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Original article

Germination, survival, and growth of grass and forb seedlings: Effects of soil moisture variability

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ABSTRACT

Seed germination and seedling growth, survivorship, and final biomass and their responses to watering interval were studied in two grass and six forb species to assess germination and seedling growth responses to increased soil moisture variability as might occur with future increases in precipitation variability. Seeds were planted in prairie soil and watered at 1, 2, 4, or 7 d intervals ($\boldsymbol{I}$). Seed germination peaked at $\boldsymbol{I} = 4$ d whereas leaf growth in grasses and forbs, and final biomass in grasses peaked at $\boldsymbol{I} = 7$ d, suggesting that growth and biomass were favored at greater soil moisture variability than seed germination. Biomass responses to $\boldsymbol{I}$ were stronger than the germination responses, suggesting that soil moisture variability more strongly influenced post germination growth. Individual species responses to $\boldsymbol{I}$ fell into three groups; those with responses to $\boldsymbol{I}$ for: (1) seed germination and seedling survival, (2) biomass, or (3) both germination and biomass production. These species groups may be more useful than life form (i.e., grass/forb) for understanding seed germination and seedling dynamics in grasslands during periods of soil moisture variability. Seed germination and early growth may assume more importance in grassland plant community dynamics under more variable precipitation patterns.

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Seed germination and seedling growth are critical stages of plant development leading to the establishment of new individuals in plant communities. These two aspects are highly sensitive to environmental variability, and require favorable conditions of soil moisture, which is rarely static. As a result, seeds in the soil in natural conditions routinely experience periods of alternating wet and dry conditions (Baskin and Baskin, 1982) caused by the episodic nature of precipitation. Tolerance of varying soil moisture also depends on the stage of plant development (Wilson et al., 1974). For example, in the C4 grass *Bouteloua gracilis*, levels of water stress which promoted high germination were unsuitable for seedling survival (Qi and Redmann, 1993). In shortgrass steppe, grass species that germinated well under a wide range of temperature and moisture conditions were intolerant of drought as established plants, whereas other grass species with narrow germination and establishment requirements survived drought when established (McGinnies, 1960). Thus, conditions that may favor germination may not favor continued growth and survival of seedlings or later stages (Lloret et al., 2004). Several studies have shown that differences in germination patterns associated with growth form or life history reflect adaptations to environmental variability (Matthews, 1976; Qi and Redmann, 1993; Dubrovsky, 1998; Perez-Fernandez et al., 2000; Flores and Briones, 2001).

Understanding how seeds and seedlings fare under varying soil moisture is important for determining how soil moisture variation may affect recruitment into plant communities. For example, several studies report that pulses of seed germination and seedling establishment in field populations follow pulses of precipitation (Wilson, 1973; Vincent and Cavers, 1978; Roberts and Potter, 1980). The timing of such events may have a marked effect on competitive success (Larsen et al., 2004; Weltzin and McPherson, 2000). The duration between precipitation inputs is a primary determinant of soil moisture variability. Most climate change scenarios forecast increasingly extreme precipitation patterns (Christensen and Hewitson, 2007). These will likely be manifest as longer droughts broken by large precipitation events. Increases in the frequency of extreme precipitation events have been documented (Groisman et al., 2005; IPCC, 2007). Knapp et al. (2002) reported that experimental rainfall applications that increased the occurrence of extreme events resulted in increased plant diversity and species turnover in grassland. Changes in plant community composition under more extreme precipitation patterns, particularly during spring, could arise in part from changes in seed and seedling success.

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To evaluate the association between seed/seedling success and soil moisture variability we conducted a watering interval experiment addressing two questions: (1) How does soil moisture variation arising from longer periods (***I***) between water inputs affect seed germination and seedling survivorship and initial growth? (2) How do species and growth forms differ in germination and growth responses to soil moisture variation? The approach was a greenhouse study using seeds planted in soil, to approximate the substrate and drying rate encountered by seeds in natural populations. The primary hypothesis was that soil moisture variability would affect germination and seedling growth differently both among species and growth forms.

1. Methods

The study focused on two grasses, *Andropogon gerardii* Vitman and *Sorghastrum nutans* (L.) Nash, and six forbs, *Amorpha canescens* Pursh, *Asclepias tuberosa* L., *Echinacea purpurea* (L.) Moench, *Lespedeza capitata* Michx., *Liatris punctata* Hook., and *Psoralea tenuiflora* (Pursh) Rydb. *A. gerardii* and *S. nutans* are C_4 tall grasses and dominant in large portions of their ranges, accounting for over 50% of net primary production in some cases (Freeman, 1998; Silletti and Knapp, 2001). The forbs are also widespread and locally abundant in the North American grasslands. These species were of further interest because of their inclusion in other precipitation variability studies (Fay et al., 2008)

1.1. Culture method and treatments

The experiment was conducted in a temperature-controlled greenhouse in Duluth, MN U.S.A. during July and August, 2004. The mean afternoon air temperature was 25.1 ± 0.5C and the mean nighttime minimum was 17.6 ± 0.3 C, which represented spring temperatures commonly encountered by these species during germination and establishment. Illumination was from natural daylight, with midday peaks varying between 500 and 1800 μmol m^{-2} s^{-1} photosynthetic photon flux density.

We prepared 640 plastic tubes (3.8 cm diameter × 21.0 cm deep, 164 cm^3, Conetainer™, Stuewe and Sons, Corvallis, OR, U.S.A.) containing 80% sieved native prairie soil, 15% peat and 5% vermiculite (v:v:v). Eighty tubes per species were planted with 3 seeds per tube at 1 cm depth in the soil mix. Seeds were obtained from commercial sources, and were not pre-conditioned, but the resulting germination rates were adequate for the objective of comparing watering interval treatments. The tubes were top-dressed with 2 g of slow release fertilizer (Osmocote®, The Scotts Company, Marysville, OH, U.S.A.). Twenty tubes per species were then randomly assigned to be watered at 1, 2, 4 or 7 d intervals (***I***). Watering was performed with a hand nozzle with a gentle flow pattern. Water was applied to the tubes until the soil appeared fully infiltrated. The small diameter of the tubes made watering individual tubes impractical, so all tubes assigned to an ***I*** were grouped on the greenhouse bench and watered together. Care was taken that individual tubes (the experimental unit) were always consistently watered, and the groups were rotated on the greenhouse bench biweekly to prevent confounding the spatial arrangement of plants and groups with watering treatment.

1.2. Soil moisture, germination, and growth measurements

Gravimetric soil moisture determinations were made by daily weighing of unplanted tubes placed among the planted tubes during several watering cycles at the end of the experiment. Soil moisture was expressed as a percent of the maximum (saturated) tube mass. Seed germination was recorded at 4 d intervals. Germination was scored when a seedling had emerged at least 2 mm above the soil surface. When no further germination occurred (day 21), seedlings were thinned to one per tube. Growth of these post germination seedlings was recorded at 10–14 d intervals by measuring plant height from the soil surface to the distal leaf tip in the grasses, and by counting expanded leaves for the forbs. Survivorship of the seedlings was estimated from the number of tubes containing plants at the last growth measurement (day 56). The plants were then harvested and the roots were carefully washed free of soil. The roots and tops were separated, dried to constant mass, and weighed to determine biomass and allocation above vs. belowground.

1.3. Data analysis

The tube was the experimental unit for statistical analysis. Percent germination in each tube was computed for each observation day. Germination and growth curves were analyzed for ***I***, day, and ***I*** × day effects by life form (grass/forb) and by species using a repeated measures ANOVA. Logistic regression was used to analyze the number of seeds germinated per tube on day 21 and the number of surviving plants at day 56. Biomass and allocation variables were assessed for ***I***, life form, and ***I*** × life form effects using ANOVA. Analyses were conducted using Proc Mixed and Proc Logistic in SAS 9.1 (SAS Institute, Cary, NC, U.S.A.).

2. Results

2.1. Soil moisture

The mean and variability in soil moisture was strongly affected by watering interval. The soil dried between waterings at about the same rate in all four treatments, with tubes losing approximately 2% of their mass, approximately 3 g, of H_20 d^{-1} (Fig. 1). Thus, the soil in tubes watered at longer intervals varied more and became significantly drier between successive waterings than those with shorter watering intervals ($F_{3,59} = 226.1$, $p < 0.0001$; Fig. 1 inset).

2.2. Germination

Germination in the grasses averaged 30–45%, compared to 20–25% for the forbs ($p < 0.0001$, Table 1, Fig. 2). Germination for both forbs and grasses were affected by the watering treatments, with significant ***I*** and days since planting effects for grasses and forbs,

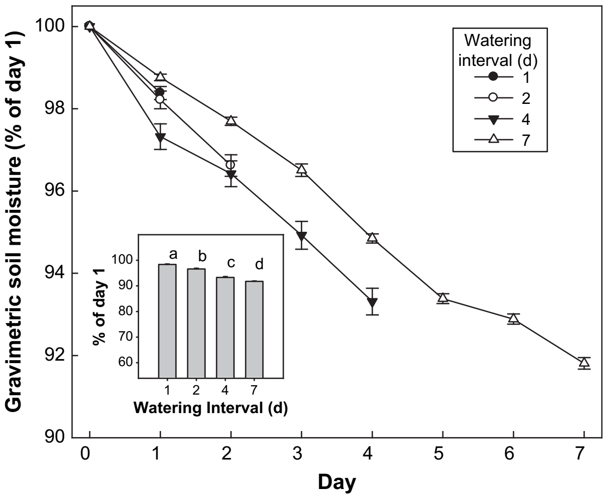

Fig. 1. Gravimetric soil water content (mean ± SE) each day of the four watering interval treatments. Inset: Mean change in soil water content relative to the saturated value immediately after watering. Letters denote significant differences among means.

Table 1
Analysis of variance (ANOVA) and logistic regression statistics for grass and forb germination, growth, and biomass.

Response		ANOVA			
		Effect	df	*F*	*p*-value
Germination	Forbs	Interval	3, 476	21.2	<0.0001
		Day	4, 1904	11.1	<0.0001
		Interval × Day	12, 1904	2.0	0.0186
	Grasses	Interval	3, 156	12.5	<0.0001
		Day	4, 624	8.5	<0.0001
		Interval × Day	12, 624	0.5	0.9354
Growth	Forbs (# leaves)	Interval	3, 476	4.4	0.0045
		Day	5, 2372	56.3	< 0.0001
		Interval × Day	15, 2372	1.8	0.0283
	Grasses (height)	Interval	3, 156	7.6	< 0.0001
		Day	5, 750	93.5	< 0.0001
		Interval × Day	15, 750	0.9	0.6045
Biomass – Total		Interval	3, 293	2.8	0.0398
		Life form	1, 293	23.1	< 0.0001
		Interval × Life form	3, 293	4.4	0.0045
	Forbs	Interval	3192	2.12	0.0992
	Grasses	Interval	3.101	3.60	0.0161
Biomass – Aboveground		Interval	3, 293	3.53	0.0154
		Life form	1, 293	14.60	0.0002
		Interval × Life form	3, 293	2.95	0.0329
	Forbs	Interval	3, 192	2.08	0.1047
	Grasses	Interval	3, 101	2.67	0.0518
Biomass – Belowground		Interval	3, 293	1.35	0.2571
		Life form	1, 293	13.89	0.0002
		Interval × Life form	3, 293	3.40	0.0183
	Forbs	Interval	3, 192	1.69	0.1703
	Grasses	Interval	3, 101	2.64	0.0538
Allocation		Interval	3, 293	2.98	0.0319
		Life form	1, 293	5.42	0.0206
		Interval × Life form	3, 293	0.05	0.9834
	Forbs	Interval	3, 192	1.99	0.1174
	Grasses	Interval	3, 101	2.98	0.0352

		Logistic Regression			
		Effect	df	X^2	*p*-value
Germination (Day 21)		Interval	3	6.99	0.0720
		Life form	1	47.20	< 0.0001
		Interval × Life form	3	1.79	0.6179
	Forbs	Interval	3	6.76	0.0801
	Grasses	Interval	3	3.29	0.3490
Survival (Day 56)		Interval	3	4.63	0.2012
		Life form	1	31.67	< 0.0001
		Interval × Life form	3	3.49	0.3214
	Forbs	Interval	3	6.35	0.0957
	Grasses	Interval	3	3.18	0.3652

and ***I*** × day effects for forbs (Table 1). Forb germination percentages were highest when ***I*** = 4 d (Figs. 2 and 3A). Forb germination was initially slower to proceed at ***I*** = 7 d (Fig. 2A) than for the other ***I*** treatments (***I*** × day $p = 0.02$, Table 1). Grass germination was highest at ***I*** = 4 d and lowest at ***I*** = 7 d for all dates combined ($p < 0.0001$, Table 1, Fig. 2B), and it followed a similar trajectory in all ***I*** treatments (***I*** × day $p = 0.93$).

2.3. Growth and survivorship

Forb leaf numbers showed significant effects of ***I***, days since planting, and their interaction ($P \leq 0.03$; Table 1). The timing of forb leaf production differed among the watering intervals. Forb leaf numbers were initially greatest for ***I*** = 4 d. However after an initial delay, leaf numbers for ***I*** = 7 d increased more rapidly than the other treatments, and were greatest by the final growth measurement (***I*** × day $p = 0.03$; Fig. 2A). Grass plant height also showed significant effects of ***I*** and day ($p < 0.0001$, Table 1), but not for their interaction ($P = 0.60$). Grass plant height was higher at ***I*** = 2 and 4 d compared to ***I*** = 1 and 7 d (Fig. 2B). Survival of seedlings from the conclusion of germination to harvest was unaffected by watering interval ($p \geq 0.20$, Table 1). Survival was much higher for the grasses overall (60–80%) than for the forbs (30–45%, $p < 0.0001$, Table 1, Fig. 3B).

2.4. Biomass

Plant total biomass showed significant ***I*** and ***I*** × life form effects ($p \leq 0.04$, Table 1). Total biomass was 37% greater for grass than for forb seedlings ($P < 0.0001$, Table 1, Fig. 3C), because of increases in both above- and belowground biomass (35–38%, $P = 0.0002$, Table 1, Fig. 3D–E). Total biomass of grass seedlings increased with longer ***I*** treatments ($P = 0.016$, Table 1). In contrast, total, aboveground, and belowground biomass of forb seedlings was not responsive to the ***I*** treatments ($P = 0.10$–0.17). The grasses allocated less biomass aboveground than the forbs (Fig. 3F), and increased allocation aboveground with longer ***I*** ($P = 0.03$, Fig. 3F).

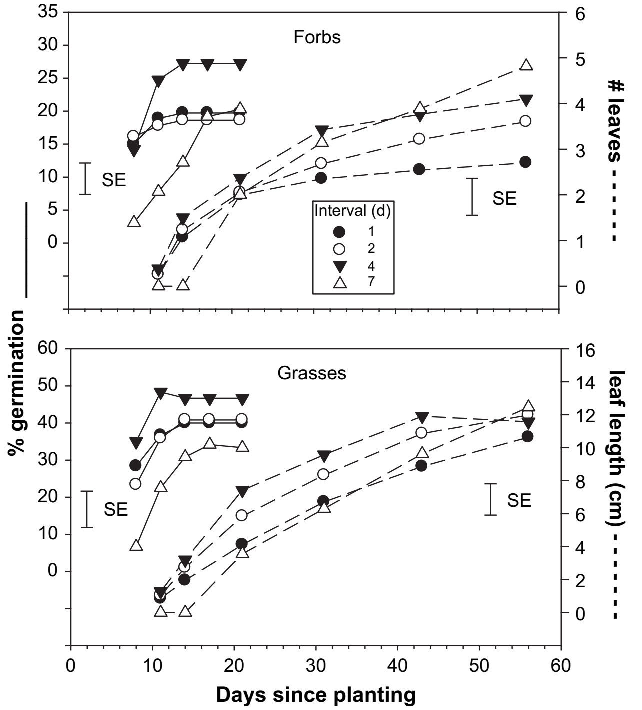

Fig. 2. Time courses of seed germination (solid lines) and seedling leaf growth (dashed lines) grouped by life form. Table 1 contains the ANOVA statistics for these data.

2.5. Response groups

All but one of the species exhibited significant responses to ***I*** in either germination, survival, and biomass respectively (Table 2). However, each species tended to have its own pattern of response to ***I*** at each stage. The species fell into four groups of response (Table 2). One group consisted of *Sorghastrum* and *Psoralea*, which showed statistically significant responses to the ***I*** treatments in germination and survival ($P \leq 0.07$, Table 2). A second group consisted of *Andropogon*, *Amorpha*, and *Lespedeza*, which showed significant responses to ***I*** in two or more aspects of biomass but not in germination or survivorship. The third group included *Liatris* and *Echinacea* which were found to be responsive to ***I*** in germination, survival, and biomass. Fourth, *Asclepias* was unresponsive to ***I*** in these parameters.

3. Discussion

Our results show that the watering interval treatments caused differences in soil moisture variability that affected the germination, growth, survival, and final biomass of these species. Tolerance of variability in soil moisture during germination and early growth varies among species. For example, some species may exhibit enhanced germination following cycles of hydration and dehydration compared to seeds maintained at constant hydration ('priming', Hegarty, 1978). In other species, periods of dehydration may reduce germination or induce dormancy compared to constant hydration (Downs and Cavers, 2000), especially with lengthening periods of dehydration (Walck et al., 1997; Kagaya et al., 2005) or slower rates of dehydration (Griswold, 1936).

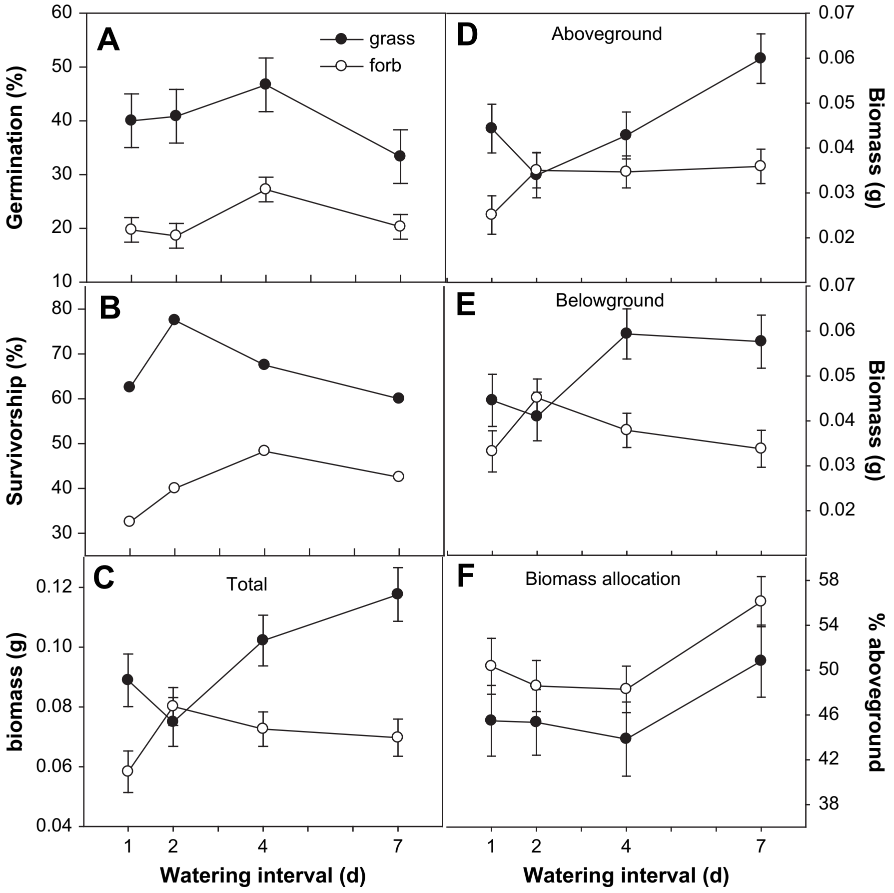

Fig. 3. Seed germination (day 21), and seedling survivorship and final biomass (day 56) components by plant life form and watering interval. Means ± 1 SE. Table 1 contains the ANOVA statistics for these data.

Table 2
p-values for the effect of watering interval on seed germination (day 21), seedling survivorship (day 56), and final seedling biomass by species and life form. Shaded values highlight the marginal or better ($p \leq 0.08$) responses to the interval treatment. Bold lines separate the species into response groups (see text).

Species	Life form	Germination	Survivorship	Biomass		
				Total	Above ground	Below ground
Psoralea tenuiflora	f	**0.0315**	**0.0671**	0.2050	0.5528	0.1142
Sorghastrum nutans	g	**0.0172**	**0.0545**	0.1410	0.2819	0.1134
Liatris punctata	f	**0.0001**	**0.0264**	**0.0263**	0.2339	**0.0093**
Echinacea purpurea	f	**0.0410**	**0.0208**	**0.0025**	**0.0020**	**0.0001**
Amorpha canescens	f	0.4956	0.1800	**0.0238**	**0.0100**	0.1976
Lespedeza capitata	f	0.2383	0.1300	**0.0380**	**0.0443**	**0.0312**
Andropogon gerardii	g	0.3717	0.3080	**0.0015**	**0.0007**	**0.0040**
Asclepias tuberosa	f	0.7860	0.7400	0.1700	0.1470	0.0978

The germination percentages in this study were comparable to previously reported values from studies conducted in both soil and petri dishes (Griswold, 1936; Baskin et al., 1992; Allen et al., 1993; Perez-Fernandez et al., 2000; Batlla and Benech-Arnold, 2006) and for a variety of species native to Central Plains grasslands (McGinnies, 1960; Beckman et al., 1993; Madakadze et al., 2001). Overall, germination percentages increased up to $\boldsymbol{I} = 4$ d but then declined when $\boldsymbol{I} = 7$ d. The differences in germination among these $\boldsymbol{I}$ treatments were 14% for grasses and 9% for forbs. The peak of germination at $\boldsymbol{I} = 4$ was consistent with a priming effect (Hegarty, 1978), and suggested that the cumulative physiological development of seeds was maintained at this watering interval without apparent damage between waterings. It is likely that $\boldsymbol{I} > 7$ d would further depress germination (Walck et al., 1997; Kagaya et al., 2005). There is a threshold in the germination process where deleterious effects of dehydration on actively metabolizing seeds increases (Berrie and Drennan, 1971).

In contrast, leaf growth and final seedling biomass were highest at the longest watering interval where soil moisture variability was highest. This suggests that the seedlings showed greater tolerance of variability than the germinating seeds. Hegarty (1978) reported that seedlings grew successfully at lower water potentials than were required for germination. In that study, the optimum water potential shifted over about 30 d, which matched the seasonal progression of rainfall patterns for the species considered. It is common for rainfall to be relatively frequent in spring and for dry periods to lengthen as the growing season progresses. Seedlings produced from seeds that germinated during the spring wet period would thus be exposed to these subsequent periods of greater soil drying. Greater tolerance of drying in seedlings versus germinating seeds may represent an adaptation to shifting precipitation patterns that could reduce post germination seedling losses (Matthews, 1976).

The species fell into four groups in terms of being responsive to water interval in germination, survival, and/or growth and biomass (Table 2). Two of the groups contained a grass and forbs, suggesting that life form was not useful for classifying seed/seedling responses to soil moisture variability in these species. The groups did not identify optimum watering intervals for growth, germination, survivorship, or biomass because each species had its own distinct pattern of response, likely reflecting each species unique adaptations to climate variability (Griswold, 1936; Matthews, 1976).

Overall, these results suggest that increases in soil moisture variability will impact seed germination more strongly than seedling growth in these species. If precipitation patterns become more episodic, and dry periods lengthen, germination and seedling growth events may become more episodic (Wilson, 1973; Vincent and Cavers, 1978; Roberts and Potter, 1980). Only a subset of the species that germinate and produce viable seedlings become established members of plant communities (Abrams, 1988). Germination and early growth responses to soil moisture variability may affect which of these species establish under more variable precipitation regimes.

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