Seed Developmental Temperature Regulation of Thermotolerance in Lettuce

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Abstract. Lettuce (Lactuca sativa L.) seeds can fail to germinate at temperatures above 24 °C. The degree of thermotolerance is thought to be at least partly related to the environment under which the seed developed. In order to study the effects of temperature during seed development on subsequent germination, various lettuce genotypes were screened for their ability to germinate at temperatures ranging from 20 to 38 °C. Seeds of the selected genotypes ‘Dark Green Boston’ and ‘Valmaine’ (thermosensitive), ‘Floricos 83’, ‘Everglades’, and PI 251245 (thermotolerant) were produced at 20/10, 25/15, 30/20, and 35/25 °C day/night temperature regimes in plant growth chambers. Seeds were germinated on a thermostatic bar from 24 to 35 °C under 12-h light/dark cycles. As germination temperature increased, the number of seeds that failed to germinate increased. Above 27 °C, seeds matured at 20/10 or 25/15 °C exhibited a lower percent germination than seeds that matured at 30/20 or 35/25 °C. Seeds of ‘Dark Green Boston’ and ‘Everglades’ that matured at 30/20 °C exhibited improved thermotolerance over those that matured at lower temperatures. Seeds of ‘Valmaine’ produced at 20/10 °C exhibited 40% germination at 30 °C, but seeds that matured at higher temperatures exhibited over 95% germination. Germination of ‘Valmaine’ at temperatures above 30 °C was not affected by seed maturation temperature. The upper temperature limit for germination of lettuce seed could thus be modified by manipulating the temperature during seed production. The potential thermotolerance of seed thereby increased, wherein thermosensitive genotypes became thermotolerant and thermostolerant genotypes (e.g., PI 251245) germinated fully at 36 °C. This information is useful for improving lettuce seed germination during periods of high soil temperature, and can be used to study the biology of thermotolerance in lettuce.

The primary method of planting lettuce (Lactuca sativa L.) is by direct seeding. Lettuce seed germination is temperature dependent, with the optimum temperature for seed germination of most cultivars in a range between 15 and 22 °C while some cultivars can tolerate temperature as high as 33 °C (Gray, 1975). When temperature rises 2 to 3 °C above the maximum level for a specific genotype, germination sharply declines. This phenomenon is termed thermoinhibition. Subsequently, if the temperature is quickly lowered, this inhibition can be reversed and germination proceeds. However, if the imbibed seeds are subjected to high temperature for an extended period of time, a secondary dormancy, called thermodormancy, is induced. Such dormant seeds exhibit delayed germination even if they are returned to low temperatures (Khan, 1980–81).

To avoid poor stands in the field under conditions of high temperature, it is necessary to bypass thermoinhibition in lettuce seed before planting. This, in turn, leads to rapid emergence and stand uniformity, which is extremely important in order to maximize yields from crops such as lettuce. Thermoinhibition is a more transient condition than thermodormancy, so preventing thermoinhibition prevents the onset of thermodormancy.

The level of thermotolerance and its effects on lettuce seed germination are genotype-dependent (Gray, 1975; Thompson et al., 1979). A number of lettuce genotypes that germinate at high temperature have been identified. One of these, PI 251245, is particularly thermotolerant (Bradford, 1985). The Spanish bibb type lettuce ‘Maturo’ has also been widely used as parental material in many breeding programs and it is thought that its thermotolerant character was transferred to other cultivars such as ‘Tall Guzmaint’ and ‘Floricos 83’ (Guzman, 1986; Guzman et al., 1992; Guzman and Zitter, 1983). A wild lettuce accession, PI 251245, has been studied for its thermotolerant character. Seeds of PI 251245 had 100% germination at 30 °C (Bradford, 1985); however, the expression of thermotolerance was not consistent and was suggested by Nagata (personal communication) to be dependent on where the seeds were produced. Thus seed thermotolerance may be improved by breeding since the thermotolerant character may be inherited.

Light and the environment in which the seed matures can affect germination performance at supraoptimal temperature. Photosensitive lettuce seed has a functional phytochrome system and therefore germination responses are affected by red or far-red light irradiation (Borthwick et al., 1952). Evenari et al. (1953) have reported that there are two possible photomechanisms influencing germination. One mechanism ensures that germination is not affected by light and operates down to a certain temperature limit. Below that limit germination cannot be decreased by light alone. The other mechanism is light-sensitive, responding to the effects of red as well as far-red light and operates up to the temperature limit above which germination cannot be increased by light alone. Scheibe and Lang (1965) surmised that low temperature prevents the transformation of the physiologically active Pfr form to the inactive Pr form. Fielding

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et al. (1992) reported that increasing Pfr levels caused a successive increase in the upper temperature limit for germination.

The upper germination temperature limit can be modified by manipulating the environment during lettuce seed production (Harrington and Thompson, 1952). Damania (1986) evaluated 62 genotypes of lettuce obtained from several locations and indicated that seeds collected from hot climatic zones tended to germinate at higher temperatures. Moreover, seed maturation at high temperature can affect the seed’s subsequent germination behavior (Gray et al., 1988b; Kolier, 1962). Seed germination percentage at high temperature can be increased, but seed size, weight, and yield may be reduced (Drew and Brocklehurst, 1990; Steiner and Opoku-Boateng, 1991).

The objective of this investigation was to determine if temperature at which the seed developed could alter the level of thermostolerance at germination in various thermostressive lettuce genotypes. By applying a range of developmental temperatures during seed development, it may be possible to precisely define the trigger needed to improve germination at formerly supraoptimal temperatures.

**Materials and Methods**

**GERmplASM SELECTION.** Seed of 21 genetic lines known to display various levels of thermostolerance were obtained from the breeding program at the University of Florida, Everglades Research and Education Center, Belle Glade. In a preliminary test, plants from the 21 lines were grown and, as the flower buds became visible, 20 plants from each line were moved into growth chambers (F-15, Conviron, Winnipeg, Manitoba, Canada) that maintained temperatures of 20/10, 25/15, 30/20, and 35/25°C (day/night) in a 12-h photoperiod (500 \( \mu \text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1} \)) and 75% to 80% relative humidity (RH). As the plants grew, they were irrigated daily and were fertilized as needed with 3500 mg L\(^{-1}\) of 20N-8.6P-16.7K. Mature seeds were harvested from plants growing in each growth chamber, then stored at 10°C and 40% RH for 2 months to afterripen.

**PRELIMINARY GERMINATION TESTS.** Genotypes were selected according to their seed’s ability to germinate under high temperature. Germination tests were conducted on a one-dimensional thermogradient bar (Type DB 5000, Van Dok and De Boer B.V., Enkhuizen, the Netherlands) in a linear temperature gradient of 20, 24, 27, 30, 33, and 35°C.

Twenty seeds from each genotype, matured at each of the four temperatures, were placed on 5-cm-diameter blue blotters (Anchor Paper Co., Inc., St. Paul, Minn.) moistened with 6 mL of distilled water and positioned at areas of the bar set at 20, 24, 27, 30, 33, 35, and 38°C. Blotters were covered with 5.5-cm petri dish lids and were remoistened with distilled water as needed. Germination was in the dark and was documented when a visible radicle protruded through the seed coat. All treatments were replicated three times.

Seeds of an additional 10 lettuce genotypes produced in the Salinas area of California in 1992 were germinated. Germination tests, replicated three times for each genotype, were conducted at temperatures of 20, 24, 27, 30, 33, 35, and 38°C.

**SELECTION OF VARIOUS THERMOSENSITIVE GENOTYPES.** Various genotypes were selected according to their germination potential (data not shown) and classified as thermostressive ('Valmaine' and 'Dark Green Boston') or thermotolerant ('Floricos 83', 'Everglades' and PI 251245). 'PI 251245' is a wildtype. 'Everglades' and 'Dark Green Boston' are butterhead types 'Floricos 83' and 'Valmaine' are cos types.

**SEED PRODUCTION.** Seedlings of selected genotypes were cultivated in 15 cm diameter pots containing media consisting of a mixture of coarse vermiculite and Speedling Fortified Tobacco Mix (Bushnell, Fla.) (1:5 v/v). The pots were placed in a greenhouse located in Gainesville, Fla. In the greenhouse, the average day/night temperature in summer was 40/28°C and in winter 25/15°C, light was 550 \( \mu \text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1} \) and RH was 75% to 80%. As the plants grew, they were irrigated daily as needed and were fertilized once every 14 days using 3500 mg L\(^{-1}\) of 20N-8.6P-16.7K. As the flower buds became visible, 20 plants from each genotype were moved to each of four growth chambers, for a total of 80 plants per genotype. All growth chambers were programmed for a 12-h photoperiod, light intensity of 500 \( \mu \text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1} \) and a RH of 75% to 80%. Day/night temperatures were 20/10, 25/15, 30/20, or 35/25°C. Seed production was repeated in May 1993, January 1994, and June 1994.

Pollination occurred naturally in all genotypes at all temperatures except 35/25°C and for ‘Everglades’ at 30/20°C. In order to ensure adequate pollination, flowers were hand-pollinated by means of cotton swabs (Johnson & Johnson, Skillman, N.J.). When seeds matured, they were harvested by hand, bulked, threshed, and cleaned. Seeds were stored at 10°C and 45% RH for 6 months to afterripen. After storage, 100 seeds of each genotype and treatment were weighed.

**GERMINATION TEST.** Germination temperatures on the thermogradient bar were 24, 27, 30, 33, and 36°C. Thirty seeds of each genotype and each seed maturation temperature were placed on one layer of 5-cm-diameter blotter paper and moistened with distilled water. Two layers of blotter paper were used for the 33 and 36°C treatments. Germination tests were conducted under fluorescent light (=26 \( \mu \text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1} \)) in a 12-h photoperiod or in the dark. Germination was measured as radicle protrusion and normal seedling development was recorded daily for 7 d. Percent germination and mean days to germination (MDG) were calculated as a measure of response to each treatment. The MDG was

<table>
<thead>
<tr>
<th>Temp (°C)</th>
<th>Dark Green Boston</th>
<th>Everglades</th>
<th>Floricos 83</th>
<th>Valmaine</th>
<th>PI 251245</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>L/D</td>
<td>D</td>
<td>L/D</td>
<td>D</td>
<td>L/D</td>
</tr>
<tr>
<td>24</td>
<td>100.0</td>
<td>100.0</td>
<td>100.0</td>
<td>100.0</td>
<td>100.0</td>
</tr>
<tr>
<td>27</td>
<td>74.0</td>
<td>0.0</td>
<td>100.0</td>
<td>100.0</td>
<td>100.0</td>
</tr>
<tr>
<td>30</td>
<td>3.3</td>
<td>0.0</td>
<td>100.0</td>
<td>100.0</td>
<td>99.0</td>
</tr>
<tr>
<td>33</td>
<td>0.0</td>
<td>0.0</td>
<td>43.0</td>
<td>37.0</td>
<td>83.0</td>
</tr>
<tr>
<td>36</td>
<td>0.0</td>
<td>0.0</td>
<td>6.0</td>
<td>3.3</td>
<td>4.7</td>
</tr>
</tbody>
</table>

**N** = Non-significant or significant at P = 0.05 or 0.01, respectively, by F test.
Table 2. Mass (mg/100 seeds) of lettuce seeds matured under four temperatures.

<table>
<thead>
<tr>
<th>Genotype</th>
<th>20/10</th>
<th>25/15</th>
<th>30/20</th>
<th>35/25</th>
<th>LSD&lt;sub&gt;0.05&lt;/sub&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dark Green Boston</td>
<td>169*</td>
<td>146</td>
<td>125</td>
<td>107</td>
<td>13</td>
</tr>
<tr>
<td>Everglades</td>
<td>171</td>
<td>163</td>
<td>143</td>
<td>133</td>
<td>6</td>
</tr>
<tr>
<td>Valmaine</td>
<td>146</td>
<td>147</td>
<td>142</td>
<td>103</td>
<td>31</td>
</tr>
<tr>
<td>Floricos 83</td>
<td>156</td>
<td>138</td>
<td>125</td>
<td>107</td>
<td>22</td>
</tr>
<tr>
<td>PI 251245</td>
<td>217</td>
<td>155</td>
<td>160</td>
<td>145</td>
<td>10</td>
</tr>
</tbody>
</table>

*Mean separation within genotypes by LSD test at P = 0.05.

calculated according to the formula $\Sigma T_i N_i/\Sigma N_i$, where $N_i$ is the number of newly germinated seeds at day $T_i$ (Maguire, 1962).

Experimental design and statistical analysis. Five genotype and four seed maturation temperature effects were evaluated in the germination tests. The study was conducted using a split-block experimental design. Germination temperature was the main block and seed lots or treatments were the split-block. The experiment was replicated three times.

Germination percentages were transformed to a square root arc sine basis before statistical analysis. Analysis of variance (ANOVA) of data was performed by means of Statistical Analysis System (SAS) software. The main effect of germination temperature was partitioned into linear, quadratic, or cubic orthogonal contrasts. The effect of seed maturation temperature was partitioned using a single degree of freedom orthogonal contrasts. The first contrast compared the response between the lower temperatures (20/10 and 25/15 °C) and the higher temperatures (30/20 and 35/25 °C), the second contrast tested the response within the higher temperatures. Means were separated by the Fisher’s protected least significant difference (LSD) test, 5% level of confidence.

Results

Effect of light on seed germination. All seeds that were produced in the Salinas area in California germinated at 24 °C, regardless of genotype or light condition (Table 1). At 27 °C, germination of ‘Dark Green Boston’ (a thermosensitive genotype) was 74% in light, but did not germinate in the dark or at any temperature above 24 °C. Germination of ‘Valmaine’ (a thermosensitive genotype) was partially inhibited in light at 30 °C and seeds did not germinate above 30 °C. ‘Floricos 83’, ‘Everglades’, and PI 251245, all thermotolerant genotypes, germinated well at 30 °C in light or dark. Above 30 °C, germination of ‘Everglades’ declined in light and dark. For ‘Floricos 83’ and PI 251245, germination in light at 33 °C was 83% and 94%, respectively, but fell to ≈40% and 50% in the dark. At 36 °C, PI 251245 germination was 31% in light and 18% in dark. Thus, temperature had a profound influence on the ability of these genotypes to germinate. Light generally had a small influence. Some genotypes were clearly more thermotolerant than others, i.e., ‘Dark Green Boston’ vs. PI 251245.

Seed mass and shape. Seed weight of all five genotypes decreased as temperature during seed maturation increased (Table 2). Seeds matured at 20/10 and 25/15 °C were significantly heavier than those matured at 35/25 °C. Seed weights were 37% and 22% greater at the lowest temperature regime for ‘Dark Green Boston’ and ‘Everglades’, respectively. In the other three genotypes, weight was ≈30% to 33% greater at the 20/10 and 25/15 °C seed maturation temperatures. Seeds that matured at 20/10 and 25/15 °C were larger in surface area than those matured at 35/25 °C (data not shown).

Effect of seed maturation temperatures on seed germination. The upper temperature limit for germination of ‘Dark Green Boston’ was significantly enhanced when the seeds matured at 30/20 and 35/25 °C (Fig. 1). When seeds matured at 30/20 °C, the percentage of germination was 54 at 36 °C, while seeds from plants grown at 20/10 and 25/15 °C essentially did not germinate above 27 °C. Seeds matured at 25/15 °C had greater germination at 27 °C than seeds matured at 20/10 °C. When ‘Everglades’ seeds were germinated at 33 and 36 °C, seeds matured at 30/20 °C had better germination than those matured at 35/25 °C (Fig. 2). At 33 and 36 °C, seeds that matured at 30/20 and 35/25 °C exhibited higher germination than those that matured at 20/10 and 25/15 °C.

At 27 °C, all seeds of ‘Valmaine’ germinated >90% regardless of maturation temperature (Fig. 3). Seeds matured at 20/10 °C had <50% germination at 30 °C while germination was maintained at 100% for seeds matured at the other three temperature regimes. ‘Valmaine’ essentially did not germinate above 30 °C, regardless of maturation temperature.

Seeds of ‘Floricos 83’ matured at 35/25 and 30/20 °C had more than 40% germination at 36 °C (Fig. 4). At 33 and 36 °C, germination of seeds matured at 20/10 and 25/15 °C was below 40%.

Seeds of PI 251245 matured at 35/25 °C had nearly 100% germination at 36 °C (Fig. 5). Seeds matured at 30/20 and 25/15 °C had >75% germination percentages at 36 °C. Seeds matured at 20/10 °C had a linear decrease in germination as temperature increased from 27 to 36 °C. Germination at 36 °C of seeds from this maturation temperature was significantly less than that of seeds produced under the other temperatures. Except for ‘Floricos 83’ and PI 251245, there were no significant interactions between seed maturation and germination temperature on the average MDG (Table 3). Otherwise average MDG increased as temperature increased from 27 to 36 °C, regardless of maturation temperature (Table 4). MDG were delayed more in thermosensitive genotypes such as ‘Dark Green Boston’ (Table 4) than in thermotolerant types such as PI 251245 (Table 3). The genotypes generally germinated more slowly than when seed

Fig. 1. Germination percentage of ‘Dark Green Boston’ lettuce seeds matured under four temperatures in 12 h light/12 h dark. Vertical bars indicate standard error.
matured at the lower temperatures (20/10 and 25/15°C) rather than at the higher temperatures (30/20 and 35/25°C).

**Discussion**

In the present research, all five genotypes germinated well at 24°C either in light or dark. The addition of light during germination caused an increase of ≈ 3°C in the upper temperature limit in all genotypes but 'Everglades'.

Seeds that matured at high temperature had increased thermostolerance. Generally, the upper germination limit was increased when seeds were matured above 30/20°C compared to the two lower temperature regimes. Koller (1962) reported that when 'Grand Rapids' lettuce seeds matured at 30/23°C, the high-temperature tolerance for germination was improved. Gray et al. (1988b) reported that more seeds of 'Saladin' germinated at 30°C when they were produced at 30/20°C than those matured at 25/15 or 20/10°C. All of these observations demonstrated that, in certain lettuce genotypes, increasing the temperature at which seeds matured resulted in greater seed thermostolerance.

Koller (1962) indicated that good seed set in lettuce occurred at night temperatures between 17 and 23°C. In California, most lettuce seed is produced in the central portion of the San Joaquin Valley where daytime temperatures may exceed 38°C for many

Table 3. Mean days to germination (MDG) of ‘Floricos 83’ and ‘PI 251245’ lettuce seed matured under four day/night temperatures with a 12-h photoperiod.

<table>
<thead>
<tr>
<th>Seed maturation temp (SMT) (°C)</th>
<th>Floricos 83</th>
<th>Germination temp (°C)</th>
<th>PI 251245</th>
</tr>
</thead>
<tbody>
<tr>
<td>20/10</td>
<td>27  30  33</td>
<td>27  30  33  36</td>
<td>27  30  33  36</td>
</tr>
<tr>
<td>1.3</td>
<td>1.9</td>
<td>1.9</td>
<td>1.6</td>
</tr>
<tr>
<td>1.0</td>
<td>1.2</td>
<td>1.3</td>
<td>1.5</td>
</tr>
<tr>
<td>2.1</td>
<td>2.9</td>
<td>1.9</td>
<td>1.9</td>
</tr>
<tr>
<td>1.0</td>
<td>1.0</td>
<td>1.1</td>
<td>1.3</td>
</tr>
</tbody>
</table>

**Significant at \( P = 0.05 \) (LSD_{0.05} value for seed maturation temperature × germination temperature = 1.7) or 0.01 (LSD_{0.01} value for seed maturation temperature × germination temperature = 1.3) by F test.

Table 4. Mean days to germination (MDG) of 'Dark Green Boston' (DGB), 'Everglades' (EG), and 'Valmaine' (VAL) lettuce seed matured under four day/night temperatures with a 12-h photoperiod.

<table>
<thead>
<tr>
<th>Seed maturation temp (°C)</th>
<th>DGB</th>
<th>EG</th>
<th>VAL</th>
</tr>
</thead>
<tbody>
<tr>
<td>20/10</td>
<td>5.9</td>
<td>1.9</td>
<td>3.9</td>
</tr>
<tr>
<td>25/15</td>
<td>4.1</td>
<td>1.6</td>
<td>3.3</td>
</tr>
<tr>
<td>30/20</td>
<td>2.2</td>
<td>1.3</td>
<td>3.2</td>
</tr>
<tr>
<td>35/25</td>
<td>2.4</td>
<td>1.7</td>
<td>2.8</td>
</tr>
</tbody>
</table>

Germination temperature (°C)

- 27: 2.6, 1.1, 1.4
- 30: 3.2, 1.4, 2.1
- 33: 4.4, 1.8, 4.7
- 36: 4.4, 2.3, 5.0

Contrasts (day temperature, °C)

- 20 + 25 vs. 30 + 35: ** NS
- 20 vs. 25: ** NS
- 30 vs. 35: NS NS

Germination temperature

Seed maturation temperature ×

germination temperature

**NS**, **Nonsignificant or significant at P = 0.05 or 0.01, respectively, by F test. Significant germination temperature effects were linear (L), quadratic (Q), or cubic (C).

Consecutive days during lettuce seed production. Steiner and Opoku-Boateng (1991) reported that in Fresno, California, which is close to the central lettuce seed growing area, from August to September, 1988, the minimum temperatures during the day ranged from 11 to 22 °C and the maximum ranged from 30 to 40 °C. This suggested that day/night temperatures of 30/20 °C may be in the natural range of commercial lettuce seed production from California.

Lettuce seed size, weight, and total yield can be affected by seed maturation temperature (Drew and Brocklehurst, 1990; Steiner and Opoku-Boateng, 1991). When seeds in the present research were matured above 30 °C, inadequate pollination and subsequent seed set occurred resulting in small seed size. However, as seed maturation temperature decreased, seed size and weight increased. Gray et al. (1988a) noted that in carrot an increase in temperature from 20/10 to 30/20 °C reduced mean weight per seed by 17%, but there was no effect of temperature on endosperm and embryo weight, or on endosperm cell number. In lettuce, the cell number per embryo and cotyledons of 'Saladini' seed was similar at 25/15 and 30/20 °C, but both were lower as compared with seeds grown at 20/10 °C (Gray et al., 1988b).

According to Fenner (1992) reduction in seed size at high production temperature could be due to the differential effect of temperature on the seed ripening and filling processes. The further increase in weight of seed matured at low temperature was due to longer period of seed filling, which facilitated improved use of photosynthetic products and increased storage of carbohydrates. In the present experiment, plants grown at 35/25 °C had pale green to yellowish leaves two weeks after anthesis, however, plants grown at 20/10 °C had green leaves for two months. The period for full seed maturation under lower temperature was 7 to 10 d longer than those matured under high temperature. Thus seeds matured at lower temperatures may be able to accumulate more nutrients and subsequently increase their size.

There is a positive correlation between seed size and seed vigor when seeds mature in the same environment. The larger or heavier the seed, the greater the germination percentage and the more vigorous the seedling in lettuce and other crops (Pollock and Roos, 1972; Soffer and Smith, 1974; Smith et al., 1973). Our results suggest that although seed size and weight were reduced when seed matured above 30 °C, the seeds had greater thermotolerance.

Expression of thermostolerance in lettuce seed is regulated by environmental seed maturation temperature regardless of genotype. Thus, if plant breeders or seed producers were seeking thermostolerant germplasm or attempting to develop more thermotolerant lettuce seeds, the environment in which the seeds are produced becomes extremely important. Temperature data during seed maturation should be recorded and maintained in order to better predict the potential for developing greater thermostolerance in lettuce seeds. Likewise, unless temperature during lettuce seed development is considered, plant breeders cannot adequately screen populations for thermostolerance.

One of the more significant factors from this research is the potential for better study the physiological-biochemical factors that govern thermomorphy and the ability of a seed, especially lettuce, to germinate at high temperature. Seed development temperature can regulate relative thermostolerance or thermosensitivity. Potentially one might be positioned to characterize and elucidate genes and the mechanism responsible for conferring germination heat tolerance.

Literature Cited


