January 1, 1999

Temporal Patterns of Seedling Emergence and Early Survival of Great Basin Perennial Plant Species

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TEMPORAL PATTERNS OF SEEDLING EMERGENCE AND EARLY SURVIVAL OF GREAT BASIN PERENNIAL PLANT SPECIES

L. David Humphrey and Eugene W. Schupp

ABSTRACT—We seeded Agropyron cristatum and 16 native Great Basin perennial species on Bromus tectorum-dominated sites to compare temporal patterns of seedling emergence and early survival among species. To indicate variability between sites and between years, plots were planted on 2 sites in western Utah in autumn 1994, and plantings were repeated near 1 site in autumn 1995. Two sites included burned and unburned seedbed treatments. We monitored seedling emergence and survival from early winter until July of the 1st year. Four seasonal patterns of emergence were evident, indicating considerable potential for different seasonal patterns of precipitation to favor recruitment of different species. Emergence of all shrubs, except Ephedra nevadensis, began in February and essentially ended by April. Seedlings of Ephedra nevadensis and of the grasses Agropyron and Pseudoroegneria spicata emerged over an extended period from February through June. Most other grasses and the 2 forbs began emerging in April and continued into June. Pleuraphis jamesii emergence did not begin until May. Although many seedlings of the 3 chenopod shrubs emerged, none survived, suggesting their periodic recruitment is more a function of survival than of emergence. Survival of 2 Chrysothamnus species was also low. Pseudoroegneria and Agropyron had the highest numbers of seedlings surviving on the moister site, followed by Elymus elymoides and Stipa comata. Survival of Agropyron, but not the native Elymus, was more depressed on the drier of the 2 sites planted in 1994. Stipa, Oryzopsis hymenoides, Pleuraphis, and Ephedra survived as well on the drier site as on the moister site, or better. On the 1995 planting site Bromus was greatly reduced by the burn treatment, and, in contrast to the effect of burn treatments on the 1994 site, survival of all species except Oryzopsis and Ephedra was higher on burned than on unburned treatments. Overall, Stipa, Oryzopsis, and Pleuraphis had low emergence but consistently high survival.

Key words: seedling emergence, seedling survival, semiarid area, Great Basin, grasses, shrubs, forbs, Bromus tectorum, vegetation dynamics.

Control and timing of germination are considered to be key elements in the survival of populations of plant species that reproduce primarily by seeds (Harper 1977). In arid and semiarid environments, timing of germination may be especially crucial because the amount and timing of precipitation are highly variable (Evenari 1985, Kigel 1995). In the Intermountain West, spring moisture and temperature conditions change rapidly, and narrow windows exist for emergence and establishment of perennial seedlings (Kitchen and Monsen 1994). Consequently, germination and seedling establishment of many desert and steppe perennials are rare and episodic (Ackerman 1979, Romney et al. 1980, Gutterman 1993, Kigel 1995).

Germination characteristics are important components of adaptive life history strategies of individual species (Angevine and Chabot 1979). Even within the same semiarid site, different species often possess different germination strategies (Gutterman 1993, Kigel 1995).

Thus, the high variability of precipitation and temperatures typical of semiarid sites can result in conditions favoring recruitment of different species in different years. Although longer-term survival is also important, emergence and early survival play critical roles in determining recruitment of plants on semiarid sites. Emergence characteristics determine which species have seedlings initially present under what conditions, and the early period after emergence is often the time of greatest mortality. Knowledge of seasonal timing of seedling emergence and of patterns of early survival, coupled with information on the site and weather conditions under which emergence and survival occur, will aid in restoration and revegetation efforts. It is also essential in understanding natural dynamics of vegetation of semiarid sites and ultimately managing such vegetation. Community composition and dynamics may be strongly altered by periodic flushes of recruitment of particular species that occur when weather conditions favor their
emergence and early survival (e.g., Westoby 1980, Neilson 1986, Westoby et al. 1989). These processes of episodic establishment of different species at different times can also lead to greater community diversity, as species established at different times accumulate on the site (Chesson 1994).

Most Great Basin germination studies have involved laboratory experiments on dormancy and effects of temperature and photoperiod on germination, while studies of field emergence have usually dealt with only a single or a few species. Few researchers have compared patterns of emergence of a variety of species. A notable exception is Ackerman (1979), who described natural seedling emergence and survival in relation to season and weather for 11 perennial species in a Mojave-Great Basin ecotonal community. Young et al. (1994) compared recruitment of 6 native and introduced perennials in relation to precipitation on arid sites in Nevada, but timing of germination was not compared. We present a comparison of patterns of seedling emergence and early survival of 16 species native to semiarid areas of the Great Basin and 1 nonnative species planted in a single seeding experiment. To better understand the variability that occurs across different types of semiarid sites, we performed experimental seedings on 2 sites in a single year. Because conditions can differ between years, favoring different species in different years, a 3rd experiment was planted near 1 of these sites in the following, drier year. As the experimental plantings were on sites dominated by the alien annual Bromus tectorum (cheatgrass), inferences that we can make about emergence and early survival of these species are pertinent to reclamation on semiarid Great Basin sites. As well as removing litter and standing vegetation, fires usually greatly reduce Bromus seedbanks (Young and Evans 1978). Thus, we included burned and unburned seedbed treatments to test the effects of reduction of Bromus competition and other changes produced by fires on emergence and early survival of the seeded species.

**METHODS**

**Study Sites**

In late October–December 1994, we planted plots at 2 substantially different Bromus-dominated sites at the U.S. Army Dugway Proving Grounds, Tooele County, Utah, USA, with another experiment planted near 1 of the sites the following year. One site served as the main experiment site where all 17 species were planted. Subsets of these 17 species were planted in the other 2 experiments. The main experiment site, the "Hill" site, is a gently sloping area at an elevation of 1620 m at the southeastern end of the Cedar Mountains (40°16′00″N, 112°49′40″W). The 2nd site, the "Near-Dune" site, is near the base of the Cedar Mountains at 1480 m elevation (40°14′30″N, 112°50′10″W), nearly level, and about 5 km southwest of the Hill site. Mean annual precipitation for the nearest weather station, about 8 km southwest of the Near-Dune site at a slightly lower elevation in an open flat, is 20 cm (U.S. Army Dugway Proving Ground, Meteorological Operations Office). Situated at the base of Cedar Mountains and in the path of weather fronts approaching from the south and west, the Near-Dune site probably receives slightly more than this. The somewhat higher-elevation Hill site, located at the end of the Cedar Mountains range, probably receives substantially more; we observed it to receive more snow in winter. The following autumn (December 1995) we planted another site, the "Dune Area" site, about 0.5 km from and at approximately the same elevation as the Near-Dune site. The 1st year was unusually wet, with 29.4 cm of precipitation from October 1994 through June 1995 at the weather station mentioned, but the 2nd year was considerably drier, with 14.3 cm from October 1995 through June 1996.

A partial analysis and description of soils of the 3 sites was done so we could identify ecologically meaningful soil differences among the 3 sites. Soil texture was determined by feel. Mean sand size was estimated using a dissecting microscope and digital calipers. Water-soluble cations were determined by atomic absorption spectrophotometry of saturation paste extracts, and nitrate nitrogen and available phosphorus were determined. Soil texture and particle size analyses were provided by J.L. Boettinger of the Plants, Soils and Biometeorology Department, Utah State University, Logan, Utah. Nitrogen, phosphorus, and cation data were provided by the Analytical Labs, Utah State University.

Soils of the 3 sites were similar in most respects. All 3 sites had deep soils (>1.5 m) derived from eolian deposits. All 3 soils were...
very low in nitrogen and phosphorus but high in calcium and potassium (Table 1). Concentrations of sodium were also substantial, but salinity was well below problem levels. The greatest difference among sites was soil texture. Soils of all 3 sites were dominated by sand-size particles. Soil of the Hill site had the lowest percentage of sand and smallest mean sand size (Table 1). The Done-Area site had the highest percentage of sand and largest mean sand size. The Near-Dune site had percent sand and mean sand size intermediate between the other 2 sites. All 3 soils were sandy enough to allow rapid to very rapid infiltration (J.L. Boettinger personal communication). Of these 3 sites, the finer-textured soil of the Hill site has greater estimated available water-holding capacity. As with infiltration, all soils are sandy enough that little available water would be lost by evaporation once the soil surfaces dry out (J.L. Boettinger personal communication). Thus, though differences are minor, we interpret the soils of the Hill site to be least droughty and those of the Dune-Area site to be most droughty. Considering the greater precipitation as well as the somewhat less droughty soils, the Hill site should have substantially more favorable moisture conditions than the Near-Dune site. As the Dune-Area site was planted in a much drier year, it had still less favorable moisture conditions than the Near-Dune site.

Experiments

We planted 1 nonnative species commonly used in rangeland seedings, *Agropyron cristatum* (crested wheatgrass), and 16 native perennial grasses, shrubs, and forbs occurring on or near the sites (Table 2). Seeding rates (Table 2) were based on recommendations of pounds of pure live seeds per acre by Vallentine (1989) and by Granite Seed Co., Lehi, Utah. All seeds were commercially obtained from Granite Seed Co. except *Grayia spinosa* and *Oenothera palida*, which were from Comstock Seed Co., Reno, Nevada. (After their first mention in the text, we refer to species by genus name only except for *Chrysothamnus*, which was represented by more than 1 species.) Our gross seeding rates were adjusted to obtain the desired amount of pure live seed per unit area using percent pure live seed listed by the commercial providers for our seed lots.

The design of the main experiment, located at the Hill site, consisted of 2 blocked replicates, each with a burned and an unburned macroplot (i.e., a split-plot design with respect to burn treatment within each of the 2 blocks). Within each macroplot we delineated 68 individual 3 x 3-m plots, each planted with 1 of the 17 species at 1 of 4 depths (surface, or simulated drilling at 1 cm, 2 cm, or 3 cm). Each plot contained 10 planted rows 30 cm apart. Rows within plots were treated as subsamples in the analyses. Burned and unburned macroplots were paired approximately 20 m apart on each side of the border of a wildfire that burned in a Bromus-dominated community the previous July. The burn border location was not related to site or vegetation characteristics; the fire was advancing slowly in this direction and fire fighters extinguished it at this particular location.

Designs of the other 2 experiments were modified from that of the main experiment. The Near-Dune site did not include a burn.
We planted by simulated drilling using a curved metal plate in a wood frame. The plate, after being adjusted to 1-cm, 2-cm, or 3-cm depth, was used to cut grooves for planting. We dropped seeds into grooves by hand, after which we heavily raked over the rows to close the grooves. Surface seeding was done in rows about 10 cm wide which were then raked over. For species whose individual seeds were difficult to identify because the commercially supplied seeds were mixed with fragments of inflorescences (Artemisitridentata, Chrysothamnus nauseosus, C. viscidiflorus), and species with very small seeds (Sporobolus cryptandrus, Oenothera, Sphaeralcea munroana), we used weighed portions of seeds corresponding to the desired number of seeds per row.
In the first 2 experiments (Hill and Near-Dune), emergence of some species began during a warm period in February. In a 1st census to quantify this early emergence, we simply counted seedlings per row on 20–26 February. In 2 following censuses we mapped locations of seedlings along rows using a 3-m ruler laid along the row. If seedlings were relatively sparse, 8 of the 10 rows per plot were mapped, excluding 1st and last. If seedlings were very dense (>50/row), only 4 rows were mapped, excluding the 4 central rows, as well as 1st and 10th. We conducted the 2nd census, in which seedlings were first mapped, for the 1st replicate (block) of both sites on 29 March–29 April 1995 and censused the 2nd replicate on 30 April–19 May (weather intermittently prevented fieldwork). The 3rd census, in which we relocated seedlings using these maps to determine seedling survival and mapped newly emerged seedlings, occurred 27 June–3 July and 8–19 July for replicates (blocks) 1 and 2, respectively. Because emergence of Pleuraphis jamesii and Sporobolus occurred much later than that of the other species and none were found in earlier censuses, we first mapped seedlings of these 2 species on 17–22 June and recensused them on 10–20 July. On the Dune-Area site planted in the 2nd year, emergence was censused in mid-February but found to be very low. The initial seedling mapping was done 21–31 March 1996, with a 2nd mapping census 28–31 May. Survival was censused 29 June–2 July. Pleuraphis was included in the May and June–July censuses.

On the Hill and Near-Dune sites, we calculated survival as the proportion of seedlings recorded in the April census (the 1st mapping) that were alive in the June–July census. For later-emerging Pleuraphis and Sporobolus, survival was the proportion of seedlings recorded in June that were alive in the July census. For the Dune-Area site, survival was the proportion of all seedlings recorded as emerging in either the late March or May censuses that were alive in the June–July census.

Analyses

We analyzed emergence and survival until July by analysis of variance (ANOVA). The response data consisted of emergence or proportional survival per row with rows constituting subsamples within plots. In addition to the analyses of proportional survival, we also ran ANOVAs with number of seedlings surviving as the response, so that we could make some individual comparisons of the actual numbers of seedlings recruited in the 1st growing season. All ANOVA analyses were done with the GLM Procedure (SAS 1990). Univariate and Frequency Procedures (SAS 1990) were used to verify that data distributions did not differ greatly from a normal distribution. We used the Frequency Procedure for this purpose, in addition to the Univariate Procedure, because a "heavy tailed" distribution with many zeros was the predominant way data sets differed from a normal distribution, and this procedure more clearly identified this problem. Arcsin square root transformations were used on proportional survival data and yielded acceptable data distributions. Natural log transformations were used on emergence data. Square root transformations were used on number of seedlings surviving. We analyzed emergence separately for each sampling period that had sufficient emergence. Data sets for some time periods with very low emergence had many zeros, violating the assumptions of ANOVA. For this reason emergence was not analyzed for the last emergence sampling period for each site nor for the February sampling periods on the Near-Dune and Dune-Area sites. When 2 time periods per site were analyzed (Hill site), they were analyzed separately; thus, repeated-measures ANOVA was not used. Species with a mean of <1 seedling per plot were omitted in all ANOVAs.

We made statistical comparisons between the 2 sites planted the same year (Hill and Near-Dune sites) using the subset of data from the Hill site that conformed to the reduced experimental design of the Near-Dune site (see above): data from unburned macroplots and the 2-cm planting depth for the 14 species shared between the 2 sites. A statistical comparison of the 2 experiments on very similar sites planted in different years (Near-Dune and Dune-Area) was not done because the 2 sites had only 5 species in common, some of which had insufficient emergence for analysis. Instead, we statistically compared the Hill and Dune-Area sites, i.e., a comparison across years and sites, including burn treatments nested within site. This provided a much more extensive comparison than comparing the Near-Dune and Dune-Area sites because both sites had burn treatments and more species were
shared between the 2 sites. Furthermore, since the Dune-Area site is a lower-elevation site planted in the drier year, this comparison is of interest because it compares sites with the most favorable and least favorable moisture conditions.

RESULTS

Preliminary to the other analyses, we conducted an initial analysis of emergence on the Hill site for the April census when most emergence occurred, with depth included as a factor. In this analysis the Species x Burn x Depth interaction was significant (F = 18.1, df = 84, P < 0.001). The major effects responsible for this 3-way interaction were that, of all species, only the 2 Chrysothamnus species had substantial emergence on surface-seeded plots, and their emergence on surface plots was much higher on burned than unburned seedbed treatments. Even the Chrysothamnus species had reduced emergence with surface seeding relative to the 3 drilling depths, however. Emergence was generally similar among the 3 simulated drilling depths, but some species (Atriplex canescens and Sarcobatus vermiculatus) had poorer emergence at 3-cm depth. Differences in emergence between planting depths were apparently reduced because plots were wet when planted, and rows subsequently dried and cracked open, reducing effective differences in planting depth.

The major difference in emergence associated with seeding depth was between surface seeding, with very low emergence, and the 3 simulated drilling depths, all with similar emergence that was considerably higher than that of surface seeding. Consistently very low emergence on surface plots greatly increased the number of zeros in the data sets, making it questionable, in some cases, whether ANOVA could be used validly for the analyses. Therefore, to provide a more statistically sound (and simpler, with the depth factor removed) ANOVA analysis, we omitted surface seeded plots and pooled the 3 drilling depths for our main analyses. As differences with seeding depth were almost entirely between surface seeding and the 3 simulated drilling depths (very few of the many paired comparisons among drilling depths were significant in this initial analysis), we considered changing our overall statistical design in this way to be valid.

Emergence

At the Hill site all shrubs and 2 grasses (Agropyron and Pseudoroegneria) began emerging in February (Fig. 1). First emergence was recorded in April for the 2 forbs and the other grasses, except for the C₄ grasses Pleuraphis and Sporobolus, which began emerging even later. Emergence was greatest on the April census for all 4 Triticeae (Agropyron, Pseudoroegneria, Elymus, Pascopyrum smithii) and for Oryzopsis, Stipa, Ephedra, and Oenothera (Fig. 1). However, the 2 Chrysothamnus species and the 3 chenopod shrubs (Atriplex, Grayia, Sarcobatus) had similar, if not higher, emergence in February versus April. Emergence of Artemisia was very low throughout (<0.5 seedling/row) but occurred mainly in February. No emergence for the chenopod shrubs and very little for Chrysothamnus occurred after April (Fig. 1). All other species had emergence through June. Agropyron, Pseudoroegneria, and Ephedra had the most extended period of emergence, from February through June (Fig. 1). Pleuraphis emergence continued into July.

Mean comparisons we present throughout (e.g., comparisons between species or comparisons of the same species between 2 sites) were done by t-test comparisons of LSMeans (least squares estimates of marginal means for unbalanced designs). Because several of these mean comparisons per ANOVA were often used, chances of incorrectly rejecting a null hypothesis in at least 1 of the comparisons may be somewhat higher than the P-values indicate. Therefore, we used the customary 0.05 probability level as the cutoff for declaring means significantly different, but we note those means that were more marginally significant (0.01 < P < 0.05) by individually stating those P-values. Thus, unless otherwise stated, all means declared significantly different had P < 0.01.

In the Hill site analyses with surface-seeded plots omitted and other depths pooled, the Species x Burn interaction was significant for both February and April emergence (F = 5.5, df = 9, P < 0.001; F = 13.3, df = 14, P < 0.001; respectively), indicating species responded differently to burn treatment. In February, Atriplex (P < 0.05) and the 2 Chrysothamnus species had significantly higher emergence on burned than unburned plots. In April, C. nauseosus continued to have higher emergence on burned plots, along with Oenothera, Agropyron,
Elymus, and Stipa. In contrast, Atriplex, Grapia, and Ephedra had significantly more emergence on unburned than on burned plots in April.

In the comparison of April emergence between Hill and Near-Dune sites, the Species × Sites interaction was significant ($F = 5.1$, df = 10, $P < 0.001$). Oryzopsis, Stipa, Sphaeralcea, Atriplex, and Oenothera had significantly more emergence on the Near-Dune site than on the Hill site (Fig. 2). Emergence of Agropyron and Elymus was less distributed over time on the Near-Dune site than on the Hill site (Fig. 2).

On the Dune-Area site, the Species × Burn interaction was again significant ($F = 2.6$, df = 6, $P < 0.05$). In the comparison of emergence between the Dune-Area and Hill sites (April census on the Hill site and March census on the Dune-Area site, with data from the smaller Dune-Area plots standardized to emergence per 3-m row), the Species × Burn (within Sites) and Species × Site interactions were significant ($F = 3.8$, df = 12, $P < 0.001$; $F = 20.6$, df = 6, $P < 0.001$; respectively). On the Dune-Area site, Pseudoroegneria, Pascopyrum, C. nauseosus, and C. viscidiflorus had significantly higher emergence on unburned than on burned plots (Fig. 3), whereas on the Hill site emergence was similar on burned and unburned plots for all these species except C. nauseosus, which had higher emergence on burned plots. Elymus, with its similar emergence on burned and unburned plots on the Dune-Area site, also had higher emergence on burned plots on the Hill site. Emergence of the 2 Chrysothamnus species on the Dune-Area site also differed from the other 2 sites in that only a few seedlings emerged in February, and emergence was lower overall (Fig. 3).
Emergence of *Ephedra* was concentrated in March (Fig. 3) rather than distributed from early to late spring as on the other sites in the wetter year. *Pleuraphis* had no emergence in this drier year. *Pseudoroegneria* had no February emergence on the Dune-Area site. Thus, both *Pseudoroegneria* on this site and *Agropyron* on the Near-Dune site lacked February emergence on the lower-elevation sites where they were planted.

Proportion of Seedlings Surviving

The Species × Burn interaction for the Hill site was significant ($F = 3.1$, df = 10, $P < 0.001$). Survival of the 3 chenopod shrubs was nearly zero by July, and survival of *Oenothera* and the 2 *Chrysothamnus* species was low (Fig. 4). Survival until July was good for *Agropyron*, *Pseudoroegneria*, and *Elymus*, but that of *Pascopyrum*, the other Triticeae species, was lower (Fig. 4). Of the shrubs, only *Ephedra* had good survival, especially on unburned plots where its survival was significantly higher than on burned plots. *Oryzopsis* and *Stipa* had the highest proportion of seedlings surviving, along with *Pleuraphis* on unburned plots, where its survival was significantly higher than on burned plots (Fig. 4). Survival of *C. viscidiflorus* was somewhat higher on unburned than on burned plots ($P < 0.05$). No species had higher survival on burned than on unburned plots.

The Species × Site interaction in the comparison between Hill and Near-Dune sites was significant ($F = 6.0$, df = 7, $P < 0.001$). On both sites survival of the chenopods, *Chrysothamnus* species, and *Oenothera* was very low. The Triticeae planted on the Near-Dune site, *Agropyron* and *Elymus*, tended to have lower survival than on the Hill site, but only *Agropyron* significantly so ($P < 0.05$; Fig. 5). In contrast, *Oryzopsis*, *Stipa*, *Pleuraphis*, and *Ephedra* tended to have higher survival.
on the Near-Dune than Hill site, but only *Stipa* significantly so.

On the Dune-Area site, the Species × Burn interaction was significant (*F* = 5.9, df = 6, *P* < 0.001). In comparing the Hill and Dune-Area sites, the Species × Burn (within Sites) and Species × Site interactions were significant (*F* = 5.8, df = 12, *P* < 0.001; *F* = 6.4, df = 6, *P* < 0.001; respectively). Survival of the 3 Triticeae on unburned plots was lower on this site in the drier year than on the Hill site in the wetter year. The burn at the Dune-Area site was more intense and reduced *Bromus* density much more than the burn on the Hill site, and survival on the Dune-Area site was much greater overall on burned than unburned plots: all species except *Ephedra* and *Oryzopsis* had significantly higher survival on burned than on unburned plots (Fig. 6). In contrast, on the Hill site survival was similar on burned and unburned plots, except for *Pleuraphis* and *Ephedra*, which had higher survival on unburned plots. *Chrysothamnus* survival was very low on unburned plots of the Dune-Area site, but on burned plots it was similar to its best survival on other sites, e.g., unburned plots on the Hill site. Similarly, survival of *Ephedra* on burned plots of the Dune-Area site was comparable to its survival on the moister Hill site in a wetter year. Only *Oryzopsis*, *Ephedra*, and *Pseudoroegneria* had substantial survival on unburned Dune-Area plots (Fig. 6).

**Number of Seedlings Surviving**

As with survival and emergence, Species × Burn interactions on both the Hill and Dune-Area sites, the Species × Site interaction in the comparison between the Hill and Near-Dune sites, and Species × Burn (within Sites) and Species × Site interactions in the comparison between the Hill and Dune-Area sites were all highly significant (*P* < 0.001 for all; *F* = 6.9,
Fig. 5. Proportion of seedlings surviving until the 1st July after emergence on the Hill site and the Near-Dune site for each species that differed between sites. For each species on each site, mean proportion surviving/3-m row and standard errors for the 2-cm simulated drilling depth plots are presented.

A wildfire burned both the Hill and Near-Dune sites late in the 1st summer following seedling emergence, and only grasses survived this fire. On the Hill site there was some survival of all 7 grass species. Proportional survival of Stipa and Pleuraphis through the 2nd growing season following the fire was >0.05 of the recorded emergence, but survival of the other species was mostly well under 0.01. On the Near-Dune site, only Stipa and Pleuraphis survived the fire, and only Pleuraphis had >0.05 proportional survival. It is unknown what this later survival would have been without the wildfire.

DISCUSSION
Seasonal Patterns

Based on results of the Hill and Near-Dune site experiments, we identified 4 relatively distinct seasonal patterns of emergence. In the 2 Chrysothamnus species, chenopod shrubs, and Artemisia, emergence began very early and ended early. Winter snowcover is important to Artemisia recruitment, as seedling emergence occurs immediately after spring snowmelt (Meyer and Monsen 1990, Meyer 1994). Although our emergence of Artemisia was very limited, it occurred very early. Similarly, other reports of field emergence and laboratory studies (Meyer et al. 1989) are consistent with our early spring emergence of Chrysothamnus. Grayia is also capable of very rapid germination (Wood et al. 1976), and in the Great Basin, after seeds have experienced a cool, moist period, they can emerge in early spring (e.g., February to early March) when soil and air temperatures are still near freezing (Shaw and Haferkamp 1994). Sarcobatus also germinates rapidly at cool temperatures (optimal germination at 4–10°C; Eddleman 1979).

Emergence and early seedling survival of Grayia are very dependent on precipitation, and establishment is episodic, occurring only in years with above-average precipitation (Shaw and Haferkamp 1994). Similarly, only episodic establishment of seeded Atriplex has been reported (Stevens and Van Epps 1984). In our experiment many seedlings of Atriplex, Grayia, and Sarcobatus emerged very early, even on the drier Near-Dune site, but were very short lived. This supports the premise that winter snow and early spring soil moisture are important to these shrubs, but suggests that
Fig 6. Proportion of seedlings surviving until the 1st July after emergence on unburned and burned plots of the Dune-Area site planted in the 2nd, drier year. For each species and burn treatment, mean proportion surviving/2.5-m row and standard errors are presented.

episodic recruitment may be limited more by early survival of seedlings than by emergence itself. Similarly, Ackerman (1979) reported considerable natural emergence of shrubs at a Mojave-Great Basin transition site, but almost none of the seedlings survived beyond 2 yr. However, the absence of mature shrubs on our Bromus-dominated sites and the removal of some standing annual-plant litter during planting may have reduced seedling survival of shrubs in our experiment. Seedling survival of *Craysia* can be enhanced by litter and nurse plants (Shaw and Haferkamp 1994), and that of *Artemisia* by snow accumulation around shrubs (Sturges and Tabler 1981, Monsen et al. 1992).

A 2nd pattern of emergence was exhibited by the grasses *Agropyron* and *Pseudoroegneria* and the shrub *Ephedra*. In these species substantial emergence occurred over an extended period of time, from February into June. This pattern may be a bet-hedging adaptation (sensu Stearns 1976) similar to that of desert annuals for coping with the unpredictable climate of arid and semiarid regions (Went 1979, Freas and Kemp 1983, Philippi 1993). If rainy periods are cut short, annuals that germinate under ideal conditions may not be able to complete their life cycle. This risk is spread if, even under ideal conditions, some seeds remain dormant to germinate later. Similarly, the extended seasonal period of germination of these perennials may spread the risk of germinating in wet periods that are not long enough to allow seedlings sufficient growth to be able to survive summer drought. It may also afford these species greater potential to establish seedlings in any given year in an unpredictable environment because some seedlings can take advantage of wet periods whenever they occur from late winter to late spring. On the Near-Dune and Dune-Area sites, where conditions were less favorable or favorable less often, emergence of these “bet-hedging” species was more confined to the mid-spring period.

A 3rd pattern of emergence was displayed by the grasses *Elymus*, *Pascopyrum*, *Oryzopsis*, and *Stipa* and by the 2 forbs. Emergence began in April, later than that of species showing the first 2 patterns, and continued into June. Later emergence of *Elymus* than of *Pseudoroegneria* is consistent with laboratory results (Hardegree 1994).

The 4th pattern was that of the C₄ grasses *Pleuraphis* and *Sporobolus* for which all seedling emergence occurred after April. These species require warmer temperatures for emergence than any of the other species, and thus on Great Basin sites are usually dependent on late spring weather conditions.

As we used only a single accession of each species, our data do not represent the variation in emergence characteristics that can exist among different populations of some of these
species (e.g., Meyer and McArthur 1987, Meyer and Monsen 1992). However, the same pattern of emergence was often common to species within the same broad taxonomic or functional groups; e.g., the Asteraceae and Chenopodiaceae shrubs shared 1 pattern, the 2 forbs and 2 Stipeae another, and the C₄ grasses a 3rd pattern, suggesting that these general patterns are characteristic of some of these species or groups of species. Still, the 4 Triticeae displayed 2 different patterns. Some species, such as the 4 Triticeae, also can be expected to exhibit some autumn emergence, but none occurred in our study because planting was done too late for autumn emergence to occur.

Based on seasonal patterns of emergence observed in this experiment, different seasonal patterns of precipitation may favor either recruitment of shrubs or recruitment of grasses and forbs, largely to the exclusion of the other. Favorable winter and early spring moisture conditions could allow shrub establishment.

In the drier year of the Dune-Area planting, early emergence of the Chrysothamnus species was almost nonexistent, and their emergence was lower overall relative to sites planted in the wetter year. A drier winter and early spring coupled with ample precipitation later might prevent shrub establishment but allow abundant recruitment of perennial grasses and forbs. Favorable moisture conditions even later could promote recruitment of Pleuraphis. Substantial Pleuraphis emergence and 1st-year survival occurred on both sites in the wetter year of 1994-95, but Pleuraphis failed to emerge on the Dune-Area site in the drier spring of 1996.

**Site/Treatment Differences**

Survival of Agropyron was lower on the Near-Dune than Hill site. Agropyron is considered unsuitable for sites with <20–25 cm annual precipitation (Young and McKenzie 1982). Precipitation at the nearest weather station exceeded this amount in the wet year of
1994–95 with 33 cm October–September. The Near-Dune site probably received at least this amount and the Hill site even more, but the Near-Dune site is more droughty because of its coarser soil. Our results are consistent with Agropyron’s unsuitability for drier portions of the Great Basin. The native Triticeae, however, appeared better suited than Agropyron to these drier sites. In contrast to Agropyron, survival of Elymus did not differ between the Hill and Near-Dune sites. Comparable seedling emergence of Pseudoroegneria and Agropyron on the Hill site and similar to better survival of Pseudoroegneria are at odds with the commonly held concept of Pseudoroegneria having weak seedlings (e.g., Jones et al. 1991).

Species with Potential for Revegetation

Species with earlier seedling emergence are predicted to have better seedling survival in the face of competition from Bromus, which is thought to gain its competitive advantage through very early seedling emergence and growth (Young and Evans 1982, Hardegree 1994). Our early emerging Chrysothamnus and chenopod shrubs clearly did not support this, but the 2 early emerging grasses, Pseudoroegneria and Agropyron, showed good potential for establishment, at least on the Hill site, due to a combination of high emergence and high survival. Two later emerging grasses, Elymus and Stipa, also showed potential. Ephedra, another early emerging species, was the only shrub with good survival.

The Triticeae, especially Agropyron, showed less potential for establishment on drier sites, though Pseudoroegneria joined Ephedra and Oryzopsis as the only species with substantial seedling survival under the most severe conditions of our experiments, the unburned plots of the Dune-Area site with dry conditions and abundant Bromus. Stipa (not planted on the Dune-Area site) and Ephedra also had high numbers surviving on the other dry site, the Near-Dune site. Oryzopsis and Pleuraphis never had high numbers of seedlings surviving because they had low emergence. However, they may be useful for revegetation on drier sites because they consistently had high survival, even under severe conditions. Pleuraphis may largely escape competition from Bromus because its seedlings emerge in late spring when Bromus has completed most of its growth.

Consequences of Different Seasonal Patterns of Emergence

There were some distinct differences in seedling emergence between the 2 yr of our
experiment. In 1995, with more precipitation in both winter and spring, there was considerable February emergence of Chrysothamnus and considerable emergence of Pleuraphis in late spring, while in 1996 such very early emergence of Chrysothamnus was almost non-existent, and there was no emergence of Pleuraphis. A wider sampling of years might reveal considerable temporal segregation of recruitment of different species into different years due to different years having seasonal patterns of precipitation favorable to recruitment of different species. As most of these species are long lived, and yearly variation in precipitation is likely to affect survival of established plants less severely than it affects recruitment, much of the gain in abundance that each species makes in years favorable to its recruitment is likely to remain through unfavorable periods. This temporal separation of recruitment of different species with a considerable lag in the removal of individuals recruited can lead to a greater number of species on the site than would exist without variation among years (storage effect; Chesson 1994).

Although variation in the pattern of precipitation at the scale of years can promote greater species coexistence, Neilson (1986) linked major and persistent shifts in vegetation composition in the Chihuahuan Desert region to species-specific or species group-specific responses to decades-long changes in seasonal patterns of precipitation. Intensification of monsoonal summer precipitation in the western USA is a major prediction of many global climatic change scenarios (Lin et al. 1996). Changes in precipitation patterns of the Great Basin to more summer precipitation, with more frequent El Niño events and/or global warming, could cause shifts to greater recruitment of grasses, particularly C4 grasses, and reduced recruitment of shrubs.

Knowledge of seasonal patterns of seedling emergence of different species could be useful in rangeland vegetation management if used in an opportunistic rangeland management approach (sensu Westoby et al. 1989). Establishment of shrubs, C3 grasses and forbs, and C4 grasses could be considered as 3 possible alternative states, along with a catalog of conditions (i.e., seasonal patterns of precipitation) that should induce a transition to each of these states. A desired transition could be attempted when the necessary conditions appear likely (e.g., seed C3 grasses when a wet spring is predicted). It should also be noted that years with reduced precipitation in winter and early spring, periods important to Bromus, could provide an enhanced opportunity for recruitment of other species on Bromus-dominated sites.

ACKNOWLEDGMENTS

We thank J. Martin and the Conservation and Preservation Division of the Environmental Program Office, U.S. Army Dugway Proving Grounds, for their cooperation. We also thank S. Kelly, J.M. Gómez, S. Russell, and R. Walkenhorst for assistance with fieldwork, and J.L. Boettinger for soil descriptions and interpretations. This research was supported by the U.S. Department of Defense Legacy Resource Management Program (Project No. 94-0095), the Utah Agricultural Experiment Station (UAES), and the Ecology Center, Utah State University, Logan UT. Approved as UAES Journal Paper No. 6051.

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Received 23 September 1997
Accepted 16 May 1998