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Seed Germination Response of Four Southwestern Range Grasses to Equilibration at Subgermination Matric-Potentials

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ABSTRACT

Seed priming at subgermination water potential has been shown to enhance the germination response of a wide number of plant species. Optimal priming conditions for germination enhancement are usually found to be at the least negative water potential that prevents radicle emergence. Equilibration of seeds at more negative water potentials may have detrimental effects on germination relative to control treatments. Seeds of *Bouteloua curtipendula* (Michx.) Torr., *Cenchrus ciliaris* L., *Eragrostis lehmanniana* Nees, and *Panicum coloratum* L. were equilibrated over the matric potential range of −1.6 to −17.5 MPa and germinated over the matric potential range of 0 to −1.6 MPa. Matric-priming at −1.6 MPa frequently increased germination percentage and rate at reduced water potential. Matric-priming at water potentials more negative than −1.6 MPa had a less positive and sometimes detrimental effect on germination relative to control treatments. Germination response of primed seeds showed a tendency toward, but not necessarily achievement of, control levels at the most negative priming-water potentials.

SEED PRIMING is a treatment in which seeds are equilibrated at a water potential that allows water uptake but prevents radicle emergence (Heydecker and Coolbear, 1977; Bradford, 1986). Increased germination rate and uniformity have been attributed to metabolic repair during imbibition (Bray et al., 1989; Burgass and Powell, 1984), a buildup of germination-enhancing metabolites (Khan et al., 1978; Coolbear et al., 1980), osmotic adjustment (Bradford, 1986), and, for seeds that are not redried after treatment, a simple reduction in the lag time of imbibition (Bewley and Black, 1982; Brocklehurst and Dearman, 1983; Heydecker, 1977).

Hardegree and Emmerich (1992) investigated the effects of priming on germination of four grass species and found that maximum germination enhancement was confined to treatments of the shortest duration and least negative water potential. Priming treatments were less effective or were found to be detrimental relative to control treatments as the priming-water potential was lowered to −7.7 MPa (Hardegree and Emmerich, 1992). The objective of the current experiment was to determine whether germination response to priming would return to control levels as priming water potential was lowered below −7.7 MPa. Primed seeds were germinated over the water potential range of 0 to −1.6 MPa to broaden the range of treatments over which priming effects could be evaluated.

MATERIALS AND METHODS

Bouteloua curtipendula, C. ciliaris, E. lehmanniana, and *P. coloratum* seeds were obtained from the same seed lots used by Hardegree and Emerich (1992). These species were chosen because they occur over large areas of rangeland in the southwestern United States and in previous studies had shown a wide range of germination response to different environmental variables (Hardegree and Emmerich, 1990a; Emmerich and Hardegree, 1990).

Seeds were primed and germinated using the matric potential control system described by Hardegree and Emmerich (1992). This system consists of a membrane-bottom germination cup which is in contact with an osmotic solution of polyethylene glycol 8000 (PEG). The PEG solution and germination cup are contained within a clear plastic snap-top vial. The cellulose-membrane has a molecular weight exclusion limit of 3500, which allows water to pass through but excludes the higher molecular weight PEG. The seeds rest on the membrane surface which maintains a matric potential equal to the osmotic potential of PEG in the solution reservoir (Hardegree and Emmerich, 1992).

Polyethylene glycol was mixed with water to yield eight priming-solutions over the water potential range of −1.6 to −17.5 MPa, and seven germination-solutions over the range of 0 to −1.6 MPa. The lower water potential limit for priming-solutions was determined by the maximum amount of PEG that would go into solution at 25 °C (1.56g PEG/gH_2O). Over the concentration range of 0 to 0.71 gPEG/gH_2O, solution water potential was calculated using a previously derived equation (Hardgree and Emmerich, 1990b). The PEG-solution water potentials over the concentration range of 0.71 to 1.56 gPEG/gH_2O were measured three times each, in random order, without filter paper (Hardegree and Emmerich, 1990b) in an SC-10A thermocouple psychrometer (Decagon Devices, Pullman, WA)[1]. The psychrometer was calibrated with standard salt solutions (Lang, 1967; Greenspan, 1977).

Each priming/germination treatment was replicated three times on samples of 35 seeds of each species. Non-primed control treatments were replicated six times. Seeds were placed on the membrane surface of the priming/germination cup and allowed to equilibrate with PEG solutions of −1.6, −3.1, −5.3, −7.7, −10.6, −12.9, −15.7 and −17.5 MPa water potential. Forty-eight hours had been determined in a previous study to be the optimal priming duration for these seed lots over the priming-water potential range of −1.5 to −7.7 MPa (Hardegree and Emmerich, 1992). Hardegree and Emmerich (1992) also found that these seeds achieve an equilibrium water content within 48 h when primed over this water potential range. The priming/germination cup was removed after equilibration for 48 h, blotted of excess solution and placed in another germination vial containing water or PEG solution with a water potential of either −0.1, −0.3, −0.6, −1.0, −1.3, or −1.6 MPa for 14 d. Seeds were primed and germinated in a controlled-temperature room at 25 ± 1°C under both fluorescent and incandescent light for 12 h d^{-1}. Germination vials were opened and checked for germination on Days 1–5, 7, 9, 11, and 14 after priming. Seeds were considered germinated and were counted and removed from the membrane surface when they exhibited radicle extension of ≥2 mm. The cellulose membranes were treated with a 50 μL suspension of fungicide (Daconil, Diamond Shamrock Chemical Co., Cleveland, OH; 2, 4, 5,6-tetrachloro-1,3-benzenedicarbonitrile; 2.5g/100 mL H_2O) before the seeds were placed on

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Abbreviations: PEG, Polyethylene glycol; *G*, total percent germination; and D_{50}, days required to 50% of *G*.

[1]Mention of a trademark name or proprietary product does not constitute endorsement by the USDA and does not imply its approval to the exclusion of other products that may also be suitable.

the membrane surface. Seeds that developed fungal growth were removed and counted as non-viable.

Eragrostis lehmanniana seeds required mechanical scarification to remove dormancy. The mechanical scarification treatment followed that reported by Wright (1973) with 0.5-mL seed samples and an 8-s scarification interval.

Two germination indices were calculated for the seeds from each germination vial: total percent germination (G), and days required to reach 50% of G (D_{50}) as an index of germination rate.

Cubic response surfaces were calculated relating G, and D_{50} to priming-water potential and germination-water potential. Cubic equations were also calculated relating germination index values to germination-water potential for the control treatments. Regression equations were recalculated deleting first cubic then quadratic then linear terms that were not significant ($P \leq 0.10$). Lower order terms that were not significant were left in the equation if a higher order term was significant. Germination index values were estimated from the regression equations and model confidence intervals were ($P \leq 0.05$) determined for each treatment combination following the procedure outlined by Evans et al. (1982). Priming was considered to have had a significant effect on germination in treatments where the confidence interval of the response surface model did not overlap the estimated germination index value of the control treatment.

The D_{50} was highly variable in treatments with a mean $G < 10\%$ because these treatments generally had some sample replicates with zero germination and only a few seeds determined D_{50} for the entire sample. Values for D_{50} were, therefore, included in the regression analysis only if the measured mean of G for the respective treatment was $\geq 10\%$.

RESULTS

Effect of Priming-Water Potential on Germination at 0 MPa

Matric-priming did not increase G of any treatment for seeds germinated at 0 MPa but decreased G relative to the controls, for *C. ciliaris* and *P. coloratum* at lower priming water potentials (Table 1). Detrimental priming effects on G appeared to return to control levels in the driest priming treatment only for *C. ciliaris* (Table 1).

The D_{50} decreased (germination rate increased) at high priming-water potentials but was not different from control levels of D_{50} at lower priming-water potentials for *C. ciliaris* and *P. coloratum* (Table 2). The D_{50} also decreased for *B. curtipendula* at high priming-water potentials but increased relative to the controls in the driest priming treatments (Table 2). The D_{50} of *E. lehmanniana* was unaffected by priming-water potential except for one intermediate treatment for which D_{50} increased (Table 2).

Effect of Priming at −1.6 MPa on Germination at Reduced Water Potential

Priming at −1.6 MPa increased G of *B. curtipendula* and *P. coloratum* relative to the control at reduced germination-water potentials (Table 1). Priming at −1.6 MPa had no affect on G of *C. ciliaris* at reduced water potential (Table 1). Priming at −1.6 MPa increased G at *E. lehmanniana* at higher germination-water potentials but decreased G relative to the control treatments at lower germination-water potentials (Table 1).

Matric-priming at −1.6 MPa significantly decreased D_{50} (increased germination rate) of *B. curtipendula* and *C. ciliaris* over the entire germination-water potential range. Matric-priming decreased D_{50} over some of the germination-water potential range for *E. lehmanniana* and *P. coloratum* (Table 2).

Interaction between Priming- and Germination-Water Potential

Germination response to the combined variables of priming- and germination-water potential did not always conform to the patterns of priming-water potential effects on seeds germinated at 0 MPa or germination-water potential effects on seeds primed at −1.6 MPa.

Bouteloua curtipendula and *P. coloratum* had relatively large regions of the response surface with significantly higher G than the controls (Table 1). These regions of increased G were mostly in the lower germination-water potential ranges. *Cenchrus ciliaris* and *E. lehmanniana* had relatively large regions of decreased G relative to the controls (Table 1). Decreased G was primarily in the lower priming-water potential range for *C. ciliaris* and the lower germination-water potential range for *E. lehmanniana* (Table 1). In general, for all species except *P. coloratum*, all increases and decreases in G appeared to be following a trend toward, but did not necessarily achieve, control levels at the lowest priming-water potentials (Table 1).

The predominant treatments resulting in decreased D_{50} (increased germination rate) were in regions of least negative priming-water potential (Table 2). Decreases in D_{50} were further confined to the lower germination-water potentials for *E. lehmanniana* and the higher germination-water potentials for *P. coloratum* (Table 2). Increased D_{50} relative to the controls appeared mostly at the lower priming- and germination-water potentials for all species except *B. curtipendula* (Table 2). The majority of treatments either achieved or showed a trend toward control-levels of D_{50} at lower priming-water potentials but the absolute magnitude and direction of change was dependent upon species and germination-water potential (Table 2).

Interpretation of Regression Models

Confidence limits were included in Tables 1 and 2 to provide an estimate of model variability and a basis for evaluating the relative magnitude of differences between treatment and control models (Evans et al., 1982). All of the regression models were significant at the $P \leq 0.01$ level. The R^2 values for regression models are included in Tables 1 and 2.

The regression models were not constrained with respect to absolute possible maximum and minimum levels of G as this would have masked some of the variability in the data for high and low germination-water potential treatments. The unconstrained models provided the best fit for the data but resulted in some seemingly erroneous predictions of G greater than 100% and less than 0% (Table 1). In all but one case, however, the model confidence interval of these values overlapped either the maximum or minimum possible value for G.

Table 1. Calculated total percent germination (G) as a function of priming-water potential and germination-water potential. Numbers in parentheses represent one-half confidence interval widths ($P \leq 0.05$) calculated from the regression model. R^2 values for the control (C) treatment regression, and response surface (R.S.) regression models appear under the species names.

Species	Priming Water Potential (MPa)	Germination Water Potential (MPa)						
		0	−0.1	−0.3	−0.6	−1.0	−1.3	−1.6
B. curtipendula C. R^2 = 0.84 R.S. R^2 = 0.84	Control	92 (6)	95 (5)	98 (4)	95 (5)	83 (5)	64 (4)	31 (7)
	−1.6	96 (4)	97 (3)	99 (3)	96 (3)	†87 (3)	†74 (3)	†52 (4)
	−3.1	94 (3)	95 (3)	96 (2)	94 (2)	85 (2)	†72 (2)	†50 (4)
	−5.3	92 (3)	94 (3)	†95 (2)	†92 (2)	83 (2)	†70 (2)	†48 (3)
	−7.7	92 (3)	94 (2)	†95 (2)	†92 (2)	83 (2)	†70 (2)	†48 (3)
	−10.6	93 (3)	95 (2)	96 (2)	93 (2)	84 (2)	†71 (2)	†49 (3)
	−12.9	95 (3)	96 (3)	97 (2)	94 (2)	85 (3)	†72 (3)	†49 (3)
	−15.7	95 (3)	96 (3)	97 (2)	94 (2)	85 (2)	†72 (3)	†49 (4)
	−17.5	94 (4)	95 (4)	96 (3)	93 (3)	84 (3)	†71 (4)	†48 (5)
C. ciliaris C. R^2 = 0.91 R.S. R^2 = 0.89	Control	67 (7)	74 (5)	80 (5)	69 (5)	42 (5)	17 (6)	−2 (8)
	−1.6	67 (5)	74 (4)	79 (4)	67 (4)	40 (4)	17 (5)	4 (6)
	−3.1	65 (4)	71 (3)	77 (3)	†64 (3)	†38 (3)	14 (4)	2 (5)
	−5.3	†62 (4)	†69 (3)	†74 (3)	†62 (3)	†35 (3)	†12 (3)	−1 (4)
	−7.7	†60 (4)	†67 (3)	†72 (3)	†60 (3)	†33 (3)	†10 (3)	−2 (4)
	−10.6	†58 (4)	†65 (3)	†71 (3)	†59 (3)	†32 (3)	† 9 (3)	−3 (4)
	−12.9	†59 (4)	†66 (3)	†71 (3)	†59 (3)	†32 (3)	† 9 (3)	−3 (4)
	−15.7	†60 (4)	†67 (3)	†72 (3)	†60 (3)	†34 (3)	†11 (4)	−1 (5)
	−17.5	62 (5)	†69 (4)	†74 (4)	†62 (4)	†36 (4)	13 (5)	1 (6)
E. lehmanniana C. R^2 = 0.90 R.S. R^2 = 0.92	Control	92 (7)	94 (6)	96 (5)	89 (6)	70 (6)	43 (5)	−4 (9)
	−1.6	94 (6)	†100 (5)	†103 (5)	90 (4)	†61 (4)	†32 (5)	3 (7)
	−3.1	92 (5)	98 (4)	†101 (4)	88 (4)	†59 (4)	†30 (4)	1 (6)
	−5.3	90 (4)	96 (3)	99 (3)	†85 (3)	†56 (3)	†27 (4)	−2 (5)
	−7.7	89 (4)	94 (3)	97 (4)	†83 (4)	†54 (3)	†25 (4)	−5 (5)
	−10.6	88 (4)	93 (3)	96 (4)	†82 (4)	†53 (4)	†23 (4)	−6 (5)
	−12.9	89 (4)	94 (3)	97 (4)	†83 (3)	†53 (3)	†23 (4)	−7 (5)
	−15.7	90 (5)	96 (4)	98 (4)	†84 (4)	†54 (4)	†24 (4)	−6 (6)
	−17.5	92 (6)	97 (5)	100 (5)	86 (5)	†56 (5)	†26 (5)	−5 (7)
P. coloratum C. R^2 = 0.93 R.S. R^2 = 0.93	Control	73 (6)	73 (4)	65 (5)	41 (5)	12 (5)	−4 (5)	2 (7)
	−1.6	76 (5)	†80 (4)	†78 (4)	†57 (4)	†25 (4)	† 3 (4)	2 (6)
	−3.1	74 (4)	†78 (3)	†77 (3)	†57 (3)	†26 (3)	† 3 (3)	1 (5)
	−5.3	73 (3)	†77 (3)	†76 (3)	†57 (3)	†26 (3)	† 4 (3)	1 (4)
	−7.7	71 (3)	76 (3)	†76 (3)	†57 (3)	†27 (3)	† 4 (3)	0 (4)
	−10.6	†69 (3)	74 (3)	†76 (3)	†58 (3)	†28 (3)	† 5 (3)	0 (4)
	−12.9	†68 (3)	74 (3)	†76 (3)	†59 (3)	†29 (3)	† 6 (3)	0 (4)
	−15.7	†67 (4)	73 (3)	†76 (3)	†60 (3)	†30 (3)	† 7 (4)	0 (5)
	−17.5	†66 (5)	72 (4)	†76 (4)	†61 (4)	†32 (4)	† 8 (4)	1 (6)

† Confidence interval did not overlap predicted mean for control treatment.

DISCUSSION

The optimal water potential for seed priming is usually found to be the least negative water potential that prevents radicle emergence (Dell'Aquila and Tritto, 1990; Evans and Pill, 1989; Hardegree and Emmerich, 1992). Priming has a less positive and sometimes detrimental effect on germination at lower priming-water potentials (Gray et al., 1990; Ely and Heydecker, 1981; Coolbear et al., 1980; Hardegree and Emmerich, 1992). Wallace (1960) found a similar germination response for seeds equilibrated in soil of subgermination water content. Wallace (1960) determined, however, that germination response returned to control levels when seed were equilibrated in the driest (air-dry soil) treatments. The seeds in this experiment exhibited a trend toward, but not always a return to, control germination response as priming-water potentials approached −17.5 MPa (Tables 1–2). This trend toward control levels of germination response was most apparent for seeds germinated at 0 MPa. Except for G of *P. coloratum* and D_{50} of *B. curtipendula*, germination response at 0 MPa returned to control levels by the lowest priming-water potential treatment (Tables 1 and 2). Germination response at germination-water potentials more negative than 0 MPa did not always return to control levels for treatments primed at −17.5 MPa. These results indicate that physiologic processes detrimental to seed germination are still active for these species at water potentials as low as −17.5 MPa. A water potential of −17.5 MPa is within Region 3 of the moisture sorption isotherm for seeds as defined by Leopold and Vertucci (1989) and Vertucci (1989). The potential for seed degradation is highest in Region 3 of the moisture sorption isotherm but it is surprising that a detrimental germination response would become apparent after only 2 d of equilibration at a water potential as low as −17.5 MPa.

Osmotic adjustment has been proposed as a possible mechanism contributing to germination enhancement of primed seeds (Bradford, 1986). Osmotic adjustment would lower seed water potential relative to the environment, increased the rate of imbibition and allow for seed germination at lower water potentials (Bradford, 1986). In almost every case, matric-priming at the optimal water potential (−1.6 MPa) either enhanced or had no effect on G and D_{50} for seeds germinated at reduced water potential. The only exception was for G of *E. lehmanniana*. Some enhancement of D_{50} for these species can be accounted for by

Table 2. Calculated days to 50% of G (D_{50}) as a function of priming water potential and germination water potential. Numbers in parentheses represent one-half confidence interval widths ($P \leq 0.05$) calculated from the regression model. R^2 values for the control (C.) treatment regression, and response surface (R.S.) regression models appear under the species names.

Species	Priming Water Potential (MPa)	Germination Water Potential (MPa)						
		0	−0.1	−0.3	−0.6	−1.0	−1.3	−1.6
B. curtipendula C. R^2 = 0.78 R.S. R^2 = 0.78	Control	1.1 (0.8)	1.4 (0.6)	1.7 (0.7)	1.6 (0.7)	1.9 (0.6)	3.3 (0.7)	7.8 (1.0)
	−1.6	†0.4 (0.3)	†0.3 (0.3)	†0.3 (0.3)	†0.5 (0.3)	†1.3 (0.3)	†2.3 (0.3)	†4.1 (0.3)
	−3.1	†0.7 (0.3)	†0.6 (0.2)	†0.5 (0.2)	†0.8 (0.2)	†1.5 (0.2)	†2.6 (0.2)	†4.4 (0.3)
	−5.3	1.0 (0.2)	†0.9 (0.2)	†0.8 (0.2)	†1.1 (0.2)	1.8 (0.2)	†2.9 (0.2)	†4.7 (0.3)
	−7.7	1.2 (0.3)	1.2 (0.2)	†1.1 (0.2)	1.4 (0.2)	2.1 (0.2)	3.1 (0.2)	†4.9 (0.3)
	−10.6	1.4 (0.3)	1.4 (0.2)	†1.3 (0.2)	1.6 (0.2)	†2.3 (0.2)	3.3 (0.2)	†5.1 (0.3)
	−12.9	†1.5 (0.2)	1.4 (0.2)	†1.4 (0.2)	1.7 (0.2)	†2.4 (0.2)	3.4 (0.2)	†5.2 (0.3)
	−15.7	†1.5 (0.3)	1.4 (0.2)	†1.4 (0.2)	1.6 (0.2)	†2.4 (0.2)	3.4 (0.2)	†5.2 (0.3)
	−17.5	†1.5 (0.3)	1.4 (0.3)	†1.3 (0.3)	1.6 (0.3)	†2.3 (0.3)	3.4 (0.3)	†5.2 (0.4)
C. ciliaris C. R^2 = 0.66 R.S. R^2 = 0.90	Control	2.4 (0.8)	2.3 (0.6)	2.4 (0.7)	3.7 (0.7)	6.6 (0.9)		
	−1.6	†1.2 (0.6)	†0.9 (0.5)	†0.8 (0.4)	†2.3 (0.4)	†5.3 (0.7)		
	−3.1	†1.5 (0.4)	†1.2 (0.3)	†1.3 (0.4)	†2.9 (0.3)	†6.0 (0.5)		
	−5.3	†1.9 (0.4)	†1.7 (0.3)	†1.8 (0.3)	3.6 (0.3)	6.9 (0.4)		
	−7.7	2.2 (0.4)	2.0 (0.3)	2.3 (0.3)	†4.2 (0.3)	†7.6 (0.4)		
	−10.6	2.5 (0.4)	2.3 (0.3)	2.6 (0.3)	†4.6 (0.3)	†8.1 (0.5)	11.8 (0.8)	
	−12.9	2.6 (0.4)	2.4 (0.3)	2.7 (0.3)	†4.6 (0.3)	†8.1 (0.4)		
	−15.7	2.5 (0.4)	2.3 (0.3)	2.5 (0.3)	†4.4 (0.4)	†7.8 (0.4)	11.5 (0.8)	
	−17.5	2.4 (0.6)	2.1 (0.5)	2.3 (0.4)	†4.1 (0.5)	†7.4 (0.6)		
E. lehmanniana C. R^2 = 0.98 R.S. R^2 = 0.94	Control	1.6 (0.2)	1.7 (0.2)	1.8 (0.2)	2.2 (0.2)	4.0 (0.2)	7.8 (0.3)	
	−1.6	1.6 (0.3)	1.4 (0.3)	†1.2 (0.2)	†1.8 (0.3)	3.9 (0.3)	†6.8 (0.4)	
	−3.1	1.8 (0.2)	1.6 (0.2)	†1.5 (0.2)	2.4 (0.2)	†4.7 (0.2)	7.8 (0.3)	
	−5.3	†1.9 (0.2)	1.7 (0.2)	1.8 (0.2)	†2.9 (0.2)	†5.4 (0.2)		
	−7.7	1.8 (0.2)	1.8 (0.2)	2.0 (0.2)	†3.3 (0.2)	†5.9 (0.2)	†9.4 (0.4)	
	−10.6	1.7 (0.2)	1.7 (0.2)	2.0 (0.2)	†3.3 (0.2)	†6.1 (0.2)		
	−12.9	1.7 (0.2)	1.6 (0.2)	1.9 (0.2)	†3.3 (0.2)	†6.1 (0.3)		
	−15.7	1.7 (0.2)	1.7 (0.2)	1.9 (0.2)	†3.1 (0.2)	†5.8 (0.3)		
	−17.5	1.9 (0.3)	1.8 (0.3)	1.9 (0.2)	†3.1 (0.3)	†5.6 (0.4)		
P. coloratum C. R^2 = 0.33 R.S. R^2 = 0.84	Control	2.7 (0.3)	2.8 (0.3)	3.2 (0.2)	3.6 (0.4)			
	−1.6	†1.8 (0.5)	†1.5 (0.4)	†1.6 (0.4)	3.4 (0.4)	6.7 (0.6)		
	−3.1	†2.1 (0.4)	†1.8 (0.3)	†1.9 (0.3)	3.5 (0.3)	6.5 (0.4)		
	−5.3	2.5 (0.3)	†2.2 (0.2)	†2.2 (0.3)	3.6 (0.3)	6.3 (0.3)	8.9 (0.8)	
	−7.7	2.8 (0.4)	2.5 (0.3)	†2.5 (0.3)	3.8 (0.3)	6.1 (0.4)		
	−10.6	3.0 (0.4)	2.7 (0.3)	†2.8 (0.3)	3.9 (0.3)	5.9 (0.4)		
	−12.9	3.0 (0.3)	2.8 (0.3)	2.9 (0.3)	†4.0 (0.3)	5.8 (0.4)		
	−15.7	2.9 (0.4)	2.8 (0.3)	3.0 (0.3)	†4.2 (0.3)	5.8 (0.4)		
	−17.5	2.7 (0.5)	2.7 (0.4)	3.0 (0.4)	†4.2 (0.5)	5.8 (0.5)	6.6 (0.8)	

† Confidence interval did not overlap predicted mean for control treatment.

a reduction in the lag time of imbibition as primed seeds were not dried back before being switched to the germination treatments. Hardegree and Emmerich (1992), however, measured seed water uptake for these species, and found that a reduction in the lag time of imbibition accounted for only a small number of treatments exhibiting reduced values of D_{50}. Increased G and decreased D_{50} at reduced germination-water potentials is, consistent with, but does not necessarily confirm, the hypothesis of Bradford (1986) that osmotic adjustment contributes to positive seed-priming effects.

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