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Afterripening Requirements and Optimal Germination Temperatures for Nuttall's Alkaligrass (*Puccinellia nuttalliana*) and Weeping Alkaligrass (*Puccinellia distans*)

Catherine S. Tarasoff, Daniel A. Ball, and Carol A. Mallory-Smith*

In the Grande Ronde Valley of eastern Oregon, two perennial grass species in the genus *Puccinellia*, weeping alkaligrass and Nuttall's alkaligrass, are weeds of Kentucky bluegrass grass-seed production fields. Weeping alkaligrass is introduced from Eurasia, whereas Nuttall's alkaligrass is native to the region. These two species were studied to determine dormancy attributes and optimal temperature conditions for seed germination. Results from the current studies indicate that both species have a high level of embryonic dormancy immediately following seed harvest, which is primarily eliminated through dry storage (afterripening) and an incubation temperature of 20 C. Following adequate afterripening, a prechill treatment of 5 d at 5 C had an inconsistent effect on germination of weeping alkaligrass ($P = 0.012$ in 2002, 0.156 in 2003) and improved germination of Nuttall's alkaligrass over both years ($P < 0.0001$). The afterripening requirement for weeping alkaligrass was more than 90 d, whereas Nuttall's alkaligrass required more than 180 d. Following adequate afterripening, both species had rapid and well-synchronized germination at fluctuating day/night temperatures of 30/10 C given unlimited moisture conditions. Given these results, it is unlikely that seeds of either species would germinate in eastern Oregon during the summer months. The data predict a long viability period under dry storage for both species. Weeping alkaligrass and Nuttall's alkaligrass should exhibit a rapid, well-synchronized germination in the spring as observed in the field.
Nomenclature: Nuttall's alkaligrass, *Puccinellia nuttalliana* Hitchc.; weeping alkaligrass, *Puccinellia distans* (L.) Parl.; Kentucky bluegrass, *Poa pratensis* L.
Key words: Afterripening, dormancy, germination, halophytes.

Weeping alkaligrass and Nuttall's alkaligrass are weeds within Kentucky bluegrass grass-seed production fields in the Grande Ronde Valley of eastern Oregon. Both perennial grass species typically occupy sites with high pH soils throughout North America (Brotherson 1987; Hughes 1972; Macke and Ungar 1971). Weeping alkaligrass, an introduced species from Eurasia, is widespread across moist, more or less alkaline environments of North America (Hitchcock 1971), whereas Nuttall's alkaligrass, native to North America, occupies moist, usually alkaline soils from Wisconsin to British Columbia, south to Kansas, New Mexico, and California (Hitchcock 1971). Both species are considered to be among the most saline-tolerant C_3 grasses in North America (Ashraf et al. 1986; Harivandi et al. 1983; Macke and Ungar 1971), with weeping alkaligrass perhaps more salt tolerant than Nuttall's alkaligrass (Moravcova and Frantik 2002; Salo et al. 1996).

Kentucky bluegrass seed is a crop of primary importance in the Grande Ronde Valley of Eastern Oregon (Union County). Approximately 90% of grass-seed crops in Union County are grown under contract with seed companies as certified seed (D. Walenta, personal communication). In 2004, in Union County, there were 2,428 ha of harvested Kentucky bluegrass, which represented 34% of Oregon's total production. It is well documented that weeds compete with the crop species for limited resources, such as nutrients, water, and sunlight. However, of greater importance for grass-seed producers is that weedy grasses, such as alkaligrass, contaminate the harvested grass-seed crop, resulting in reduced seed quality and market value. For Kentucky bluegrass seed producers of eastern Oregon, control of these grassy weeds can be difficult because of the complexity of selectively controlling grass weeds in grass-seed crops.

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* First and third authors: Department of Crop and Soil Science, Oregon State University, Corvallis, OR 97331-3002; second author: Columbia Basin Agricultural Research Center, Oregon State University, Pendleton, OR 97801. Corresponding author's E-mail: catherine.tarasoff@oregonstate.edu

An understanding of a plant's dormancy and germination is a primary step toward a better understanding of its biology, ultimately adding to the development of effective control strategies. Seed dormancy is an adaptation that prevents the germination of newly dispersed seed and, based on the length and type of dormancy, may help to preserve a supply of seed in the soil seed-bank. Farmers need to understand the potential for seed-bank persistence due to seed dormancy attributes that control the timing of germination to maximize the probability of seedling survival (Meyer et al. 1990). Understanding the dormancy attributes of weeping alkaligrass and Nuttall's alkaligrass could help land managers to predict the possible longevity of an infestation.

Afterripening requirements of weeping alkaligrass were studied by Moravcova and Frantik (2002). They found that the percentage of germination increased after 90 d of dry storage, up to a maximum of nearly 100% germination. However, in their experiment, dormancy-breaking treatments, such as chilling and potassium nitrate (KNO_3), were not tested. Field observations by Macke and Ungar (1971) documented that these species are likely to germinate the spring following a winter chill. Macke and Ungar (1971) cited alternating day/night temperatures of 20/5 C as optimal for Nuttall's alkaligrass germination; however, that was not verified through experimentation. Moravcova and Frantik (2002) documented the optimal day/night temperature combination for germination of weeping alkaligrass at 30/15 C; however, that experiment reported only the final germination percentage at 12 fluctuating temperature combinations and 6 constant temperatures but not germination over time.

To determine the overriding effect of afterripening, chilling, and temperature on dormancy, it was necessary to investigate the effect of dormancy-breaking treatments in combination with afterripening. To evaluate optimal temperatures for germination of nondormant seeds, a wider range of temperatures was tested, especially extreme high and low temperatures that are common within the shallow layers of soil (top 2.5 cm) of

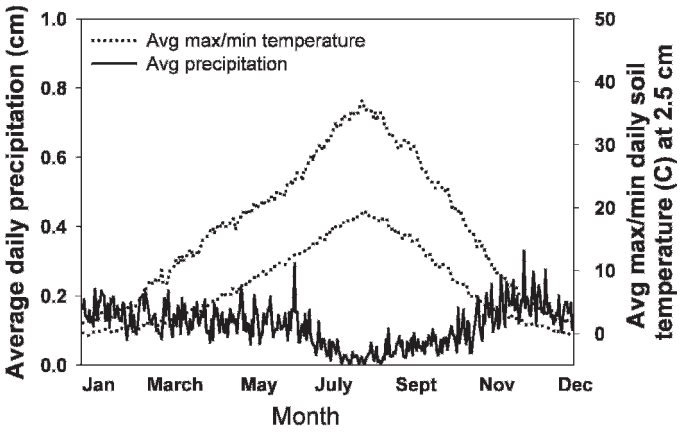

Figure 1. Twenty-year average daily maximum and minimum soil temperatures at 2.5 cm depth with 20-yr average daily precipitation (data collected from Columbia Basin Agricultural Research Center, Pendleton, OR).

eastern Oregon, where summer temperatures can reach upward of 40 C (Figure 1).

This article presents the results of two experiments studying the loss of dormancy during afterripening in combination with dormancy-breaking treatments and the effect of temperature on germination following adequate afterripening.

Materials and Methods

Factors Regulating Loss of Dormancy During Afterripening. An afterripening experiment was conducted to study the loss of seed dormancy in Nuttall's alkaligrass and weeping alkaligrass. Nuttall's alkaligrass and weeping alkaligrass seeds were collected from multiple distinct sites within a large acreage in the Grande Ronde valley at the "Imbler Site" (45°29′15.9″N, 117°56′4″W) on July 8, 2002. In 2003, the Imbler site was removed from grass-seed production, thereby eliminating the 2002 collection site. Therefore, weeping alkaligrass was collected in the same manner previously described at "Market Ln" site (45°22′57.5″N, 117°54′37.7″W) and Nuttall's alkaligrass at "Hull Ln" (45°26′57.8″N, 117°56′22.1″W); both species were collected on July 29, 2003. Seeds were hand-thrashed, sorted, and air-dried at 20 C for 5 d. Seeds were afterripened for 10, 30, 90, 180, and 365 d after harvest (DAH). All seeds were surface sterilized for 20 s with a 5% solution of bleach, and triple rinsed. At each afterripening date, 50 seeds of each species were counted onto two layers of germination paper placed in a 9-cm-diam petri dish. Treatment options used at each germination time were a wet prechill for 5 d at 5 C vs. no prechill and an incubation fluid of KNO_3 (20 mM) or deionized water combined with a germination temperature of 20 or 30 C.[1]

All possible combination options for each species resulted in eight treatments in a two by two by two factorial arrangement, with each petri dish assigned to a treatment in a completely randomized design. Each treatment combination was replicated four times, and the protocol was identical for both species. Prechilled treatments were wetted before placing seeds into the prechill chamber. Seeds were germinated under dark conditions except for limited exposure to ambient light conditions as necessary to count germinated seeds on days 3, 7, 14, and 21. Seeds were considered germinated when the coleoptile was 2 mm long and a radicle was present. Germinated seeds were removed from the petri dish as they were counted. At day 21, the remaining ungerminated seeds were counted and recorded to allow accurate calculation of percentage of germination. Because of the small seed size, accurate tetrazolium tests could not be conducted, but by day 21, most ungerminated seeds were soft to the touch and moldy. Differences in probability of germination between treatments were analyzed using the logistic link function, PROC GENMOD.[2] Logistic regression considers the probability of germination as a function of each seed's response to the treatment calculated by the fraction of germinated seeds in relation to the total number of seeds in a petri dish. Many forms of pseudoreplication occur during the study of seed germination through the lack of true replication of each independent treatment (Morrison and Morris 2000). Logistic regression calculates the probability of germination by assuming all seeds in a given petri dish are subjected to the same conditions.

Effect of Temperature on Germination of Nondormant Seed. Nuttall's alkaligrass and weeping alkaligrass seeds were collected from the Grande Ronde Valley at the Imbler Site on July 8, 2002 and open air dried at 20 C for 18 mo to ensure adequate afterripening. All seeds were surface sterilized for 20 s with a 5% solution of bleach and triple rinsed. Following the bleach treatment, 200 seeds were placed on two layers of germination paper, which was placed on top of 80 ml (0.5 cm deep) of sterilized 20-grit silica sand in an 8 cm by 8 cm plastic germination box. The silica sand was wetted to maximum holding capacity to provide a buffer against desiccation and water puddling. After wetting, all seeds were prechilled for 48 hr at 5 C.

Following the prechill treatment, each germination box was randomly assigned to one of 32 temperature combinations located on a two-way thermogradient plate (Larsen et al. 1973). The germination boxes were placed on the thermogradient plate in a checkerboard pattern resulting in day/night temperature combinations of approximately: 5/5, 5/15, 5/25/, 5/35, 10/10, 10/20, 10/30, 10/40, 15/5, 15/15, 15/25, 15/35, 20/10, 20/20, 20/30, 20/40, 25/5, 25/15, 25/25, 25/35, 30/10, 30/20, 30/30, 30/40, 35/5, 35/15, 35/25, 35/35, 40/10, 40/20, 40/30, and 40/40 C. The experiment was a completely randomized design with 200 sample seeds per treatment. The experiment was repeated. The thermogradient plate required approximately 2 hr of heating and cooling to the specific temperature. No specific photoperiod was used, and seeds were exposed to ambient indoor lighting conditions. Temperature of each treatment was measured by a copper-constantan thermocouple at 15-s intervals, and the data were averaged over 10 min using a datalogger[3] attached to a multiplexer.[4] Germinated seeds were counted and removed 3, 6, 9, 12, 15, and 18 d after the experiments were initiated. Seeds were considered germinated when the coleoptile was 2 mm long and a radicle was present. On day 18, the remaining ungerminated seeds were counted. Differences in probability of germination among treatments were analyzed using logistic link function (PROC GENMOD).[2]

Results and Discussion

Factors Regulating Loss of Dormancy During Afterripening. Unequal variances in germination between 2002

Table 1. Statistical results of logistic regression analysis of afterripening data for weeping alkaligrass (2002 and 2003 separately) and Nuttall's alkaligrass (2002 and 2003 combined).

Species	Year	Treatment[a]	*F* value	P
Weeping alkaligrass	2002	Afterripening	$F_{4,120} = 4.67$	< 0.001
		KNO_3	$F_{1,120} = 1.63$	0.202
		Temperature	$F_{1,120} = 13.16$	< 0.001
		Chill	$F_{1,120} = 6.24$	0.012
		Afterripening × temp	$F_{4,120} = 1.35$	0.248
		Afterripening × chill	$F_{4,120} = 1.38$	0.238
Weeping alkaligrass	2003	Afterripening	$F_{4,120} = 97.5$	< 0.0001
		KNO_3	$F_{1,120} = 0.76$	0.383
		Temperature	$F_{1,120} = 247.47$	< 0.0001
		Chill	$F_{1,120} = 2.01$	0.156
		Afterripening × temp	$F_{4,120} = 28.86$	< 0.0001
		Afterripening × chill	$F_{4,120} = 9.30$	< 0.0001
Nuttall's alkaligrass	2002/3	Afterripening	$F_{4,280} = 36.82$	< 0.0001
		KNO_3	$F_{1,280} = 0.96$	0.327
		Temperature	$F_{1,280} = 116.75$	< 0.0001
		Chill	$F_{1,280} = 48.70$	< 0.0001
		Afterripening × temp	$F_{4,280} = 40.2$	< 0.0001
		Afterripening × chill	$F_{4,280} = 8.3$	< 0.0001

[a] Unlisted treatment combinations were not significant at $\alpha = 0.05$.

and 2003 prevented data combination for weeping alkaligrass. Although the germination values of weeping alkaligrass were lower in 2002, and the data could not be combined, the trends were similar between years. Nuttall's alkaligrass had acceptable variances in germination between years and, therefore, those data were combined.

Weeping Alkaligrass. Incubation temperature was the most important factor affecting germination across both years (Table 1). Total germination was greatest in 2002 with an incubation temperature of 20 C combined with 365 d of afterripening (55 ± 19%). There was no significant difference between seeds given a prechill treatment (51 ± 8%) and those that were unchilled (55 ± 19%). The effect of the interactions of afterripening, temperature, and prechill treatments varied by year (Table 1). In 2002, the afterripening, temperature, and prechill treatments improved germination of weeping alkaligrass (Table 1). In 2002, weeping alkaligrass seed dormancy was beginning to decline by 90 DAH with 29 ± 11% of the seeds germinated at 20 C and a prechill treatment (Figure 2A).

In 2003, interactions between temperature and afterripening and between afterripening and chill were significant ($P < 0.0001$). Therefore, germination was improved with temperatures of 20 C or a chill treatment combined with afterripening but not all three. Although in 2003, weeping alkaligrass seeds began to lose dormancy by 10 DAH (Figure 2B), not until 90 DAH did the seeds exhibit higher germination values (81 ± 4%). In 2003, weeping alkaligrass was able to germinate at incubation temperatures of 30 C with a prechill treatment at 90 and 180 DAH; however, by 365 DAH, the seeds were no longer able to germinate at 30 C, regardless of a prechill treatment (Figure 2B) possibly due to embryonic death. Although prechilling improved germination in both years at 90 DAH, its effect was reduced over time and was inconsistent between 2002 and 2003 (Table 1). Overall, there did appear to be a dormancy-breaking effect of prechilling for weeping alkaligrass at 90 DAH regardless of year. However, for both years, by 180 DAH, the prechill treatment marginally and inconsistently

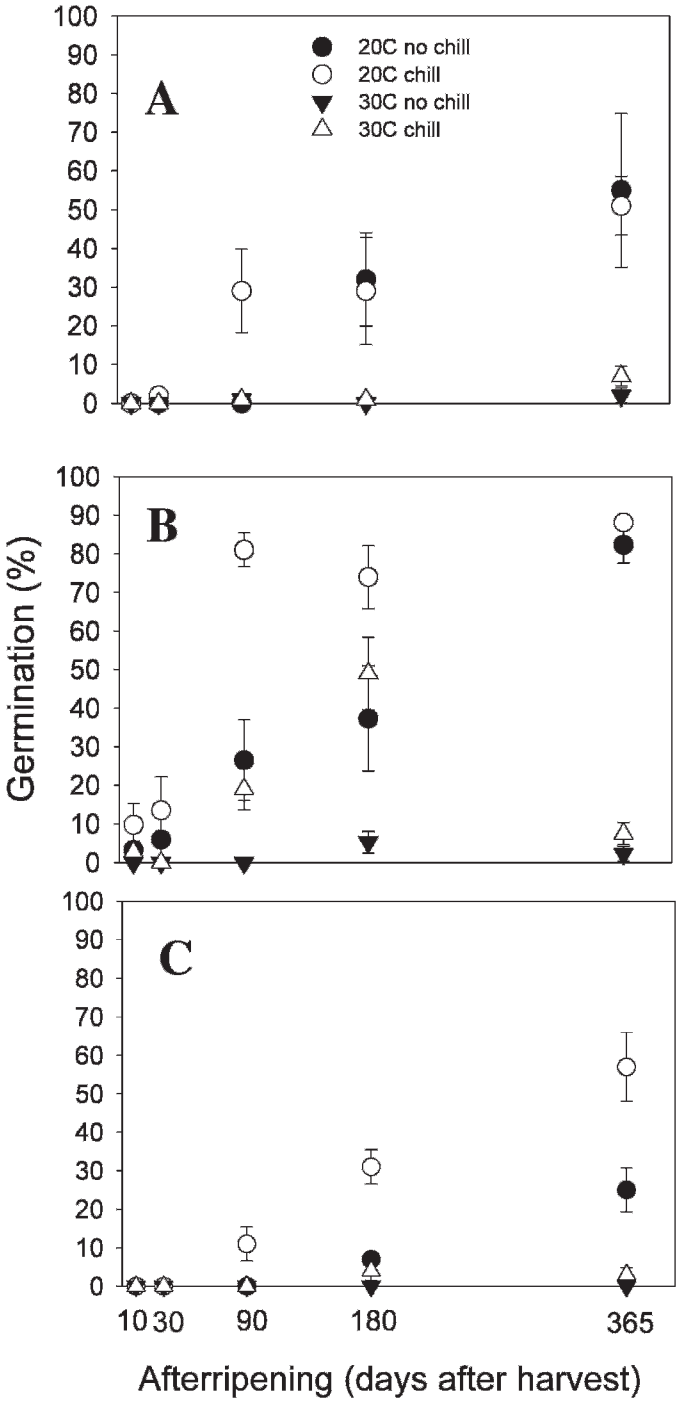

Figure 2. Effect of afterripening, chill, and germination temperature on germination at day 18 for weeping alkaligrass in (A) 2002 and (B) 2003 and (C) for Nuttall's alkaligrass, with 2002 and 2003 data combined. Data are presented with 95% confidence intervals ($\alpha = 0.05$).

improved germination values. Weeping alkaligrass did not respond to the solution of 20-mM KNO_3 in either year (Table 1). The results for weeping alkaligrass are consistent with the findings of Moravcova and Frantik (2002) and indicate that although afterripening is the most important factor relating to loss of dormancy, afterripening combined with suitable temperatures of 20 C are necessary for non-dormant seeds to germinate.

Table 2. Germination at 3, 7, 14, and 21 d after treatment (DAT) with 365 d of afterripening for weeping alkaligrass (2002 and 2003 separately) and Nuttall's alkaligrass (2002 and 2003 combined).

Species	Year	Treatment	Germination			
			3 DAT	7 DAT	14 DAT	21 DAT
			% (± 95% CI)			
Weeping	2002	20 C + chill	0	65 (6.6)	89 (4.3)	89 (4.3)
		20 C no chill	0	17 (5.2)	33 (6.5)	33 (6.5)
		30 C + chill	0	4 (2.7)	4 (2.7)	4 (2.7)
		30 C no chill	0	0	0	0
Weeping	2003	20 C + chill	0	85 (4.9)	91 (4.0)	91 (4.0)
		20 C no chill	0	72 (6.2)	82 (5.3)	82 (5.3)
		30 C + chill	0	5 (3.0)	5 (3.0)	5 (3.0)
		30 C no chill	0	2 (1.9)	2 (1.9)	2 (1.9)
Nuttall's	2002/3	20 C + chill	0	44 (6.9)	45 (6.9)	45 (6.9)
		20 C no chill	0	14 (4.8)	16 (5.1)	16 (5.1)
		30 C + chill	0	1 (1.4)	1 (1.4)	1 (1.4)
		30 C no chill	0	0	0	0

Nuttall's Alkaligrass. Under no circumstances was Nuttall's alkaligrass able to germinate at 30 C (Figure 2C), nor did this species respond to the KNO_3 treatment (Table 1).

Prechill treatments were highly significant in germination response in Nuttall's alkaligrass (Table 1) because this species consistently responded to the chilling treatment with higher germination values (Figure 2C). Germination response to the prechill treatment increased linearly with length of afterripening. The increased germination, from 90 to 365 DAH, indicates a gradual loss of dormancy through afterripening that was stimulated via a prechill treatment.

Although Nuttall's alkaligrass began to exhibit dormancy breaking at 90 DAH at 20 C and a prechill treatment (11 ± 4%), higher germination values were not noted until 180 DAH (31 ± 5%) with the same treatment combinations (Figure 2C). Within Nuttall's alkaligrass, germination increased linearly and at a greater rate with afterripening when a prechill treatment was combined with an incubation temperature of 20 C. Although the precise dormancy-breaking mechanisms associated with chilling treatments are not clearly understood, the effects of low temperatures on plant cells generally result in an overall decrease in metabolic rates, a qualitative change in metabolism, a structural change in membranes (i.e., lipid composition) (Hara et al. 2003), and changes in hormone abundance, such as gibberellin (Yamauchi et al. 2004) and abscisic acid (Ali-Rachedi et al. 2004). Although the effect of low temperature (chilling) on germination is species specific and interrelated with other environmental factors, such as light, salinity, moisture, and oxygen to name a few (Silvertown 1980), embryonic development or afterripening is known to influence the overall effect of temperature on germination (Baskin and Baskin 1998). Therefore, it is not surprising that both species demonstrated increased germination when they were adequately afterripened, given a prechill treatment, and subjected to an incubation temperature of 20 C. Germination responses to various KNO_3 concentrations appear to be inconsistent within the literature (Adkins and Adkins 1994; Larsen et al. 1973), with no particular rate providing optimum germination across species (Adkins and Adkins 1994; Mekki and Leroux 1991). It is apparent that the rate of KNO_3 required to break dormancy is dependant on the species being studied and was not significant within this study.

Germination Rate. Rate of germination was not altered or improved with any of the dormancy-breaking treatment combinations (Table 2). At 365 d of afterripening, both species had the least amount of dormancy remaining; therefore, any germination stimulation as a result of the treatments should be apparent. For both species, after 365 d of afterripening, regardless of treatment, the majority of germination occurred between 3 and 7 d after treatment (DAT) (Table 2).

Effect of Temperature on Germination of Nondormant Seed. The germination data for both species were assessed for equal variance between runs. Variability was not found to be

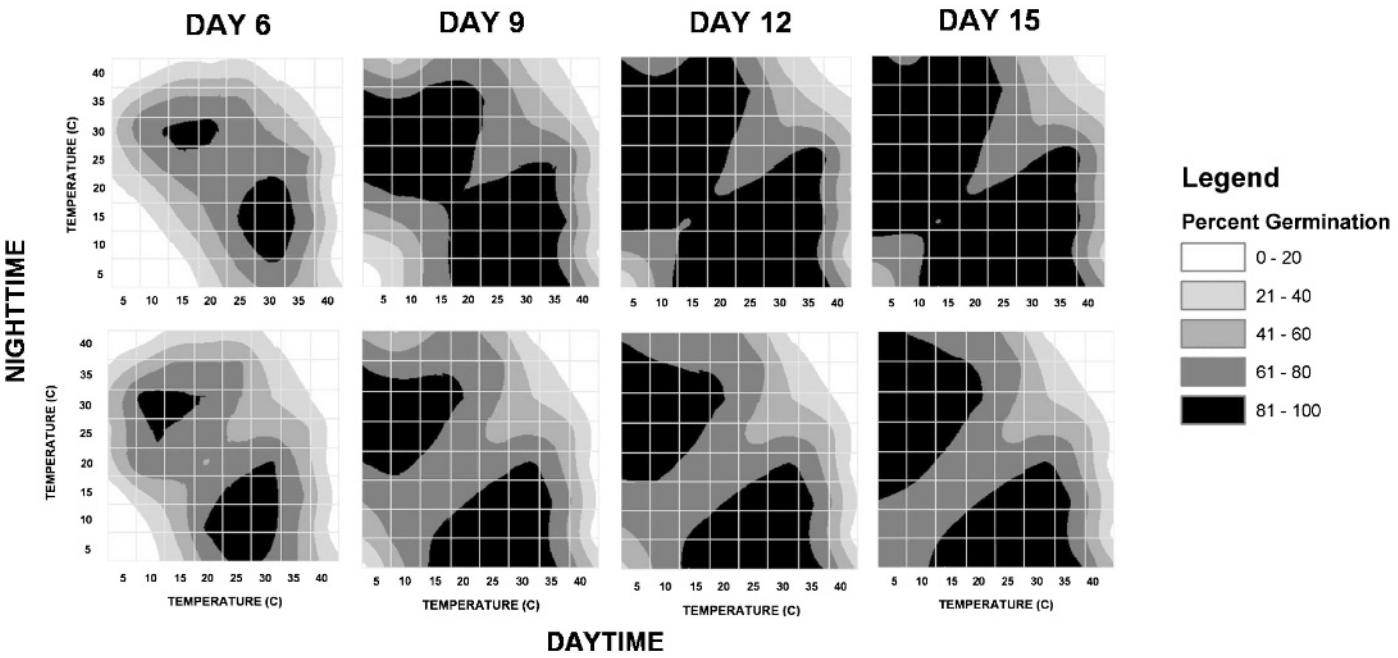

Figure 3. Germination over time of (A) weeping alkaligrass and (B) Nuttall's alkaligrass from days 6 to 15 at various day/night temperature-treatment combinations.

significant ($P \leq 0.05$ at $\alpha = 0.05$); therefore, 2002 and 2003 data were combined before analysis. To accommodate the quadratic relationship between temperature and germination, the independent variables of day and night temperatures were squared and incorporated into the logistic regression analysis (PROC GENMOD).[2] Because of the large number of treatment combinations, germination rate is presented as a figure created using mathematical interpolation formulae within geographic information system (GIS) software (Figure 3) (Tarasoff et al. 2005). Not surprisingly, the interaction of day and night temperatures was found to affect germination for both species ($P \leq 0.05$ at $\alpha = 0.05$) because both species benefited from fluctuating temperatures. Rates of germination were slightly slower at temperature combinations involving the extreme high and low temperatures as well as at constant temperatures (Figure 3).

Similar to the afterripening results and regardless of temperature, most germination occurred by day 9 (Figure 3). Germination was less than 20% for all treatment combinations for both species at day 3 (data not shown); as well, germination at day 18 was the same as at day 15 for all treatment combinations for both species (data not shown).

Although both species germinated across a variety of temperature combinations, in general, weeping alkaligrass had higher germination at most temperature combinations, in particular, at constant temperatures. For weeping alkaligrass, greater than 80% germination occurred on day 6 at the optimal daytime temperature of 30 C with a nighttime temperature of 10 to 15 C. Although Nuttall's alkaligrass was less vigorous, greater than 80% germination occurred on day 6 with daytime temperatures between 25 and 30 C and nighttime temperatures of 10 to 15 C.

In the Grande Ronde Valley of eastern Oregon, high summer soil temperatures are associated with dry soil conditions (Figure 1). However, average soil-temperature conditions throughout the summer should be suitable to initiate some germination in both species. Therefore, because neither species emerges in the summer (personal observation), it is likely that the combination of adequate afterripening and soil moisture are more critical for germination than specific temperature requirements.

Weed seeds with short afterripening periods and concentrated germination flushes and emergence should be easier to control than those with long afterripening periods and drawn-out germination characteristics. Both species of alkaligrass exhibit relatively long afterripening characteristics, making control and prevention of alkaligrass seed-bank development more difficult for land managers. As well, seeds of either species of alkaligrass will remain viable for at least 1 yr within dry stored Kentucky bluegrass. Newly establishing Kentucky bluegrass fields could be subjected to competition from either species because of alkaligrass's ability to germinate at low temperatures, allowing for the establishment of dense monocultures early in the season. Early establishment by either species of alkaligrass would limit resources available for the development of other plant species, an obvious competitive advantage.

Sources of Materials

[1] Incubation chamber, Hoffman Manufacturing, Inc., P.O. Box 547, Albany, OR 97321.

[2] SAS statistical software, version 9.1, SAS Institute Inc., 100 SAS Campus Drive, Cary, NC 27513.

[3] CR 10 Datalogger, Campbell-Scientific Inc., 815 West 1800 North, Logan, UT 84321.

[4] AM 16/32 multiplexer, Campbell-Scientific Inc., 815 West 1800 North, Logan, UT 84321.

Literature Cited

Adkins, S. W. and A. L. Adkins. 1994. Effect of potassium nitrate and ethephon on fate of wild oat (*Avena fatua*) seed in soil. Weed Sci. 42:353–357.

Ali-Rachedi, S., D. Bouinot, M. Wagner, M. Bonnet, B. Sotta, P. Grappin, and M. Jullien. 2004. Changes in endogenous abscisic acid levels during dormancy release and maintenance of mature seeds: studies with the Cape Verde Islands ecotype, the dormant model of Arabidopsis thaliana. Planta (Berl.) 219: 479–488.

Ashraf, M., T. McNeilly, and A. D. Bradshaw. 1986. The potential for evolution of salt (NaCl) tolerance in seven grass species. New Phytol. 103:299–309.

Baskin, C. C. and J. M. Baskin. 1998. Seeds: Ecology, Biogeography, and Evolution of Dormancy and Germination. San Diego, CA: Academic Press.

Brotherson, J. D. 1987. Plant community zonation in response to soil gradients in a saline meadow near Utah Lake, Utah County, Utah. Great Basin Nat. 47:322–333.

Hara, M., S. Terashima, T. Fukaya, and T. Kuboi. 2003. Enhancement of cold tolerance and inhibition of lipid peroxidation by citrus dehydrin in transgenic tobacco. Planta (Berl.) 217:290–298.

Harivandi, M. A., J. D. Butler, and P. N. Soltanpour. 1983. Effects of soluble salts on ion accumulation in *Puccinellia* spp. J. Plant Nutr. 6:255–266.

Hitchcock, A. S. 1971. Manual of the grasses of the United States. 1st ed. New York: Dover Publications.

Hughes, T. D. 1972. Illinois Turfgrass Conference. Champaign, IL: Illinois Cooperative Extension Service.

Larsen, A. L., D. P. Montgillion, and E. M. Schroeder. 1973. Germination of dormant and nondormant Rescuegrass seed on the thermogradient plate. Agron. J. 65:56–59.

Macke, A. J. and I. A. Ungar. 1971. The effects of salinity on germination and early growth of *Puccinellia nuttalliana*. Can. J. Bot. 49:515–520.

Mekki, M. and G. D. Leroux. 1991. False chamomile seed germination requirements and its enhancement by ethephon and nitrate. Weed Sci. 39:385–389.

Meyer, S., S. Monson, and E. McArthur. 1990. Germination response of *Artemesia tridentata* (Asteraceae) to light and chill: patterns of between-population variation. Bot. Gaz. 151:176–183.

Moravcova, L. and T. Frantik. 2002. Germination ecology of *Puccinellia distans* and *P. limosa*. Biologia (Bratisl.) 57:441–448.

Morrison, D. and E. Morris. 2000. Pseudoreplication in experimental designs for the manipulation of seed germination treatments. Austral Ecol. 25:292–296.

Salo, L. F., J. F. Artiola, and J. W. Goodrich-Mahoney. 1996. Plant species for revegetation of a saline flue gas desulfurization sludge pone. J. Environ. Qual. 25:802–808.

Silvertown, J. 1980. Leaf-canopy-induced seed dormancy in a grassland flora. New Phytol. 85:109–118.

Tarasoff, C. S., M. Louhaichi, C. Mallory-Smith, and D. A. Ball. 2005. Using geographic information systems to present nongeographical data—an example using a two-way thermogradient plate. Range. Ecol. Manag. 58:315–318.

Yamauchi, Y., M. Ogawa, A. Kuwahara, A. Hanada, Y. Kamiya, and S. Yamaguchi. 2004. Activation of gibberellin biosynthesis and response pathways by low temperature during imbibition of *Arabidopsis thaliana* seeds. Plant Cell 16:367–378.

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