*Weed Science* 2007 55:305–310

# Extreme Ionic and Temperature Effects on Germination of Weeping Alkaligrass (*Puccinellia distans*), Nuttall's Alkaligrass (*Puccinellia nuttalliana*) and Kentucky Bluegrass (*Poa pratensis*)

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The introduced species weeping alkaligrass, and the native species Nuttall's alkaligrass, two of the most salt-tolerant $C_3$ grasses found in arid and semiarid environments of western North America, occur within the Grande Ronde valley of eastern Oregon. Both species occur as weeds within Kentucky bluegrass seed fields and subsequently as grass seed contaminants. Two separate germination experiments were conducted to understand better the seed germination biology of these two species compared to Kentucky bluegrass under negative water potentials or high temperature conditions. Results of these studies indicate that although all three species benefited from an ionic enhancement associated with NaCl, weeping alkaligrass was the most drought and salt tolerant of the three species. Dry seeds of weeping alkaligrass were also particularly tolerant to high temperatures with no differences in germination at temperatures below 50 C, indicating that seed viability under nonirrigated field conditions should be unaffected by high soil temperatures. Under soil temperature conditions as high as 40 C, moist Kentucky bluegrass seeds had the greatest germination rates, indicating that this species should benefit from irrigation more than the other two species.

**Nomenclature:** Nuttall's alkaligrass, *Puccinellia nuttalliana*; weeping alkaligrass, *Puccinellia distans*; Kentucky bluegrass, *Poa pratensis* L.
**Key words:** Germination, halophytes, water potential.

Two of the most salt-tolerant $C_3$ grasses commonly found in arid and semiarid environments of western North America, weeping alkaligrass and Nuttall's alkaligrass (Ashraf et al. 1986; Harivandi et al. 1983a; Macke and Ungar 1971), occur within the Grande Ronde valley of eastern Oregon. Both species are commonly referred to as alkaligrass and have been defined as facultative halophytes (Beyschlag et al. 1996; Macke and Ungar 1971; Moravcova and Frantik 2002). Generally, these two species occupy moist, alkaline to somewhat alkaline soil conditions (Hitchcock 1971), often occupying sites unsuitable to most crop species. Weeping alkaligrass is suspected to have been introduced to North America from Eurasia at the turn of the century in the vicinity of Michigan (Cusick 1982). Nuttall's alkaligrass, native to North America, occurs from Wisconsin to British Columbia, south to Kansas, New Mexico, and California (Hitchcock 1971).

These two species pose a problem for Kentucky bluegrass seed farmers of the Grande Ronde valley in eastern Oregon through seed contamination. The seed size of both alkaligrass species are almost identical to Kentucky bluegrass making them extremely difficult to remove during the cleaning process. As a result, alkaligrass seed was reported as a contaminant in 8% of Kentucky bluegrass samples submitted for certification by Oregon State University Extension Service in 2000 (D. Walenta, Oregon State University, personal communication).

Drought and salinity are major factors that reduce crop yields worldwide. Increasing salinity generally reduces germination in most species due to two processes: an osmotic effect due to increasing soil solutes and an ionic effect due to toxic ion uptake and accumulation (Ungar 1991). Uncoupling the osmotic from the ionic effects of a negative water potential can be challenging. Therefore, researchers often eliminate the osmotic effect by using two mediums of equal osmotic potential—one created with a salt such as sodium chloride (NaCl) versus a medium created using polyethylene glycol (PEG). The differences in seed germination between the PEG and NaCl solutions can be attributed to ionic effects (Dodd and Donovan 1999).

Salinity may affect seed germination by decreasing the ease with which seed imbibes water and/or by facilitating the entry of ions in amounts high enough to be toxic and/or reducing the absorption of nutrients through ion imbalances (Romo and Eddleman 1985). Generally, germination is delayed and reduced when salt stress exceeds a critical level. The level of salinity at which germination is reduced varies with species, genotype, environmental conditions, osmotic potential, and specific ions (Ungar 1991). Conversely, the accumulation of salt ions by the embryo may function to promote a water potential gradient between the embryo and substrate, making germination conditions more favorable than substrates of similar osmotic potentials without salt (Romo and Eddleman 1985).

Macke and Ungar (1971) reported 34% ($\pm$ 4%) germination of Nuttall's alkaligrass under negative water potentials of $-$ 1.2 MPa created with NaCl versus only 10% ($\pm$ 2%) with polyethylene glycol. However, the seeds were germinated in growth chambers with widely fluctuating temperatures of 12 h at 5 C (night) and 12 h at 20 C (day). The water potential of a solution is affected by temperature such that lower temperatures make the water potential less negative, whereas higher temperatures have the opposite effect (Kramer and Boyer 1995). Earlier work indicated that weeping alkaligrass germination was 50% in solutions equivalent to 75% seawater (Harivandi et al. 1983a). However, it is difficult to attribute the results to a specific ion or to make cross comparisons to other research, because the seawater solution used was comprised of 12 ions (Harivandi et al. 1983b). Horst and Taylor (1983) studied many Kentucky bluegrass cultivars for salinity tolerance; however, for reasons unexplained, germination results were averaged across all salt concentrations, making the results difficult to interpret.

DOI: 10.1614/WS-06-170.1
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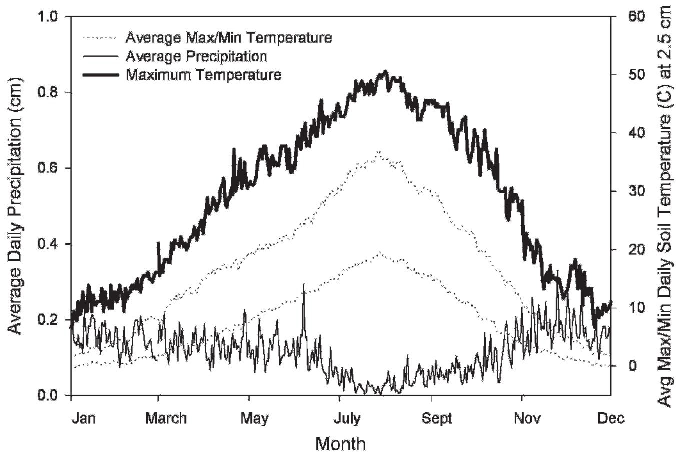


Figure 1. Twenty-year average daily maximum and minimum soil temperatures at 2.5-cm depth with 20-yr maximum recorded daily temperature and 20-yr average daily precipitation (data collected from Columbia Basin Agricultural Research Center, near Pendleton, OR).

Extreme osmotic and ionic conditions are not the only environmental stresses a seed may encounter in arid environments. Within the arid environments of eastern Oregon, where the uppermost layer of soil (top 2.5 cm) can reach temperatures in excess of 50 C (Figure 1), extreme soil temperatures also may inhibit seed germination. Under natural rangeland conditions, high temperatures may never coincide with enough soil moisture to promote seed germination; however, irrigation used in Kentucky bluegrass seed production could mitigate this obstacle. Although irrigation may enhance crop germination and seedling growth, the benefits to weeping alkaligrass and Nuttall's alkaligrass germination are unknown.

Once seeds are imbibed, high temperatures effects include leakages of amino acids related to an increase in permeability of the plasmalemma (Hendricks and Taylorson 1976). The effect of high temperature on unimbibed (dry) nondormant seeds may include a reentry into dormancy due to unfavorable environmental conditions (Baskin and Baskin 1998). As seeds reenter dormancy, they progress through conditional dormancy into secondary dormancy wherein dormancy breaking may be unpredictable (Baskin and Baskin 1998). This could be partly a response to a hypothesized theory that high temperatures degrade the receptors that interact with active phytochromes (Vleeshouwers et al. 1995).

This article presents results of experiments studying the relative ionic effects of NaCl on Kentucky bluegrass, weeping alkaligrass, and Nuttall's alkaligrass germination. Additionally, the germination response of moist and dry seeds under optimal temperatures of 10/15 C versus supraoptimal temperatures of 30, 35, 40, and 50 C (Moravcova and Frantik 2002; Tarasoff et al. 2007) is reported.

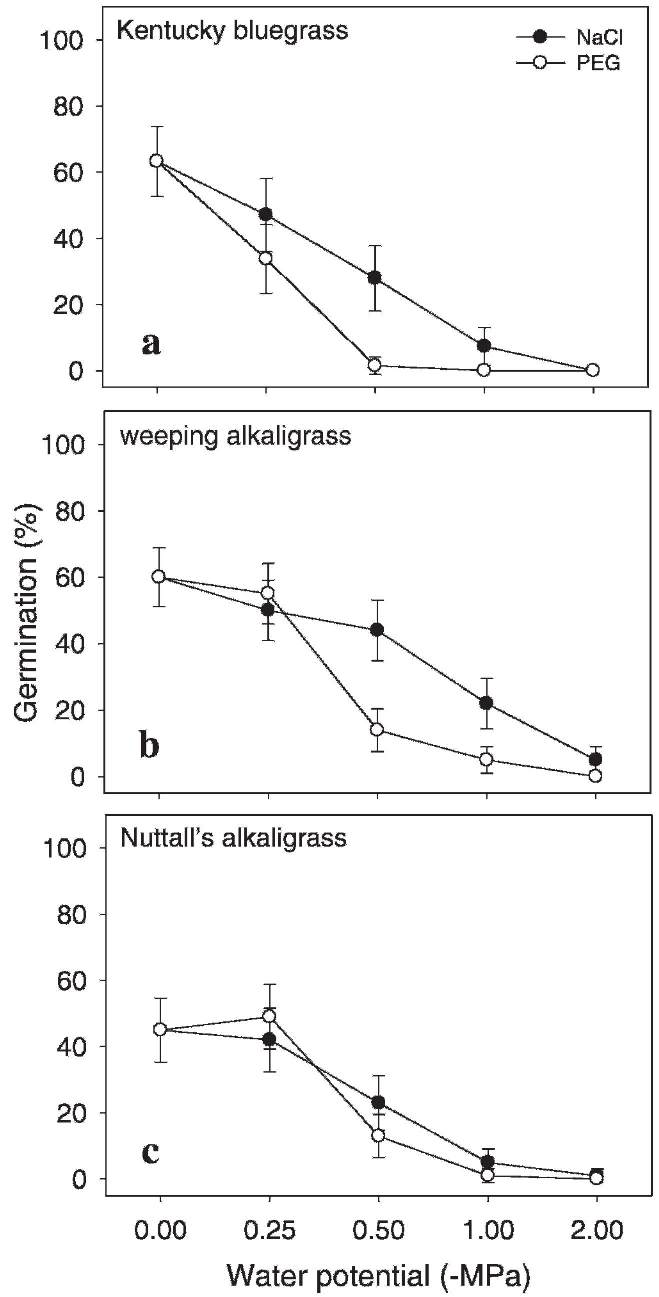


Figure 2. Germination response of Kentucky bluegrass (a), weeping alkaligrass (b), and Nuttall's alkaligrass (c) to negative osmotic potentials created with the use of NaCl versus PEG.

## Materials and Methods

**Osmotic Stress.** Nuttall's alkaligrass and weeping alkaligrass seeds were hand collected from the Grande Ronde valley at the Imbler Site (45°29′15.9″N, 117°56′4″W) on July 8, 2002. Seeds were hand thrashed, and air dried at 20 C for 18 months to ensure adequate afterripening. Kentucky bluegrass var. 'Brilliant' seeds were supplied by a local seed-cleaning facility.

Seeds were surface sterilized with a 5% solution of bleach for 20 s and triple rinsed with deionized water. After seed sterilization, an 8 by 8–cm germination box[1] was filled with 50 ml of 20-grit silica sand.[2] Within each box, 10 seeds of one species were placed approximately 1 mm below the surface. Because of the difficulty comparing the various aforementioned research, the three species in our study were tested with a constant temperature of 20 C and a simple NaCl salt medium rather than a complex seawater medium. Treatments consisted of NaCl[3] or PEG 6000[4] media with five different osmotic potentials: 0.0, − 0.25, − 0.5, − 1.0, or − 2.0 MPa for a total of 10 treatments. The PEG 6000

Table 1. Comparison of differences in germination between species for various osmotic potential treatments with NaCl or PEG ($\alpha$ = 0.05).

| | NaCl | | PEG 6000 | |
|---|---|---|---|---|
| Species comparison | − MPa | % difference | − MPa | % difference |
| Weeping vs. Kentucky | 0 | − 3.2 ± 13.4 | 0 | − 3.2 ± 13.4 |
| Weeping vs. Nuttall's | 0 | 15.0 ± 13.7 | 0 | 15.0 ± 13.7 |
| Kentucky vs. Nuttall's | 0 | 18.2 ± 13.6 | 0 | 18.2 ± 13.6 |
| Weeping vs. Kentucky | 0.25 | 2.9 ± 13.8 | 0.25 | 21.2 ± 13.4 |
| Weeping vs. Nuttall's | 0.25 | 8.0 ± 13.7 | 0.25 | 6.0 ± 13.8 |
| Kentucky vs. Nuttall's | 0.25 | 5.1 ± 13.7 | 0.25 | − 15.2 ± 13.5 |
| Weeping vs. Kentucky | 0.5 | 16.1 ± 13.1 | 0.5 | 12.5 ± 7.2 |
| Weeping vs. Nuttall's | 0.5 | 21.0 ± 12.7 | 0.5 | 1.0 ± 9.5 |
| Kentucky vs. Nuttall's | 0.5 | 4.9 ± 12.1 | 0.5 | − 11.5 ± 7.0 |
| Weeping vs. Kentucky | 1.0 | 14.6 ± 9.6 | 1.0 | 5.0 ± 4.3 |
| Weeping vs. Nuttall's | 1.0 | 17.0 ± 9.2 | 1.0 | 4.0 ± 4.7 |
| Kentucky vs. Nuttall's | 1.0 | 2.4 ± 6.6 | 1.0 | − 1.0 ± 2.0 |
| Weeping vs. Kentucky | 2.0 | 5.0 ± 4.2 | 2.0 | NG[a] |
| Weeping vs. Nuttall's | 2.0 | 4.0 ± 4.6 | 2.0 | NG |
| Kentucky vs. Nuttall's | 2.0 | − 1.0 ± 2.0 | 2.0 | NG |

[a] NG = No germination of either species.

(Michel and Kaufman 1973) and NaCl (Lang 1967) treatments created were verified with a dew-point potentiometer WP4[5] at a constant temperature of 20 C.

Each germination box was filled to water-holding capacity with a randomly assigned treatment and placed inside an unilluminated germination chamber at 20 C. Each treatment was replicated five times and the experiment was repeated. Seeds were considered germinated when the coleoptile was 2 mm long and a radicle was present. On day 18 (after treatment), the number of germinated seeds were counted.

**Temperature Stress.** Seeds of all three species were collected and sterilized following the same procedures previously described.

*Moist Conditions*. Following the sterilization treatment, 25 seeds were placed on top of two layers of germination paper[6] wetted to maximum holding capacity in an 8 by 8-cm germination box. After wetting, seeds were prechilled for 48 h at 5 C. Following the prechill treatment, each germination box was randomly assigned to an unilluminated growth chamber at one of five temperature treatments: the optimal germination temperature of 10/15 C on a 12-h day/night cycle, or one of four supraoptimal constant temperatures of 30, 35, 40, or 50 C. Germinated seeds were counted as previously described. Each treatment was replicated seven times and the experiment repeated.

*Dry Conditions*. Approximately 500, dry, afterripened seeds of each of the three species were randomly assigned to a growth chamber set at one of five temperature treatments: Control (dry stored at 20 C), 30, 35, 40, or 50 C for 18 d. After this, the seeds were removed and 25 seeds were placed on top of two layers of germination paper wetted to maximum holding capacity in an 8 by 8-cm germination box. After wetting, seeds were prechilled, in the dark, for 48 h at 5 C. All temperature-treated seeds were then placed in an unilluminated germination chamber at 10/15 C on a 12-h day/night cycle. Germinated seeds were counted and removed as previously described. Each treatment was replicated seven times and the experiment was repeated.

Temperature treatment seed germination under initially moist conditions will heretofore be referred to as "moist germination." Germination of seeds initially dry, then moistened, will be referred to as "rebound germination," because the seeds are rebounding from the dry temperature treatment conditions and germinating in the ideal moist and 10/15 C growth chamber conditions.

*Statistical Analysis*. All experiments were analyzed for equal variance between runs with the use of the link logit function (PROC GENMOD,[7] SAS v.9.1). No significant differences were found between runs; therefore, the data sets for each experiment were combined. 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. The probability of germination calculated by this procedure assumes all seeds in a given petri dish are subjected to the same conditions (Ramsey and Schafer 2002). Germination results for all experiments were analyzed as binary response variables and 95% confidence intervals were created and contrasted for the total proportion of germination.

## Results and Discussion

**Osmotic Stress.** *Comparison of Treatments Within Species*. Kentucky bluegrass and weeping alkaligrass germination was reduced by PEG treatments more than NaCl treatments with the same osmotic potential indicating an ionic enhancement associated with NaCl (Figure 2). Kentucky bluegrass benefited from the ionic effects at the moderate osmotic potential of − 0.5 MPa, with an average germination of 28% with NaCl versus 2% when PEG was used (Figure 2a). Weeping alkaligrass had 44% germination at osmotic potentials of − 0.5 MPa with NaCl versus 14% with PEG. Weeping alkaligrass also had 22% germination at water potentials of − 1.0 MPa with NaCl versus 5% with PEG (Figure 2b). Regardless of medium osmotic potential, there were no differences among NaCl and PEG treatments for Nuttall's alkaligrass at $\alpha$ = 0.05, indicating that this species may be equally affected by NaCl as PEG (Figure 2c). These results conflict with those of Macke and Ungar (1971) and may be due to differences in our controlled experiment versus their experiment done with the use of fluctuating temperature conditions, differences in length of seed afterripening, and/or ecotypic differences among populations.

*Comparison of Treatments Between Species*. At − 0.25 MPa, seed germination of all three species was similar in the NaCl medium ($\alpha$ = 0.05) (Table 1). However, at osmotic potentials of − 0.50 MPa with NaCl, weeping alkaligrass germination was 21% greater than Nuttall's alkaligrass and 16% greater than Kentucky bluegrass. This trend continued at − 1.0 MPa with NaCl, where weeping alkaligrass germination was 17% greater than Nuttall's alkaligrass and 15% greater than Kentucky bluegrass (Table 1). At water potentials of − 2.0 MPa, weeping alkaligrass germination was not different from Nuttall's alkaligrass and only slightly greater than Kentucky bluegrass. In conclusion, weeping alkaligrass exhibited the greatest ionic enhancement and tolerance, followed by Kentucky bluegrass and then Nuttall's alkaligrass.

When subjected to PEG treatments, there were no differences in weeping or Nuttall's alkaligrass seed germination, regardless of the osmotic potential. Yet seed germination of both species was greater than that of Kentucky bluegrass in the PEG medium at all osmotic potentials ($\alpha$ = 0.05). At − 0.25 MPa, weeping alkaligrass and Nuttall's alkaligrass were 21 and 15% greater than Kentucky bluegrass, respectively (Table 1). At − 0.50 MPa, weeping alkaligrass and Nuttall's alkaligrass were 13 and 12% greater than Kentucky bluegrass, respectively (Table 1). At − 1.0 MPa, weeping alkaligrass exhibited a 5% greater germination than Kentucky bluegrass. At − 2.0 MPa there was no germination of any of the three species. In conclusion, based on the methods used in this study, our results suggest that weeping alkaligrass is likely more drought tolerant than Nuttall's alkaligrass and Kentucky bluegrass.

Given the results of this study, one would expect weeping alkaligrass to be the most likely to germinate in the arid and sodic (sodium dominated) soils of the Grande Ronde valley, followed by Nuttall's alkaligrass and then Kentucky bluegrass.

Although, in our study, Kentucky bluegrass germination was enhanced by the ionic effects of NaCl compared to germination in the presence of PEG, personal field observations of Kentucky bluegrass germination under sodic soil conditions is often followed by seedling death before the four-leaf stage. Therefore, actual drought conditions may be too great for seedling survival and establishment.

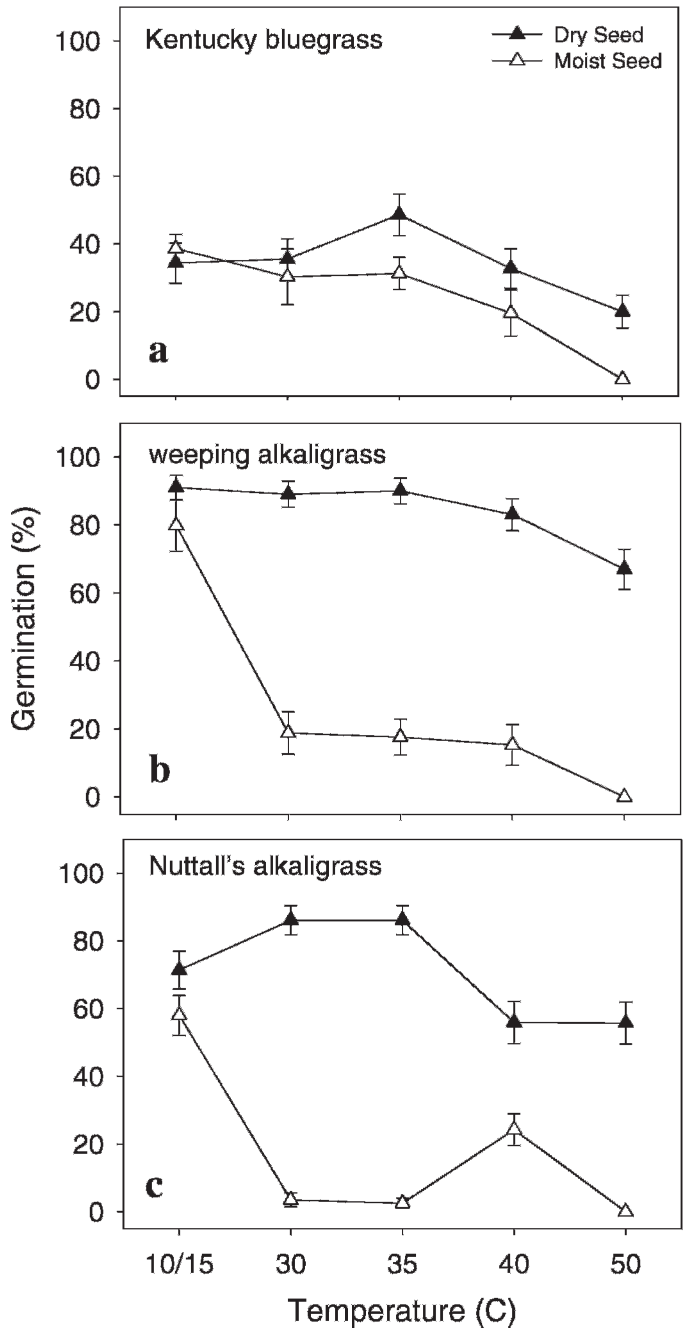


Figure 3. Germination response of Kentucky bluegrass (a), weeping alkaligrass (b), and Nuttall's alkaligrass (c) following temperature treatment of dry versus moist seeds.

**Temperature Stress.** *Comparison of Treatments Within Species*. Kentucky bluegrass moist germination was not affected by the temperature treatments of 30 or 35 C versus the control ($\alpha$ = 0.05) (Figure 3a). Germination at 40 C (20%) was lower than the control (38%). No germination occurred at 50 C for moist seed germination. Although generally greater, rebound germination of Kentucky bluegrass followed a similar pattern to moist seed germination. No difference existed between the control, 30 C, and 40 C treatments, with germination of 34, 35, and 34%, respectively. Germination at 35 C was 49%, greater than the control, whereas germination at 50 C was 24%, lower than the control (Figure 3a).

Weeping alkaligrass moist germination was relatively high at 80% in the 10/15 C control treatment but decreased to approximately 20% at temperature treatments of 30, 35, and 40 C. (Figure 3b). No germination was recorded at 50 C. Rebound germination of this grass in the control treatment was relatively high at 92%, germination was not less than that of the control until 50 C when it dropped to 68%. At each temperature treatment, rebound germination was greater than moist seed germination.

Moist Nuttall's alkaligrass seeds expressed a bimodal germination response with 58% germination at 10/15 C, 4% germination at 30 and 35 C, 24% at 40 C, and then no germination at 50 C (Figure 3c). The increase in germination at 40 C occurred in both run 1 and run 2 cannot be explained based on current knowledge. Rebound germination of Nuttall's alkaligrass at 30 and 35 C was greater than the

Table 2. Comparison of differences in germination between species for various temperature treatments of moist versus dry seeds ($\alpha = 0.05$).

| Species comparison | Dry seeds—rebound germination | | Moist seeds germination | |
|---|---|---|---|---|
| | Temperature | % difference | Temperature | % difference |
| | C | | C | |
| Weeping vs. Kentucky | 10/15 | 56.7 ± 7.1 | 10/15 | 41.2 ± 8.7 |
| Weeping vs. Nuttall's | 10/15 | 19.6 ± 9.4 | 10/15 | 21.8 ± 8.8 |
| Kentucky vs. Nuttall's | 10/15 | − 37.1 ± 15.6 | 10/15 | − 19.4 ± 9.6 |
| Weeping vs. Kentucky | 30 | 53.5 ± 7.2 | 30 | − 11.5 ± 8.4 |
| Weeping vs. Nuttall's | 30 | 2.9 ± 5.8 | 30 | 15.3 ± 6.0 |
| Kentucky vs. Nuttall's | 30 | − 50.6 ± 11.2 | 30 | 26.8 ± 6.9 |
| Weeping vs. Kentucky | 35 | 41.4 ± 7.3 | 35 | − 13.7 ± 8.3 |
| Weeping vs. Nuttall's | 35 | 3.9 ± 5.7 | 35 | 15.1 ± 5.7 |
| Kentucky vs. Nuttall's | 35 | − 37.5 ±11.5 | 35 | 28.8 ± 6.8 |
| Weeping vs. Kentucky | 40 | 50.3 ± 7.5 | 40 | − 4.3 ± 7.4 |
| Weeping vs. Nuttall's | 40 | 27.1 ± 7.8 | 40 | − 9.0 ± 7.7 |
| Kentucky vs. Nuttall's | 40 | − 23.2 ± 12.9 | 40 | − 4.7 ± 12.2 |
| Weeping vs. Kentucky | 50 | 47.0 ± 10.2 | 50 | NG[a] |
| Weeping vs. Nuttall's | 50 | 11.3 ± 11.3 | 50 | NG |
| Kentucky vs. Nuttall's | 50 | − 35.7 ± 16.0 | 50 | NG |

[a] NG = No germination of either species.

control, at 84, 84, and 72%, respectively. All three temperature treatments were greater than the 40 and 50 C treatments, both with 58% germination. At each temperature treatment, rebound germination was greater than moist seed germination.

*Comparison of Treatments Between Species*. At optimal temperatures of 10/15 C, moist-treated seeds of weeping alkaligrass had the greatest germination, followed by Nuttall's alkaligrass and then Kentucky bluegrass (Table 2). Yet, as temperatures increased to 30 and 35 C, Kentucky bluegrass had the greatest germination, followed by Nuttall's alkaligrass and then weeping alkaligrass (Table 2). At 40 C, Nuttall's alkaligrass had 9% more germination than weeping alkaligrass, and there were no differences between other species comparisons. No moist seeds from any of the species germinated at 50 C, whereas all species exhibited rebound germination at that temperature (Figure 3, Table 2).

Generally, weeping alkaligrass exhibited the greatest rebound germination response, followed by Nuttall's alkaligrass and then Kentucky bluegrass (Table 2). The only exception was at temperatures of 30 and 35 C when there was no difference between weeping and Nuttall's alkaligrass.

In our study, moist seeds of weeping alkaligrass and Nuttall's alkaligrass were more negatively affected by high temperatures than those of Kentucky bluegrass; therefore, seed germination of both species could be expected to be low in irrigated Kentucky bluegrass production fields as long as the soil temperatures remain above 30 C.

Rebound germination of Kentucky bluegrass was lower than either alkaligrass species. Weeping alkaligrass rebound germination was either equal to or greater than Nuttall's alkaligrass. These results indicate that weeping alkaligrass seeds should have the greatest germination response to fall precipitation, when rain events coincide with soil temperatures of 10 to 20 C (Figure 1), followed by Nuttall's alkaligrass and then Kentucky bluegrass.

It is possible that Nuttall's alkaligrass uses a mechanism to avoid ion uptake during seed germination. If this is the case, Nuttall's alkaligrass may rely more on salt-avoidance strategies than salt-tolerating mechanisms. If Nuttall's alkaligrass is able to avoid ion uptake, its mechanisms are yet to be elucidated.

Results from all three studies indicate that for Kentucky bluegrass farmers of the Grande Ronde valley of eastern Oregon, weeping alkaligrass may pose a greater threat than Nuttall's alkaligrass in terms of germination tolerance to the extreme soil and environmental conditions of this semiarid environment.

## Sources of Materials

[1] Germination Box, Sigma-Aldrich Co., 3050 Spruce Street, St. Louis, MO 63103.

[2] Silica sand, Struktol Company of America, P.O. box 1649, Stow, OH 44224.

[3] Sodium chloride, Asia Pacific Specialty Chemicals Ltd., 15 Park Road, Seven Hills, NSW 2147, Australia.

[4] Polyethylene glycol 6000, Sigma-Aldrich Co., 3050 Spruce Street, St. Louis, MO 63103.

[5] Dewpoint potentiometer WP4, Decagon Devices Inc., 950 NE Nelson Court, Pullman, WA 99163.

[6] Germination paper, Anchor Paper Company, 480 Broadway Street, St. Paul, MN, 55101.

[7] SAS Institute, Inc., 100 SAS Drive, Cary, NC 27513.

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*Received September 27, 2006, and approved March 6, 2007.*