Ecology of Musk Thistle (*Carduus nutans*) Seed Germination for Grasslands of Temperate Climates

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Ecology of Musk Thistle (*Carduus nutans*) Seed Germination for Grasslands of Temperate Climates

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Abstract: Musk thistle is an invasive weed that is widely distributed throughout much of North America, including grasslands in temperate climates of the midwest USA. A series of laboratory and greenhouse experiments were conducted to determine the effect of various environmental factors on germination of musk thistle seeds. In temperature-fluctuation experiments, seed germination was greater than 65% in both alternating (30/20 C) and constant (20 or 25 C) temperature regimes with an 8-h day but less (33%) in warmer regimes (35/20 C). Germination of musk thistle seeds was 37% in alternating temperature regimes of 30/20 C in total darkness, but less than 67% in pots in the greenhouse. Differences of 10 and 15 C between day and night temperatures resulted in 91 and 75% maximum germination of musk thistle, respectively. Increasingly dryer soils reduced germination of musk thistle seeds from 35% (−0.03 MPa) to 0% (−1.2 MPa), whereas saline soils (> 80 mM) reduced maximum germination to less than 10%. Musk thistle seeds collected from populations in a bare-ground area had 96% germination, which was greater than that of seeds collected from populations growing in a perennial grass pasture (71%). A residence time (i.e., period that seeds remained on the parent plant) of 9 to 12 wk after capitulum maturity resulted in seeds germinating more quickly than those dispersed earlier. Overall, reduced light levels, cool and fluctuating temperatures, and amount of time seeds remained in residence are some of the most important factors that contribute to germination of musk thistle seeds. Information on germination dynamics of musk thistle seeds provides an understanding of the interactions that affect this process and underscores the importance of timely management strategies in temperate grasslands.

Nomenclature: Musk thistle, *Carduus nutans* L. CRUNU.

Keywords: Germination, habitat, invasive species, light, moisture, osmotic potential, plasticity, residence time, salinity, temperature, viability

Musk thistle is an herbaceous monocarpic herb that was introduced to the United States from Eurasia (Kok 2001). It continuously evades control efforts and can be found in many regions of North American (Roeth et al. 2003). Musk thistle occurs in all states (except Vermont, Maine, Florida, and Hawaii) and throughout the provinces of Canada from British Columbia to Nova Scotia (U.S. Department of Agriculture Natural Resources Conservation Service [USDA-NRCS] 2012). Musk thistle has been listed as a noxious weed in many states, including Nebraska, where it is reported to cover almost 6,070 km^2 (Nebraska Department of Agriculture [NDA] 2010). Musk thistle can inhabit rangelands, pastures, rights-of-way, and wastelands (Allen and Shea 2006). In grassland regions with low diversity and richness, musk thistle may establish quite easily (Beck 2001). Musk thistle phenology depends largely on climate and habitat characteristics (Edmonds and Popay 1983; McCarty and Scifres 1969; Sindel 1991). Musk thistle can behave as a summer annual, winter annual, and short-lived perennial in Canada (Desrochers et al. 1988). In the midwest, musk thistle has been classified as a biennial and observed as a summer annual and biennial in many areas (Roeth et al. 2003).

Losses associated with musk thistle include reduced forage area, increased soil erosion, and a reduction in recreation area and habitat for wildlife (Roeth et al. 2003). The dynamic phenology of musk thistle results in seeds being dispersed and exposed to various environmental conditions in different times of the year. Musk thistle seeds germinate with adequate moisture and temperatures ranging from 15 to 30 C, which contributes to the regular occurrence of seedlings in spring and sometimes fall (Lee and Hamrick 1983; McCarty and Scifres 1969; Popay and Medd 1990). Musk thistle flowers can contribute large amounts of seeds to the seed bank, which can remain viable for more than 10 yr and facilitate continued invasion (Burnside et al. 1981; Desrochers et al. 1988). Roeth et al. (2003) found that an individual musk thistle plant could produce up to 20,000 seeds within 100 or more capitula.

Successful germination of musk thistle seeds and emergence of seedlings depends on the conditions of the surrounding environment (Hamrick and Janet 1987; Medd and Lovett 1978; Popay and Kelly 1986; Popay and Medd 1990). A well-established pasture or rangeland in good condition can suppress germination, growth, and development of musk thistle (Popay and Kelly 1986). Its occurrence in the temperate grasslands of the midwest may be an indicator of poor grassland health and/or suitable conditions that favor the establishment of this invasive plant species. In this context, it is important to understand musk thistle seed ecology in terms of the effects of temperature, light, moisture, salinity, dormancy, and habitats.

One of the most important factors in germination of seeds is the range of temperatures to which seeds are exposed (Baskin and Baskin 1998). Musk thistle seeds exposed to various weather conditions may respond differently by germinating under a range of temperature regimes and light conditions. Medd and Lovett (1978) reported 75% germination of musk thistle seeds under 30/20 C day/night alternating temperature and 25% germination when temperature was held constant at 30 C. A fluctuating day/night temperature could have a significant effect on germination of musk thistle seeds.

Moisture can affect viability of musk thistle seeds (Hamrick and Janet 1987; Sindel 1991), and although germination of musk thistle seeds can occur in dryer soil conditions, research has shown that it favors moist soil conditions (Beck 1999; Hamrick and Janet 1987). Still, research on musk thistle tolerance to a range of water stress conditions has not been studied extensively.

Granstrom (1987) reported that viability of musk thistle seeds is affected by duration of storage, and although some studies indicate musk thistle seeds lack dormancy (Desrochers et al. 1988), others have indicated that it has a period of innate dormancy (Medd and Lovett 1978; Popay and Medd 1990). Lacefield and Gray (1970) report 2% germination of fresh musk thistle seeds, and 50% germinated after 8 wk.

The length of time that musk thistle seeds stay in the capitulum may affect germination. In addition, musk thistle seeds in capitulum that remain attached to a senesced plant (dead) carcass and out of contact with the soil later in the season may benefit from the relatively dryer and less damp conditions encountered by seeds dispersed on the soil. Further, the seeds that remain on dead upright plant carcasses may benefit from trapped winter snow later in the spring as seeds are finally released to the ground and begin germination (Desrochers et al. 1988). Musk thistle seeds from erect plant carcasses could be adding seeds with greater viability to the soil seed bank. Martin and Rahman (1987) report variation in germination among musk thistle seeds collected from immature to early maturing capitulum. However, germination of musk thistle seeds under increasing maturities or amounts of time spent on the parent plant has not yet been reported.

The preconditioning effects on plants, such as competition, can influence germination responses in the subsequent offspring (Baskin and Baskin 1998). The ecotypic differences for seeds of a species can vary significantly because of exposure to environments with and without competition (Jordan et al. 1982). Because musk thistle can grow in a wide range of habitats (Roeth et al. 2003), it is critical to understand how differences in each habitat type influence germination.

To our knowledge, a comprehensive assessment on the ecology of musk thistle seed germination is lacking. Understanding the germination of musk thistle seeds in a range of environmental conditions could help in characterizing more fully the properties that make this plant species so invasive. Therefore, a range of conditions representing potential environments of temperate midwestern grasslands were applied to seeds collected from field sites. Our objective was to determine the effect of temperature regimes, light availability, moisture, salinity, residence time, and habitat type on germination and development of musk thistle seeds. The results will provide a better understanding of how musk thistle seeds are responding to changes in the environment and better assess the invasion potential, which will lead to the development of better management strategies.

Materials and Methods

Seed Collection. Seeds were collected from musk thistle plants growing in four locations that all had similar climate conditions as the West Central Research & Extension Center (WCREC) in North Platte, NE (41°7.955933'N, 100°46.47583'W). The average annual precipitation at the WCREC is 508 mm, of which 80% occurs during the growing season during late April to mid-October (USDA 1978). The first site (1) at the WCREC was a bare-ground area that had recently been invaded by musk thistle. The second site (2) was located in a field 32 km east of WCREC (41°0.606'N, 100°35.16'W). The dominant species at this location were western wheatgrass [*Pascopyrum smithii* (Rydb.) Á. Löve], blue grama [*Bouteloua gracilis* (Willd. Ex Kunth) Lag. Ex Griffiths], and sideoats grama [*Bouteloua curtipendula* (Michx.) Torr. Var. curtipendula]. The third site (3) was at the WCREC in a grass pasture dominated by smooth brome (*Bromus inermis* Leyss). The fourth (4) site was a mix of warm-season perennial grasses dominated by switchgrass (*Panicum virgatum* L.) at the WCREC that had been poorly managed (e.g., overgrazed), allowing musk thistle to invade and establish.

At sites 1 to 4, musk thistle plants produced seeds that were collected and used in experiments during 2010, 2011, and 2012 to test response to a range of environmental conditions. For collecting, musk thistle seeds were considered mature when the white pappus of capitulum had fully expanded and seeds were detaching from the receptacle (Martin and Rahman 1987). Depending on the set of experiments, seeds were separated from the capitulum, transported to the lab or greenhouse, and processed for analyses. The average weight of 50 seeds collected from sites 1, 2, and 3 was 0.15 ± 0.01, 0.16 ± 0.01, and 0.12 ± 0.02 g, respectively.

For site 1, seeds collected in 2011 were subjected to temperature regimes and salinity experiments and seeds collected in 2012 were used in the light-availability and residence-time experiments (bare ground). Seeds collected from site 2 in 2010 and 2011 were subjected to moisture stress and temperature–light-fluctuation experiments. At site 3, seeds were collected in 2010 and used for the habitat-type experiment that also involved site 1. Similar to site 1, musk thistle seeds were collected at site 4 for the residence-time experiments (warm-season grasses).

Germination tests for musk thistle seeds in all experiments were conducted according to the following procedure, except in the moisture-stress experiments. Fifty musk thistle seeds were placed on moist seed-germination paper (Anchor Paper, St. Paul, MN) in petri dishes that were sealed with Parafilm and placed into germination chambers. In each chamber, seeds received 8 h light each day and photosynthetic photon flux density was 75 to 125 lux. For treatments requiring total darkness, petri dishes were wrapped in aluminum foil. For the moisture stress experiments, 50 musk thistle seeds were placed on steel blue germination blotters (Anchor Paper) in germination boxes and placed into germination chambers. Accumulated germination was recorded for each petri dish and box following the initiation of the experiment. The criterion for germination was growth of emerged radicle had a length of 2 mm. Seeds were checked each day, initially, and then less often after 30 d or more. Germinated seeds were removed after counting. For seeds incubated in total darkness, germinated seeds were counted in a total dark condition and a green safe light was used for lighting purposes. In all experiments, each treatment had four replicates and each experiment was repeated twice. At the end of each experiment, any remaining seeds were assumed to be nonviable based on visual observations (e.g., darkened, shriveled, softened, and moldy), although an actual viability test was not performed.

Temperature and Light Fluctuation. Musk thistle seeds were placed in petri dishes and incubated in germination chambers for 16 d. Seeds were incubated in light and in darkness at two fluctuating temperature regimes (35 C day/20 C night and 30 C day/20 C night) and at two constant temperatures (25 C and 20 C) during a 24-h period. Half of the petri dishes were wrapped in aluminum foil for treatments requiring total darkness. Seed counts were determined as described previously.

Temperature Regimes. Musk thistle seeds were exposed to alternating temperature regimes with 15 C and 10 C light/dark differences (e.g., 35 C day/20 C night, 30 C day/15 C night, 30 C day/20 C night and 25 C day/15 C night). Seeds were incubated in the germination chamber for 31 days. Seed counts were determined as described previously.

Moisture Stress. The effect of osmotic potential (ψ) on germination of musk thistle seeds was measured with the use of 10 PEG (50% w/v polyethylene glycol 6000, Hampton Research, Aliso Viejo, CA) solutions. An isopiestic thermocouple psychrometer (SC-10, Decagon Devices, Pullman, WA) and a Vapro® vapor pressure osmometer (WESCOR, Logan, UT) were used to measure the osmotic potential values of solutions to which seeds were exposed. Seeds were put into 12 solutions (−0.03, −0.06, −0.07, −0.07, −0.09, −0.18, −0.19, −0.28, −0.39, −0.55, −0.72, and −1.32 MPa) that were mixed with distilled water and PEG in volumes of 370 : 10, 63 : 1, 31 : 1, 15 : 1, 7 : 1, 250 : 30, 3 : 1, 175 : 60, 165 : 60, 1 : 1, 135 : 75, and 100 : 100 ml, respectively.

Osmotic potential of the solutions was measured with either the vapor pressure osmometer or the isopiestic thermocouple psychrometer. Distilled water was used as the control. Four replicates of 50 seeds each were placed in petri dishes and incubated in darkness at 30 C day/20 C night for 21 days. Each germination box was wrapped with aluminum foil to prevent light exposure and desiccation. Counts of germinated seeds were determined as described previously.

Salinity. Salt stress was determined by adding 5-ml solutions containing 10, 40, 80, 160, and 320 mM sodium chloride (NaCl) to petri dishes containing 50 musk thistle seeds (Stanton et al. 2012). Distilled water was used as control. The range of salt concentrations used was similar to the range that can occur in temperate midwestern grasslands (Hoffman 1997). Fifty seeds were incubated in light at 30 C day/15 C night. Germinated seeds were counted as described previously over a 30-d period.

Habitat Type. Germination of seeds from musk thistle plants growing in two different habitat types was compared. Seeds were collected from plants growing in bare ground (site 1) and among smooth brome (site 3). At each site, musk thistle seeds were collected in September (2011) and July (2012), which was 3 wk after plants had set seed. In 2012, extremely dry conditions caused plants to mature earlier than normal. Seeds were tested for germination in light at 30 C day/15 C night and germination was monitored as described previously for 30 d.

Residence Time. At sites 1 and 4, seeds were collected from musk thistle plants growing on bare ground and in the warm-season grasses, respectively, at set periods from June to September, 2012. Mesh cloth bags (7 by 10 cm) were placed over mature musk thistle terminal capitulum when flowers first started to turn brown after pollen receptivity on June 1. For the next 4 d, plants were checked visually and inflorescences that had reached full maturation of seeds (e.g., color of the corolla) were bagged and left on the plants. A total of 40 bags were placed on inflorescences of 40 different musk thistle plants (20 at each site).

The first inflorescences were bagged on June 2, and 3 d later all 40 inflorescences were bagged. Bags with inflorescences were collected from standing musk thistle plants at 3-wk intervals beginning with the first one on June 23 and ending with the last one on August 26. For each collection, 10 bags were removed from plants and immediately assessed for head diameter, number of seeds, and seed mass. Following assessments, 50 seeds were placed in eight petri dishes (400 seeds total), tested for germination in light at 30 C day/15 C night, and monitored as described previously for 30 d. This same procedure was used for each of the four collection dates at each site.

Light Availability. In this experiment, shading treatments were used to simulate various light conditions at the soil surface that can occur in temperate midwestern grasslands. Musk thistle seeds collected from site 1 were placed on the surface of soil in plastic pots (22 cm in diameter, 16 cm in height) in the greenhouse. The soil in pots was Cozad silt loam collected from WCREC.

The treatments included various shade cloth fabrics (e.g., 40, 60, and 80%) and a nonshaded control. The treatments were replicated four times and pots were arranged randomly on a greenhouse bench. Pots were watered regularly to prevent surface crusting and desiccation of musk thistle seeds. Fifty seeds were sown on the surface of soil (not mixed in) of each pot. For 38 d, seedlings were measured weekly in each treatment. Following counts, seedlings were discarded from each pot.

Statistical Analysis. Musk thistle seed germination in all experiments was presented as percentage of germinated seeds of the total number of seeds in the petri dishes. Data on germination were arcsine square-root transformed to improve normality and homogeneity, and subjected to ANOVA by using PROC GLIMMIX in SAS (SAS 2009) where treatment factors were considered fixed effects and experimental repeats as random factors. Least-square means (LSMEAN) was used to separate treatment means at the $P < 0.05$ level. Model parameter estimations were conducted with the use of PROC NLIN and PROC NLMIXED.

An exponential decay model was fitted to raw data of percentage germination from moisture stress experiments with the use of Sigmaplot (Sigmaplot 12.0, Systat Software Inc., San Jose, CA). The model fitted was

$$G = G_{max} * \exp(-G_{rate} * X) \qquad [1]$$

where G represents the total germination (%) at moisture stress x, G_{max} is the maximum germination, and G_{rate} indicates the slope of the curve. For temperature and light fluctuation, temperature regimes, salinity, habitat-type, residence-time, and light-availability experiments, a three-parameter sigmoid model,

$$G = G_{max} / \{1 + \exp[-(X - X_{50}) / G_{rate}]\} \qquad [2]$$

was fitted to raw data of percentage germination, where G is total germinated seeds at day x, G_{max} is the maximum germination, X_{50} is time required for 50% of the maximum germination, and G_{rate} is the slope of the curve.

Table 1. Parameter estimates of the exponential decay (moisture stress) and three-parameter sigmoid (habitat type and residence time) models fitted to germination of musk thistle seeds.

Experiment	Treatment	Parameter estimates (± standard error)[a]		
		X_{50}	G_{max}	G_{rate}
Habitat type	Bare ground	4.7 ± 0.05	94.3 ± 0.7	0.2 ± 0.04
	Grass pasture	3.6 ± 0.7	66.2 ± 1.2	1.1 ± 0.6
Residence time	3 wk	9.9 ± 0.3	90.2 ± 1.3	2.4 ± 0.3
	6 wk	5.6 ± 0.1	91.5 ± 0.9	1.2 ± 0.1
	9 wk	3.3 ± 0.2	89.7 ± 1.1	1.0 ± 0.2
	12 wk	3.4 ± 0.5	91.8 ± 0.4	0.6 ± 0.4
Light availability	0%	19.0 ± 2.1	1.7 ± 1.2	3.6 ± 2.1
	40%	16.2 ± 3.6	14.6 ± 2.0	4.1 ± 3.4
	60%	11.8 ± 1.7	42.0 ± 2.5	3.7 ± 1.6
	80%	6.5 ± 1.6	66.5 ± 2.2	5.5 ± 1.7

a. X_{50}, days requiring for 50% maximum germination; G_{max}, maximum germination (%); G_{rate}, slope.

Parameter estimates for germination in the moisture, habitat type, residence time, and light-availability experiments are listed in Table 1.

Results and Discussion

Temperature and Light Fluctuations. At constant and alternating temperatures, seeds germinated to a higher percentage in light than in darkness (Figure 1). In light, the highest germination was at 20 C, but germination at this temperature was not statistically different from that in light at 25 C and 30/20 C. In general, photoperiod has a greater effect on germination than temperature and this is consistent with results from Medd and Lovett (1978), who found seeds of musk thistle had 76% germination at 20/30 C (8/16 h dark/light) compared to 2.2% germination at the same temperature regime in total darkness for 14 d. In darkness, germination of musk thistle seeds was poor regardless of fluctuating temperatures. This is typically the condition in healthy, vigorous, and dense temperate grasslands of the midwest, which prevent light from penetrating the canopy creating darkness at the soil surface where most musk thistle seeds are located. Alternatively, an unhealthy grassland has openings in the canopy that allow sufficient light penetration to the soil surface and results in more significant day/night temperature fluctuations, which are favorable for germination of musk thistle seeds.

Temperature Regimes. In the four temperature regimes (35/25, 30/20, 30/15, and 25/15C), the maximum germination of musk thistle seeds was greatest (91%) at the lowest regime (25/15 C) (Figure 2). This regime is often the condition in late fall or spring in the midwest and represents periods of greatest musk thistle germination in these regions (High Plains Regional Climate Center 2011; Lee and Hamrick 1983; Medd and Lovett 1978; Popay and Medd 1990). Interestingly, the highest temperature regime (35/20 C) had poor maximum germination (32%) and required 6 d to reach 50% of maximum germination (Figure 2). Under future climate scenarios, excessively warm temperatures that occur early or late in the season could negatively impact germination of musk thistle seeds.

By alternating temperature regimes either 10 C (e.g., 25/15 C and 30/20 C) or 15 C (e.g., 30/15 C) and remaining below 35 C, maximum germination was 70% or more. However, when maximum was 35 C (e.g., 35/20 C), germination dropped significantly, although the difference was 15 C. Our results are consistent with those of other studies that show musk thistle seeds germinate better under temperature regimes with a min-

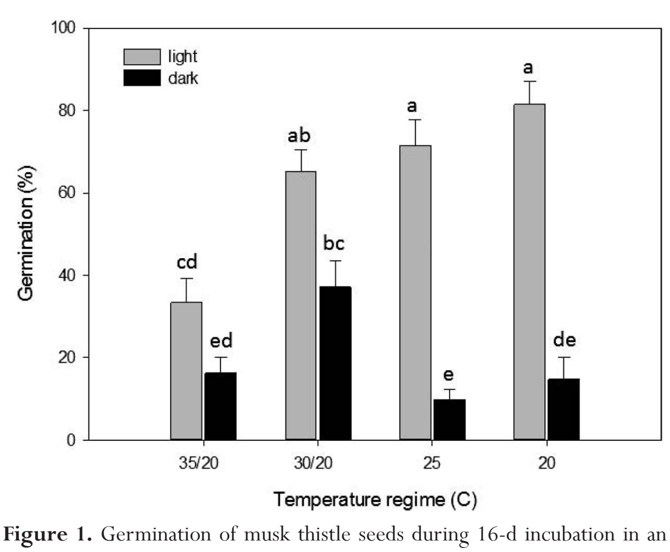

Figure 1. Germination of musk thistle seeds during 16-d incubation in an 8-h photoperiod or in darkness. Vertical bars are standard error of mean.

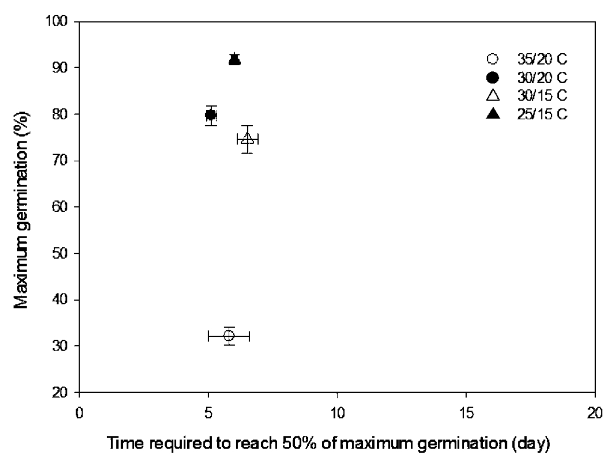

Figure 2. Germination of musk thistle seeds in light and various temperature regimes for 31 d. Vertical and horizontal bars are standard error of the coefficient with the use of a fitted three-parameter sigmoid model, $G(\%) = G_{max}/\{1 + \exp[-(X - X_{50})/G_{rate}]\}$.

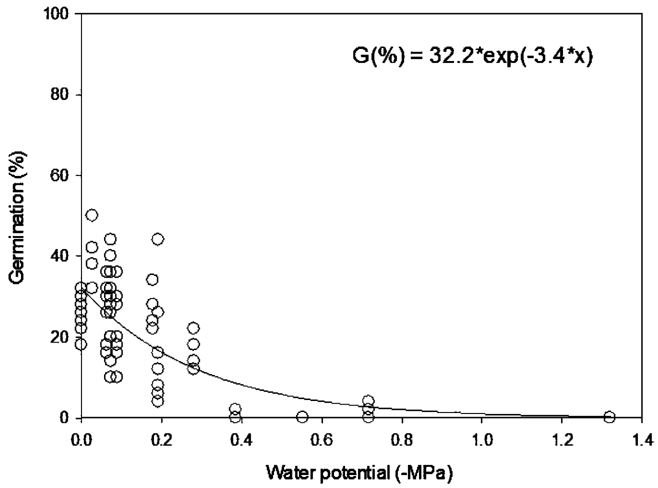

Figure 3. Germination of musk thistle seeds during 21-d incubation in wet to dry conditions, with the use of osmotic potential (MPa). Vertical bars are standard error of mean. Lines represent the exponential decay curve model, $G(\%) = G_{max} * \exp(-G_{rate} * X)$ fitted to the data.

imum of 15 C (Hull and Evans 1973; Medd and Lovett 1978; Popay and Medd 1990; Roeth et al. 2003). These low temperatures are typical for temperate grasslands in the midwest during spring and fall when musk thistle seed is more prevalent. During this time, the weather, including precipitation, in these regions is ideal for germination of musk thistle and facilitates potential establishment opportunities.

Moisture Stress. As moisture decreased from −0.0275 to −1.32 MPa, germination also declined from almost 40% to near 0 (Figure 3). There was only an average of 2% germination measured at osmotic potentials of under −0.7175 MPa. Possibly the dry conditions prevented more seeds from germinating, which is typical during dry periods between precipitation events (Beck 1999). Very low osmotic potentials inhibited germination of musk thistle seeds, indicating that although invasions might occur (e.g., new seedlings), the establishment (e.g., mature plants) of musk thistle usually does not happen.

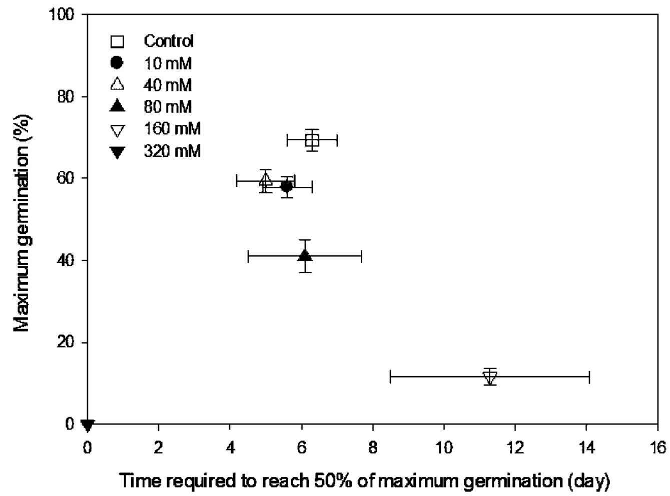

Figure 4. Germination of musk thistle seeds during 21-d incubation in sodium chloride (NaCl). Vertical and horizontal bars are standard error of the coefficient with the use of a fitted three-parameter sigmoid model, $G(\%) = G_{max}/\{1 + \exp[-(X - X_{50})/G_{rate}]\}$.

Salinity. High salinity concentrations above 160 mM reduced germination of musk thistle seeds and at 320 mM or higher, germination was completely inhibited (Figure 4). At low salt concentrations (10 to 40 mM), germination of musk thistle seeds was near 60%, which is near the control (71%), suggesting maximum germination varied little at salinity concentrations below about 45 mM salinity. Although our germination percentages at low concentrations were lower than those of Kaya et al. (2009) (92%), the variability in seeds taken from different populations could explain some of the difference (Baskin and Baskin 1998).

High salinity can inhibit germination of seeds (Gulzar and Khan 2002), although musk thistle has been found in saline soils (Beck 1999). Alternatively, frequent precipitation events can lower the concentration of salinity, which might ease saline stress on germination of musk thistle seeds. Our results show a concentration of 80 mM or less of salt will have a suppressive effect on the germination of musk thistle, reducing maximum germination to less than 50%. Although salinity is not frequently reported in temperate grasslands of the midwest, drought could create high salinity conditions, which may hinder germination of musk thistle seeds.

Habitat Type. Germination of musk thistle seeds collected from site 1 (bare ground) was more rapid than from site 3 (grass pasture) at 5 d after sowing and reached near 100% germination 25 d later (Figure 5). Seeds collected from site 3 also began to germinate earlier than seeds from site 1, but total germination failed to surpass much beyond 60%. The difference in germination between the two sites was probably due to environmental factors that preconditioned the seeds for earlier or later and total germination (Baskin and Baskin 1998). As indicated previously, all nongerminated seeds had a darkened, shriveled appearance with mold, and thus were assumed to be nonviable.

One of most common precondition factors that effects germination is competition. For example, seeds of baby blue eyes

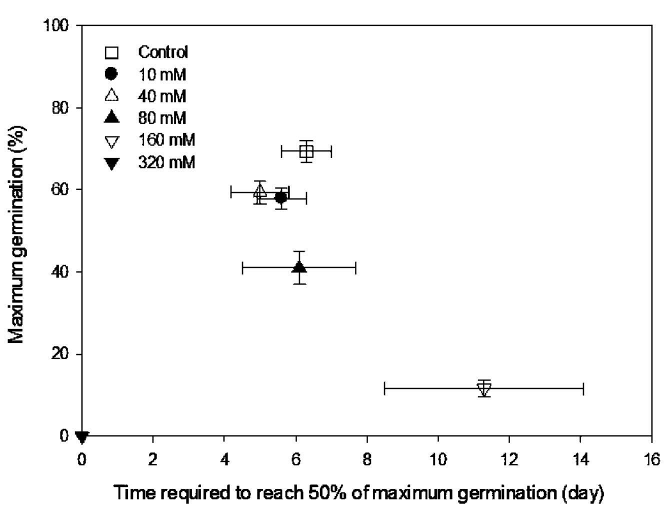

Figure 5. Germination of musk thistle seeds during 30-d incubation in response to habitat type. Vertical bars are standard error of mean. Lines represent the three-parameter sigmoid curve model, $G(\%) = G_{max} * \exp(-G_{rate} * X)$ fitted to the data.

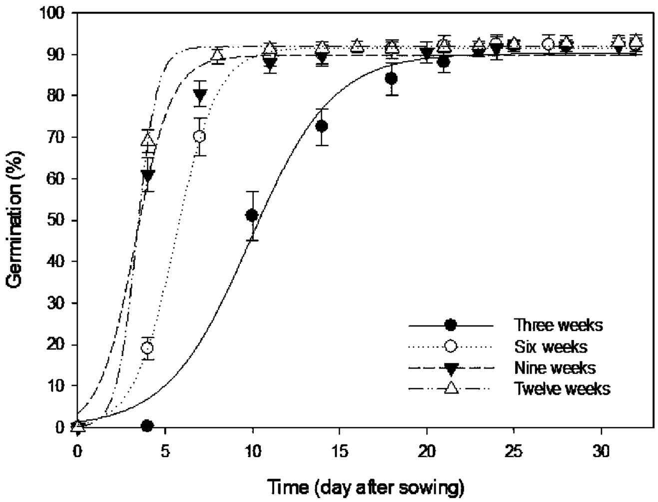

Figure 6. Germination of musk thistle seeds during 30-d incubation in response to residence time of seeds in capitula. Vertical bars are standard error of mean. Lines represent the three-parameter sigmoid curve model, $G(\%) = G_{max} * \exp(-G_{rate} * X)$ fitted to the data.

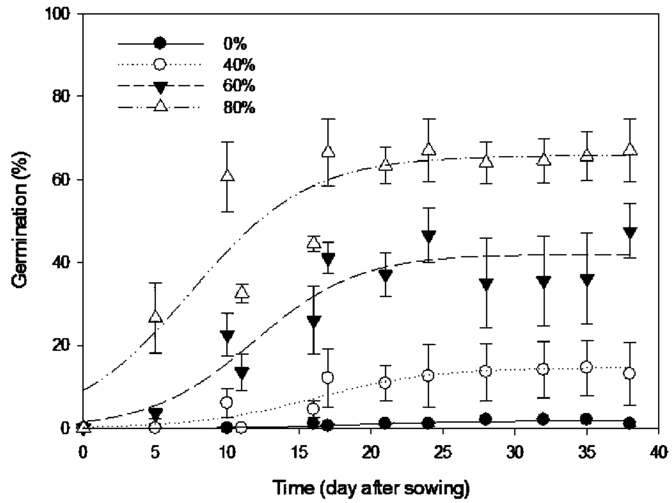

Figure 7. Germination of musk thistle seeds following exposure to shading. Vertical bars are standard error of mean. Lines represent the three-parameter sigmoid curve model, $G(\%) = G_{max} * \exp(-G_{rate} * X)$ fitted to the data.

(*Nemophila menziesii* Hook & Arn.) exhibited a decrease in germination when maternal plants were grown in competition with ripgut brome (*Bromus diandrus* Roth) (Platenkamp and Shaw 1993). The competitive conditions may cause baby blue eyes to allocate more resources into developing vegetative structures and less into reproduction, which could result in lower viability of seeds. Musk thistle plants growing on bare ground may benefit from a less competitive environment and thereby, produce more viable seeds. Kok et al. (1986) showed that habitats dominated by tall fescue [*Lolium arundinacea* (Schreb.) S.J. Darbyshire] reduced germination of musk thistle seeds and those plants that did germinate failed to reach flowering stage. Mother plants from site 3 were mature a week earlier compared to mother plants from site 1 (Han, personal observation); however, the difference in total germination between the two sites may not be caused by seed age, which is supported by the residence-time experiment.

Residence Time. Residence time had a significant effect on the germination of musk thistle seeds in capitula on mature plants (Figure 6). Seeds collected 9 and 12 wk after maturation germinated more quickly (3 d) reaching maximum germination (92%) than those collected 3 wk after maturation (10 d) (Table 1). By 30 d after sowing, germination of seeds collected at 3, 6, 9, and 12 wk was not significantly different (Figure 6).

Musk thistle seeds that remain attached to the parent plant longer in capitulum have high germination, possibly because of greater exposure to fluctuating temperatures and light/dark conditions that help break dormancy. The longer into the summer that seeds remained on the plant, the more time the seeds had for dormancy break to occur. This phenomenon has been observed for other invasive plant species, including leafy spurge (*Euphorbia esula* L.) (Chao et al. 2011) and is consistent with our temperature–light-fluctuation experiments (Figure 1). Moreover, musk thistle may have an after-ripening period (DiTomaso and Healy 2007), which indicates a period of time needed for seeds in capitula to break dormancy.

All four collection periods had similar total germination percentages at the end of the experiment. This highlights the fact that seeds that stay in capitula on the plant for a short period have a similar germination rate as seeds that are dispersed later, but the earlier-dispersed seeds require almost 3 wk longer to reach the same percentage (Figure 6). Musk thistle provides a constant seed source that is viable largely toward the end of the season. It is not known if earlier- or later-dispersed seeds result in higher numbers of new plants in the fall or early spring, but clearly these differences show the importance of control measures being applied before plants have set seeds. For those plants not controlled, it is still necessary to make follow-up treatments and avoid missing the window of opportunity for significantly reducing established populations.

Light Availability. Germination of musk thistle seedlings was greatest (67%) under 80% shade than any of the other treatments, including full sunlight (Figure 7). The darker conditions also resulted in more rapid germination, which is depicted in the three-parameter sigmoidal model (Table 1); the 80% shade had the highest maximum germination and took the fewest days to reach 50% maximum germination. The 0% shade treatment had the lowest germination (1 to 2%), which might be associated with relatively drier soil surfaces compared to soil surface in shade, although all pots were watered regularly. Light can be beneficial in the germination of musk thistle seeds, but germination is not affected solely by sufficient light. Moreover, increasing soil moisture may compensate for relatively low light penetration and allow for sufficient germination.

In the midwest, taller warm-season perennial grasses that are in good condition may create a shade environment, which is similar to the 80% shade treatment. Shade of grass canopy with adequate soil moisture may favor the initial germination of musk thistle seedlings, but as the grasses rapidly elongate and create continued or additional shade during the spring, few to no musk thistle plants will survive (Han, personal observation). This is consistent with Hamrick and Janet (1987), who reported musk thistle was suppressed under low light conditions in dense pastures.

For the few musk thistle seeds that germinate successfully in full sunlight, there is potential for them to reach full maturity and set seeds. Yet, there is an ecological trade-off for musk thistle seedlings in response to light resources. Fluctuating-light and low-light conditions are conducive to germination of musk thistle seeds, but they are created in competitive environments usually with taller, denser plants (e.g., native perennial grasses). On the contrary, intense light is not highly desirable for germination of musk thistle seeds, yet the environment is less competitive for the few seedlings that successfully germinate and establish in these conditions. The relative success of musk thistle to establish in varying light levels is an example of plasticity that is common for many successfully established invasive plant species.

The most important factors in high germination percentages of musk thistle seeds are exposure to cool temperatures and fluctuating light/dark vs. darkness condition, which are common in temperate grasslands of the midwest. Moisture stress inhibits germination of musk thistle seeds, which is not surprising and is more of a factor during intense competition when water is limited or under drought conditions. Similarly, salinity inhibits germination of musk thistle seeds, especially at higher levels. Thus, both moisture and salt stress can prevent germination of musk thistle, although saline environments might be slightly more tolerable. In some situations, precipitation events may facilitate germination of musk thistle seeds by easing osmotic and saline stress created by soil.

Germination of musk thistle seeds can vary significantly based on the effects from neighboring plants and after-ripening location. Germination of musk thistle seeds collected from plants growing in bare ground was higher than seeds collected from the grass pasture. The environmental or habitat difference could have preconditioned the seeds to be less germinable in the highly competitive environment (Baskin and Baskin 1998). Musk thistle seeds stored in capitula for 9 to 12 wk after maturity in the field germinated more rapidly than seed collected after only 3 wk of maturity. Before seeds are dispersed, a period of stratification by cool night temperatures may facilitate the breaking of dormancy for musk thistle seeds.

These results indicate that in temperate grasslands, the germination of musk thistle seeds are influenced by numerous factors. In addition to light and soil moisture, the effects of other environmental conditions (temperature, residence time, and habitat type) play a role in germination of musk thistle seeds. This series of experiments reports on some of the most important conditions that affect musk thistle seed resilience, the reasons that this species continues to be persistent throughout North America, and the potential for improving management strategies in temperate grasslands. Effectively controlling musk thistle is associated with good grassland management. A dense and healthy grassland stand with few openings in the canopy will prevent and suppress the emergence of musk thistle by creating a competitive environment. For those plants that escape management efforts and reach the flowering stage, control is still important at this point to reduce more readily germinable seed from entering the soil seed bank. From our studies, the longer the seed remains on the mother plant, the more quickly that seed will germinate under favorable conditions. Therefore, it is not too late to perform even a minimum level of control of musk thistle at or during the early flowering stage of development.

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