Journal of Experimental Botany, Vol. 43, No. 247, pp. 233–238, February 1992

Effect of Matric-Priming Duration and Priming Water Potential on Germination of Four Grasses

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Received 5 April 1991; Accepted 4 September 1991

ABSTRACT

In this study, a matric-potential control system was used to determine the effect of matric-priming duration and priming water potential on the germination response of *Bouteloua curtipendula* (Michx.) Torr., *Cenchrus ciliaris* L., *Eragrostis lehmanniana* Nees, and *Panicum coloratum* L. Seeds were primed at water potentials of −1·5 to −7·7 MPa for up to 14 d. Optimum germination generally occurred in treatments primed at high water potential for the shortest period. Germination of seeds primed at lower water potential and for longer periods exhibited a negative germination response relative to the control. Seeds were not redried after the priming treatment. Seed-water uptake measurements suggest that a reduction in the lag time of imbibition accounted for at least some germination-rate enhancement in the positive-priming treatments.

Key words: Germination, matric-priming, imbibition.

INTRODUCTION

Osmotic priming is a pre-germinative seed treatment in which seeds are immersed in an osmotic solution that allows water uptake but prevents radicle emergence (Bradford, 1986). Germination enhancement by osmotic priming may reflect metabolic repair processes (Bray, Davison, Ashraf, and Taylor, 1989; Burgass and Powell, 1984), a build-up of germination metabolites (Khan, Tao, Knypl, Borkowska, and Powell, 1978; Coolbear, Grierson, and Heydecker, 1980), and/or osmotic adjustment during imbibition (Bradford, 1986). If the seeds are not re-dried after treatment, part of the priming effect may result from a simple reduction in the lag phase of imbibition (Bewley and Black, 1982; Brocklehurst and Dearman, 1983; Heydecker, 1977).

Polyethylene glycol (PEG) is the most frequently used solute for osmotic priming. PEG with a molecular weight greater than 4000 is excluded from plant cell walls and cannot be taken up by seed (Carpita, Sabularse, Montezinos, and Delmer, 1979; Tarkow, Feist, and Southerland, 1966). Priming in an osmotic solution of PEG should, therefore, be equivalent to priming in or on an isopotential porous matrix. A matric seed-priming effect has been demonstrated by Wallace (1960) who found that germination could be stimulated by pre-equilibration in unsaturated soil. The term Solid Matrix Priming (SMP) has also been used to describe seed equilibration in a porous matrix but SMP uses a relatively saturated medium where the primary water potential control is osmotic (Taylor, Klein, and Whitlow, 1988).

One drawback to current osmotic- and porous-matrix-priming systems is that the intermixture of seed with the priming medium makes it difficult to monitor seed water relations during imbibition and limits commercial application of the priming technique. Gray, Steckel, and Hands (1990) eliminated this problem by separating the seeds from the priming solution with a cellulose dialysis membrane and found no difference in germination response of matric- and osmotic-primed seed. The purpose of this study is to use an improved matric potential control system to determine the effects of matric-priming duration and priming water potential on seed germination response of four range-grass species.

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MATERIALS AND METHODS

Seed priming and germination

B. curtipendula, *C. ciliaris*, *E. lehmanniana*, and *P. coloratum* seeds were tested for matric-priming duration and priming water potential effects on total germination, germination rate, and germination uniformity. These species were selected because they occur over large areas of rangeland in the southwestern United States and in previous studies showed a wide range of germination response to a number of environmental variables (Hardegree and Emmerich, 1990*b*; Emmerich and Hardegree, 1990).

Seeds were primed and germinated in a priming/germination cup inside a germination vial designed for control of matric potential in the seed germination environment (Fig. 1). A germination vial consisted of a 50 mm diameter by 85 mm high transparent snap-top vial (Thornton Plastics, Salt Lake City, UT)[1] containing 65 cm^3 of either water or an osmotic solution of polyethylene glycol 8000 (PEG; Union Carbide Corp., Danbury, CT). The seed priming/germination cup was constructed by cutting the top 25 mm from a 30 mm diameter, clear-plastic snap-top vial. Spectra/Por 3 cellulose dialysis membrane (Spectrum Medical Industries, Inc., Los Angeles, CA) was stretched across the mouth of the vial and held in place with the snap-top lid from which a 25 mm diameter hole had been punched. The priming/germination cup thus formed was lowered into contact with water or osmotic solution in the larger vial. The priming/germination cup was supported at the solution surface on a plastic screen resting on plastic rods glued to the inside of the larger vial. The cellulose membrane has a molecular weight exclusion limit of 3500, effectively excluding PEG from contact with the seed inside the priming/germination cup.

PEG was mixed with water to yield nine solutions over the water potential range of −1·5 to −7·7 MPa. PEG solution water potentials were measured three times each, in random order, without filter paper (Hardegree and Emmerich, 1990*a*) in an SC-10A thermocouple psychrometer (Decagon Devices, Pullman, WA). The psychrometer was calibrated with standard salt solutions (Lang, 1967).

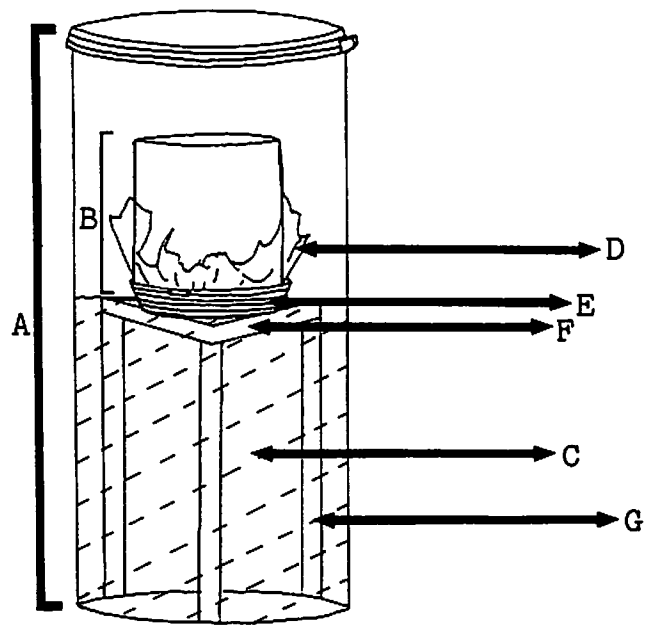

FIG. 1. Matric potential control system for seed priming and germination. A, germination vial; B, priming/germination cup; C, osmotic solution; D, cellulose membrane; E, snap-top lid with 25 mm diameter hole; F, plastic screen; G, support rods.

Thirty-five seeds were placed on the membrane surface of the priming/germination cup and allowed to equilibrate with PEG solutions of −1·5, −2·0, −2·5, −3·0, −4·0, −5·0, −5·9, −6·8, or −7·7 MPa water potential for either 0, 1, 2, 3, 4, 5, 7, 9, 11 or 14 d. After the specified period of equilibration, the priming/germination cup was removed, blotted of excess PEG solution and placed in another germination vial, containing deionized water, for 14 d. Treatments were replicated three times and vials were arranged in randomized blocks within a controlled-temperature room. All seed priming treatments were started on the same day and a set of non-primed control treatments was initiated on every day that a set of primed seed was switched to pure water.

Seeds were primed and germinated in the controlled-temperature room at 25 ± 1 °C under both fluorescent and incandescent light for 12 h d^{-1}. Germination vials were opened and checked every day of the priming and germination period. Seeds were considered germinated and were counted and removed from the membrane surface when they exhibited radicle extension of ≥2·0 mm. The cellulose membranes were treated with a 50 mm^3 suspension of fungicide (Daconil; 2·5 g/100 cm^3 H_2O) before the seed were placed on the membrane surface. The few seed that developed fungus were removed and counted as non-viable.

E. lehmanniana seed required mechanical scarification to remove dormancy. The mechanical scarification treatment followed that reported by Wright (1973) with 0·5 cm^3 seed samples and an 8 s scarification interval.

Three germination indices were calculated for the seed from each germination vial: total per cent germination (G), days required to reach 50% of G (D_{50}) as an index of germination rate, and days between attainment of 10% and 90% of G (D_{10-90}) as an index of germination uniformity.

Linear regression equations were calculated to determine the relationship between individual germination index and date of initiation for the control treatments.

Cubic response surfaces were calculated relating G, D_{50}, and D_{10-90} to priming-solution water potential and priming duration for each species. Regression equations were recalculated deleting first cubic then quadratic then linear terms that were not significant ($P \leq 0{\cdot}10$). 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 ($P \leq 0{\cdot}05$) determined for each treatment combination of priming duration and priming water potential (Evans, Easi, Book, and Young, 1982). Treatments that resulted in germination during priming were not included in regression calculations. Priming was considered to have had a significant effect on germination if the confidence interval of the regression model did not overlap the mean germination index value of the control treatment.

Seed-water uptake

Seed-water uptake was determined with the same system used for the germination experiment except that a larger number of seed were used. PEG was mixed with water to yield six solutions with water potentials of 0, −0·5, −1·5, −2·5, −5·0, and

[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.

−7·7 MPa. Seed were poured on to the membrane surface of the priming/germination cups which were in contact with PEG solution in the germination vials. The aggregate weight of air-dry seeds in each sample was approximately 0·3 g for *B. curtipendula*, 0·5 g for *P. coloratum*, and 0·6 g for *C. ciliaris*, and *E. lehmanniana*. The time at which the seeds were loaded was recorded and the seeds were allowed to equilibrate for up to 72 h. Seeds used in the water uptake experiment were not treated with fungicide in order to avoid confounding the gravimetric measurements and the relatively dense packing in the hydration experiment did not allow for removal of individual seeds that developed fungal growth. The hydration experiment was terminated after 72 h because any seed mass allowed to equilibrate for longer periods developed massive fungal infection.

Three replicate samples of each species were removed from the vials after approximately 2, 4, 6, 8, 10, 12, 24, 36, 48, and 72 h. Seeds were weighed immediately after removal from the priming/germination cups, dried at 105 °C for 24 h and reweighed. The initial air-dry water content of the seed was also determined for six samples of each species.

Quadratic regression equations were calculated for each species relating seed-water content after equilibration to water potential in the −1·5 to −7·7 MPa treatments. A regression equation was also calculated relating seed-water content to equilibration time in the pure water treatment. These equations were used to estimate a correction factor to account for the component decrease in D_{50} of primed seeds relative to the control. Only treatments exhibiting no germination were included in the regression calculations.

RESULTS

There was no relationship between date of initiation of control treatments and G, D_{50} or D_{10-90} for any species. It was concluded that conditions for seed germination did not change over the course of the priming/germination period. Mean values for G, D_{50} and D_{10-90} of the control treatments were, therefore, calculated from the data of all control treatments disregarding date of treatment initiation (Tables 1–3).

Priming enhanced G, relative to the control, for three of the species over at least part of the measured range of matric-priming duration and priming water potential (Table 1). In general, optimum G was achieved under conditions of high priming-water potential and short priming-duration (Table 1). The regression models for G were not constrained to a maximum value of 100%. The unconstrained models provided the best fit for all of the data but produced some predicted values of $G > 100\%$ for *B. curtipendula* (Table 1). In such cases, however, the calculated confidence interval overlapped the maximum actual value of 100%.

Priming enhanced D_{50} for *C. ciliaris* and *P. coloratum* in the high water potential treatments over the entire range of priming duration (Table 2). *B. curtipendula* and *E. lehmanniana* exhibited positive priming effects on D_{50} for only a very few treatments (Table 2).

Uniformity of germination was enhanced over at least part of the treatment range for all species except *B. curtipendula* (Table 3). Enhancement of D_{10-90} was confined to the wetter treatments for *C. ciliaris* and to wetter and shorter-duration treatments for *E. lehmanniana* (Table 3). The priming response of *P. coloratum* for D_{10-90} was atypical in that optimum performance was achieved in the wetter, but longer-duration, treatments (Table 3).

The majority of priming treatments in this study either had no effect or had a negative effect on germination relative to the controls (Tables 1–3). *C. ciliaris* exhibited the most dramatic positive enhancement with matric-priming. G of *C. ciliaris* could be enhanced by 17%, D_{50}

TABLE 1. *Calculated total per cent germination* (G) *as a function of priming water potential and days equilibrated*

Numbers in parentheses represent one-half confidence interval widths ($P \leq 0.05$) calculated from the regression model. G for the control treatments are listed under the species names.

Species	Water potential (MPa)	Days equilibrated							
		1	2	3	5	7	9	11	14
B. curtipendula	−1·5	98 (4)	99 (3)						
Control: 99 (1)	−3·0	101 (3)	101 (2)	101 (2)	99 (2)	96 (2)	93 (2)	92 (2)	97 (3)
	−5·0	98 (2)	98 (2)	98 (2)	95 (2)	91 (2)	87 (2)	85 (2)	89 (3)
	−7·7	102 (3)	101 (3)	100 (3)	95 (2)	90 (2)	85 (3)	82 (3)	83 (4)
C. ciliaris	−1·5	92 (6)	90 (5)	88 (4)	83 (4)	80 (5)	77 (6)		
Control: 75 (4)	−3·0	84 (4)	81 (3)	79 (2)	75 (3)	72 (3)	71 (3)	70 (3)	71 (7)
	−5·0	79 (4)	75 (4)	71 (3)	64 (3)	60 (3)	57 (3)	56 (4)	58 (6)
	−7·7	81 (7)	72 (6)	63 (5)	48 (5)	35 (5)	26 (6)	19 (6)	14 (9)
E. lehmanniana	−1·5	97 (4)	95 (3)	93 (3)	90 (3)				
Control: 92 (3)	−3·0	99 (3)	97 (2)	96 (2)	95 (2)	94 (2)	94 (2)	94 (3)	91 (4)
	−5·0	94 (3)	92 (2)	90 (2)	88 (2)	89 (2)	90 (2)	92 (3)	93 (4)
	−7·7	91 (5)	86 (4)	82 (3)	76 (3)	74 (3)	73 (4)	74 (4)	77 (6)
P. coloratum	−1·5	81 (4)	80 (3)	80 (3)	79 (2)	76 (2)	73 (3)	69 (3)	
Control: 75 (4)	−3·0	77 (3)	77 (2)	77 (2)	76 (2)	75 (2)	72 (2)	69 (2)	63 (4)
	−5·0	73 (3)	73 (2)	74 (2)	74 (2)	73 (2)	72 (2)	69 (2)	64 (4)
	−7·7	67 (4)	68 (3)	69 (3)	70 (3)	71 (3)	70 (3)	69 (4)	66 (5)

TABLE 2. *Calculated days to 50% of* G (D_{50}) *as a function of priming water potential and days equilibrated*

Numbers in parentheses represent one-half confidence interval widths ($P \leq 0.05$) calculated from the regression model. D_{50} for the control treatments are listed under the species names. Treatments marked with an asterisk did not perform better than the control when corrected for lag time of imbibition.

Species	Water potential (MPa)	Days equilibrated							
		1	2	3	5	7	9	11	14
B. curtipendula	−1·5	0·6 (0·1)	0·6 (0·1)						
Control: 0·6 (0·1)	−3·0	*0·4 (0·1)	0·5 (0·1)	0·5 (0·1)	0·5 (0·1)	0·6 (0·1)	0·6 (0·1)	0·6 (0·1)	0·5 (0·1)
	−5·0	0·5 (0·1)	0·6 (0·1)	0·7 (0·1)	0·8 (0·1)	0·9 (0·1)	1·0 (0·1)	1·0 (0·1)	0·9 (0·1)
	−7·7	0·8 (0·1)	0·9 (0·1)	1·0 (0·1)	1·1 (0·1)	1·2 (0·1)	1·2 (0·1)	1·2 (0·1)	1·0 (0·2)
C. ciliaris	−1·5	0·7 (0·2)	0·6 (0·2)	0·6 (0·1)	0·5 (0·1)	0·5 (0·2)	0·5 (0·2)		
Control: 1·9 (0·2)	−3·0	1·2 (0·1)	1·1 (0·1)	1·1 (0·1)	1·0 (0·1)	1·0 (0·1)	1·0 (0·1)	1·1 (0·1)	1·2 (0·2)
	−5·0	*1·6 (0·2)	*1·6 (0·1)	*1·6 (0·1)	*1·7 (0·1)	*1·7 (0·1)	*1·7 (0·1)	*1·7 (0·1)	1·7 (0·2)
	−7·7	2·0 (0·2)	2·1 (0·2)	2·3 (0·2)	2·5 (0·2)	2·7 (0·2)	2·8 (0·2)	2·8 (0·2)	2·7 (0·3)
E. lehmanniana	−1·5	1·0 (0·2)	1·1 (0·1)	1·2 (0·1)	1·2 (0·1)				
Control: 1·2 (0·1)	−3·0	*1·0 (0·1)	1·2 (0·1)	1·3 (0·1)	1·4 (0·1)	1·3 (0·1)	1·3 (0·1)	1·3 (0·1)	1·5 (0·2)
	−5·0	1·1 (0·1)	1·3 (0·1)	1·4 (0·1)	1·6 (0·1)	1·6 (0·1)	1·6 (0·1)	1·7 (0·1)	2·0 (0·1)
	−7·7	1·3 (0·2)	1·5 (0·1)	1·7 (0·1)	2·0 (0·1)	2·1 (0·1)	2·2 (0·1)	2·4 (0·2)	2·8 (0·2)
P. coloratum	−1·5	1·7 (0·2)	1·7 (0·2)	1·7 (0·1)	1·7 (0·1)	1·8 (0·1)	1·8 (0·2)	1·9 (0·2)	
Control: 2·5 (0·2)	−3·0	2·4 (0·1)	2·4 (0·1)	2·4 (0·1)	2·4 (0·1)	2·4 (0·1)	2·4 (0·1)	2·5 (0·1)	2·6 (0·2)
	−5·0	2·7 (0·1)	2·6 (0·1)	2·6 (0·1)	2·6 (0·1)	2·6 (0·1)	2·6 (0·1)	2·6 (0·1)	2·7 (0·2)
	−7·7	3·1 (0·2)	3·0 (0·2)	3·0 (0·2)	2·9 (0·2)	2·8 (0·2)	2·8 (0·2)	2·8 (0·2)	2·8 (0·2)

TABLE 3. *Calculated days between 10% and 90% of* G (D_{10-90}) *as a function of priming water potential and days equilibrated*

Numbers in parentheses represent one-half confidence interval widths ($P \leq 0.05$) calculated from the regression model. D_{10-90} for the control treatments are listed under the species names.

Species	Water potential (MPa)	Days equilibrated							
		1	2	3	5	7	9	11	14
B. curtipendula	−1·5	0·8 (0·2)	0·8 (0·1)						
Control: 0·9 (0·1)	−3·0	0·8 (0·1)	0·9 (0·1)	0·9 (0·1)	1·0 (0·1)	1·0 (0·1)	1·0 (0·1)	0·9 (0·1)	0·8 (0·1)
	−5·0	1·0 (0·1)	1·1 (0·1)	1·1 (0·1)	1·2 (0·1)	1·3 (0·1)	1·3 (0·1)	1·3 (0·1)	1·2 (0·1)
	−7·7	1·4 (0·2)	1·5 (0·1)	1·5 (0·1)	1·6 (0·1)	1·6 (0·1)	1·6 (0·1)	1·6 (0·1)	1·5 (0·2)
C. ciliaris	−1·5	1·6 (0·4)	1·5 (0·4)	1·4 (0·3)	1·2 (0·3)	1·1 (0·4)	1·0 (0·4)		
Control: 3·1 (0·3)	−3·0	1·8 (0·3)	1·8 (0·2)	1·8 (0·2)	1·7 (0·2)	1·7 (0·2)	1·6 (0·2)	1·6 (0·3)	1·5 (0·5)
	−5·0	2·7 (0·3)	2·7 (0·2)	2·8 (0·2)	2·9 (0·2)	2·9 (0·2)	2·9 (0·2)	2·9 (0·2)	2·7 (0·3)
	−7·7	2·7 (0·5)	2·9 (0·4)	3·1 (0·3)	3·4 (0·4)	3·6 (0·4)	3·7 (0·4)	3·6 (0·4)	3·4 (0·6)
E. lehmanniana	−1·5	1·4 (0·2)	1·6 (0·2)	1·7 (0·2)	1·9 (0·2)				
Control: 2·2 (0·3)	−3·0	1·7 (0·2)	1·9 (0·1)	2·0 (0·1)	2·2 (0·1)	2·2 (0·1)	2·2 (0·1)	2·2 (0·2)	2·3 (0·2)
	−5·0	2·1 (0·2)	2·3 (0·1)	2·4 (0·1)	2·5 (0·1)	2·6 (0·1)	2·6 (0·1)	2·5 (0·2)	2·7 (0·2)
	−7·7	2·6 (0·3)	2·8 (0·2)	2·9 (0·2)	3·1 (0·2)	3·1 (0·2)	3·1 (0·2)	3·1 (0·2)	3·2 (0·3)
P. coloratum	−1·5	3·5 (0·6)	3·4 (0·5)	3·3 (0·5)	3·1 (0·5)	3·0 (0·5)	3·0 (0·5)	3·0 (0·6)	
Control: 4·0 (0·6)	−3·0	3·9 (0·4)	3·8 (0·4)	3·6 (0·3)	3·4 (0·3)	3·3 (0·3)	3·2 (0·3)	3·2 (0·4)	3·3 (0·6)
	−5·0	3·9 (0·4)	3·7 (0·3)	3·6 (0·3)	3·3 (0·3)	3·1 (0·3)	3·0 (0·3)	2·9 (0·3)	3·0 (0·5)
	−7·7	6·0 (0·7)	5·8 (0·6)	5·6 (0·5)	5·3 (0·5)	5·0 (0·5)	4·8 (0·5)	4·7 (0·6)	4·7 (0·8)

reduced by 1·4 d and D_{10-90} reduced by 2·1 d relative to untreated seeds (Tables 1–3).

Seed-water uptake reached a plateau for most water potential treatments more negative than −1·5 MPa in less than 24 h (Fig. 2). Treatments with a positive priming effect on D_{50} were re-evaluated to determine whether germination advancement could be accounted for by a reduction in the lag time of imbibition for primed seeds. This correction reduced the number of treatments with a positive priming effect on D_{50} for *C. ciliaris* and *P. coloratum* and eliminated them for *B. curtipendula* and *E. lehmanniana* (Table 2).

DISCUSSION

Seed-priming at subgermination water content has been shown to enhance the germination response of a large number of plant species (Heydecker and Coolbear, 1977). Our study and others, however, have demonstrated detrimental priming effects for low water potential and long duration treatments (Gray *et al.*, 1990; Ely and

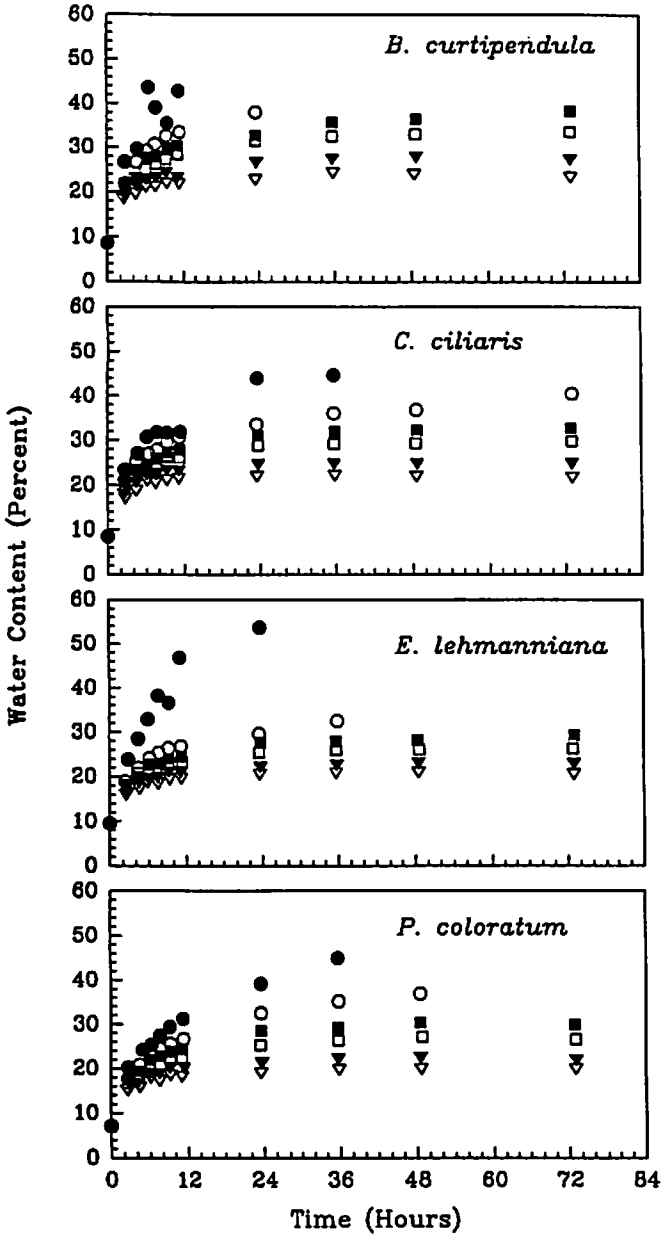

FIG. 2. Seed water uptake as a function of time at 0 (●), −0·5 (○), −1·5 (■), −2·5 (□), −5·0 (▼), and −7·7 (▽) MPa water potential. Data points represent mean water content of three replicate samples.

Heydecker, 1981; Coolbear *et al.*, 1980). The priming water potential selected for most seed-priming applications should, therefore, be the least negative that does not cause significant pre-germination (Dell'Aquila and Tritto, 1990; Evans and Pill, 1989).

Priming at lower than optimum water potential is inadvisable as a pre-germination seed treatment but does offer insight into natural priming and seed degradation processes that may occur in the soil. Our data (Tables 1–3) indicate that metabolic reactions resulting in positive priming effects may only occur at relatively high water potential. Oxidative processes detrimental to total germination appear to dominate in the more negative and longer duration priming treatments. Wallace (1960) found similar results for seed equilibrated in soil at subgermination water content. Wallace (1960) did not determine the water potential of his soil samples but found that germination enhancement was confined to wetter treatments. Seed equilibrated in soil of intermediate water content were negatively affected but seed equilibrated in very dry soil had a subsequent germination response equivalent to the control (Wallace, 1960). The results of Wallace (1960) are consistent with our study but we did not include treatments dry enough to return the germination response to control levels.

The effect of seed priming on germination response depends upon whether the seed are re-dried after treatment (Bradford, 1986; Heydecker and Coolbear, 1977). Re-drying is usually accompanied by some reversal of the priming effect (Heydecker and Coolbear, 1977). The seed in this study were not re-dried, therefore, part of the priming effect on D_{50} can be attributed to a simple reduction in the lag phase of imbibition (Bewley and Black, 1982; Heydecker and Coolbear, 1977). We found that the advanced water content of primed seeds may have accounted for some but not all of the increased germination rate in the positive priming treatments (Table 2). Several assumptions were made, however, in the determination of a correction factor for the advanced hydration of primed seeds. It was first assumed that imbibition rate was the same for both primed and non-primed seed at the same water content. Osmotic adjustment during imbibition may have increased the subsequent imbibition rate of primed seeds relative to the control. A second assumption was that imbibition rates were comparable between the priming/germination experiment and the seed-water uptake experiment. Imbibition rates in the seed-water uptake experiment may have been reduced by the greater number of seed competing for available water. A third assumption was that the water content of primed seed remained stable in treatments equilibrated for longer than 72 h. It has been demonstrated for many species that water content of primed seed remains fairly stable for prolonged periods unless radicle emergence occurs (Gray *et al.*, 1990). A fourth assumption was that imbibition rate of the seed that germinated was the same as that of the population as a whole.

The significance of individual species response to priming cannot be evaluated from our data as intraspecific variability was not determined. The absolute magnitude of germination rate enhancement, however, was found to be relatively small compared to that found for some agricultural crops (Heydecker, 1977). Other studies have also shown that germination enhancement from priming may be expressed to a greater degree at sub- or

supra-optimal temperatures (Heydecker, 1977). Positive-priming effects in this experiment may have been limited relative to that found in other studies because both priming and germination occurred at the optimal temperature for germination of these grasses.

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