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Emergence and Seedling Survival of Two Warm-season Grasses as Influenced by the Timing of Precipitation: A Greenhouse Study

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Abstract

A greenhouse study was conducted to determine seedling survival probabilities of sideoats grama *(Bouteloua curtipendula* (Mich x.) Torr.) and cochise lovegrass *(Eragrostis lehmanniana* Nees × *Eragrostis trichophora* Coss & Dur.) for selected combinations of initial wet-day and dry-day sequences. Three separate 14-day experiments were conducted using 1, 2, 3, 4, and 5 days wet followed with 5 days dry. The number of emerging seedlings growing from 10 seeds placed in a sand media in small plastic cones were counted daily. A total of 50 to 70% of the sideoats grama seeds emerged in the initial wet period, but over 50% of the seedlings died in the following 5-day dry period, resulting in less than a 35% survival rate. The cochise lovegrass was slower to germinate and less susceptible to the effect of the 5-day dry period, which resulted in 40 to 60% seedling survival. With the 1- and 2-day wet sequences, the maximum cochise lovegrass plant count was not achieved until the final rewet period. With the exception of 5 days wet, the length of the initial wet period did not significantly affect the number of surviving lovegrass seedlings. This information offers the possibility of incorporating the probablistic aspects of precipitation and soil water relations into a description of the seedling environment.

Plant establishment from seed requires a viable seed and a favorable environment for seedling development. Seeds often germinate, but the seedlings may fail to survive because inadequate soil moisture has limited the development of a root system capable of supporting the plant through later periods of less favorable moisture conditions. Available soil moisture was a factor in the establishment of blue grama (*Bouteloua gracilis* (Willd. ex H.B.K.) Lag. Ex. Griffiths), crested wheatgrass (*Agropyron desertorum* Fisch. ex Link) Schult.), and Russian wildrye (*Elymus junceus* (Fisch.)) plantings in arid portions of the Central High Plains (Briske and Wilson 1977, 1978, 1980; Wilson and Briske 1979a; Hassanyar and Wilson 1978). Water stress during germination and seedling development was detrimental to the survival of western wheatgrass (*Agropyron smithii* Rydb), alkali sacaton (*Sporobolus airoides* (Torr.) Torr.), galleta *(Hilaria jamesii* (Torr.) Benth), blue grama, mountain mahogany (*Cercocarpus mountainus* Raf.), broom snakeweed (*Gutierrezia sarothrae* (Pursh) Butt. and Rusby), and mesquite (*Prosopis juliflora* (Sw.) DC.) (Knipe 1968, 1973; Piatt 1976; Kruse 1970; Scifres and Brock 1969). Young et al. (1970) found reduction in plant survival from water stress with various legumes.

Wilson and Briske (1979b) found that blue grama required 2 to 4 days of moist soil conditions and soil temperatures above 15° C, to germinate and initiate seminal root growth, and that this period must be followed with a similar period after 2 to 8 weeks for the growth of adventitious roots to ensure plant establishment. The first wet-dry sequence after planting is probably equally important to emergence and initial establishment of other species.

One might hypothesize that if the first wet period is short, the seeds may not germinate and will survive the sequence as viable seeds. If the first wet sequence is long enough to germinate most or all of the seeds, and is followed by a long drought, a "false start" as described by Young et al. (1970) would occur. If the first wet sequence is long enough for the seedlings to develop to the stage where they can survive drought-induced quiescence, a high percentage of the plants might survive a long drought period. By identifying alternate periods of favorable soil moisture and drought conditions within the seed bed or rooting zone, techniques for achieving successful plant establishment can be enhanced.

If the duration of the first period of favorable soil moisture after planting is represented as L_1 and the duration of the following drought period as L_0, then, for any combination of (L_1 L_0), there will be a particular response in the number of viable seeds, viable seedlings, and dead seeds or seedlings at the end of the drought period.

In nonirrigated areas, the soil water used in seed germination and plant establishment is replenished by precipitation and depleted by evaporation. In arid and semiarid regions, the precipitation process is intermittent, with the periods of rainfall being much shorter than the intervening dry periods. Temperature and solar radiation, which affect the loss of soil water by evaporation, are both interrelated with precipitation and are more likely to be below average on rainy days than on dry days (Richardson 1981). For a given region, soil type, and planting date the joint distribution (L_1, L_0) can be estimated from climatic data. By evaluating the response of various range plant species to several wet-dry sequences, it should be possible to identify the species for a given planting date or the planting date for a given species that would maximize the probability of surviving the first wet-dry sequence. The first step in developing the relationships of plant response to the initial drought period is to determine the relative differences in seedling survival of selected plant species when subjected to various wet-dry water sequences.

This study was conducted in a greenhouse and designed to determine the relative effects of selected combinations of initial wet-day and dry-day sequences on the emergence and survival of 2 warm-season grasses, sideoats grama (*Bouteloua curtipendula* (Mich x.) Torr.) and cochise lovegrass (*Eragrostis lehmanianna*

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[1]Trade names are mentioned solely for the purpose of providing specific information and do not imply recommendation or endorsement by the U.S. Department of Agriculture.

Nees × *Eragrostis trichophora* Coss. & Dur.).

Methods and Materials

Two cotton balls were placed in the bottom of 3.8 cm diameter by 20 cm long tapered plastic cones (Ray Leach "conetainers")[1]. The cones were filled with 210 grams of dry 60-mesh silica sand to provide a reproducible, uniform growth media and to reduce problems of undesirable seed contamination. Ten dehulled seeds of sideoats grama or cochise lovegrass (lot germination, 98–100%) were placed on the dry surface and covered with a 2 to 3-mm layer of dry sand.

Water was applied to the cones with an overhead reciprocating spray boom sprinkling system. Two grooved tracks on each side supported the spray bar at a height of 77 cm above the top of the cones. A variable speed reversible electric motor operated a chain drive to move the spray bar across the work area at a speed of 10 cm/sec. The spray bar consisted of 1.3 cm diameter galvanized steel pipe with 2 spray nozzles (Spray Systems No. 1/8 K - SS.75 Floodjet)[1] spaced 113 cm apart, and operated at a pressure of 207 kPa. The work area under the spray bar was 175 by 250 cm.

The spray pattern was checked using cones with sealed bottoms placed in a row perpendicular to the travel direction of the spray boom. The volume of water from 10 passes of the spray bar was measured. Four areas, each 7 cone rows wide, were located in which the maximum variation of application was ± 0.2 mm of water per cone (2.5 to 3.0 mm total application). The coefficient of variation within an area ranged from 5 to 8% and the standard deviation of applied water ranged from 0.14 to 0.20.

The seeded cones were watered in predetermined wet-dry-wet sequences of 1, 2, 3, 4, and 5 days wet followed with 5 days dry. Following the dry period, the cones were sprayed daily for the remainder of the 14 day study to determine the number of viable seeds which had not previously germinated. Two separate 14-day experiments were conducted using the 5 wet-dry water sequences. One additional experiment was conducted with the 1 day and 2 day wet, 5 day dry water sequences.

Six cones in each rack were randomly selected for daily weighing to determine evapotranspiration losses and the quantity of water applied. All cones initially received 20 grams of water (≈10% moisture by weight). In the wet period, cones were sprinkled daily with sufficient water to bring the average moisture content of the cones back to the original weight. Water was not added to the cones during the dry period. Cones in a dry period were protected during sprinkling with rack covers constructed from 18-gauge galvanized sheet metal. To reduce the possibility of plants dying because of a nutrient deficiency, each cone was given 5 ml of a one-quarter strength Hoagland solution on day 10.

The study design was 5 completely randomized blocks with 6 replications for each species. The number of live plants in each cone was counted each day. The daily plant counts were analyzed by analysis of variance techniques. Duncan's new multiple range test was used to evaluate differences among means ($P \leq 0.05$).

A separate study was conducted to measure the change in the water content of the sand with depth during a dry sequence. Eighteen cones were filled with 170 g of dry sand, then 17 g of water were applied to the surface. After equilibrating for 2 h, the cones were reweighed. Three cones were randomly selected and sectioned into 3-mm layers. The moisture content of each layer was gravimetrically determined. The remaining cones were placed, uncovered, in the greenhouse adjacent to the seeded cones. Each day at 0900 and 1400 h, all of the remaining cones were reweighed and 3 cones randomly selected for moisture content with depth determination. The relationship between soil moisture content and soil moisture tension for the sand was determined using standard porous pressure plant techniques.

Results and Discussion

Daily mean plant counts for days 2, 5, 9, and 12 are shown in Table 1 for the 1 and 2 day wet, 5 day dry water sequences. Day 2 represents the period when sideoats grama had the greatest number of seedlings. Day 5 is the middle of the dry period. Day 9 was indicative of the period of plant recovery following the dry period. Day 12 represents the period when all remaining viable seeds would have emerged.

Differences of 1.0 to 1.5 plants per cone were significant ($P \leq 0.05$) (Table 1). The total average water loss for both species, for experiments 1, 2, and 3, in the 1 day wet water sequence, was 42.6, 45.2, and 43.3 mm per cone, respectively. For the 2 day wet sequence, the total average water loss was 44.9, 46.0, and 44.1 mm per cone for each experiment, respectively. Differences in the means of the total water use were not significant ($P \leq 0.05$). Differences in the daily means of the number of plants between the experiments are attributed to variability in solar radiation and air temperature caused by cloudy days, coupled with minor differences in depth of seeding. Seeds planted at deeper depths had longer periods of time when soil moisture was adequate for germination, root elongation, and seedling emergence. Even in the greenhouse on clear, sunny days, the surface layer of the sand in the cones dried

Table 1. Comparison of the mean plant count of 30 cones planted with 10 seeds of sideoats grama or Cochise lovegrass at four selected days in three experiments with 1 and 2 day wet, 5 day dry moisture sequence.

			Plants/cones					
	Moisture sequence		Sideoats grama			Cochise lovegrass		
Day after Planting	Days wet	Days dry	Exp 1	Exp 2	Exp 3	Exp 1	Exp 2	Exp 3
2	1	5	5.8a[1]	4.7b	4.1b	0.3a	N.P.[2]	0.1a
	2	5	6.6a	6.0a	6.1a	0.7a	<0.1b	0.3b
5	1	5	2.9a	0.9b	0.8b	2.7a	0.1b	0.6b
	2	5	5.0a	1.9b	2.6b	5.5a	1.5c	4.1b
9	1	5	1.6a	1.3a	1.8a	3.2b	2.2c	4.1a
	2	5	1.7a	0.5a	2.1a	3.2b	1.8c	4.6a
12	1	5	1.7a	2.1a	2.5a	3.8a	3.6a	4.5a
	2	5	1.3b	0.7b	2.5a	3.5b	2.8b	4.8a

[1]Means in rows, for each species, with different letters are significant ($P \leq 0.05$).
[2]No plants in any cone.

very rapidly. On cloudy days, the media surface remained wetter for longer periods because of reduced evaporation rates.

The daily plant count data for the 5 different wet-dry water sequences show that the sideoats grama produced seedlings very rapidly, even with the short water sequences (Fig. 1). Fifty to 70% of the seeds produced seedlings in 2 to 5 days. Over 70% of these seedlings succumbed during the dry period after the 1, 2, or 3 day wet water sequence, and over 50% died after the 4 and 5 day wet sequences (Table 2). The final plant count, after 13 days, represented 25 to 50% of the maximum number of plants counted, but only 15 to 35% of the number of seeds planted.

The cochise lovegrass was slower to germinate, and there was a more pronounced effect of the length of the first water period on the initial plant count (Fig. 1). Approximately 10% of the seeds produced a seedling in 4 days with the 1 day wet water sequence, while over 60% produced seedlings in 5 days with the 5 day wet water sequence (Table 2). Plant mortality from the dry period ranged from 10% with the 5 day wet sequence, to 30% with the 2 and 3 day wet sequences. Final plant count showed that 40 to 60% of the cochise lovegrass seeds produced seedlings, which represented 75% survival of the maximum plant count. With the exception of the 5 day wet combination, the length of the initial wet period did not affect the number of surviving seedlings.

There was a 10 to 30% increase in plants per cone following the dry period for the sideoats grama at 1 day wet and the cochise lovegrass at 1 day and 2 day wet (Table 2). This increase, following resumption of watering, is a result of new plants from seeds which had not germinated in the initial wetting and, possibly, a few plants which were not completely dead in the dry period. The increased plant count, following the dry period, was not evident for the 4 and 5 day initial wet sequences. Total water use among the 5 water sequences was not significantly different ($P \leq 0.05$).

The relation of seed germination of sideoats grama and cochise lovegrass to soil moisture tension is unknown. The germination of alkali sacaton, western wheatgrass, lehmann lovegrass (*Eragrostis lehmanniana* Nees.), Arizona cottontop (*Trichachne insularis* Nees.), and plains bristlegrass (*Setaria macrostachy* H.B.K.) and some range legumes have been reduced by 50% at soil moisture tensions of 1 to 4 bars, compared to germination at 0 bars (Knipe 1968, 1973; Young et al. 1970; Tapia and Schmutz 1971).

The potential effect of surface drying of the soil on seedling establishment is demonstrated in Figure 2. Moisture tensions of 4 bars were attained when the sand had dried to slightly less than 2% moisture by weight. The 2% moisture level was reached in the top 15 mm after approximately 48 h. If a moisture tension of 4 bars is critical to survival of sideoats grama or cochise lovegrass seedlings, then germinated seeds with a seminal root of less than 15 mm by the end of 48 h probably did not survive. This would explain the relatively high percentage of sideoats grama plants which died during the 5 day dry period following 1 and 2 day wet periods.

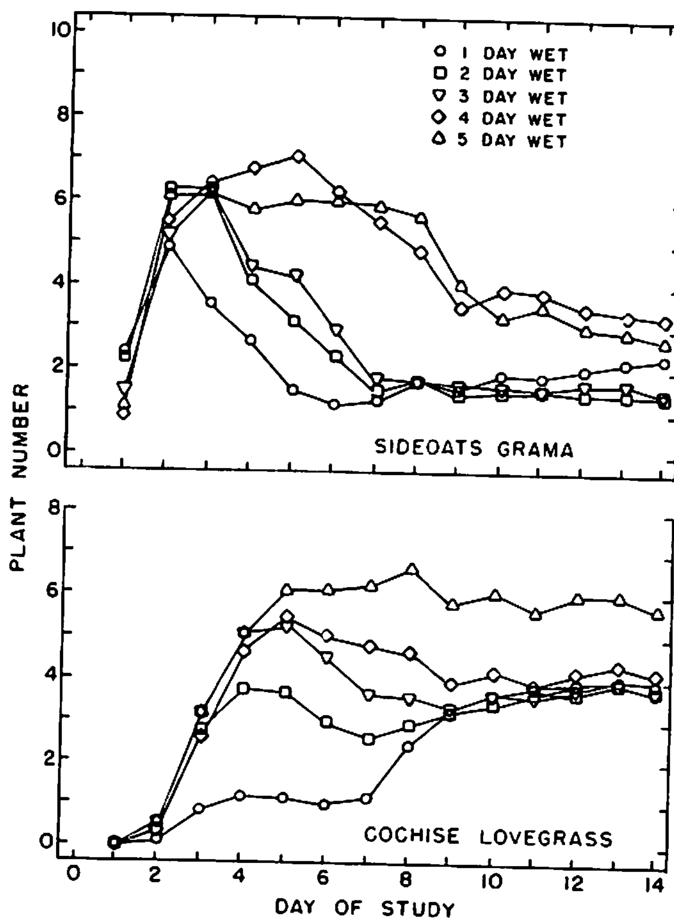

Fig. 1. *Daily mean plant count from 10 seeds of sideoats grama and Cochise lovegrass during 5 different lengths of wet periods each followed with 5 dry days.*

The probability of a plant or viable seed surviving the first wet and subsequent dry period after planting can be denoted as $q(L_1, L_0)$, $0 \leq q \leq 1$, where L_1 = length of wet sequence in days, and L_0 =

Table 2. The effect of five wet-dry sequences on the initial, minimum, and final plant counts of sideoats grama and Cochise lovegrass.

Moisture sequence		Total water loss per	Plants per cone		
Days wet	Days dry	cone in mm	Initial	Minimum	Final
		Sideoats			
1	5	43.8	4.9 (2)[1]c[2]	1.2 (6) b	2.3 (13) bc
2	5	44.9	6.3 (3) b	1.5 (7) b	1.5 (13) d
3	5	44.5	6.2 (3) b	1.7 (8) b	1.8 (13)cd
4	5	41.5	7.1 (5) a	3.4 (13) a	3.4 (13) a
5	5	44.3	6.1 (5) b	3.0 (13) a	3.0 (13) ab
		Cochise			
1	5	43.8	1.2 (4) d	1.0 (6) d	4.1 (13) b
2	5	44.9	3.8 (4) c	2.6 (7) c	3.9 (13) b
3	5	44.5	5.3 (5) b	3.6 (8) b	4.0 (13) b
4	5	41.5	5.5 (5) b	4.0 (9) b	4.4 (13) b
5	5	44.3	6.7 (8) a	6.0 (13) a	6.0 (13) a

[1]The number in parenthesis is the day of that plant count.
[2]Means in a column for each species with different letters are significant ($P \leq 0.05$).

Table 3. Survival probability for Cochise lovegrass and sideoats grama for various combinations of the first wet-dry days (L_1, L_0) sequence following planting.

Dry days	Cochise lovegrass Wet days (L_1)					Sideoats grama (Wet days (L_1))				
(L_0)	1	2	3	4	5	1	2	3	4	5
1	<.1 (.3)[1]	.3 (.1)	.5	.6	.6	.5 (.1)	.6	.4	.7	.6
2	.1 (.3)	.4 (.1)	.5	.5	.6	.4 (.1)	.4	.4	.6	.6
3	.1 (.3)	.4 (.1)	.5	.5	.7	.3 (.1)	.3	.3	.6	.6
4	.1 (.3)	.3 (.1)	.4	.5	.6	.2 (.1)	.2	.2	.5	.4
5	.1 (.3)	.3 (.1)	.4	.4	.6	.1 (.1)	.1	.2	.4	.3

[1]Numbers in parentheses are the inferred probabilities that a viable seed has not germinated during the wet period for that (L_1, L_0) combination.

length of dry sequence in days. In this study, the survival probability, $q(i, 5), i = 1, 2, \ldots, 5$, is simply the number of plants counted on a given day after the dry sequence divided by 10, the number of seeds planted. This probability does not account for additional water, nutrient, or plant competition factors. We can also estimate the intervening values. For the longer wet sequences, we assume that all seeds would have germinated, and that the average number of surviving plants is only a function of the length of the dry period, L_0. For short wet sequences with dry sequences less than 5 days, we can estimate the average number of viable seeds that did not germinate in the initial wetting from the increase in the number of plants following the termination of the 5 day dry sequence. From these data, we can compute the discrete function $q(L_1, L_0)$, $L_1, L_0 = 1, 2, \ldots, 5$ (Table 3). These survival probabilities are a function of the random variables L_1 and L_0, which in turn are affected by solar radiation, temperature, wind, seedbed microtopography and other factors.

The survival probability for 1 wet day followed by 5 dry days is approximately 0.4 for the cochise lovegrass and 0.2 for sideoats grama. Both probabilities include viable, but ungerminated, seeds which have survived this sequence. This demonstrates that a rapid response by sideoats grama to a simple signal (rain on one day) may reduce plant reproductive potential.

The expected survival probability can be estimated by the equation:

$$E(q) = \sum_{L_0=1}^{\infty} \sum_{L_1=1}^{\infty} q(L_1, L_0)\, P_n(L_1, L_0) \quad (1)$$

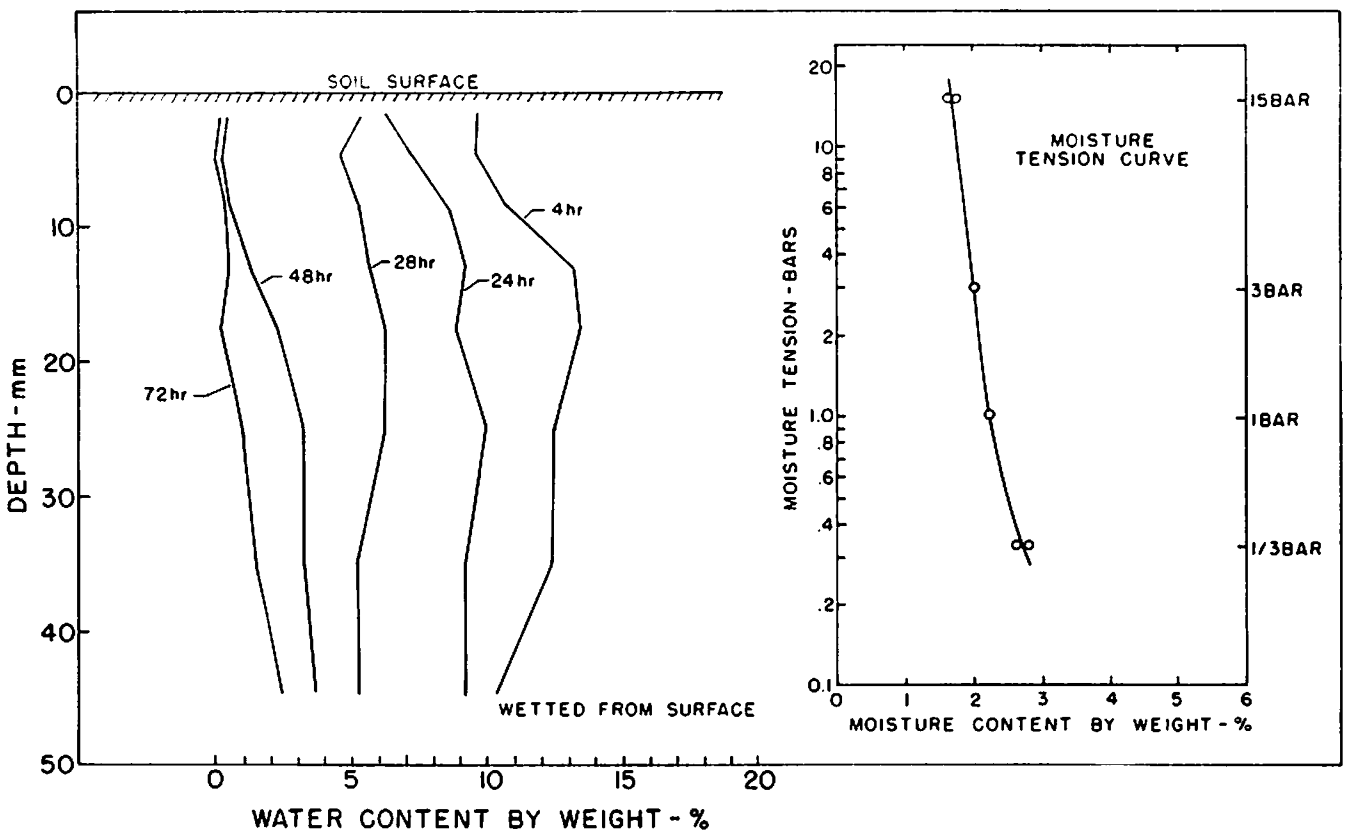

Fig. 2. *Soil moisture profiles of 60-mesh silica sand in cones during the dry period following initial wetting and moisture tension curve as determined from pressure plate studies.*

where $P_n(L_1, L_0)$ is the discrete joint density function of the first wet-dry sequence after planting on day (n). The function $P_n(L_1, L_0)$ can be estimated by simulation or simplified analytic models. In the field, the planting date will be further constrained by temperature considerations.

As an approximation, let us define a wet-dry sequence of length k + j as the sequence of k consecutive wet days followed by j consecutive dry days bounded by a dry day and a wet day at the beginning and end of the sequence, respectively. Given that a wet-dry sequence begins on day i, it is defined as the event:

$$\{X_{i-1} = 0, X_i = 1, X_{i+1} = 1 \ldots X_{i+k-1} = 1, X_{i+k} = 0, X_{i+k+1} = 0, \ldots X_{i+k+j-1} = 0, X_{i+k+j} = 1\}$$

where $X_i = 1$ if rain occurred on day i;
$X_i = 0$ otherwise.

If the sequence X_i, i = 1, 2... is described by a Markov chain, the probability of this sequence is (cf. Roldan and Woolhiser 1982).

$$P\{L_1 = k, L_0 = j\} = P\{X_{i-1} = 0, X_i = 1, \ldots X_{i+k-1} = 1, X_{i+k} = 0 \ldots X_{i+k+1} = 0, \ldots X_{i+k+j-1} = 0, X_{i+k+j} = 1 | X_{i-1} = 0, X_i = 1\} = p_{11}^{k-1}(1-p_{11})p_{00}^{j-1}(1-p_{00}) \quad (2)$$

where p_{11} is the probability of a transition from a wet day to a wet day, and p_{00} is the probability of a transition from a dry day to a dry day.

The probability that a wet-dry sequence is included in the sample space shown in Table 3 is

$$P\{L_1 \leq 5, L_0 \leq 5\} = \sum_{j=1}^{5} \sum_{k=1}^{5} p_{11}^{k-1}(1-p_{11})p_{00}^{j-1}(1-p_{00}) \quad (3)$$

This probability is 0.88 for Tombstone, Ariz., for the 14-day period beginning July 19, and 0.44 for the 14-day period beginning June 21, so the sequences covered in our experiments are relevant. Of course, a more realistic description of the joint density function of the wet day period would account for the random amounts of rainfall on a wet day as well as the rate of evaporation from the soil.

For a particular grass species, the best planting date, (N), is that which maximizes E(q) (Equation(1)). Our hypothesis is that the first wet-dry sequence is critical, and the most adapted species has the largest maximum E(q). In many cases, this hypothesis seems plausible. A notable exception, however, is blue grama grass. Wilson and Briske (1979a) found that a favorable first wet sequence is necessary, but not sufficient for plant establishment. The occurrence of hard seeds is a survival mechanism that nature uses to increase survival probablity, and thus reduce the importance of the first wet-dry sequence.

There are many other factors which must be evaluated and field verified before this approach can be used for achieving improved seeding success or developing a better understanding of species adaptability. However, this approach offers the possibility of incorporating the probabilistic aspects of precipitation quantity and frequency with basic understanding of plant-water relations into a description of the seedling environment.

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