selected to be used in further experiments, including genotypes with a high germination percentage at 34 °C and some standard and thermosensitive genotypes. The selected genotypes have uniform seed germination at 24 °C and their seeds were produced in greenhouses at the USDA, Salinas, CA, and stored at -20 °C. This may minimize the effect of the environmental conditions, at which the seeds were matured, on seed germination.

Seed germination. Four replicates of 25 seeds each were placed in petri dishes (100 × 20 mm) over one layer of Whatman #1 filter paper and 4.5 mL of deionized water was added. The petri dishes were covered with lids to prevent evaporation. The petri dishes were placed in incubators maintained at 24, 29, and 34 °C under a 12-h fluorescence light (80 μmol·m⁻²·s⁻¹) for 14 d. We used this light intensity because the optimal temperature for seed germination in lettuce was noted to be higher in light than in darkness (Deng and Song, 2012). Seed germination was recorded as the emergence of the radicle after 2, 4, 7, and 14 d or until no additional germination occurred. Percentage of seed germination was calculated and the germination rate was determined based on the method of Meguire (1962) using the following equation: germination rate = $\frac{\sum GT1/T1 + \dots + GTn/Tn}{n}$. GT1 = number of germinated seeds on first count; GTn = number of germinated seeds on last count; T1 = days at first count; Tn = days at last count. The percentage reduction in seed germination at 29 and 34 °C from that at 24 °C was also calculated.

Field germination. Seeds of lettuce genotypes were planted on 10 July 2012 in a field at the West Side Research and Extension Center, University of California, Five Points, CA. The experiment was arranged in a randomized complete block with four replications per treatment. Fifty seeds from each genotype were planted in rows 6 m long. The experimental unit consisted of one row per entry. Seed germination was evaluated after 7 and 14 d. The average maximum and minimum air temperatures for the 14 d were 34.9 and 16.1 °C and the average maximum and minimum soil temperatures at 15-cm depth were 27.2 and 24.9 °C, respectively.

Statistical analysis. Analysis of variance was conducted using the JMP program (SAS Institute Inc., Cary, NC). Treatment means

were separated by the least significant difference at the 0.05 level of probability. The correlation coefficients between field seed germination and germination at 29 and 34 °C were determined by the JMP program using genotype means.

Results and Discussion

Butterhead lettuce. All the butterhead genotypes showed a high germination percentage and germination rate at 24 °C (Table 1). Annecy exhibited the lowest germination

percentage (83%) and germination rate among all genotypes tested. There were highly significant differences in germination percentage and germination rates among genotypes at 29 and 34 °C. At 29 °C, Annecy, Anthem, Dark Green Boston, and Winter Marvel showed the lowest germination percentage and germination rates compared with other genotypes. The reductions in seed germination at 29 °C in these were 54%, 93%, 70%, and 100%, respectively (Fig. 1). These genotypes were the most sensitive genotypes to thermoinhibition at 29 °C. Significant cultivar

Table 1. Effect of temperature on seed germination in butterhead lettuce.

Genotype	Germination (%)			Germination rate			Field germination (%)
	24 °C	29 °C	34 °C	24 °C	29 °C	34 °C	
Annecy	83 b ^a	37 c	3 h	34.0 d	10.1 cd	0.4 i	2 i
Anthem	100 a	7 d	4 h	50.0 a	2.5 de	0.1 i	1 i
Aquarius	100 a	78 b	11 gh	48.0 ab	28.6 b	2.3 i	40 abc
Arcade	100 a	100 a	11 gh	50.0 a	47.5 a	3.4 i	33 a-e
Averya	97 a	93 a	69 cd	45.7 b	44.3 a	22.0 def	14 ghi
Belluro	100 a	100 a	65 d	50.0 a	50.0 a	18.3 fg	44 a
Bibb	100 a	100 a	39 ef	50.0 a	50.0 a	19.5 efg	8 hi
Big Hoss	100 a	97 a	65 d	49.3 a	48.5 a	30.9 c	19 fgh
Buttercrunch	100 a	94 a	38 ef	50.0 a	46.6 a	19.0 fg	28 b-g
Calibra	100 a	100 a	55 de	49.0 a	46.8 a	7.6 hi	9 hi
Clinton	100 a	100 a	73 bcd	50.0 a	50.0 a	20.2 ef	20 e-h
Dark Green Boston	96 a	29 c	3 h	40.3 c	13.6 c	1.3 i	9 hi
Deciso	100 a	100 a	26 fg	50.0 a	50.0 a	12.3 gh	1 i
Dukaat	100 a	100 a	56 de	50.0 a	50.0 a	26.8 cde	25 d-g
Elizabeth	100 a	100 a	98 a	50.0 a	50.0 a	46.7 ab	14 ghi
Florida Buttercrisp	100 a	100 a	88 abc	50.0 a	50.0 a	41.4 ab	29 b-f
Kitty	100 a	100 a	58 de	50.0 a	50.0 a	28.6 cd	32 a-f
Kordaat	100 a	100 a	88 abc	50.0 a	50.0 a	41.0 b	37 a-d
Magnet	100 a	100 a	69 cd	50.0 a	50.0 a	31.5 c	37 a-d
Mantilia	100 a	100 a	62 d	50.0 a	50.0 a	24.7 c-f	42 ab
Margarita	100 a	73 b	7 gh	50.0 a	35.7 b	3.5 i	29 b-f
PI 342533	100 a	100 a	93 ab	50.0 a	50.0 a	45.8 ab	33 a-f
PI 358025	100 a	100 a	98 a	50.0 a	50.0 a	49.0 a	33 a-f
Summer Bibb	100 a	100 a	4 h	50.0 a	50.0 a	0.4 i	26 c-g
Winter Marvel	100 a	0 d	0 h	50.0 a	0.0 e	0.0 i	1 i

^aMeans with the same letter in the same column are not significantly different at $P \leq 0.05$.

Table 2. Effect of temperature on seed germination in crisphead lettuce.

Genotype	Germination (%)			Germination rate			Field germination (%)
	24 °C	29 °C	34 °C	24 °C	29 °C	34 °C	
Barrier Reef	99 ab ^a	87 ab	0 j	48.1 ab	40.7 bcd	0.0 i	5 jk
Batavian Cybele	100 a	100 a	39 d-g	50.0 a	50.0 a	19.1 bcd	26 c-f
Batavia Gloire	100 a	99 a	71 ab	49.3 ab	46.4 abc	23.2 bc	13 g-j
Batavian Reine	98 ab	100 a	56 bcd	48.3 ab	50.0 a	24.7 b	25 c-g
Bayview	100 a	94 a	0 j	50.0 a	35.0 d	0.0 i	1 jk
Calmar	97 ab	8 e	2 j	47.3 b	4.0 f	0.3 i	0 k
Celtic	100 a	100 a	36 efg	50.0 a	49.0 a	17.0 cde	25 c-g
Command	97 ab	95 a	45 cde	47.8 ab	47.3 ab	5.3 ghi	19 f-i
Empire	96 b	100 a	42 def	47.5 ab	50.0 a	13.1 def	21 e-h
Headmaster	100 a	100 a	15 hij	50.0 a	50.0 a	7.5 fgh	45 ab
Huron	98 ab	100 a	62 abc	48.5 ab	50.0 a	8.2 fg	28 c-f
Marleen	100 a	100 a	44 def	50.0 a	50.0 a	12.0 ef	37 abc
Mid Queen	100 a	100 a	16 hij	50.0 a	50.0 a	8.0 fg	47 a
Premiere	100 a	79 bc	4 j	50.0 a	39.5 cd	2.0 ghi	24 d-g
PRO 839	100 a	100 a	0 j	50.0 a	50.0 a	0.0 i	35 a-d
PRO 874	100 a	100 a	27 fgh	50.0 a	50.0 a	12.9 def	41 ab
Pybas 101	100 a	100 a	50 cde	47.3 b	50.0 a	13.2 def	27 c-f
Salinas	100 a	43 d	8 ij	50.0 a	14.6 e	4.0 ghi	23 d-h
Sinano-Summer	100 a	100 a	79 a	50.0 a	50.0 a	37.8 a	35 a-d
Vanguard 75	100 a	90 ab	4 j	50.0 a	45.0 abc	2.0 ghi	33 b-e
Vista Verde	98 ab	100 a	0 j	48.5 ab	50.0 a	0.0 i	7 ijk
Westlake	100 a	71 c	0 j	50.0 a	11.9 e	0.0 i	1 jk
Winter Select	100 a	100 a	3 j	50.0 a	50.0 a	1.5 hi	4 jk
Wintercut	100 a	100 a	22 h	50.0 a	50.0 a	8.1 fg	11 h-k
Winterhaven	98 ab	47 d	5 ij	49.0 ab	8.8 ef	2.5 ghi	19 f-i

^aMeans with the same letter in the same column are not significantly different at $P \leq 0.05$.

Batavia Gloire = Batavia Gloire du Dauphine; Batavian Reine = Batavian Reine Des Glaces.

differences in the ability to germinate were observed at 34 °C (Table 1). Elizabeth, PI 358025, PI 342533, Kordaat, and Florida Buttercrisp exhibited the highest percentage of seed germination (greater than 80%) and germination rates at 34 °C. These genotypes also showed the lowest reduction in seed germination (less than 20%) at 34 °C from that at 24 °C (Fig. 1). The results showed that these varieties were the most tolerant butterhead genotypes to thermoinhibition at 34 °C. In addition to Annecy, Anthem, Dark Green Boston, and Winter Marvel, the most sensitive genotypes to thermoinhibition at 34 °C were Summer Bibb, Margarita, Aquarius, and Arcade. These genotypes exhibited a substantial reduction (greater than 80%) in seed germination at 34 °C (Fig. 1). Dark Green Boston has been previously considered a thermosensitive cultivar, which was consistent with our results (Sung et al., 2008).

Seed germination in the field was low with the highest germination percentages (greater than 30%) observed in Belluro, Mantilia, Aquarius, Kordaat, Magnet, PI 342533, PI 358025, Arcade, and Kitty (Table 1). There was a significant positive correlation between seed germination at 29 and 34 °C and field germination in butterhead lettuce (Table 7). Thus, seed germination of some lettuce genotypes is inhibited at 29 °C, but others can tolerate higher temperatures (34 °C), which indicated that the maximum temperature for seed germination is genotype-dependent (Coons et al., 1990).

Crisphead lettuce. All crisphead genotypes showed a high percentage germination (greater than 95%) and germination rate at 24 °C (Table 2). There were significant differences in percentage germination and germination rate among all genotypes at higher temperatures. At 29 °C, most crisphead genotypes germinated well except Calmar, Salinas, and Winterhaven, which showed the lowest germination percentage (8%, 43%, and 47%, respectively). These genotypes also showed the largest reduction (greater than 50%) in seed germination at 29 °C (Fig. 2). The results indicated that Calmar was the most thermosensitive genotype followed by Salinas and Winterhaven. At 34 °C, Sinano-Summer, Batavia Gloire du Dauphine, Huron, and Batavian Reine Des Glaces showed the highest germination percentages (79%, 71%, 62%, 56%, respectively) among crisphead genotypes. These genotypes also showed the highest germination rates at 34 °C (Table 2) and the smallest reduction (less than 50%) in germination at 34 °C (Fig. 2). All the other genotypes had lower germination and some of them were completely inhibited with no germination at 34 °C such as Barrier Reef, Bayview, Pro 839, Vista Verde, and Westlake. Sinano-Summer was the only crisphead lettuce with low reduction in germination at 34 °C and it was considered the most thermotolerant genotype (Fig. 2). Salinas exhibited thermoinhibition at 29 and 34 °C and this result was consistent with the previously reported findings (Argyris et al., 2008a, 2008b; Coons et al., 1990).

Fig. 1. Reduction in germination percentage at 29 and 34 °C from 24 °C in butterhead lettuce. Results are means $\pm$ SE (n = 4). $LSD_{0.05}$ for 29 and 34 °C are 11.9 and 20.9, respectively. LSD = least significant difference.

Fig. 2. Reduction in germination percentage at 29 and 34 °C from 24 °C in crisphead lettuce. Results are means $\pm$ SE (n = 4). $LSD_{0.05}$ for 29 and 34 °C are 14.8 and 16.7, respectively. LSD = least significant difference.

Fig. 3. Reduction in germination percentage at 29 and 34 °C from 24 °C in romaine lettuce. Results are means $\pm$ SE (n = 4). $LSD_{0.05}$ for 29 and 34 °C are 12.8 and 20.2, respectively. LSD = least significant difference.

Table 3. Effect of temperature on seed germination in romaine lettuce.

Genotype	Germination (%)			Germination rate			Field germination (%)
	24 °C	29 °C	34 °C	24 °C	29 °C	34 °C	
Amanthus	93 b ^z	100 a	71 a-e	46.5 b	50.0 a	35.3 ab	11 ijk
Black Seeded Bath	100 a	3 d	0 h	50.0 a	1.5 d	0.0 g	2 jk
Clemente	100 a	100 a	31 g	50.0 a	49.0 a	14.8 ef	13 ijk
Corsair	100 a	100 a	86 a	50.0 a	50.0 a	39.7 a	55 ab
FL 43007	100 a	100 a	45 fg	50.0 a	50.0 a	18.6 def	41 c-f
FL 49678	100 a	100 a	30 g	50.0 a	50.0 a	13.0 f	39 c-f
FL 50105	100 a	100 a	82 abc	50.0 a	50.0 a	37.2 a	57 a
Floricos 83	100 a	100 a	79 a-d	50.0 a	50.0 a	35.6 ab	40 c-f
Green Forest	100 a	93 a	0 h	50.0 a	46.1 a	0.0 g	43 b-e
Grenadier	100 a	100 a	64 b-f	50.0 a	50.0 a	31.4 abc	43 b-e
Heavy Heart	100 a	100 a	74 a-e	50.0 a	50.0 a	36.4 ab	32 d-g
Jericho	100 a	1 d	3 h	50.0 a	0.5 d	0.4 g	1 k
King Henry	98 a	100 a	55 ef	49.0 a	50.0 a	27.3 bcd	31 efg
Little Gem	100 a	0 d	0 h	50.0 a	0.0 d	0.0 g	7 jk
PI 174228	100 a	100 a	61 def	50.0 a	50.0 a	23.9 cde	28 fgh
PI 278070 BS	100 a	100 a	83 ab	50.0 a	50.0 a	38.9 a	30 efg
PRO 423	100 a	47 c	0 h	50.0 a	23.5 c	0.0 g	15 hij
PRO 425	100 a	100 a	82 abc	50.0 a	50.0 a	40.3 a	57 a
Romaine Romea	100 a	100 a	62 c-f	50.0 a	50.0 a	31.0 abc	45 a-d
Romaine SSC 1148	100 a	100 a	55 ef	50.0 a	50.0 a	27.3 bcd	48 abc
Romaine SSC 1156	100 a	100 a	33 g	50.0 a	50.0 a	15.5 ef	37 c-f
Romulus	100 a	100 a	62 c-f	50.0 a	50.0 a	27.4 bcd	21 ghi
Sweet Gem	100 a	100 a	74 a-e	50.0 a	50.0 a	36.5 ab	37 c-f
Valmaine	100 a	66 b	0 h	50.0 a	32.1 b	0.0 g	2 jk
Winter Density	100 a	1 d	1 h	50.0 a	0.3 d	0.5 g	2 jk

^zMeans with the same letter in the same column are not significantly different at $P \leq 0.05$.

Table 4. Effect of temperature on seed germination in green leaf lettuce.

Genotype	Germination (%)			Germination rate			Field germination (%)
	24 °C	29 °C	34 °C	24 °C	29 °C	34 °C	
Amazona	100 a ^z	99 a	41 d-g	50.0 a	35.9 c	19.8 cde	8 ghi
Antigua	98 a	100 a	41 d-g	41.4 b	50.0 a	19.2 cde	14 e-h
Australischer Gelber	95 b	30 e	0 k	41.3 b	7.6 f	0.0 h	5 hi
Azura	100 a	92 ab	56 b-e	49.5 a	45.0 ab	22.5 bed	5 hi
Black Seeded Simpson	100 a	87 ab	1 k	50.0 a	39.6 bc	0.5 h	4 hi
Flandria	100 a	100	29 fgh	50.0 a	50.0 a	13.9 def	5 hi
Funly	100 a	ND	28 gh	50.0 a	ND	12.2 efg	28 cd
Green Wave	100 a	100 a	50 cde	50.0 a	50.0 a	22.8 bc	42 ab
Greengo	98 a	49 d	14 h-k	38.3 b	12.1 ef	1.2 h	0 i
Loros	100 a	100 a	26 gh	50.0 a	50.0 a	4.0 gh	20 d-g
Neva	100 a	100 a	49 def	50.0 a	50.0 a	23.8 bc	27 cd
Noemie	100 a	100 a	98 a	50.0 a	50.0 a	47.5 a	42 ab
Ocean Green	100 a	100 a	5 ijk	50.0 a	50.0 a	1.7 h	21 def
PI 177420	100 a	100 a	70 bc	50.0 a	50.0 a	26.1 bc	27 cde
PI 187238 E	100 a	79 bc	73 b	50.0 a	25.4 d	30.2 b	36 abc
Royal Oak Leaf	100 a	11 f	14 h-k	50.0 a	5.0 f	3.1 h	3 hi
Simpson Elite	100 a	31 e	0 k	50.0 a	15.5 e	0.0 h	8 ghi
Slobolt	100 a	69 c	2 jk	46.5 a	27.1 d	0.6 h	10 f-i
Squadron	100 a	19 ef	12 h-k	48.5 a	7.0 f	6.0 fgh	44 a
Tendergreen	100 a	100 a	38 efg	50.0 a	50.0 a	6.6 fgh	19 d-g
Tiara	100 a	100 a	22 g-j	50.0 a	50.0 a	6.7 fgh	30 bcd
Two Star	100 a	100 a	0 k	50.0 a	50.0 a	0.0 h	5 hi
Versailles	100 a	100 a	23 ghi	50.0 a	50.0 a	8.4 fgh	5 hi
Waldmann's Green	100 a	72 c	14 h-k	50.0 a	34.7 c	7.0 fgh	24 cde
Xena	100 a	100 a	61 bcd	50.0 a	50.0 a	30.1 b	44 a

^zMeans with the same letter in the same column are not significantly different at $P \leq 0.05$.

ND = not determined.

The highest germination percentages (greater than 30%) in the field were observed in Mid Queen, Headmaster, PRO 874, Marleen, PRO 839, Sinano-Summer, and Vanguard 75 (Table 2). There was no significant correlation between field germination and germination at 29 or 34 °C among crisphead genotypes (Table 7).

Romaine lettuce. Germination percentage and germination rates for romaine lettuce genotypes are shown in Table 3. There were significant differences in percentage germination

and germination rates among genotypes at 29 and 34 °C. Seeds of Little Gem, Jericho, Winter Density, and Black Seeded Bath exhibited thermoinhibition at 29 °C as indicated by the lowest germination percentages and germination rates of the romaine genotypes tested. These genotypes also showed the largest reduction in seed germination at 29 °C compared with other genotypes (Fig. 3). In addition to these genotypes, Green Forest, Valmaine, and PRO 423 exhibited substantial reductions in seed germination at 34 °C

(Fig. 3). These genotypes were more sensitive to thermoinhibition at 34 °C than the other genotypes. The most thermotolerant genotypes were Corsair, PI 278070, FL 50105, Pro 425, Floricos 83, Amanthus, Heavy Heart, and Sweet Gem, which showed the smallest reduction in seed germination (less than 30%) at 34 °C compared with other romaine genotypes (Fig. 3). Green Forest exhibited thermotolerance at 29 °C and thermoinhibition at 34 °C. This indicated that the maximum temperature for thermoinhibition depends on lettuce cultivar and germplasm.

The highest field germination percentages (greater than 50%) were observed in PRO 425, FL 50105, and Corsair (Table 3). The field tolerance of these genotypes was consistent with their thermotolerance at 29 and 34 °C. There was a significant positive correlation between field seed germination and germination at 29 and 34 °C among romaine genotypes (Table 7).

Green leaf lettuce. The effect of temperature on seed germination percentage and germination rate in green leaf lettuce is presented in Table 4. High germination percentages (greater than 95%) were observed in all genotypes at 24 °C. At 29 and 34 °C, there were significant differences in percentage germination and germination rates among green leaf genotypes. The most sensitive genotypes to thermoinhibition were Royal Oak Leaf, Squadron, Australischer Gelber, Simpson Elite, and Greengo, which had significantly lower germination percentages (less than 50%) and germination rates at 29 °C than other green leaf genotypes (Table 4). The reduction in germination percentages at 29 °C in these genotypes was 89%, 81%, 69%, 69%, and 50%, respectively (Fig. 4). The differences in germination percentages and germination rates among lettuce genotypes were greater at 34 °C than at 29 °C. Noemie was the most thermotolerant genotype followed by PI 187238 E and PI 177420. These genotypes had the highest germination percentages and germination rates at 34 °C as compared with the other genotypes (Table 4). The reductions in seed germination in these genotypes at 34 °C were 2%, 27%, and 30%, respectively (Fig. 4).

The largest field germination percentages (greater than 40%) were observed in Squadron, Xena, Noemie, and Green Wave (Table 4). There was a significant correlation between field seed germination and germination at 34 °C among green leaf genotypes (Table 7).

Red leaf lettuce. Cultivars and genotypes of red leaf lettuce also differ in their tolerance to thermoinhibition. All red leaf lettuce genotypes exhibited high germination percentages and germination rates at 24 °C (Table 5). However, at 29 and 34 °C, there were highly significant differences in germination percentages and germination rates among genotypes. At 29 °C, most of the red lettuce genotypes exhibited high germination percentages and rates except Big Red, Red Flower, Prizehead, Red Rage, Red Prize, Ibis, Merlot, Red Tide, and Hyper Red Rumble Waved, which showed the lowest germination

Fig. 4. Reduction in germination percentage at 29 and 34 °C from 24 °C in green leaf lettuce. Results are means $\pm$ SE (n = 4). LSD_{0.05} for 29 and 34 °C are 13.7 and 20.6, respectively. Black Seeded = Black Seeded Simpson. LSD = least significant difference.

Fig. 5. Reduction in germination percentage at 29 and 34 °C from 24 °C in red leaf lettuce. Results are means $\pm$ SE (n = 4). LSD_{0.05} for 29 and 34 °C are 12.9 and 15.1, respectively. LSD = least significant difference.

Fig. 6. Reduction in germination percentage at 29 and 34 °C from 24 °C in wild species. Results are means $\pm$ SE (n = 4). LSD_{0.05} for 29 and 34 °C are 10.8 and 18.3, respectively. LSD = least significant difference.

percentages and rates. However, at 34 °C, most of the genotypes showed very low germination percentage and rates except Picarde, Gaillarde, and Valdai (Table 5). The reduction in germination percentages at 34 °C from that at 24 °C in Picarde, Gaillarde, and Valdai was 5%, 12%, and 25%, respectively (Fig. 5). These red leaf genotypes were considered the most tolerant to thermoinhibition at 34 °C.

The highest field germination percentages (greater than 30%) were observed in Picarde, Red Giant, Medera DMR, Marimba, Grenoble N 65, Gaillarde, and Black Jack (Table 5). Picarde showed the highest germination in the field and at 34 °C. There was a significant positive correlation between field seed germination and germination at 29 and 34 °C among red leaf genotypes (Table 7).

Wild species. There were significant differences in germination percentages and rates among primitive and wild lettuce species at 29 and 34 °C (Table 6). PI 281877, PI 204753, and PI 491000 had the lowest germination percentages and rates at 29 °C. The reduction in germination percentages in PI 281877, PI 204753, and PI 491000 at 29 °C was 94%, 91%, and 63, respectively (Fig. 6). These genotypes were the most thermosensitive genotypes at 29 °C. In addition to these genotypes, PI 491089 and PI 202349 C exhibited thermoinhibition at 34 °C as determined by germination percentages and rates (Table 6). Genotypes with high tolerance to thermoinhibition were PI 491112, UC96US23, PI 187238 A, PI 274378 D, PI 491147, and PI 289063 C as indicated by high germination percentages (greater than 80%) and germination rates at 34 °C (Table 6). The reductions in seed germination in these genotypes were 6%, 6%, 9%, 14%, 14%, and 18%, respectively (Fig. 6). This shows that all three wild species (*L. serriola*, *L. saligna*, and *L. virosa*) and primitive lettuce have thermoinhibition. The observed thermotolerance in UC96US23 (*Lactuca serriola*) was consistent with previous results of Argyris et al. (2008a, 2008b).

All of the wild species showed very low germination in the field (Table 6). The highest percentage germination (33%) was observed in PI 289063 A. There was no significant correlation between field seed germination and germination at 29 or 34 °C among wild species (Table 7). This variation in seed germination could be the result of field conditions, which were not optimal for germination like in the laboratory or growth chambers. Disease and insect damage may also lower germination percentage. It has been observed that poor field emergence at high temperature in broccoli was the result of an inhibition of root growth (Jett et al., 1996). The presence of high salt in the irrigation water or in the upper soil surface may lower seed germination (Coons et al., 1990).

The observed variations in the sensitivity to high-temperature inhibition of seed germination among lettuce genotypes may depend on lettuce cultivars and germplasm (Coons et al., 1990; Gray, 1975; Thompson et al., 1979). The regulation of seed germination in

Table 5. Effect of temperature on seed germination in red leaf lettuce.

Genotype	Germination (%)			Germination rate			Field germination (%)
	24 °C	29 °C	34 °C	24 °C	29 °C	34 °C	
Big Red	89 b ^z	1 e	0 f	37.1 b	0.3 g	0.0 e	5 jk
BlackJack MT	100 a	100 a	0 f	50.0 a	50.0 a	0.0 e	30 c-f
Flashy Trout Back	100 a	100 a	13 ef	50.0 a	50.0 a	6.1 de	22 e-h
Gaillarde	100 a	100 a	88 ab	50.0 a	50.0 a	43.5 a	33 b-e
Grenobloise N 65	100 a	100 a	50 c	50.0 a	50.0 a	23.4 c	34 b-e
Hyper Red Rumpel	99 a	10 de	0 f	49.5 a	1.2 fg	0.0 e	2 k
Ibis	100 a	19 d	0 f	50.0 a	7.6 ef	0.0 e	0 k
Madera DMR	100 a	100 a	8 f	50.0 a	50.0 a	1.9 e	39 abc
Mariachi AMR	100 a	100 a	3 f	50.0 a	50.0 a	1.5 e	8 ijk
Marimba	100 a	100 a	26 de	50.0 a	50.0 a	11.1 d	37 a-d
Merlot	100 a	39 c	3 f	50.0 a	19.5 cd	1.5 e	11 h-k
New Red Fire	100 a	100 a	1 f	50.0 a	50.0 a	0.5 e	25 d-g
Picarde	100 a	100 a	95 a	50.0 a	50.0 a	46.8 a	49 a
Prizehead	100 a	7 de	0 f	50.0 a	3.5 efg	0.0 e	22 e-h
Red Salad Bowl	100 a	66 b	29 d	47.0 a	25.7 c	11.4 d	3 jk
Red Flower	100 a	2 e	0 f	50.0 a	1.0 fg	0.0 e	3 jk
Red Fox	100 a	98 a	25 de	50.0 a	47.1 a	12.5 d	12 h-k
Red Giant	100 a	99 a	1 f	50.0 a	43.6 a	0.3 e	43 ab
Red Prize	80 c	18 d	2 f	40.0 b	8.8 e	0.6 e	3 jk
Red Rage	100 a	10 de	9 f	50.0 a	1.4 fg	1.0 e	15 g-j
Red Rebosa	100 a	100 a	15 def	50.0 a	50.0 a	6.8 de	6 jk
Red Tide	100 a	41 c	2 f	50.0 a	16.5 d	1.0 e	1 k
Redina	100 a	66 b	2 f	50.0 a	33.0 b	0.5 e	19 f-i
Valdai	100 a	100 a	75 b	50.0 a	50.0 a	36.3 b	25 d-g

^zMeans with the same letter in the same column are not significantly different at $P \leq 0.05$.

Table 6. Effect of temperature on seed germination in wild species lettuce.

Genotype	Species	Germination (%)			Germination rate			Field germination (%)
		24 °C	29 °C	34 °C	24 °C	29 °C	34 °C	
IVT 280	VIR	100 a ^z	100 a	76 abc	50.0 a	48.7 ab	24.0 efg	1 ef
PI 187238 A	PRI	100 a	100 a	91 ab	50.0 a	50.0 a	30.8 b-e	14 bc
PI 187238 D	PRI	100 a	100 a	51 de	50.0 a	50.0 a	23.2 e-h	13 bcd
PI 190906	PRI	100 a	100 a	69 cd	48.5 ab	50.0 a	19.8 gh	15 bc
PI 202349 C	PRI	100 a	100 a	7 g	50.0 a	50.0 a	2.3 i	19 b
PI 204753	PRI	95 a-d	8 h	0 g	46.8 a-d	2.1 i	0.0 i	5 ef
PI 271938	VIR	100 a	100 a	78 abc	49.3 ab	50.0 a	22.0 fgh	7 c-f
PI 274378 A	VIR	94 bcd	86 d	41 ef	42.8 e	34.9 d	5.7 i	2 ef
PI 274378 D	VIR	100 a	98 abc	86 abc	43.8 cde	45.5 bc	31.0 b-e	8 cde
PI 274901	VIR	96 a-d	100 a	75 bc	48.0 ab	50.0 a	36.1 abc	17 b
PI 281877	SER	100 a	6 h	0 g	50.0 a	3.0 i	0.0 i	4 ef
PI 289063 A	PRI	100 a	100 a	79 abc	50.0 a	50.0 a	38.9 ab	33 a
PI 289063 C	PRI	100 a	100 a	82 abc	50.0 a	50.0 a	25.1 efg	13 bc
PI 490999	SAL	98 abc	100 a	52 de	48.8 ab	50.0 a	24.3 efg	0 f
PI 491000	SAL	93 cd	35 g	31 f	46.0 b-e	15.8 g	15.1 h	1 ef
PI 491089	SER	100 a	53 f	1 g	48.5 ab	5.4 i	0.1 i	0 f
PI 491112	SER	100 a	100 a	94 a	48.0 ab	50.0 a	37.9 ab	1 ef
PI 491119	SER	100 a	100 a	75 bc	50.0 a	50.0 a	29.7 c-f	3 ef
PI 491134	SER	100 a	100 a	74 bc	50.0 a	50.0 a	27.5 d-g	5 def
PI 491147	SER	100 a	87 cd	86 abc	50.0 a	41.8 c	33.5 bcd	5 ef
PI 491159	SAL	91 d	88 bcd	79 abc	43.5 de	21.5 f	23.8 efg	5 ef
PI 491204	SAL	100 a	54 f	53 de	50.0 a	10.1 h	26.0 d-g	2 ef
PI 491205	SAL	99 ab	71 e	51 de	48.5 ab	33.2 d	23.7 efg	1 ef
PI 491206	SAL	100 a	73 e	49 ef	49.0 ab	28.6 e	24.0 efg	0 f
PI 491207	SAL	98 abc	100 a	37 ef	47.3 abc	50.0 a	15.3 h	0 f
UC96US23	SER	100 a	99 ab	94 a	48 ab	44 c	43 a	nd

^zMeans with the same letter in the same column are not significantly different at $P \leq 0.05$.

VIR = *L. virosa*; SAL = *L. saligna*; PRI = primitive; SER = *L. serriola*.

lettuce by temperature may involve plant hormones such as ABA and GA. High temperature stimulated ABA synthesis and inhibited GA synthesis in imbibed *Arabidopsis* seeds (Toh et al., 2008). The increase in ABA levels in seeds of the Salinas cultivar that exhibited thermoinhibition indicated that ABA plays a key role in thermoinhibition of lettuce seeds (Argyris et al., 2008a; Nambara et al., 2010). ‘Salinas’ also exhibited thermoinhibition at 29 to 34 °C as observed in this study. The observed increase in thermotolerance in UC96US23 was associated with a

decrease in ABA biosynthesis at high temperature (Argyris et al., 2011). Seed covering may also be involved in regulation of seed germination by imposing a restriction on seed germination at high temperature (Ikuma and Thimann, 1963; Speer, 1974; Sung et al., 1998). The stimulation of activities of hydrolytic enzymes is required to promote seed germination and embryo growth (Khan, 1994; Nascimento et al., 2000).

The results of this study indicated that seeds of cultivars and germplasm of various lettuce types (crisphead, romaine, butterhead,

Table 7. Correlation coefficients of percentage seed germination (24, 29, 34 °C and field) among lettuce genotypes.

Lettuce type	Germination	24 °C	29 °C	34 °C
Butterhead	29 °C	0.39*		
	34 °C	0.30	0.65**	
	Field	0.37	0.57**	0.41*
Crisphead	29 °C	0.28		
	34 °C	-0.10	0.42*	
	Field	0.28	0.38	0.33
Romaine	29 °C	-0.14		
	34 °C	-0.18	0.75**	
	Field	-0.20	0.73**	0.68**
Green leaf	29 °C	0.36		
	34 °C	0.24	0.48*	
	Field	0.30	0.20	0.57**
Red leaf	29 °C	0.40		
	34 °C	0.18	0.47*	
	Field	0.30	0.65**	0.52**
Wild species	29 °C	0.28		
	34 °C	0.18	0.72**	
	Field	0.20	0.35	0.23
All lettuce types	29 °C	0.28**		
	34 °C	0.12	0.56**	
	Field	0.27**	0.46**	0.34**

*, **Significant correlations at 5% and 1% levels of probability, respectively.

green and red leaf, and primitive and wild species) differed greatly in their ability to germinate at 29 and 34 °C. However, at 24 °C, seeds of most lettuce genotypes germinated rapidly and uniformly. Some lettuce cultivars and germplasm exhibited thermoinhibition at 29 °C, whereas others exhibited thermotolerance at high temperature (34 °C). The maximum temperatures for thermoinhibition may depend on lettuce genotype. Despite the variations in field germination, seed germination in the field positively correlated with seed germination at 29 and 34 °C. This evaluation of seed germination at 29 and 34 °C helped in identifying lettuce cultivars and germplasm that tolerate high-temperature stress. Selecting lettuce cultivars with good germination at high temperatures is essential to ensure uniform stand establishment and subsequent uniform maturity at harvest.

Most U.S. lettuce production is carried out in the central coast of California with transit to the San Joaquin Valley for a short period in spring and fall and a switch to southern California and Arizona for winter crops. Land costs in the coastal production areas are usually several times higher than in the inland regions. However, production seasons in these low land cost areas are limited by heat stress and thermoinhibition. Seed priming is commonly used to prevent thermodormancy and ensure uniform emergence, even in coastal production areas. Thermoinsensitive lettuce varieties could help expand the production seasons in warm and low land

cost areas nationwide and reduce the need for seed priming, lowering the production costs. As the costs of land, labor, fuel, fertilizer, pesticides, seeds, packing material, cooling, transportation, and overhead including food safety continue to rise, it is essential to reduce production costs of leafy vegetables to benefit producers as well as consumers.

The results from this study may help growers choose lettuce varieties to be grown in a warm environment. These data may also help lettuce breeders to improve the crop for resistance to heat stress. A breeding program usually starts from germplasm screening to find the source of beneficial traits. Because the development of a new lettuce cultivar may take up to 10 years, there is an urgent need to breed thermodormancy-resistant cultivars for adaptation to global warming and climate changes.

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