

Article

Temperature Limits for Seed Germination in Industrial Hemp (*Cannabis sativa* L.)

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Abstract: Industrial hemp (*Cannabis sativa* L.) as a grain and fiber crop is experiencing a resurgence in North America. Due to governmental prohibition, there has been limited information on regional agronomic production systems including basic information on seed germination. This study was initiated to provide basic information on the relationship between temperature and germination in hemp seed. Germination was measured at constant temperatures ranging from 3 to 42 °C. Cardinal temperatures were determined for two industrial oil crop hemp cultivars ('Georgina' and 'Victoria'). The optimal germination temperature indicated by a high mean germination percentage and rate was between 19 and 30 °C. Optimal (29.6 °C), base (3.4 °C) and ceiling (42.6 °C) temperatures were calculated from a linear regression of the germination rates to reach 50% germination for each temperature. The thermal time for 'Georgina' and 'Victoria' to reach 50% germination at suboptimal temperatures was 694 and 714 °C h, respectively. The osmotic and solid matrix-primed hemp seeds germinated faster than the untreated seeds, but the final germination percentages were not different. The primed seeds germinated faster at supraoptimal temperatures but did not impact final germination percentages in the thermally inhibited seeds.

Keywords: seed vigor; priming; osmotic priming; solid matrix priming; thermal time; cardinal temperatures; thermal inhibition



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1. Introduction

Hemp (*Cannabis sativa* L.) has been grown for its fiber, oil-rich seed and psychoactive resins for over 5000 years [1]. Today, it is estimated that over 25,000 different food, fiber and medicinal products can be derived from the hemp plant [2]. Most modern production of industrial hemp occurs in China, Canada and several European countries [3]. Industrial hemp production was common in North America until governmental restrictions were imposed after WWII. In the United States, the 2014 Farm Bill began the process of reinitiating industrial hemp production as an agricultural commodity [2].

Due to years of governmental prohibition, there is limited information on agronomic production systems, including basic information on seed germination. Temperature is an important environmental factor for scheduling field seeding. Spring sowing time can impact weed management strategies and since industrial hemp is daylength sensitive for flowering, time from seedling emergence to harvest influences crop biomass and seed yields [4]. Several crop models have been developed for hemp production in Europe [5,6]. These studies indicated that plant emergence under field conditions was faster when the minimum soil temperatures ranged between 13.5 and 18.5 °C, while temperatures under 10 °C and over 24 °C increased time to seedling emergence [6]. However, there is less information on the influence of temperature on time to initial germination under controlled conditions in hemp [7–10]. One important aspect of seed germination available for most commercially important crops is the response to temperature. Temperature impacts both germination percentage and time to radicle emergence. It is therefore important to describe

seed germination in hemp over a range of temperatures. Three cardinal temperature points represented as base (minimum), optimum and ceiling (maximum) can be designated for seed germination. Seeds germinated at optimal temperatures have the highest percentage of seeds germinated in the shortest period of time. The optimum temperature for non-dormant seeds in most commercially produced plants is between 25 and 30 °C but can be as low as 15 °C for some cool-season crops. The base cardinal temperature is the lowest temperature for effective germination, while the maximal cardinal temperature is the highest temperature at which germination occurs. Above the maximum temperature, seeds are either injured, thermally inhibited for germination or in some cases enter secondary dormancy. Global climate change has placed renewed interest in high temperature plant stress, including germination and seedling establishment [11]. Columbia *Arabidopsis* begins to lose the ability to germinate at 45 °C and seedling viability is lost after a twenty-minute exposure at that temperature [12]. Seeds exposed to high temperature stress during germination show delayed storage reserve mobilization, protein degradation, loss of enzyme activity, loss of de novo protein synthesis and loss of membrane integrity leading to cellular damage and collapse after prolonged exposure [13,14].

Seed priming is a pre-germination-controlled hydration treatment where seeds are imbibed in a situation where the water potential is kept between -1.0 and -2.0 MPa, usually using osmotic or matric forces for several days at a controlled temperature before being dried back to near their original dry weight [15]. A major benefit to seed priming is a coordinated reduction in the time from initial imbibition to radicle emergence, leading to improved germination uniformity [16]. It is generally observed that primed seeds show improved germination under less-than-optimal environmental conditions, including heat stress [17]. Responses to abiotic stress include changes in plant metabolites, hormone signaling cascades and reactive oxygen pathways [18]. Seed priming initiates early physiological processes that are important for the transition from a dry seed to germination competency, and they are retained in the primed dry seed. This “primed state” includes processes related to stress tolerance and is thought to improve the germination of a wider range of environments compared with non-primed seeds [19].

Therefore, the current study was initiated to provide basic information on the relationship between temperature and seed germination in hemp seed. The objectives were to determine the cardinal temperatures for hemp seed germination and provide estimates of thermal time required to initiate radicle protrusion at constant temperatures. In addition, the impact of seed priming on germination rate and final germination percentages were determined in relation to temperature stress.

2. Materials and Methods

2.1. Plant Materials

Industrial hemp (*Cannabis sativa* L.) seeds (achenes) of ‘Georgina’ and ‘Victoria’ were supplied by Atalo, Winchester KY. Seeds were stored in sealed plastic bags at 10 °C and were stored for less than two years.

2.2. Germination Conditions

Seed germination occurred in plastic petri dishes (100 × 15 mm) containing 2 pieces of Grade 8001 germination paper (Stults Scientific Co., Springfield, IL, USA) moistened with 6 mL of deionized water and sealed with parafilm (Bemis Flexible Packaging, Shirley, MA, USA). Standard and accelerated aging germination (8 replicates with 25 seeds per petri dish) occurred in a lighted incubator (8 h light, 16 h dark at approximately $60 \mu\text{mol m}^{-2} \text{s}^{-1}$) at 20–30 °C [20]. For accelerated aging, approximately 200 seeds were distributed in a single uniform layer on stainless steel screens and were placed in closed germination boxes (11 × 11 × 3.5 cm) containing 40 mL of deionized water below the screen. The seeds were placed in a water-jacketed accelerated aging chamber and were held at 41 °C for 72 h. Following aging, normal seedlings were recorded after 3 and 7 days [20]. The seed moisture

content on a fresh weight basis was determined before and after accelerated aging for 100 seeds placed in a forced-air oven at 105 ± 3 °C for 48 h.

2.3. Germination and Temperature

For temperature germination studies, at each temperature, four replicates of 25 seeds for each seed lot were placed in petri dishes as previously described in Section 2.2, and they were moved to an insulated two-dimension aluminum plate thermogradient table. Additional water was added to petri dishes as needed at the warm temperature treatments. For temperature studies, germination (radicle protrusion) was recorded every 4 h for the first two days and then daily until day seven. Germination was measured at temperatures ranging from 3 to 42 °C. The thermal gradient was produced by recirculating water baths containing 50% propylene glycol at opposite ends of a 5 cm thick aluminum plate. The temperature was measured each time germination data were recorded along the gradient with a Taylor 1441 E temperature probe (Taylor Precision Products, Oak Brook, IL, USA).

The germination capacity in thermally inhibited ‘Georgina’ and ‘Victoria’ seeds was evaluated by moving low- or high-temperature-exposed seeds to permissive germination conditions (lighted incubator at 20/30 °C). Imbibed seeds in petri dishes were held in an incubator at 3 °C for 7 days or at 42 °C for 24, 48, 72 and 96 h prior to moving to germination conditions. After 7 days, the non-germinated seeds were evaluated for viability using TZ (2,3,5 triphenyl tetrazolium chloride). Seeds with the seed coverings removed were soaked in a 0.1% TZ solution at 25 °C for 18 h. The seeds were considered viable if staining occurred over at least 1/3 of the radicle and cotyledon area. There were 25 seeds per petri dish with four replications per treatment.

The impact of temperature on seed germination and seedling emergence was evaluated in ‘Victoria’ by sowing seeds in cell trays containing a Pro-Mix substrate (Premier Tech Horticulture, PA, USA). Cell trays (12.3 × 12.3 × 5.9 cm) were either held at a constant temperature of 20/30 °C or 35 °C or at 20/30 °C or 35 °C for two days before moving to reciprocal temperatures. There were 20 seeds per cell trays with 10 replications.

2.4. Seed Priming

‘Victoria’ hemp seeds were primed using a solid matrix or osmotic priming systems. Solid matrix priming was used a ratio of 3.2 g of Micro-Cel with 5.6 mL of water and 4 g of seeds. The seeds were held at 10 or 24 °C for 2 to 4 days. Osmotic priming occurred in an aerated salt (KCl) solution at -1.15 MPa at 10 °C for 2 to 4 days. Following priming, the seeds were rinsed and air dried for 24 h under a laminar flow hood to their near-original moisture content. Germination occurred in petri dishes (5 replicates with 25 seeds per dish) under standard germination conditions described previously in Section 2.2.

The impact of priming on germination at high temperatures was evaluated using osmotically primed ‘Victoria’ hemp seeds germinated at temperatures between 33 and 41 °C. Germination occurred in petri dishes as previously described (5 replicates with 25 seeds per dish).

2.5. Data Analysis

The germination rate was calculated as the inverse of the time-to-germination (radicle protrusion) at each temperature for subpopulations between 20 and 80% germination percentiles. The thermal time was calculated from the inverse of the slopes of the linear regression of the germination rate for each germination subpopulation and temperature [21]. Regression models were generated using SigmaPlot 12.3 (Systat Software, Richmond, CA, USA). Where appropriate, means were statistically separated using Tukey’s test or single degree of freedom F-tests at $p \leq 0.05$.

3. Results

3.1. Germination and Vigor

Standard germination and vigor tests were conducted to provide a baseline for seed quality in each seed lot. The standard germination was statistically the same for the 'Georgina' and 'Victoria' seed lots used in this study (Table 1). 'Victoria' showed higher seed vigor compared to 'Georgina', as indicated by the accelerated aging germination, especially at the early 3-day count (Table 1). Elias et al. [22] also found accelerated aging to be effective for evaluating relative seed vigor in hemp seed.

Table 1. Standard and accelerated aging germination percentage in two hemp cultivar seed lots evaluated after 3 and 7 days. Seeds were aged at 41 °C for 3 days prior to standard germination.

| Cultivar | Standard Germination (%) | | | Accelerated Aging Germination (%) | | |
|------------|--------------------------|--------|--------------|-----------------------------------|--------|--------------|
| | 3 days | 7 days | Moisture (%) | 3 days | 7 days | Moisture (%) |
| 'Georgina' | 76.5b ^x | 89.5 a | 8.3 | 57.5 b | 74.5 b | 24.9 |
| 'Victoria' | 84.0 a | 91.5 a | 8.4 | 81.0 a | 88.0 a | 23.5 |

^x Means within a column followed by the same letter were not different at 5% level by Tukey's test.

3.2. Germination and Temperature

The germination percentage, speed and uniformity for the 'Georgina' and 'Victoria' seed lots showed a typical response to temperature (Table 2). The optimal germination temperatures indicated by a high germination percentage and rate (time to 50% germination) were between 19 and 30 °C (Table 2).

Table 2. Germination percentage, speed and uniformity related to germination temperature for two hemp cultivars after 7 days.

| Cultivar | Temperature (°C) | Germination Percentage | Time to 50% Germination (h) | (T ₈₀)–(T ₂₀) |
|------------|------------------|------------------------|-----------------------------|---------------------------------------|
| 'Georgina' | 3 | 0 | - | - |
| | 10 | 87 | 91.0 | 17.5 |
| | 15 | 96 | 63.5 | 40.5 |
| | 19 | 92 | 43.4 | 19.6 |
| | 24 | 94 | 33.2 | 14.0 |
| | 27 | 84 | 32.5 | 13.8 |
| | 30 | 68 | 31.7 | 14.0 |
| | 33 | 70 | 31.8 | 21.8 |
| | 36 | 70 | 36.8 | 27.0 |
| | 39 | 29 | - | - |
| | 42 | 0 | - | - |
| 'Victoria' | 3 | 0 | - | - |
| | 10 | 91 | 107.5 | 23.0 |
| | 15 | 98 | 76.5 | 51.2 |
| | 19 | 100 | 43.7 | 29.2 |
| | 24 | 92 | 34.6 | 17.3 |
| | 27 | 96 | 32.1 | 12.3 |
| | 30 | 84 | 30.5 | 14.8 |
| | 33 | 84 | 30.9 | 13.9 |
| | 36 | 70 | 65.4 | 39.5 |
| | 39 | 22 | - | - |
| | 42 | 0 | - | - |

The 'Georgina' and 'Victoria' seeds failed to germinate at 3 and 42 °C (Table 2), but it was unclear if this was due to thermal inhibition, thermal dormancy or thermal intolerance. The seeds held at 3 °C showed thermal inhibition and recovered their ability to germinate once transferred to 25/30 °C (Table 3). However, the seeds held at 42 °C were initially

thermally inhibited, but with longer exposure to a high temperature, the seeds progressively showed reduced viability and failed to recover germination after 4 days (Table 3). This indicated that the ‘Georgina’ and ‘Victoria’ hemp seeds showed progressive intolerance to high temperatures and became inviable after four days.

Table 3. Thermal inhibition in ‘Georgina’ and ‘Victoria’ hemp seeds held at 3 or 42 °C for various times before moving to standard germination conditions (20/30 °C).

| Initial Temperature | Cultivar | Duration (Days) | Germination (%) | Tetrazolium Staining in Non-Germinated Seeds | |
|---------------------|------------|-----------------|-------------------|--|----------------|
| | | | | Viable (%) | Non-Viable (%) |
| 3 °C | ‘Georgina’ | 0 | 87 a ^x | - | - |
| | | 7 | 82 a | - | - |
| | ‘Victoria’ | 0 | 89 a | - | - |
| | | 7 | 86 a | - | - |
| 42 °C | ‘Georgina’ | 0 | 84 a | 11 | 5 |
| | | 1 | 70 b | 5 | 25 |
| | | 2 | 64 bc | 3 | 33 |
| | | 3 | 25 c | 0 | 75 |
| | | 4 | 0 | 1 | 99 |
| | ‘Victoria’ | 0 | 86 a | 11 | 3 |
| | | 1 | 73 b | 13 | 13 |
| | | 2 | 44 c | 10 | 45 |
| | | 3 | 8 d | 0 | 92 |
| | | 4 | 0 | 0 | 100 |

^x Means within a column for each cultivar followed by the same letter were not different at 5% level by Tukey’s test.

In a seedling growth study, the ‘Victoria’ seeds were germinated in a greenhouse substrate and were held for two days at 25/30 °C or 35 °C prior to being moved to the reciprocal temperature (Table 4). Seedling emergence was reduced when the germination temperature was held at a constant 35 °C or in seedling trays held for two days at 35 °C prior to moving to the permissive temperature. However, seedling emergence was not reduced in the trays held at the permissive temperature for two days prior to movement to 35 °C (Table 4).

Table 4. Seedling emergence (%) in ‘Victoria’ hemp seed sown in growth chambers and held at 20/30 °C or 35 °C for two days prior to moving to the reciprocal temperature.

| Temperature (°C) | Time (Days after Sowing) | | | | | |
|-------------------|--------------------------|----|----|----|----|------|
| | 2 | 3 | 4 | 5 | 6 | 7 |
| 20/30 constant | 0 | 27 | 72 | 88 | 88 | 91 a |
| 35 constant | 7 | 36 | 55 | 63 | 71 | 71 b |
| 20/30 moved to 35 | 1 | 51 | 76 | 83 | 90 | 90 a |
| 35 moved to 20/30 | 1 | 12 | 51 | 70 | 71 | 71 b |

Means for seven-day emergence followed by the same letter were not different at 5% level by Tukey’s test.

3.3. Thermal Time

Cumulative germination time courses for each cultivar at constant temperatures ranging from 10 to 39 °C followed sigmoidal relationships (Figure 1; r^2 between 0.87 and 0.99). The time-to-germination across temperatures was extrapolated from sigmoidal curves and the germination rates were calculated as the reciprocal of the time-to-germination for subpopulations in the 20, 30 40, 50, 60, 70 and 80% germination percentiles. Although cardinal temperatures can vary depending on the germination percentile subpopulation being used [18], the mean germination or time to 50% germination is often used to represent these values [16,19,20]. Using the 50% percentile averaged for both cultivars, the optimal

germination temperature was 29.6 °C, the base temperature was 3.4 °C and the upper ceiling temperature was 42.6 °C (Figure 2).

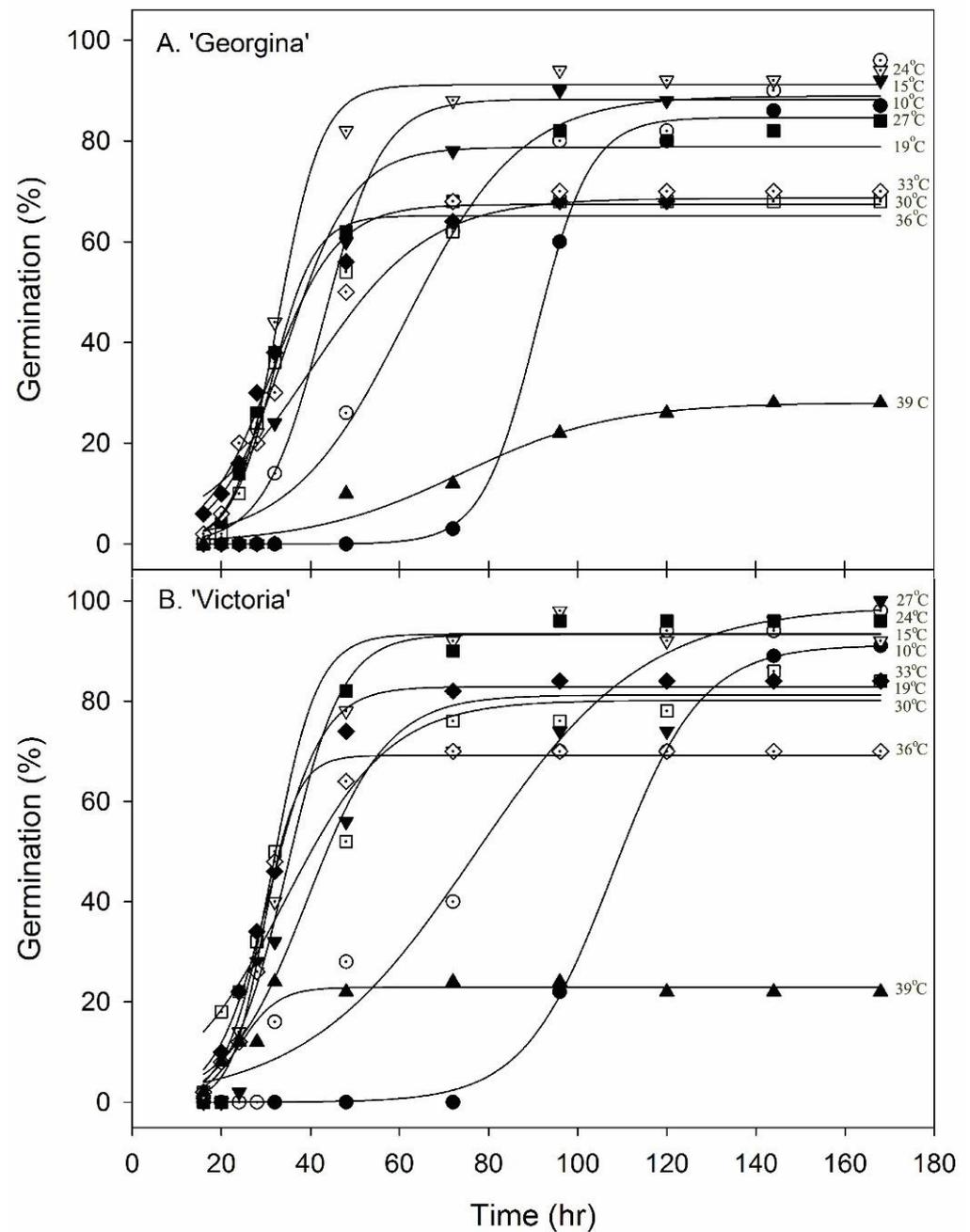


Figure 1. Cumulative germination percentage in (A) 'Georgina' and (B) 'Victoria' hemp seeds at constant temperatures ranging from 10 to 39 °C. Filled circle: 10 °C; open circle: 15 °C; filled inverted triangle: 19 °C; open inverted triangle: 24 °C; filled square: 27 °C; open square: 30 °C; filled diamond: 33 °C; open diamond: 36 °C; filled triangle: 39 °C.

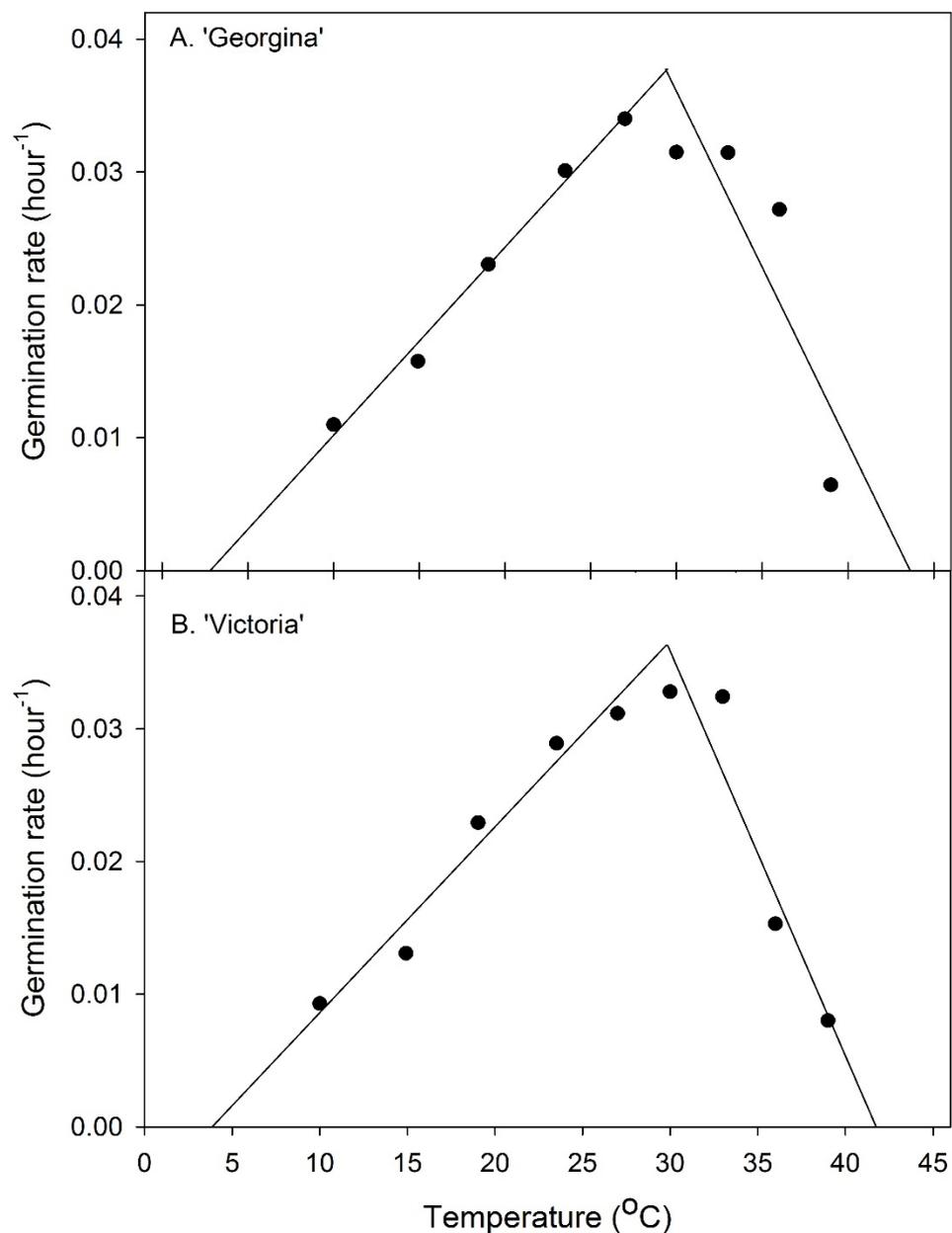


Figure 2. Germination rates for the 50 percent germination subpopulation in ‘Georgina’ and ‘Victoria’ hemp seeds across temperatures from 10 to 39 °C. (A) ‘Georgina’ linear regression for suboptimal ($y = 0.00144x - 0.0043$; $r^2 = 0.98$) and supraoptimal ($y = -0.00265x + 0.115$; $r^2 = 0.73$) temperatures; (B) ‘Victoria’ linear regression for suboptimal ($y = 0.00140x - 0.0054$; $r^2 = 0.97$) and supraoptimal ($y = -0.0026x + 0.108$; $r^2 = 0.87$) temperatures.

The germination rates were linear over the optimal temperature range and showed a sharp decline at supraoptimal temperatures (Figure 2). The germination rate across suboptimal temperature and thermal time for ‘Georgina’ and ‘Victoria’ are presented in Table 5. Using the representative 50% germination percentile, the thermal time required to reach 50% germination for ‘Georgina’ and ‘Victoria’ was 714 and 694 °C h, respectively. The thermal time to reach benchmark germination percentiles was linear (Figure 3; r^2 0.99 and 0.98 for ‘Georgina’ and ‘Victoria’, respectively). The slopes for each cultivar were comparable (0.202 and 0.175 for ‘Georgina’ and ‘Victoria’, respectively), but it required less thermal time to reach each germination percentile for ‘Victoria’ compared with ‘Georgina’ (Figure 3).

Table 5. Thermal time calculated for each germination percentage subpopulation for ‘Georgina’ and ‘Victoria’ hemp seeds across suboptimal temperatures (10 to 30 °C).

| Germination Percentage Subpopulation | ‘Georgina’ | | | ‘Victoria’ | | |
|--------------------------------------|------------------|----------------|---------------------|------------------|----------------|---------------------|
| | Germination Rate | R ² | Thermal Time (°C h) | Germination Rate | R ² | Thermal Time (°C h) |
| 20 | 0.00163 | 0.99 | 612.11 | 0.00190 | 0.99 | 526.87 |
| 30 | 0.00148 | 0.96 | 677.97 | 0.00170 | 0.96 | 587.20 |
| 40 | 0.00136 | 0.99 | 733.20 | 0.00157 | 0.99 | 637.76 |
| 50 | 0.00144 | 0.98 | 693.96 | 0.00140 | 0.98 | 714.08 |
| 60 | 0.00119 | 0.99 | 839.98 | 0.00137 | 0.99 | 728.92 |
| 70 | 0.00115 | 0.99 | 867.30 | 0.00129 | 0.99 | 775.31 |
| 80 | 0.00103 | 0.96 | 974.75 | 0.00120 | 0.96 | 832.22 |

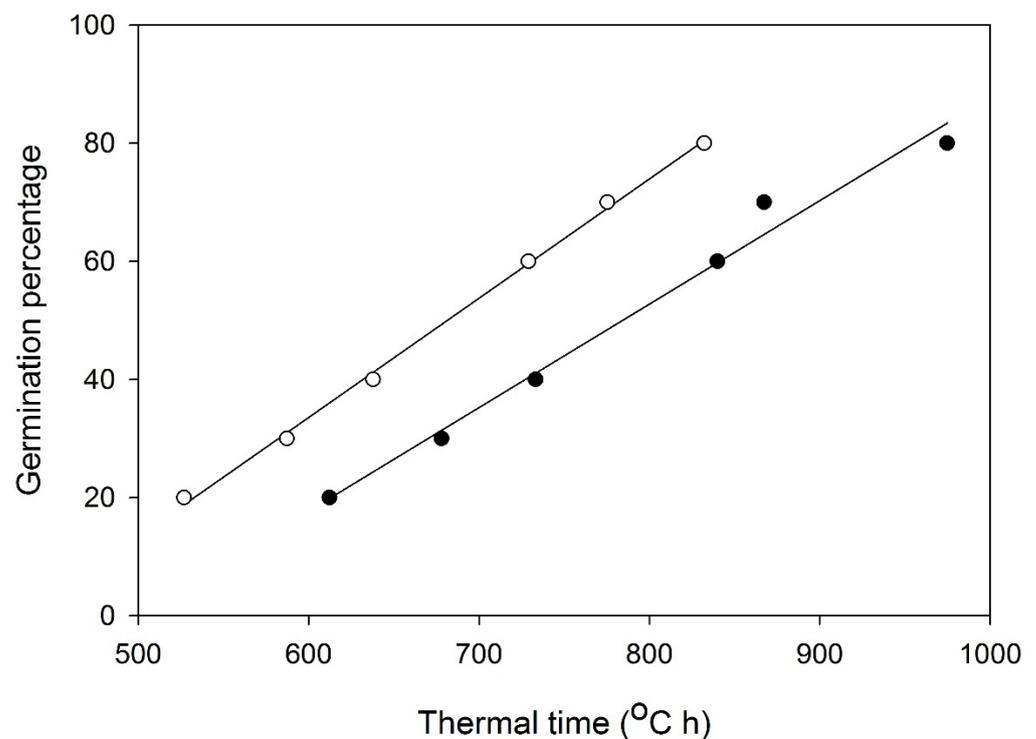


Figure 3. Thermal time required to reach different germination percentages in ‘Georgina’ and ‘Victoria’ hemp seeds across suboptimal temperatures (10 to 30 °C). ‘Georgina’: filled circle ($y = 0.202x - 87.65$; $r^2 = 0.99$); ‘Victoria’: open circle ($y = 0.175x - 87.36$; $r^2 = 0.98$).

3.4. Seed Priming

The ‘Victoria’ seeds responded to solid matrix and osmotic priming for faster germination but there were no significant differences seen in the final germination (Tables 6 and 7). For both methods, the better priming conditions were seen in the seeds held for 4 days at 10 °C, where approximately 20% more seeds germinated after 40 h compared with the untreated seeds. For the primed ‘Victoria’ hemp seeds germinated at supraoptimal temperatures, there was an enhancement in early germination up to 40 h compared with the untreated seeds (Table 8). However, there were no differences in the final germination percentages between the primed and untreated seeds over the temperature range from 30 to 41 °C (Table 8).

Table 6. Germination percentage over time in ‘Victoria’ hemp seed following solid matrix priming at two temperatures for up to four days.

| Temperature (°C) | Days | Time (h after Imbibition) | | | | | | Final |
|------------------|------|---------------------------|------|------|------|------|------|-------|
| | | 16 | 24 | 40 | 48 | 64 | 72 | |
| No priming | | 0 | 7 | 56 | 71 | 82 | 83 | 90 |
| | 2 | 0 | 17 * | 63 | 74 | 83 | 83 | 88 |
| Priming at 24 °C | 3 | 4 * | 17 * | 54 | 61 | 77 | 82 | 84 |
| | 4 | 4 * | 12 * | 45 | 50 | 67 | 68 | 74 |
| Priming at 10 °C | 2 | 1 | 18 * | 76 * | 80 * | 88 * | 88 * | 90 |
| | 3 | 14 * | 29 * | 75 * | 78 * | 85 | 87 | 87 |
| | 4 | 16 * | 36 * | 77 * | 80 * | 88 * | 88 * | 90 |

Means followed by an * within a column were significantly different from the control, as determined by single degree of freedom F-tests at $p \leq 0.05$.

Table 7. Germination percentage over time in ‘Victoria’ hemp seed following osmotic priming at 10 °C for up to four days.

| Days of Priming | Time (h after Imbibition) | | | | | | Final |
|-----------------|---------------------------|------|------|------|------|------|-------|
| | 16 | 24 | 40 | 48 | 64 | 72 | |
| 0 | 0 | 11 | 64 | 78 | 79 | 79 | 88 |
| 2 | 25 * | 39 * | 64 | 66 | 76 | 78 | 80 |
| 3 | 37 * | 46 * | 62 | 63 | 76 | 71 | 73 |
| 4 | 51 * | 66 * | 82 * | 85 * | 87 * | 87 * | 87 |

Means followed by an * within a column were significantly different from the control, as determined by single degree of freedom F-tests at $p \leq 0.05$.

Table 8. Germination percentage in ‘Victoria’ hemp seed following solid matrix priming at 10 °C for three days at various high temperatures.

| Temperature (°C) | Treatment | Time (Days after Planting) | | | | |
|------------------|------------|----------------------------|------|------|----|----|
| | | 16 | 24 | 40 | 48 | 64 |
| 33 | No priming | 1 | 17 | 61 | 80 | 85 |
| | Priming | 17 * | 54 * | 72 | 82 | 84 |
| 35 | No priming | 1 | 14 | 53 | 64 | 73 |
| | Priming | 11 * | 35 * | 63 | 71 | 77 |
| 37 | No priming | 0 | 9 | 53 | 55 | 73 |
| | Priming | 15 * | 39 * | 54 | 54 | 61 |
| 39 | No priming | 0 | 3 | 29 | 31 | 41 |
| | Priming | 9 * | 16 * | 43 * | 43 | 50 |
| 41 | No priming | 0 | 1 | 3 | 3 | 5 |
| | Priming | 2 * | 7 * | 8 | 6 | 6 |

Means followed by an * were significantly different from the control, as determined by single degree of freedom F-tests at $p \leq 0.05$.

4. Discussion

4.1. Germination and Vigor

Standard germination for ‘Georgina’ and ‘Victoria’ were not significantly different after seven days, but it was higher in ‘Victoria’ after three days (Table 1). Additionally, ‘Victoria’ seeds showed a higher normal germination after accelerated aging treatment. Both early germination and accelerated aging are standard tests for relative seed vigor assessment [20], and these results indicated that initial seed vigor differed between the two seed lots. Elias et al. [22] also found accelerated aging to be effective for evaluating relative seed vigor in hemp seeds.

4.2. Germination and Temperature

The hemp seed germination percentage and rate were highest between 19 and 30 °C (Table 2). Similarly, Qi et al. [8] found that the germination percentage and rate were highest between 20 and 25 °C. Parihar et al. [23] also reported that the highest final germination percentages in three hemp seed lots were at 20, 25 or 20/30 °C. However, in their study, the final germination percentages were reduced to approximately 15% at 30 °C and no germination was observed at 35 or 15 °C. In contrast, seed germination for the ‘Georgina’ and ‘Victoria’ seeds remained high at 36 °C (70%) and 10 °C (87 and 91%, respectively). In the current study, 40 °C was the maximum temperature for germination (Table 2). Byrd [10] observed germination percentages of less than 15% at 40 °C. In contrast, Lisson et al. [7] working with ‘Kompolti’ hemp, found good but declining germination (~40%) at 40 °C and still observed germination at 18% when the temperature was elevated to 54 °C. In these three reports, the maximal high temperature threshold differed from 35, 40 and >50 °C. It is difficult to reconcile these differences except with the possibility that hemp germination is cultivar dependent. Byrd’s work [10] suggests this possibility and he found that southern European lines showed higher germination at temperatures above 30 °C compared with northern European and Canadian hemp lines.

To further explore the high-temperature intolerance of hemp seeds, a reciprocal temperature greenhouse study was devised to separate temperature impact on seed germination versus seedling development. There was lower seedling emergence when ‘Victoria’ seeds were sown at 35 °C prior to moving to the permissive temperature, but no impact when seeds were held at 25/30° for two days prior to moving to higher temperatures (Table 4). This suggests that seed germination rather than seedling growth was the sensitive developmental stage for high temperature inhibition in ‘Victoria’ hemp seeds. This high temperature response would be significant for producers sowing late in the season. Growers sow later in the season to avoid early season weed competition and to control final plant height at harvest (personal communication). Hemp is a quantitative short-day plant for flowering and plant growth is considerably reduced following flower initiation [24].

4.3. Thermal Time

Thermal time models can be important for determining germination speed across a range of temperatures [25,26]. Using equations generated from the 50% percentile from cumulative germination time courses, the optimal germination temperature was 29.6 °C, the base temperature was 3.4 °C and the upper ceiling temperature was 42.6 °C (Figure 2). These values correspond to the observed germination (Table 2), but as seen in many germination/temperature profile studies [21], the optimal germination temperature is better represented as a range (24 to 30 °C in the current study) rather than a single temperature.

Seed germination for seeds in a seed lot is normally distributed over time, and using the linear relationship between germination rates at specific temperatures can generate thermal time for predicting germination for different proportions of a seed lot (Figure 2). Germination rates showed a sharp decline at supraoptimal temperatures, as has been observed in numerous other species [27,28]. Therefore, there were insufficient data within the high temperatures to have confidence in accurate thermal time calculations in that range [29]. The seeds required less thermal time to reach each germination percentile for ‘Victoria’ compared to ‘Georgina’ (Figure 3). Thermal time variance between cultivars has been observed in other crops [30,31], and in the current study, it was most likely related to the higher seed vigor observed in ‘Victoria’ compared to ‘Georgina’ (Table 1). Lisson et al. [7] also developed a thermal simulation germination model for ‘Kompolti’ hemp and calculated a thermal time at 18.4 °C d, which was lower than the thermal time reported here. The difference is accounted for by the faster germination rate reported in ‘Kompolti’ hemp, especially at temperatures above 35 °C.

4.4. Seed Priming

Seed priming is a controlled hydration treatment that can reduce the time to radicle emergence and may improve germination under environmental stress. Similar to other small-seeded agronomic crops [32,33], hemp seeds responded to priming for faster but not higher overall germination (Tables 6 and 7). It has been generally observed that primed seeds tend to germinate better than untreated seeds under stressful conditions, including high temperature stress [17,34]. However, in hemp seeds exposed to supraoptimal temperatures, there was higher early germination but no differences in final germination percentages (Table 8). It does not appear that seed priming will have a significant ameliorating impact on hemp seed thermal intolerance, but it may be useful for improving early germination.

5. Conclusions

This study was designed to provide a better understanding of seed germination in hemp relative to temperature. The observed optimal germination temperatures for industrial hemp ranged between 19 and 30 °C. The optimal, base and ceiling germination temperatures were calculated to be 29.6, 3.4 and 42.6 °C, respectively. The current study provided additional information on a thermal time model for seed germination at suboptimal temperatures under controlled conditions. Heat sums models have been described for time from sowing to field emergence within the same suboptimal temperature range. Tamm [35] estimated time to seedling emergence in hemp to be 96 °C d, while Werf et al. [36] provided a range between 68 to 109.5 °C d for seedling emergence. Since temperature influences seed germination differently than seedling growth, it is difficult to directly compare these thermal time values with the current study, but the overall response to temperature was similar. Seedling emergence under field conditions was faster at air temperatures between 13.5 and 18.5 °C, while temperatures under 10 °C and over 24 °C reduced time to seedling emergence [6]. Hemp seed germination appeared to be more sensitive to high temperature stress than seedling growth (Table 4). Seed priming did provide faster germination at high temperatures compared with the untreated seeds, and seed priming may offer some benefit during field germination and stand establishment (personal observation in preliminary trials). However, seed priming would probably not provide substantial thermotolerance at supraoptimal temperatures.

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Abbreviations

2,3,5 triphenyl tetrazolium chloride: TZ.

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