Weed Science

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Research Article

Cite this article: Yadav R, Jha P, Kniss AR, Lawrence NC, Sbatella GM (2023) Effect of osmotic potential and temperature on germination of kochia (*Bassia scoparia*) populations from the U.S. Great Plains. Weed Sci. **71**: 133–140. doi: 10.1017/wsc.2023.12

Received: 15 June 2022
Revised: 20 January 2023
Accepted: 23 February 2023
First published online: 6 March 2023

Associate Editor:
Ramon G. Leon, North Carolina State University

Keywords:
Germination duration; germination rate; maximum germination; optimum temperature

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Effect of osmotic potential and temperature on germination of kochia (*Bassia scoparia*) populations from the U.S. Great Plains

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Abstract

Development of integrated weed management strategies requires knowledge of weed emergence timing and patterns, which are regulated primarily by water and thermal requirements for seed germination. Laboratory experiments were conducted in fall 2017 to fall 2018 to quantify the effect of osmotic potential and temperature on germination of 44 kochia [*Bassia scoparia* (L.) A.J. Scott] populations under controlled conditions. *Bassia scoparia* populations were collected in fall 2016 from northern (near Huntley, MT, and Powell, WY) and southern (near Lingle, WY, and Scottsbluff, NE) regions of the U.S. Great Plains. Ten osmotic potentials from 0 to −2.1 MPa and eight constant temperatures from 4 to 26 C were evaluated. Response of *B. scoparia* populations to osmotic potential did not differ between the northern and southern regions. At an osmotic potential of 0 MPa, all *B. scoparia* populations had greater than 98% germination, and the time to achieve 50% germination (t_{50}) was less than 1 d. At −1.6 MPa, 25% of seeds of all *B. scoparia* populations germinated. Osmotic potentials of −0.85 and −1.9 MPa reduced *B. scoparia* germination by 10% and 90%, respectively. Regardless of temperature regime, all populations exhibited greater than 88% germination. The germination rate was highest at temperatures between 15 to 26 C and did not differ between populations from northern versus southern regions. At this temperature range, all populations had a t_{50} of less than 1 d. However, at 4 C, *B. scoparia* populations from the northern region had a higher germination rate (5 h) and cumulative germination (7%) than populations from the southern region. Overall, these results indicate a wide range of optimum temperatures and osmotic potential requirements for *B. scoparia* germination.

Introduction

Kochia [*Bassia scoparia* (L.) A.J. Scott] is a summer annual, broadleaf weed in the Amaranthaceae family (formerly Chenopodiaceae), native to central and eastern Europe and western Asia (Georgia 1914; Whitson et al. 1991). *Bassia scoparia* is the most troublesome weed in arid and semiarid regions of the North American Great Plains (Kumar et al. 2019). Several unique biological characteristics such as early and rapid germination, significant outcrossing, high genetic variation, high seed production, and tumble mechanism of seed dispersal contribute to the weediness of this species in the region (Gressel and Segel 1978; Kumar et al. 2019; Mengistu and Messersmith 2002). Low temperature and osmotic potential requirements for germination are the most important characteristics that allow *B. scoparia* to compete with spring-planted crops in the region (Eberlein and Fore 1984; Evetts and Burnside 1972).

Bassia scoparia is often the first species to emerge in spring in the Northern Great Plains (Dyer et al. 1993; Schwinghamer and Van Acker 2008). Seeds are either nondormant or exhibit very little (less than 5%) dormancy (Dyer et al. 1993). Therefore, mature seeds germinate as soon as germination requirements are met. Furthermore, seeds can germinate over a wide range of temperatures from 3.5 to 40 C (Eberlein and Fore 1984). Alternate versus constant temperature regimes do not affect *B. scoparia* seed germination (Everitt et al. 1983).

Moisture is often a limiting factor for crop production in the semiarid U.S. Great Plains. *Bassia scoparia* can germinate at soil moisture levels at which other species fail to germinate (Everitt et al. 1983) or certain preemergence soil-residual herbicides are not biologically active (Sebastian et al. 2017). Therefore, many preemergence herbicides do not provide consistent control of this species in this region. Early emergence in the spring enables *B. scoparia* to acquire limited soil moisture and provides a competitive advantage over crops and other weed species

(Dyer et al. 1993). Additionally, *B. scoparia* is highly water-use efficient because of its C_4 photosynthetic pathway (Chu and Sanderson 2008).

Competitive dominance of weeds in crops is largely determined by their relative time of emergence (Cousens et al. 1987). This is regulated primarily by soil temperature and water potential (Bradford 2002). In addition, timing of weed control practices and weed emergence should coincide to obtain the full potential of those weed control practices (Ogg and Dawson 1984). Therefore, improved knowledge of temperature and osmotic potential requirements for *B. scoparia* seed germination is important to predict the timing and duration of weed emergence (Ogg and Dawson 1984), which would ultimately aid in designing effective weed management programs.

Variable germination requirements and emergence patterns for *B. scoparia* have been reported in different geographic regions (Anderson and Nielsen 1996; Dille et al. 2017; Kumar et al. 2018a; Schwinghamer and Van Acker 2008). Dille et al. (2017) reported that under field conditions, *B. scoparia* populations from Kansas required 690 growing degree days (GDD) to achieve 90% emergence, compared with only 230 GDD for Nebraska and Wyoming populations. Kumar et al. (2018a) also observed a differential emergence pattern of *B. scoparia* populations collected from the U.S. Great Plains, suggesting the presence of different emergence "biotypes" among *B. scoparia* field populations. These differences in germination requirements or emergence patterns are not unusual, as there is a substantial genetic/phenotypic variation present among *B. scoparia* populations (Bell et al. 1972; Mengistu and Messersmith 2002).

Although some studies quantified thermal requirements for *B. scoparia* germination (Kumar and Jha 2017; Kumar et al. 2018b), it is unclear whether observed differences in *B. scoparia* emergence patterns across the geographic sites are due to differential thermal requirements or differential osmotic potential requirements among populations. Additionally, information on germination requirements of weed populations collected across a wide geographic area may help in developing robust models to predict weed emergence patterns (Myers et al. 2004). Therefore, the objectives of this research were to (1) quantify the temperature and osmotic potential requirements of *B. scoparia* populations collected from 44 locations across three states (Montana, Wyoming, and Nebraska) in the U.S. Northern Great Plains and (2) compare thermal or osmotic potential requirements for germination of *B. scoparia* populations between northern and southern parts of the three-state region.

Materials and Methods

Seed Collection

Mature seeds of *B. scoparia* plants growing in fields were collected in fall 2016 from three states of the U.S. Northern Great Plains. Eleven kochia populations each were collected from sites surrounding Huntley, MT, and Powell, WY, in the northern region, and Lingle, WY, and Scottsbluff, NE, in the southern region (Figure 1). Ten different crop field locations (approximately 10 km apart from one another) and one rangeland or non-crop collection site were located in each of the four areas. Therefore, a total of 44 *B. scoparia* seed samples were collected and considered to be 44 separate populations. To quantify the effect of geographic regions (across a latitudinal transect) on the germination requirements, populations were divided into two groups, northern and southern regions. The Huntley and Powell sites were included in the northern region, whereas the Lingle and Scottsbluff sites were included in the southern region. All *B. scoparia* seed samples collected were dried for 4 wk at room temperature (25 C), hand threshed, and then cleaned using mesh sieves. Cleaned seed samples were stored at 4 C until being used for the germination experiments.

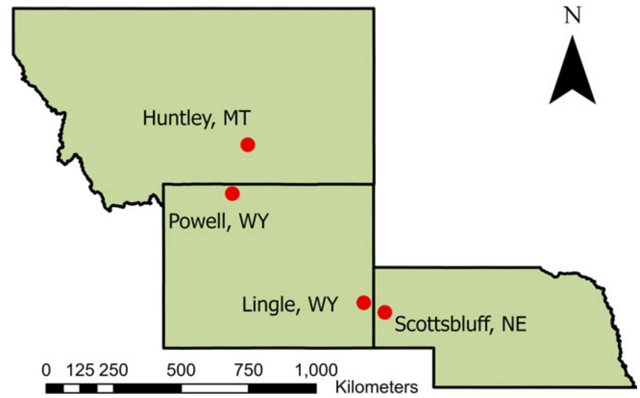

Figure 1. Geographic map of four sites where 44 *Bassia scoparia* populations were collected in 2016 across a three-state region in the U.S. Great Plains.

Osmotic Potential Experiment

Laboratory experiments were conducted at the Montana State University Southern Agricultural Research Center (MSU SARC), Huntley, MT, in fall 2017 to quantify osmotic potential requirements for germination of *B. scoparia* populations. Ten osmotic potential treatments ranging from 0 to −2.1 MPa were created by using polyethylene glycol (PEG 8000, Fisher Scientific, One Reagent Lane, Fair Lawn, NJ 07410) based on the methods described by Michel (1983). The ten treatments included 0, −0.1, −0.3, −0.5, −0.7, −0.9, −1.2, −1.6, −1.8, and −2.1 MPa. Each treatment was replicated three times. For each experimental unit, 50 seeds from each population were counted out and placed between two layers of filter paper (Whatman® Grade 2, Sigma-Aldrich, St Louis, MO 68178) in a 10-cm-diameter petri dish (Fisher Scientific). Filter paper in each petri dish was moistened with 7 ml of PEG solution, except in the 0 MPa treatment, in which 7 ml of distilled water was used. Petri dishes were sealed with a thermoplastic wrapper (Parafilm™ M, Fisher Scientific) to prevent water loss through evaporation. Because light is not required for *B. scoparia* seed germination (Everitt et al. 1983), petri dishes were placed in the dark in an incubator (VWR® Signature™, VWR, 100 Matsonford Road, Radnor, PA 19087) set to a constant temperature of 20 C. The 20 C temperature was selected because PEG solution was prepared for this temperature and it is the optimum temperature for germination of *B. scoparia* seeds (Eberlein and Fore 1984; Everitt et al. 1983; Kumar and Jha 2017). Treatments were arranged in a completely randomized design.

Temperature Experiment

Temperature requirements for germination of *B. scoparia* populations were quantified in laboratory experiments conducted at the MSU SARC, Huntley, MT, in fall 2018. Eight constant temperature treatments ranging from 4 to 26 C were used. The treatments included 4, 8, 12, 15, 18, 21, 24, and 26 C. Separate growth chambers (VWR® Signature™) were assigned for each temperature

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treatment. Petri dishes were prepared and maintained as described for the osmotic potential experiment. Petri dishes in all treatments were watered with 7 ml of distilled water.

Data Collection and Statistical Analysis

Bassia scoparia seed germination was observed on a daily basis for 2 wk. Germinated seeds were counted and removed from petri dishes at each observation time. A seed was considered germinated when the tip of the protruding radicle uncoiled (Dyer et al. 1993; Young et al. 1981). *Bassia scoparia* germination data from each experiment were analyzed in the R statistical environment (R Core Team 2019) using the R extension package DRC (Ritz et al. 2015). Data from each observation period were arranged in an event-time format (Ritz et al. 2013), then a three-parameter log-logistic model was fit (Equation 1; Ritz et al. 2013).

$$F(t) = \frac{d}{1 + \exp\{b[\log(t) - \log(t_{50})]\}} \quad [1]$$

In Equation 1, F(t) denotes the proportion of seeds germinated between time 0 (start of the experiment) and time t; d denotes the upper limit (expected maximum germination at very large t); t_{50} denotes the time required to observe 50% germination (relative to the upper limit, d); and b denotes the slope of germination curve at time t_{50}. In the osmotic potential experiment, overall seed germination from all populations decreased to less than 30% at osmotic potentials of −1.6 and −1.8 MPa and ceased completely at −2.1 MPa. The lower germination proportions at −1.6 and −1.8 MPa did not allow model fit and parameter estimations. Therefore, only seven osmotic potential treatments ranging from 0 to −1.2 MPa were used to fit the model and generate germination curves. However, in the temperature experiment, *B. scoparia* seeds germinated in high proportions at all temperatures; therefore, all eight treatments were used to fit the model and generate germination curves. The accuracy of model fit was tested using the lack of fit test in the DRC package (Ritz et al. 2015).

Additionally, a second three-parameter log-logistic model was fit using Equation 2 (Ritz et al. 2015) to quantify germination response of *B. scoparia* populations to osmotic potential treatments.

$$y = \frac{d}{1 + \exp\{b[\log x - \log e]\}} \quad [2]$$

In Equation 2, y denotes the percent reduction in germination (relative to an osmotic potential of 0 MPa); x denotes the osmotic potential; d denotes the upper limit; e denotes the ψ_{50} (osmotic potential required to reduce the germination by 50%); and b denotes the relative slope around ψ_{50}. Values of ψ_{10} and ψ_{90} were calculated using the *ED* function of the DRC package.

To compare northern *B. scoparia* populations with southern populations for germination requirements, a two-step procedure described by Jensen et al. (2017) was used. In the first step, parameters of interest—t_{50} and duration of germination (t_{95}–t_5)—were obtained for each population using Equation 1. Then, in the second step, these parameters were analyzed using a mixed-effects model in the *lmer* function of the LME4 package in R (Bates et al. 2015). In the model, populations were considered to be random effects, whereas treatments and regions were considered to be fixed effects. Results were visualized in graphs using the GGPLOT2 package in R (Wickham 2016).

Results and Discussion

Effect of Osmotic Potential

Bassia scoparia populations germinated in high proportions (>60%) at osmotic potentials of −1.2 MPa or higher (Table 1; Figure 2). At an osmotic potential of 0 MPa, almost all *B. scoparia* seeds (>98%) from each site germinated during the observation period. *Bassia scoparia* exhibits rapid and high germination percentages when optimum conditions are met. Dyer et al. (1993) and Thompson et al. (1994) also reported greater than 95% germination of *B. scoparia* in less than 3 d under optimum seed germination conditions. At osmotic potentials of −0.9 MPa or higher, *B. scoparia* populations from all four sites achieved 50% of the maximum germination within 2 d. Similarly, at an osmotic potential of −1.2 MPa, *B. scoparia* populations took 4 to 8 d to achieve 50% germination; populations from northern Wyoming (near Powell) took the shortest time (4 d) and populations from Nebraska (near Scottsbluff) took the longest time (8 d). In addition, populations from Powell achieved 15% higher germination than populations from Scottsbluff at an osmotic potential of −1.2 MPa.

A proportion of *B. scoparia* seeds from each site were able to germinate within the range of osmotic potentials from 0 to −1.8 MPa (Table 2). However, decreases in the osmotic potential (more negative) significantly reduced *B. scoparia* germination rate (Figure 2) and cumulative germination (Figure 3) for all populations. Cumulative germination of *B. scoparia* populations from all the sites started declining rapidly at an osmotic potential of −0.9 MPa and declined to less than 20% at −1.8 MPa (Figure 3). A −0.85 MPa osmotic potential or lower reduced *B. scoparia* cumulative germination by 10%. These results agree with Everitt et al. (1983), who previously reported that *B. scoparia* germination did not decline until osmotic potential reached −0.8 MPa. In the current experiment, a −1.9 MPa osmotic potential or lower reduced *B. scoparia* germination by 90%. Populations from Scottsbluff were more sensitive to the osmotic potential (ψ_{50} of −1.32 MPa) than the populations from Powell (ψ_{50} of −1.46 MPa). However, no differences were observed between these two sites for ψ_{90} values (Table 2).

Time to achieve 50% of the maximum germination (t_{50}) increased with decreasing osmotic potential, but did not differ between *B. scoparia* populations from northern versus southern regions based on the mixed-effects analysis (Figure 4). Similarly, the duration of germination (t_{95}–t_5) increased with decreasing osmotic potential, but no differences were observed between *B. scoparia* populations from northern versus southern regions. On average, populations from northern and southern regions completed germination in 25 d at an osmotic potential of −1.2 MPa. Individual populations within a site or region had a greater variability in rate and duration of germination than the variability between the regions.

Effect of Temperature

Populations from all four sites had a high germination percentage (≥88%) across the temperatures tested (Table 3). The germination rate ($1/t_{50}$) was lowest at 4 C for all populations (Figure 5); however, 50% of the maximum germination was achieved in 3 d at this temperature. This indicates that temperatures above 4 C are not likely to reduce germination rate and cumulative germination of *B. scoparia* seeds. At 15 C or above, all populations achieved 50% germination in less than 1 d. Therefore, germination rate was highest at temperatures of 15 to 26 C for all populations,

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Table 1. Effect of osmotic potential on germination characteristics of *Bassia scoparia* populations collected in 2016 from four sites across a three-state region (MT, WY, NE) in the U.S. Great Plains.

Osmotic potential	Parameter estimates (±SE)[a]					
	b	t_{50}	d	b	t_{50}	d
—MPa—	Huntley, MT			Powell, WY		
0	−1.06 (0.45)	0.11 (0.11)	99 (1.4)	−2.45 (1.12)	0.37 (0.18)	100 (0.1)
−0.1	−1.27 (0.33)	0.35 (0.13)	97 (2.0)	−2.16 (0.65)	0.46 (0.13)	100 (0.1)
−0.3	−0.94 (0.21)	0.41 (0.14)	94 (2.8)	−2.23 (0.52)	0.61 (0.11)	99 (1.0)
−0.5	−1.14 (0.19)	0.78 (0.17)	94 (3.0)	−1.71 (0.31)	0.73 (0.12)	98 (1.3)
−0.7	−1.19 (0.17)	1.23 (0.22)	94 (3.4)	−1.74 (0.26)	0.94 (0.13)	98 (1.7)
−0.9	−1.14 (0.15)	2.36 (0.42)	87 (4.7)	−1.33 (0.18)	1.45 (0.23)	95 (3.3)
−1.2	−0.99 (0.13)	6.15 (1.29)	72 (7.1)	−1.03 (0.13)	3.84 (0.75)	79 (5.9)
		Lingle, WY			Scottsbluff, NE	
0	−0.93 (0.40)	0.08 (0.08)	98 (1.5	−0.90 (0.35)	0.10 (0.10)	98 (1.6)
−0.1	−1.32 (0.34)	0.36 (0.12)	98 (1.5)	−1.08 (0.29)	0.27 (0.12)	97 (1.9)
−0.3	−1.23 (0.27)	0.48 (0.12)	96 (2.3)	−0.98 (0.21)	0.45 (0.14)	95 (2.7)
−0.5	−1.11 (0.20)	0.71 (0.13)	94 (2.9)	−1.01 (0.17)	0.79 (0.19)	93 (3.3)
−0.7	−1.15 (0.18)	1.00 (0.19)	92 (3.2)	−1.06 (0.16)	1.24 (0.25)	92 (3.9)
−0.9	−1.05 (0.14)	2.20 (0.42)	85 (4.7)	−1.01 (0.14)	2.24 (0.45)	85 (4.9)
−1.2	−0.90 (0.12)	6.39 (1.48)	69 (7.0)	−0.81 (0.12)	7.53 (1.98)	64 (6.9)

[a]Parameter estimates were obtained using the log-logistic model (Equation 1). b, relative slope around t_{50}; t_{50}, time (days) taken to achieve 50% of the maximum germination; d, maximum germination (%) at the end of the observation period.

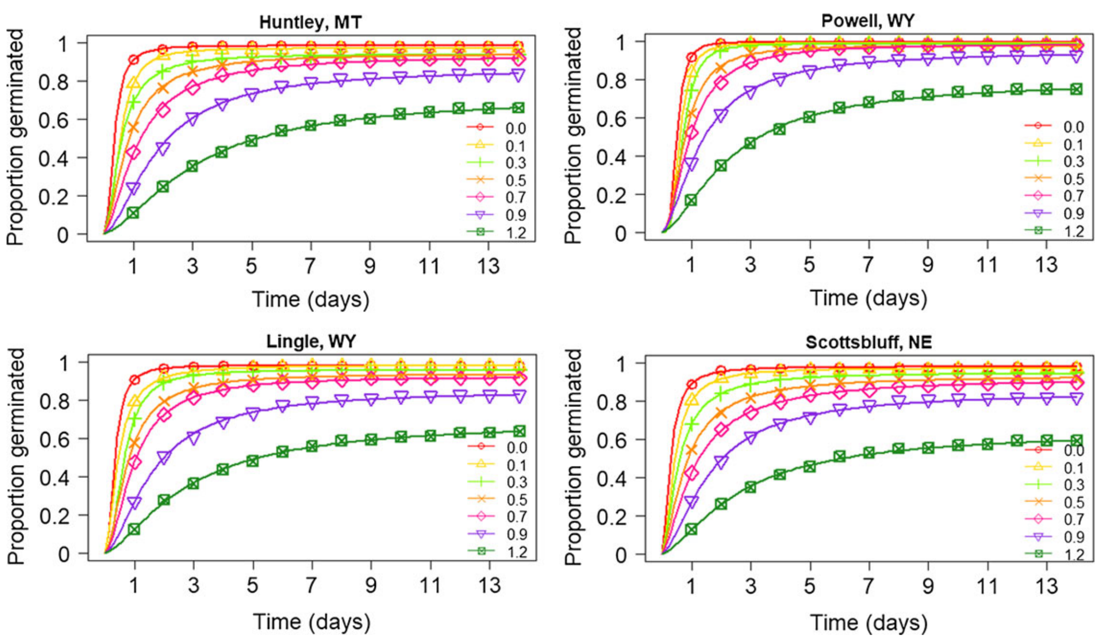

Figure 2. Germination response of *Bassia scoparia* populations to different levels of osmotic potential. Populations were collected in 2016 from four sites across a three-state region (MT, WY, NE) in the U.S. Great Plains. Curves were generated using a three-parameter log-logistic model (Equation 1). Each curve represents germination response (cumulative proportion) at a given osmotic potential (−MPa) over time (days). Symbols on the curves are the observed means of 11 populations.

indicating a wide range of temperatures favorable for *B. scoparia* germination. All populations had a cumulative germination of at least 90% over the range of temperatures tested. Dyer et al. (1993) reported greater than 99% cumulative germination by *B. scoparia* at 17 C in a 2-d period.

Time taken to achieve 50% of the maximum germination (t_{50}) by *B. scoparia* populations decreased with increasing temperatures, but did not differ between populations from northern versus southern regions at temperatures of 8 C or above based on the mixed-effects analysis (Figure 6). Similarly, the duration of germination (t_{95}–t_5) decreased slightly with temperatures above 4 C, but did not differ between populations from northern versus southern regions. Regardless of temperature treatment, *B. scoparia* populations from both regions completed their germination in less than 10 d. These results are consistent with previous findings that *B. scoparia* can germinate as soon as the minimum soil temperature rises above 3 or 4 C (Everitt et al. 1983; Nussbaum et al. 1985). Regional differences in emergence patterns of *B. scoparia* populations are likely to occur at low temperatures. For example, at 4 C, populations from the northern region took 5 h fewer to achieve 50% germination than populations from the southern region of the U.S. Great Plains (Table 4; Figure 7). Although this is not a large difference, it is likely to increase with further reductions in temperatures below 4 C, which needs to be investigated.

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Table 2. Effect of osmotic potential on the maximum germination of *Bassia scoparia* populations collected in 2016 from four sites across a three-state region (MT, WY, NE) in the U.S. Great Plains.

	Parameter estimates (±SE)[a]				
Site	*b*	ψ_{10}	ψ_{50}	ψ_{90}	*d*
Huntley, MT	6.46 (0.47)	0.98 (0.03)	1.37 (0.02)	1.93 (0.04)	98 (1.09)
Powell, WY	6.54 (0.48)	0.91 (0.03)	1.46 (0.02)	2.03 (0.05)	99 (1.06)
Lingle, WY	5.50 (0.40)	1.04 (0.03)	1.36 (0.02)	2.04 (0.05)	98 (1.14)
Scottsbluff, NE	5.16 (0.36)	0.86 (0.03)	1.32 (0.02)	2.03 (0.06)	97 (1.16)

[a]Parameter estimates were obtained using the log-logistic model (Equation 2). *b*, relative slope around ψ_{50}; ψ_{10}, ψ_{50}, and ψ_{90}, osmotic potential (−MPa) required to reduce the germination by 10%, 50%, and 90%, respectively; *d*, maximum germination (%) at the end of the observation period.

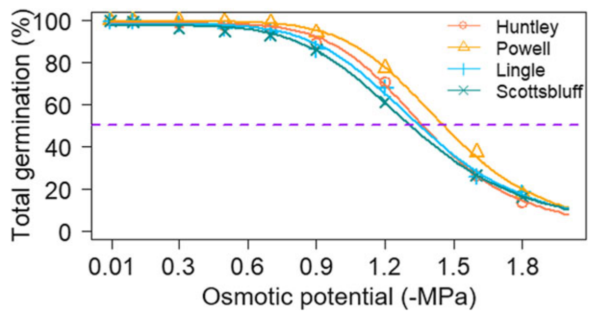

Figure 3. Effect of osmotic potential on the cumulative germination of *Bassia scoparia* populations collected in 2016 from four sites across a three-state region (MT, WY, NE) in the U.S. Great Plains. Curves were generated using a three-parameter log-logistic model (Equation 2). Each curve represents percent maximum germination over a range of osmotic potentials. Symbols on the curves are the observed means of 11 populations.

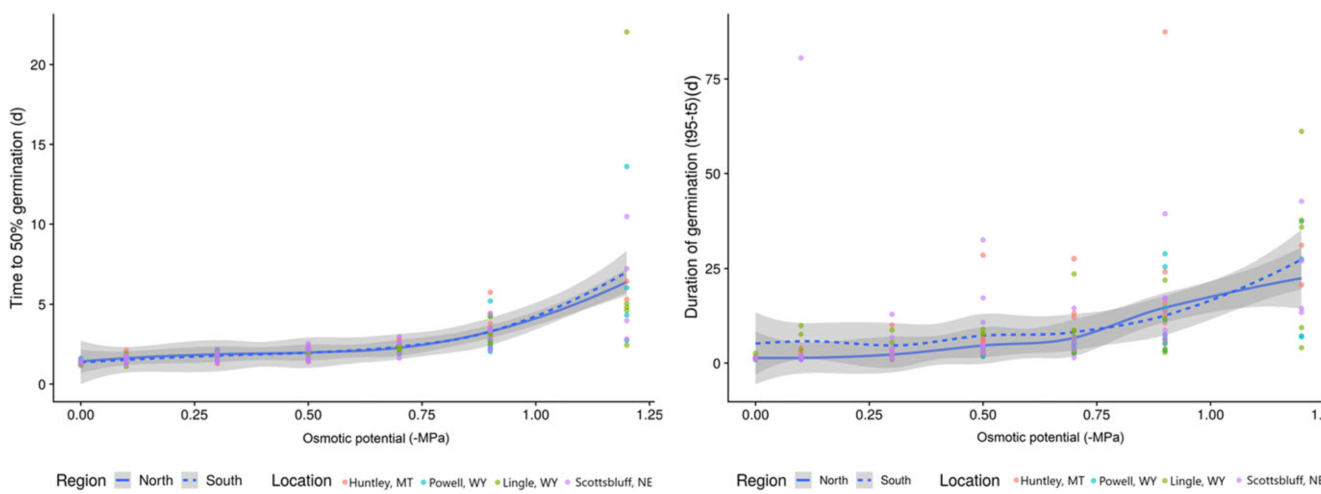

Figure 4. Effect of osmotic potential on the germination rate (left) and the germination duration (right) of *Bassia scoparia* populations collected in 2016 from four sites across a three-state region (MT, WY, NE) in the U.S. Great Plains. Response lines were fit with a mixed-effects model. The Huntley and Powell sites were included in the northern region, whereas the Lingle and Scottsbluff sites were included in the southern region. Colored round symbols along the lines represent parameter values of individual populations. Shaded gray bands along the lines represent 95% confidence intervals.

Management Implications

The results of this research indicate a wide range of optimum temperatures and osmotic potentials requirements for *B. scoparia* germination. Mengistu and Messersmith (2002) previously reported higher levels of genetic diversity within a *B. scoparia* population than across populations, and this may contribute to the lack of differences in response to temperature or water potential attributable to the northern versus southern location. The ability of *B. scoparia* to germinate in high proportions in a short period of time at low temperatures reinforces its competitive advantage over other weed species and crops. For example, *B. scoparia* achieved 80% of its maximum emergence at the time when other weed species common to the Northern Great Plains started emerging (Bullied et al. 2003; Schwinghamer and Van Acker 2008). In these studies, a minimum of 530 GDD were required to achieve 50% emergence for wild oat (*Avena fatua* L.), wild buckwheat (*Polygonum convolvulus* L.), field pennycress (*Thlaspi arvense* L.), common lambsquarters (*Chenopodium album* L.), and redroot

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Table 3. Effect of temperature on germination characteristics of *Bassia scoparia* populations collected in 2016 from four sites across a three-state region (MT, WY, NE) in the U.S. Great Plains.

	Parameter estimates (±SE)[a]					
	b	t_{50}	d	b	t_{50}	d
Temperature —C—		Huntley, MT			Powell, WY	
4	−4.42 (0.49)	2.85 (0.14)	92 (3.1)	−4.99 (0.53)	2.96 (0.14)	98 (1.7)
8	−3.41 (0.40)	1.64 (0.11)	92 (3.1)	−4.24 (0.48)	1.67 (0.13)	98 (1.8)
12	−2.83 (0.40)	1.14 (0.09)	94 (2.7)	−3.76 (0.51)	1.15 (0.09)	99 (1.2)
15	−2.85 (0.58)	0.81 (0.08)	93 (3.0)	−4.20 (0.60)	0.87 (0.07)	99 (0.1)
18	−3.60 (0.72)	0.88 (0.07)	94 (2.8)	−4.25 (0.85)	0.92 (0.07)	99 (0.1)
21	−3.33 (0.71)	0.83 (0.07)	92 (3.2)	−4.25 (0.96)	0.86 (0.06)	99 (1.1)
23	−2.25 (0.48)	0.84 (0.09)	95 (2.6)	−4.15 (0.95)	0.85 (0.06)	99 (1.1)
26	−2.15 (0.40)	0.86 (0.10)	90 (3.4)	−2.57 (0.46)	0.86 (0.09)	98 (1.4)
		Lingle, WY			Scottsbluff, NE	
4	−4.17 (0.47)	2.99 (0.16)	88 (3.7)	−4.22 (0.47)	3.21 (0.17)	88 (3.7)
8	−3.58 (0.42)	1.67 (0.10)	90 (3.5)	−3.49 (0.40)	1.75 (0.11)	90 (3.4)
12	−3.10 (0.44)	1.15 (0.08)	92 (3.1)	−2.79 (0.39)	1.17 (0.10)	92 (3.2)
15	−2.82 (0.59)	0.79 (0.09)	97 (3.1)	−2.57 (0.49)	0.83 (0.09)	92 (3.2)
18	−4.68 (0.73)	0.89 (0.06)	97 (2.1)	−3.56 (0.66)	0.92 (0.06)	93 (2.9)
21	−4.67 (0.86)	0.80 (0.07)	96 (2.2)	−3.79 (0.81)	0.86 (0.06)	94 (2.6)
23	−4.21 (0.75)	0.76 (0.08)	96 (2.3)	−3.34 (0.73)	0.80 (0.07)	94 (2.7)
26	−2.49 (0.48)	0.81 (0.09)	96 (2.3)	−2.32 (0.41)	0.89 (0.10)	95 (2.5)

[a]Parameter estimates were obtained using the log-logistic model (Equation 1). b, relative slope around t_{50}; t_{50}, time (days) taken to achieve 50% of the maximum germination; d, maximum germination (%) at the end of the observation period.

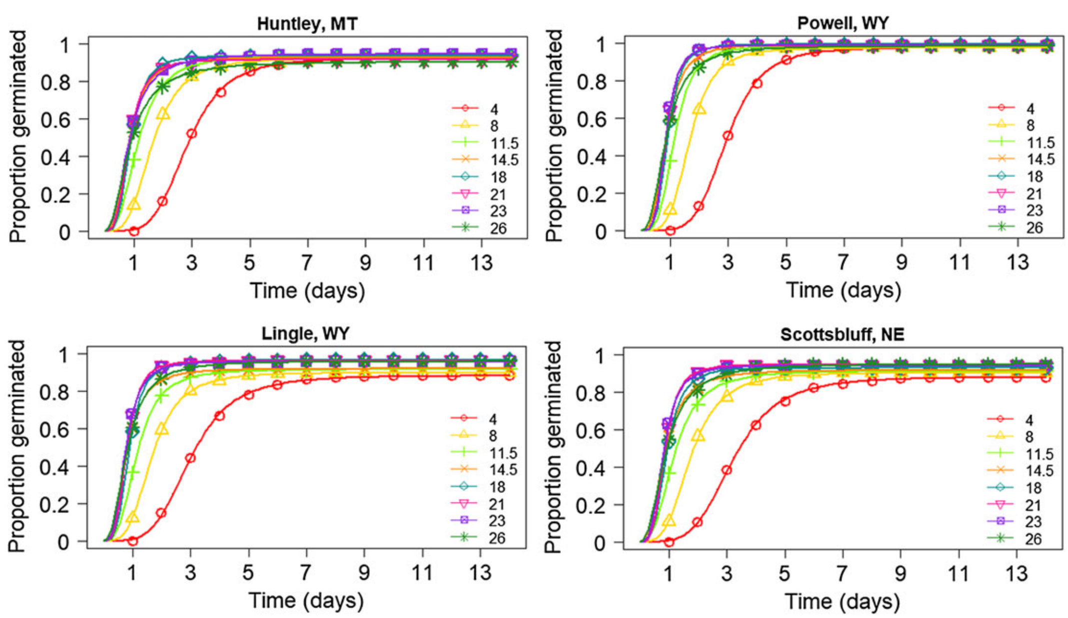

Figure 5. Germination response of *Bassia scoparia* populations collected in 2016 from four sites across a three-state region (MT, WY, NE) in the U.S. Great Plains to different temperature treatments. Curves were generated using a three-parameter log-logistic model (Equation 1). Each curve represents germination response (cumulative proportion) at a given temperature (C) over time (days). Symbols on the curves are the observed means of 11 populations.

pigweed (*Amaranthus retroflexus* L.) compared with 175 GDD for *B. scoparia*. The ranges of optimum temperatures and osmotic potentials required for germination in the current study were consistent across geographic regions. However, *B. scoparia* from the southern region had lower germination than *B. scoparia* from the northern region, especially at low temperatures tested, indicating the need for site-specific management practices for this early-emerging weed.

In osmotic potential experiments, 25% of *B. scoparia* seeds germinated at an osmotic potential of −1.6 MPa, an osmotic potential at which some weeds and crop species are unable to germinate (Guillemin et al. 2013; Hoveland and Buchanan 1973). For example, downy brome (*Bromus tectorum* L.), a problem weed in the U.S. Great Plains (Stougaard et al. 2004; Thill et al. 1984), did not germinate when osmotic potential dropped below −1.5 MPa (Thill et al. 1979). Similarly, wheat (*Triticum aestivum* L.), an important crop in this region, did not germinate at an osmotic potential of −1.5 MPa (Singh et al. 2013). The ability of *B. scoparia* to germinate at such a low osmotic potential may provide a competitive advantage over other species that are not present at the

https://doi.org/10.1017/wsc.2023.12 Published online by Cambridge University Press

Table 4. Effect of low temperature (4 C) on the rate and maximum germination of *Bassia scoparia* populations collected in 2016 across a north–south transect (MT, WY, NE) in the U.S. Great Plains.

Region[b]	Parameter estimates (±SE)[a]				
	b	t_{10}	t_{50}	t_{90}	d
Northern	−4.19 (0.11)	1.82 (0.03)	2.91 (0.03)	4.64 (0.07)	95 (0.53)
Southern	−4.19 (0.10)	1.84 (0.03)	3.11 (0.03)	5.26 (0.09)	88 (0.82)

[a]Parameter estimates were obtained using the log-logistic model (Equation 1).
b, relative slope around t_{50}; t_{10}, t_{50}, and t_{90}, time (days) taken to achieve 10%, 50%, and 90% of the maximum germination, respectively; *d*, maximum germination (%) at the end of the observation period.
[b]Huntley, MT, and Powell, WY, sites were included in the northern region; Lingle, WY, and Scottsbluff, NE, sites were included in the southern region.

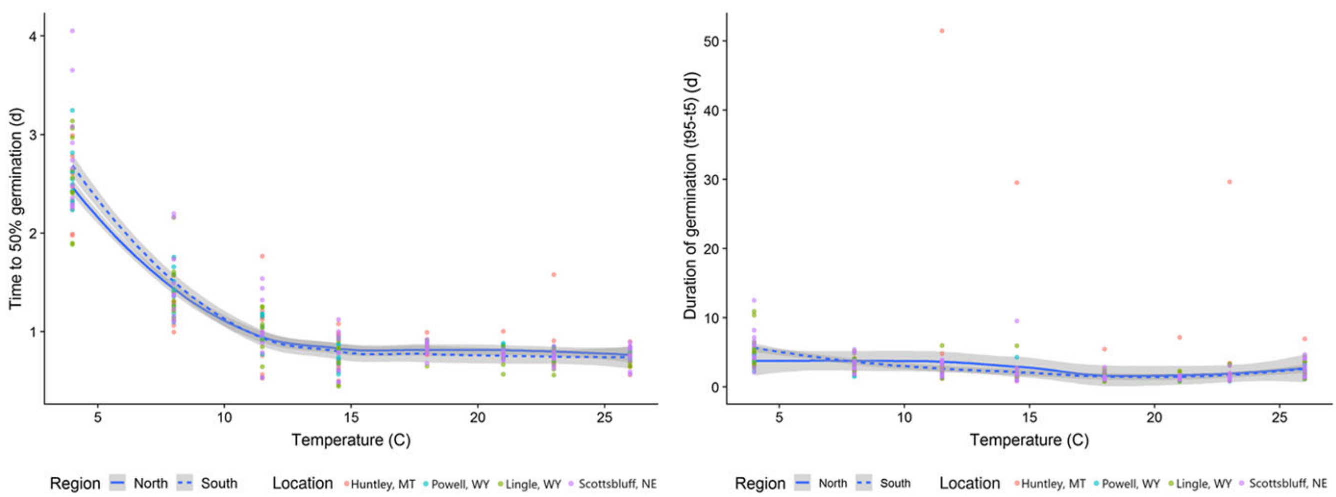

Figure 6. Effect of temperature on the germination rate (left) and the germination duration (right) of *Bassia scoparia* populations collected in 2016 from four sites across a three-state region (MT, WY, NE) in the U.S. Great Plains. Response lines were fit with a mixed-effects model. The Huntley and Powell sites were included in the northern region, whereas the Lingle and Scottsbluff sites were included in the southern region. Colored round symbols along the lines represent parameter values of individual populations. Shaded gray bands along the lines represent 95% confidence intervals.

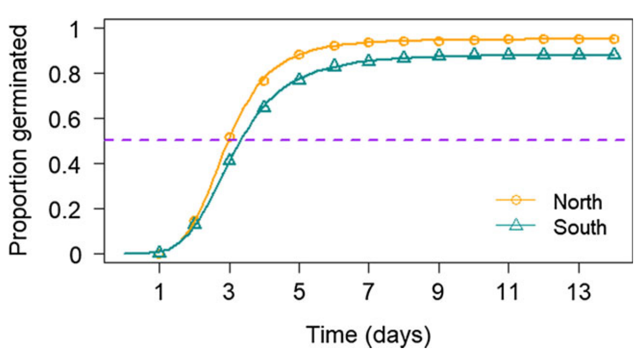

Figure 7. Effect of low temperature (4 C) on the rate and cumulative germination of *Bassia scoparia* populations collected in 2016 across a north–south transect (MT, WY, NE) in the U.S. Great Plains. Curves were generated using a three-parameter log-logistic model (Equation 1). Each curve represents germination response over time (days). Symbols on the curves are the observed means of 22 populations. The Huntley and Powell sites were included in the northern region, whereas the Lingle and Scottsbluff sites were included in the southern region.

time of *B. scoparia* germination (Bullied et al. 2003; Schwinghamer and Van Acker 2008). Additionally, the efficacy of certain preemergence soil-residual herbicides for *B. scoparia* control was reduced linearly with decreasing osmotic potentials (Sebastian et al. 2017). These results indicate that *B. scoparia* may become difficult to control in dry years (Teasdale et al. 2003) given the reported (Wienhold et al. 2018) trends of frequent droughts in the U.S. Northern Great Plains.

One of the practical ways to deplete soil seedbanks of troublesome weed species is to identify and manipulate the environmental factors that control their germination and emergence (Schonbeck and Egley 1980). Models have been used to predict weed emergence in a specific region or across regions. However, these models often rely solely on GDD to predict weed emergence (Myers et al. 2004). Use of a hydrothermal time, which includes both soil temperature and osmotic potential parameters can improve the accuracy of predicting emergence of weed species in the field (Bradford 2002; Forcella 1998; King and Oliver 1994). Therefore, parameter estimates generated from this study could be used to develop *B. scoparia* emergence models and predict emergence patterns across the three-state region using historical climate data. Knowledge of the timing and duration of *B. scoparia* emergence in a particular geographic location can then be used to modify crop practices and develop ecological strategies to manage the weed seedbank. For example, seedbanks of early-emerging populations of this weed can be exhausted using a stale seedbed approach before planting of crops in irrigated regions of the U.S. Great Plains. Similarly, the late-emerging populations can be suppressed using competitive crops such as wheat and barley (*Hordeum vulgare* L.), planted in the fall or early spring in this region (Kumar et al. 2018a). In conclusion, this research indicates that *B. scoparia* has rapid germination under a wide range of temperatures and osmotic potentials, which should be exploited using ecologically based strategies for its to control.

Osmotic potential requirements for *B. scoparia* seed germination in the current study were determined using PEG solutions (Michel 1983). Although this has been the most widely used method to create different water potentials in seed germination experiments, it may not simulate soil water potentials accurately (Camacho et al. 2021). For instance, 18% of Palmer amaranth (*Amaranthus palmeri* S. Watson) seeds germinated at water potential of −1.2 MPa in PEG solution, compared with 67% in a silty loam soil at the same water potential (Camacho et al. 2021). Therefore, development of germination predictive models for field use based on the parameters generated in this study would require additional considerations, such as soil texture.

Acknowledgments. This work was supported by the USDA National Institute of Food and Agriculture (grant no. 2016-70006-25831). We thank the MSU SARC, Huntley, MT for providing resources and support to conduct this study. Vipan Kumar provided helpful comments on an earlier draft of this article. No conflicts of interest have been declared.

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