EFFECTS OF PLANTING DATE AND SPECIES CHOICE ON THE FATE OF

PLANTED WARM-SEASON PERENNIAL GRASS SEEDS:

IMPLICATIONS FOR REVEGETATION

by

Laurie Belle Abbott

A Dissertation Submitted to the Faculty of the

SCHOOL OF RENEWABLE NATURAL RESOURCES

In Partial Fulfillment of the Requirements
For the Degree of

DOCTOR OF PHILOSOPHY
WITH A MAJOR IN RANGE MANAGEMENT

In the Graduate College

THE UNIVERSITY OF ARIZONA

1999

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As members of the Final Examination Committee, we certify that we have

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entitled __Effects of planting date and species choice on the fate_____

__of planted warm-season perennial grass seeds:_____

__implications for revegetation_____

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and recommend that it be accepted as fulfilling the dissertation

requirement for the Degree of __Doctor of Philosophy_____

Mitchel P. McClaran   Date __9 July 99__

Guy R. McPherson   Date __9 July 1999__

Bruce A. Roundy   Date __9 July 1999__

Steven E. Smith   Date __9 July 1999__

Thomas L. Thompson   Date __9 July 1999__

Final approval and acceptance of this dissertation is contingent upon
the candidate's submission of the final copy of the dissertation to the
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I hereby certify that I have read this dissertation prepared under my
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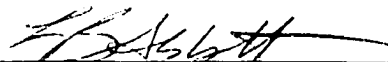Dissertation Director   Bruce A. Roundy   Date   9 July 1999

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DEDICATION

I dedicate this dissertation to Wayne and Skyler, in gratitude for sharing love, patience, joy, encouragement, and daily reminders that 'you can do it, Mom'.

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ABSTRACT

Attempts to establish native grasses in revegetation projects in semidesert grasslands in the southwestern United States often fail whereas revegetation of non-native lovegrasses (*Eragrostis* spp.) is frequently more successful. The reasons for differential establishment are unclear. Species may be differentially vulnerable to variable patterns of soil moisture availability during germination and seedling growth. Field experiments described within this dissertation investigated the effects of planting date and species on germination, emergence, mortality, survival, and seedling growth of native and non-native warm-season perennial grasses seeded in southeastern Arizona.

Native species [Sideoats grama (*Bouteloua curtipendula* (Michx.) Torr.), cane beardgrass (*Bothriochloa barbinodis* (Lag.) Herter), green sprangletop (*Leptochloa dubia* (H.B.K.) Nees), and Arizona cottontop (*Digitaria californica* (Benth.) Chase)] germinated rapidly, produced a few, large cohorts of seedlings, and retained limited residual germinability following initial rain events. In contrast, Lehmann lovegrass (*Eragrostis lehmanniana* Nees) germinated more slowly, produced more, smaller cohorts throughout the growing season, and retained more residual germinable seeds following initial rains. Mortality of all species was highest in the first week following emergence. Early development of adventitious roots and relatively high rates of biomass accumulation exhibited by Lehmann lovegrass are potentially advantageous under variable environmental conditions. Establishment of fast-germinating native species is favored by rainfall patterns that support early seedling growth subsequent to initial rains; the risk of seeding failure for these species increases when lengthy dry periods follow initial rain events. Years in which summer soil moisture conditions are highly variable would tend to favor Lehmann lovegrass establishment. Gradual depletion of the seedbank, early seedling growth characteristics,

and rapid production of seed in response to drought increase the probability that at least one cohort will establish or will survive long enough to replenish the seedbank for subsequent years. In southeastern Arizona, the probability of intermittent dry periods decreases as rainstorm frequency increases near the end of July, yet the recommended time to reseed is early summer. Adjusting the planting date to late July or early August may improve the potential for successful revegetation of native species that germinate rapidly and produce few cohorts following initial rains.

CHAPTER 1

INTRODUCTION

Restoration of semidesert grasslands in southeastern Arizona has been attempted, with varying success, since a decline in the abundance of perennial grass was detected (Cox et al. 1982, Cox and Jordan 1983, Bahre 1991, Roundy and Biedenbender 1995). Early research reported relatively high germination of native grass species, but field revegetation trials often failed (Wilson 1931, Bridges 1941). Low success rates with native grasses compelled researchers to investigate the revegetation potential of non-native species. Several species of lovegrass (*Eragrostis* spp.) native to Africa exhibited superior revegetation potential due to their tendency to establish in years when seedings of native species failed (Bridges 1941, Flory and Marshall 1942, Cox et al. 1982). In general, attempts to establish non-native lovegrasses have been met with greater success than attempts to establish native grasses. The reasons for differential establishment are unclear.

Two major tenets of range seeding are: 1) it is essential to plant species that are adapted to local conditions, and 2) plant seeds at a time when moisture and temperature conditions favor germination and establishment (Jordan 1981, Vallentine 1989). Flory and Marshall (1942) recognized the importance of planting date on grass establishment; native warm-season perennial grasses sown in late June may be vulnerable to seedling desiccation if early rains are followed by lengthy dry periods. Due to this potential rainfall pattern, mid-July planting dates were recommended over mid- to late-June plantings in semidesert grasslands of the southwestern United States (Flory and Marshall 1942). However, successful plantings of non-native lovegrasses were obtained by planting earlier (Bridges 1941, Herbel et al. 1973), leading some researchers to recommend late-spring to early-

summer planting dates for revegetation of warm-season perennial grass (Bridges 1941, Jordan 1981).

Two main goals of early revegetation efforts were to stabilize eroding soils and provide forage for livestock; thus, early selection trials focused on species that would meet those criteria and could establish reliably in most years (Roundy and Biedenbender 1995). Several native grasses were identified as promising candidates, although their suitability varied widely with site. For example, Rothrock grama (*Bouteloua rothrockii* Vasey) was rated satisfactory and sideoats grama (*B. curtipendula* [Michx.] Torr.), black grama (*B. eriopoda* [Torr.] Torr.), and bush muhly (*Muhlenbergia porteri* Scribn.) showed promise after revegetation trials in southern New Mexico (Bridges 1941); good results were also reported in trials of Arizona cottontop (*Digitaria californica* (Benth.) Chase), little bluestem (*Andropogon scoparius* Michx.), and plains bristlegrass (*Setaria macrostachya* H. B. K.) (Flory and Marshall 1942). However, over many years of revegetation trials, the species that have most consistently established in southeastern Arizona are non-native lovegrasses: Lehmann lovegrass (*Eragrostis lehmanniana* Nees), Boer lovegrass (*E. chloromelas* Steud.), and Cochise lovegrass (*E. lehmanniana* Nees X *E. tricophera* Coss and Dur.) (Cox et al. 1982).

Recent land management goals include increased biodiversity and restoration of ecosystem structure and function on degraded sites. Lehmann lovegrass spreads aggressively into unseeded areas (Cox and Ruyle 1986), and quickly re-establishes after drought or fire (Cable 1965, 1971; Fourie and Roberts 1977, Robinett 1992, 1994; Biedenbender and Roundy 1996), which portends its ability to alter structure and function of grasslands where it occurs (Bock et al. 1986, Anable et al. 1992, Whitford 1997). These factors re-

emphasize the need to concentrate revegetation efforts on establishment of native species, yet problems associated with native grass establishment remain.

Successful reseeding of native warm-season perennial grasses on rangeland depends on the ability of individuals to germinate, emerge, and survive. Differential establishment may result from species-specific differences in total germination, germination rate, emergence, and growth and development of seedlings during periods when soil moisture availability is not limiting (Cox 1984, Frasier et al. 1984, 1985; Adams 1997). Furthermore, species may differ in their ability to tolerate periods of limited soil moisture availability during these stages, which ultimately affects survival and recruitment (McGinnies 1960, Wright 1971, 1975; Roundy et al. 1996). Several studies have focused on the effects of soil moisture availability on germination, emergence, and seedling development of grasses commonly seeded in revegetation efforts. However, the majority of this work has been conducted under controlled-environment conditions, and it is often difficult to extend these results to explain species responses exhibited under field conditions (Frasier et al. 1987, Roundy 1994). Increased knowledge of germination, emergence, survival, and seedling development of grass species to specific environmental conditions under field conditions will address these needs (Livingston 1992, Roundy 1994). A better understanding of the patterns and processes underlying species establishment could facilitate planning and implementation of revegetation strategies in this region.

The purpose of the work presented in this dissertation was to determine the fate of warm-season perennial grass seeds planted under field conditions during summer in southeastern Arizona. Fundamental research questions centered on the response of species to patterns of soil moisture availability that occurred in the field. Do species exhibit different rates and patterns of germination, and do germination responses vary with variable moisture

availability patterns? Do emergence patterns mirror germination patterns? What are the relationships between soil moisture availability and emergence, mortality, survival, and establishment? Does the timing of germination and emergence relative to moisture availability affect mortality and survival? Do patterns of seedling growth and development vary among species, and how are these factors affected by soil moisture availability and drought? Effects of species and planting date on germination and establishment response are described in Chapter 2. Effects of species and planting date on emergence, mortality, and survival of seedlings are described in Chapter 3. Effects of variable moisture and environmental conditions on early growth and development of seedlings are described in Chapter 4. The final chapter provides a synthesis of these results and a brief discussion of their relevance to revegetation strategies in southeastern Arizona.

CHAPTER 2

EFFECTS OF PLANTING DATE ON GERMINATION AND ESTABLISHMENT OF WARM-SEASON PERENNIAL GRASS SPECIES IN SOUTHEASTERN ARIZONA

SUMMARY

Successful multi-species reseeding of native warm-season perennial grasses on rangeland depends on the ability of individuals to germinate, grow, and establish. Sporadic rainstorms in semi-arid regions result in variable soil moisture patterns that may contribute to differential survival of seeded species. In this two-year study, seven native and two non-native grass species were planted before and during the summer rainy season to determine the germination response of seeds exposed to variable patterns of soil moisture under field conditions. Sideoats grama (*Bouteloua curtipendula* (Michx.) Torr.), cane beardgrass (*Bothriochloa barbinodis* (Lag.) Herter), green sprangletop (*Leptochloa dubia* (H.B.K.) Nees), Arizona cottontop (*Digitaria californica* (Benth.) Chase), and bush muhly (*Muhlenbergia porteri* Scribn.) exhibited high germination percentages and limited residual germinability following initial rainfall events. Lehmann lovegrass (*Eragrostis lehmanniana* Nees) germinated fewer seeds in response to initial and subsequent rainfall events, but retained more residual germinable seeds than all other species studied. The ability of Lehmann lovegrass to retain a viable seedbank after multiple rainfall events is advantageous when long dry periods are interspersed between rainfall events. Lehmann lovegrass exhibited relatively greater recruitment in a summer with infrequent precipitation. Following a summer with more consistent rainfall, native species recruitment was greatest

when planted during the summer rainy season. Probability of successful establishment of native grass species used for revegetation in southern Arizona may increase if planting date is delayed until late July or early August.

INTRODUCTION

Establishment of native plants has become a common goal for revegetation projects. However, in semidesert grasslands, seedings of native warm-season perennial grasses often fail while plantings of non-native species are successful (Cox et al. 1982, Roundy and Biedenbender 1995). For example, Lehmann lovegrass (*Eragrostis lehmanniana* Nees), a warm-season perennial bunchgrass introduced from South Africa, has been commonly used in rangeland revegetation in southern Arizona because of its reliable establishment (Cox et al. 1982).

Reasons for differential establishment between native and non-native grasses are unclear. Frequency of summer precipitation in this region is sporadic, resulting in variable total precipitation and distribution of rain throughout the growing season (Humphrey 1958, McClaran 1995). The duration and frequency of rainfall directly affects the availability of soil moisture and therefore germination of seeds and growth and development of seedlings (Beatley 1974, Cox and Jordan 1983, Elberse and Breman 1990). The ability of seeds to tolerate hydration and dehydration prior to germination varies among species, and is sensitive to the water potential of the soil as well as the duration of wet and dry soil moisture conditions (Hegarty 1978, Bewley and Black 1982, Bradford 1990, Hardegree and Emmerich 1992a, Adams 1997). Thus, differences in native and non-native grass species establishment after reseeding suggest that some native grass species and non-native

lovegrasses may respond differently to patterns of soil moisture availability (Roundy et al. 1996). Differential establishment may result from species-specific differences in total germination, germination rate, and seedling growth and development during periods when soil moisture availability is not limiting (Cox 1984, Frasier et al. 1984, 1985; Adams 1997). Furthermore, species may also vary in their ability to tolerate periods of limited soil moisture availability during germination and seedling growth, which ultimately affects survival and recruitment (McGinnies 1960, Wright 1971, 1975; Roundy et al. 1996). Increased understanding of the patterns and processes underlying species establishment could facilitate planning and implementation of revegetation strategies in this region.

Careful selection of species and planting dates are two strategies that land managers may use to improve reseeding success (Roundy and Call 1988, Wester 1995). The most practical way to accommodate soil moisture conditions without using irrigation is to adjust planting date. Revegetation of arid and semiarid rangelands generally focuses on species that tolerate conditions of low soil moisture. Historically, species used in revegetation have been selected based on reseeding trials initiated before the onset of summer rains. Large inter-annual variability in summer precipitation patterns has been documented in Arizona (Sellers and Hill 1974). Long-term records from southeastern Arizona indicate that storms are generally less common in the beginning of the summer monsoon season, but the frequency of storms usually increases by the third week of July (Smith and Schreiber 1973, Frasier and Lopez 1990, Roundy et al. 1996). However, in southeastern Arizona, the recommended time to reseed warm-season grasses is in May or June, prior to the beginning of the summer rainy season (Jordan 1981). Utilizing these seeding practices, successful rangeland reseedings can be expected in 1 of 10 years in regions characterized by low precipitation (Cox and Jordan 1983). Therefore, the high failure rate of reseedings may result, at least in part, from the tradition of early planting dates that expose seeds and

seedlings to fluctuating and variable soil moisture conditions during the period of infrequent storms early in the summer rainy season (Frasier et al. 1987, Roundy et al. 1996).

Germination is the first essential process that seeds must complete to become established plants, and in semi-arid regions moisture availability is typically the predominant resource limiting germination (Wright 1971, Noy-Meir 1973); therefore, considerable research has focused on how germination is affected by moisture availability. Although this research has provided valuable insight into germination response to static water potentials, it is often not measured and related to revegetation responses in the field (Frasier et al. 1987, Roundy 1994). For example, laboratory studies of germination response to water stress often expose seeds to static osmotic or matric potentials (Knipe 1968, Tapia and Schmutz 1971, Bokhari et al. 1975, Hardegree and Emmerich 1991, Romo et al. 1991, Adams 1997), but static conditions seldom occur in field environments. Several studies have focused on germination or emergence response to dynamic soil moisture conditions by exposing seeds to sequentially decreasing static osmotic conditions (Qi and Redmann 1993) or imposing wet-dry-wet cycles (Frasier et al. 1984, 1985; Frasier 1989). However, dynamic soil moisture and temperature conditions associated with field conditions are difficult to reproduce under controlled-environment conditions. In addition, seedling emergence is often used as a proxy for germination of seeds sown into soil in both field and controlled environment studies (Glendening 1942, Coukos 1944, Frasier et al. 1984, 1985; Frasier 1989, Elberse and Breman 1990, Klink 1996). However, studies that use emergence as a proxy for germination do not always account for the proportion of seeds that successfully germinate but do not emerge, and thus potentially underestimate total germination (Chambers and MacMahon 1994). Direct evaluation of germination of seeds sown into soil is relatively rare due to inherent difficulties associated with retrieving seeds. Direct retrieval

of seeds sown into soil may be appropriate to determine field germination of large-seeded species, but consistent retrieval of small-seeded species may be difficult (Livingston 1992). Retrieval of small-seeded species may be facilitated if they are enclosed in cloth mesh bags prior to burial in soil (Livingston 1992).

The fate of planted seeds depends on the combined effects of several factors: 1) species response to environmental conditions (e.g., species-specific germination requirements, seedling growth and development, and stress tolerance of seedlings); and 2) environmental conditions that influence seed and seedling response (e.g., ambient climatic and edaphic factors that affect the amount, duration, and frequency of soil moisture available to seeds and seedlings). Thus, the duration of initial soil moisture availability and relative frequency and duration of subsequent wet- and dry-periods may have differential effects on species establishment. Seed and seedling survival may be favored by the following scenarios: 1) an initial wet period of short duration that results in low germination would enable ungerminated seeds to survive the following dry period and then germinate in response to subsequent rains; or 2) an initial wet period that promotes germination is of sufficient duration that seedlings develop adequate root systems to enable survival during subsequent dry periods; or 3) a dry period that follows a germination-promoting initial wet period is of short duration and is insufficient to result in seedling desiccation, but is followed by soil moisture conditions that promote continued seedling development and growth (Frasier et al. 1985, Roundy et al. 1997). Alternatively, soil moisture dynamics that promote seed germination but do not support continued seedling growth would likely result in seedling desiccation and death. Thus, the duration and amount of soil moisture available during the initial wet period and the nature of subsequent soil moisture dynamics could result in differential survival and establishment of fast-germinating or slow-germinating species. The purpose of these experiments was to determine the germination response of seeds

planted under field conditions. Seedling establishment was evaluated after the first

growing season to elucidate the relationship between germination, soil moisture dynamics,

and subsequent recruitment. Increased understanding of the conditions under which seeds

germinate and establish may provide valuable insights into species selection and the timing

of planting.

METHODS

Study Site

These studies were conducted in a semidesert grassland site at the Santa Rita Experimental

Range, approximately 40 km southwest of Tucson, Arizona. The site is located on an

alluvial fan with a maximum slope of 5%; elevation is 1,075 m (Cox et al. 1990). Annual

precipitation averaged 415 mm over the last 30 years, and varied between 205 and 765 mm

(SRER 1999). Precipitation is bimodally distributed, with approximately 60% falling as

rain between July and September, and most of the remaining 40% falling as rain or snow

between October and April (Cox et al. 1990, Roundy et al. 1997). Air temperatures range

annually between 0° and 40° C.

Soils are classified as coarse-loamy, mixed, superactive, nonacid, thermic Typic Ustic

Torrifluvents and coarse-loamy, mixed, superactive, thermic Ustic Haplargids of the

Combate-Diaspar complex, and the site is classified as a complex of sandy loam upland and

deep sandy loam range sites in the 12- to 16-inch precipitation zone (Breckenfeld and

Robinett 1997, D. Robinett *pers. comm.*). Reclassification of soils on this site occurred in

1997; the soil was previously classified as sandy loams of the Comoro series (Roundy et

al. 1997). Research was conducted within a livestock exclosure that had been fenced since 1984; prior to fencing, the site had been used as an airstrip, cleared of woody vegetation and graded several times, and grazed by cattle. The area inside the exclosure supports a herbaceous community dominated by Lehmann lovegrass. Nearby vegetation is typical semidesert grassland with an overstory dominated by velvet mesquite (*Prosopis velutina* Woot.) and a shrubby understory of burroweed [*Happlopappus tenuisectus* (Green) Blake], acacia [*Acacia greggii* Gray], false mesquite (*Calliandra eriophylla* Benth.) and prickly pear and cholla (*Opuntia* spp.). Common native perennial grasses include three-awns (*Aristida* spp.), Arizona cottontop, Rothrock grama (*Bouteloua rothrockii* Vasey), black grama (*B. eriopoda* Torr.), sideoats grama, slender grama [*B. filiformis* (Fourn.) Griffiths], and sprucetop grama [*B. chondrosioides* (H.B.K.) Benth.] (Martin 1966).

Before initiation of research, experimental plots were mowed, raked, and sprayed with glyphosate (N-[phosphonomethyl] glycine, a non-selective herbicide) to reduce the influence of vegetation on the site. Throughout the study, plots were maintained relatively free of non-target vegetation by mowing, hoeing, and raking.

Two separate field studies were conducted concurrently during the summers of 1992 and 1993 to examine the effect of different rainfall and soil moisture patterns on germination response and establishment of seedlings at the end of the growing season for nine warm-season perennial grass species (Table 2.1). Cleaned seed is commonly used in revegetation to facilitate flow of seed through mechanical equipment (Vallentine 1989); therefore, prior to planting all seeds were mechanically cleaned to remove appendages from caryopses. The first planting occurred prior to the onset of summer rains, and the second planting occurred later, after summer rains had typically begun; seeds were planted on 16 June and

30 July in 1992, and on 15 June and 2 August in 1993. Experiments were replicated in three blocks.

Germination Response Study

This experiment employed a randomized complete block design in a split-split-split-plot arrangement, in which year was the main plot, planting date was the sub-plot factor, species was the sub-sub-plot factor, and retrieval date was the sub-sub-sub-plot factor. Seed were retrieved twice after each planting to determine changes in germination response over time. The first retrieval occurred as the top 1 cm of soil was drying after the initial rainfall event. The second retrieval followed after at least one subsequent rainfall and drying event.

Seeds were placed in nylon mesh bags prior to burial to facilitate recovery of all planted seeds. Individual bags contained 10 pure live seeds of onespecies and were buried at 3-5 mm depth; bags contained seeds only, and did not contain soil. Sample sizes differed in the two years. Six bags of each species were buried in each block on each planting date in 1992 (N = 18), resulting in a sample size of nine bags per planting date/species/retrieval date. In 1993, four bags of each species were buried on each planting date in each of three blocks (N = 12), resulting in six bags per planting date/species/retrieval date.

A subset of the bags were unearthed and opened at each retrieval date. Seeds were inspected for germination; a seed was considered germinated if the radicle visibly protruded beyond the testa. Ungerminated seeds were placed on filter paper in petri dishes, wetted, and placed in a 25° C constant-temperature germination chamber. Seeds were checked daily for germination, and those that germinated in the germination chamber were

considered germinable. Seeds that did not germinate after two weeks in the germination chamber were considered dead or dormant. Due to difficulties in differentiating between dead and dormant seeds following this procedure, dead and dormant seeds were excluded from analysis and interpretation; subsequent analyses were conducted on the proportion of seeds that had germinated in the field or were germinable after retrieval.

Establishment Study

This experiment employed a randomized complete block design in a split-split-plot arrangement, in which year was the main plot, planting date was the sub-plot factor, and species was the sub-sub-plot factor. Within each planting date/species treatment combination there were 10 circular sub-plots (rings), each of which was 15 cm in diameter. Rings were constructed by excavating 15 X 15 cm pits to a depth of approximately 5 cm, placing a 15-cm diameter by 7.5-cm deep ring of PVC pipe into the pit, and backfilling around the outside of the ring. Each ring was then filled with sandy loam soil. Precautions were taken to reduce the potential of contamination of the rings with Lehmann lovegrass seeds of the extant seedbank. In 1992, rings were filled with autoclaved soil collected from the study site. In 1993, off-site soil was imported from a location where Lehmann lovegrass density was low and the soil profile supported a deep layer of sandy loam very similar to the soil at the study site (D. Post, *pers. comm.*). To further reduce the risk of contamination from Lehmann lovegrass, the top 10 cm of soil was removed and discarded before harvesting the deeper soil. On each planting date, 25 pure live seeds of a single species were planted into each ring. Consistent with typical recommendations for the species (Jordan 1981), small-seeded species (lovegrasses) were covered with approximately 0.5 cm of soil, and larger-seeded species were covered with approximately 1 cm of soil. The number of established seedlings in each ring was recorded at the end of

each season. Percent establishment values are based on the ratio between the number of established seedlings and the number of seeds sown.

Environmental Data

Throughout the observation period, soil moisture and temperature were recorded in each block, as described by Roundy et al. (1997). Soil moisture was estimated with calibrated Colman fiberglass soil cells (Colman and Hendrix 1949) at five depths in the soil: 1-3, 4-6, 8-10, 12-14, and 18-20 cm. Temperature was measured with copper-constantan thermocouples buried at 1, 2, 5, 9, 13, and 19 cm. At each depth, soil moisture measurements were replicated with five soil cells in each of three blocks, and temperature measurements were replicated using three thermocouples. Ambient climatic data (precipitation, air temperature, relative humidity, wind speed, and incident solar radiation) were measured on site. Measurements were recorded every minute using Campbell Scientific Inc. CR-10 microloggers, and stored as an hourly sum for precipitation and as hourly averages for all other variables.

Data Analysis

The data were analyzed using likelihood-based methods appropriate for general linear mixed models (MIXED procedure in SAS; Littel et al. 1996). Blocks were considered random effects, whereas all other factors (year, planting date, species, and retrieval date) were treated as fixed effects. The data were not normally distributed, and consequently were rank-transformed prior to analysis (Conover and Iman 1981). When appropriate, means were separated with Fisher's LSD mean separation test. Nylon bags served as

replicates in the germination response study; rings served as the replicates in the seedling establishment study.

Planting date was randomly assigned within each block, and species were randomly assigned to a row within each planting date plot. Each species row contained replicates that had identical species/planting date treatment combinations. Therefore, although the locations of planting date and species were randomized, the location of the individual bags or rings (in the germination response and seedling establishment studies, respectively) was not randomly assigned. As such, caution must be exercised in the extension of these results to other sites due to the potential confounding effects of pseudoreplication.

RESULTS

Eight of the nine species planted exhibited >70% combined germination and germinability throughout the two study years (70 to 91% in 1992, and 73 to 99% in 1993). One species, plains bristlegrass, exhibited an 11-fold decrease in combined germination and germinability from 80% in 1992 to 7% in 1993; thus, approximately 93% of the plains bristlegrass seeds were considered dead or dormant in 1993. Plains bristlegrass was therefore excluded from all analyses because of the likelihood that the low germination response in 1993 was due to a loss of viability instead of a response to environmental conditions. In the germination response study, two retrieval bags (one each of sideoats grama and Cochise lovegrass) contained fewer than four seeds, and were excluded from analysis.

Rainfall and Soil Moisture Patterns

Total precipitation and distribution of precipitation during the summer months differed

greatly between 1992 (Fig. 2.1) and 1993 (Fig. 2.2). Between 15 June and 10 September,

238 mm and 157 mm of rain fell in 1992 and 1993, respectively. However, due to the

number of days in which measurable rain fell, and the distribution of rain, the total number

of days in which soil water potential at the 1-3 cm depth was above -1.5 megapascals

(MPa) was greater in 1993 (41 days) than in 1992 (38 days). Perhaps more important than

the number of days in which the soil moisture potential was above or below a threshold

level is the relative length of the dry periods to which seeds were exposed after the initial

rain event. The soil water potential of the sandy loam at this site equals -1.5 MPa at a

volumetric soil moisture content of 0.0627 (Roundy et al. 1997). This value was

considered a threshold value, below which the soil was considered dry, and above which

the soil was considered wet. Between the initial rain event in July and 10 September, four

periods in which dry soil conditions existed occurred in 1992, lasting 5, 7, 5, and 10 days

(Fig 2.1). In 1993, five periods of dry soil conditions occurred between the initial rain

event and 10 September, lasting 4, 15, 1, 2, and 7 days (Fig. 2.2). Thus, in 1993 only

two dry periods lasting five or more days occurred after the initial rain, whereas four such

periods occurred in 1992.

Germination Response Study

The 4-way interaction of year, planting date, species, and retrieval date affected seed

germination in the field (Table 2.2) and residual germinability (Table 2.3). Of all possible

3-way interactions, the interaction of year, planting date, and retrieval date was the greatest

for germination and germinability. Of all possible 2-way interactions, the interaction of

year and planting date was greatest for germination and germinability. One of the principal objectives of the study was to determine seed response to different patterns of soil moisture availability that occurred following the two planting dates in each of the two years. Given that objective, the complexity of these higher-order interactions, and the strength of the interaction between year and planting date for both response variables, the data were re-analyzed using reduced models for each planting trial (planting date-year combination).

16 June 1992 planting

Germination varied among species and among retrieval dates, but not with the interaction of these factors (Table 2.2). Germination of Lehmann lovegrass (mean = 33.1%) was lower than that of all other species, which varied between 63.1% (plains lovegrass) and 97.3% (cane beardgrass) (Figure 2.3a). Germination increased from the first (68.8%) to the second retrieval date (80.4%) (Fig. 2.3a).

Germinability exhibited an inverse pattern with germination. Germinability varied among species and among retrieval dates, but not with the interaction of these factors (Table 2.3). Residual germinability of Lehmann lovegrass (64.7%) was higher than all other species; mean germinability of the remaining species varied between 1.7% (cane beardgrass) and 17.1% (Arizona cottontop) (Fig. 2.3b). Germinability decreased from the first (24.2%) to the second retrieval date (7.8%) (Fig. 2.3b).

30 July 1992 planting

Germination varied among species, but did not vary with retrieval date or the interaction of species and retrieval date (Table 2.2). Germination of Lehmann lovegrass (11.5%) was lower than all other species (Fig 2.4a). Cochise lovegrass and plains lovegrass also had low mean germination relative to the other species (28.3% and 29.4%, respectively);

sideoats grama and cane beardgrass exhibited the highest germination (77.1% and 81.3%, respectively) (Fig. 2.4a).

Germinability was affected by the interaction of species and retrieval date (Table 2.3). Lehmann lovegrass exhibited the highest residual germinability in both the first (83.0%) and second (49.2%) retrieval dates (Fig. 2.4b). Cane beardgrass had the lowest residual germinability (3.3%) in the first retrieval date, and sideoats grama, green sprangletop, and cane beardgrass each had zero germinability remaining in the second retrieval date (Fig. 2.4b). In general, germinability in the first retrieval date was either higher or not different from germinability in the second retrieval date for all species (Fig. 2.4b).

15 June 1993 planting

Germination was affected by the interaction of species and retrieval date (Table 2.3). None of the seeds of plains lovegrass or Cochise lovegrass had germinated by the first retrieval date, at which time sideoats grama exhibited the highest germination (48.5%) (Fig. 2.5a). In the second retrieval date, Lehmann lovegrass had the lowest germination (25.5%), and the highest germination was exhibited by cane beardgrass (93.6%) (Fig. 2.5a). In general, germination for all species except sideoats grama was greater in the second retrieval date relative to the first, although the magnitude of the difference varied among species.

Germinability was affected by the interaction of species and retrieval date (Table 2.4). Lehmann lovegrass had the highest germinability remaining in the first (98.9%) and second (74.5%) retrieval dates (Fig. 2.5b). Sideoats grama had the lowest remaining germinability (51.6%) in the first retrieval date, whereas sideoats grama, green sprangletop, Arizona cottontop, and bush muhly each had zero residual germinability in the second retrieval date

(Fig. 2.5b). In general, germinability for all species was greater in the first retrieval date relative to the second, although the magnitude of the difference varied among species.

2 August 1993 planting

Germination was affected by the interaction of species and retrieval date (Table 2.3). Lehmann lovegrass had the lowest germination in the first (14.5%) and second (49.1%) retrieval dates (Fig. 2.6a). Sideoats grama, green sprangletop, and Arizona cottontop each exhibited 100% germination in both retrieval dates (Fig. 2.6a). For all species except plains lovegrass, germination in the first retrieval date was either lower or not different than germination in the second retrieval date; germination of plains lovegrass was higher in the first retrieval date than in the second (Fig. 2.6a).

Germinability was affected by the interaction of species and retrieval date (Table 2.4). Lehmann lovegrass had the highest residual germinability in the first (83.8%) and second (49.2%) retrieval dates (Fig. 2.6b). Sideoats grama, green sprangletop, cane beardgrass, Arizona cottontop, and bush muhly each had no residual germinability after either retrieval date (Fig. 2.6b). In general, there was no difference in germinability between the two retrieval dates for any species except Cochise lovegrass, which had higher germinability in the first retrieval date relative to the second (Fig. 2.6b).

Establishment Study

Seedling establishment to the end of the growing season was affected by all possible 2-way interactions of year, planting date, and species, but was not affected by the 3-way interaction of those factors (Table 2.4). Of all possible 2-way interactions, the interaction of year and planting date was strongest (F = 41.46). In 1992, more seedlings established

from the 16 June planting (2.6%) than from the 30 July planting (0.6%) (Fig. 2.7a). In

1993, the 2 August planting (16.7%) resulted in more established seedlings than did the 15

June planting (7.2%) (Fig. 2.7a).

In general, more seedlings established for each species in 1993 than in 1992, but the

magnitude of the difference among years differed among species (Fig. 2.7b). For

example, seedling establishment was lowest for bush muhly in 1992 (0.2%) and in 1993

(3.7%). In 1992, Lehmann lovegrass (3.1%) and Cochise lovegrass (3.1%) had the

highest seedling establishment, whereas in 1993 green sprangletop had the highest seedling

establishment (19.5%) (Fig. 2.7b).

When considering the interaction of species and planting date, bush muhly had the lowest

seedling establishment for all species in both the pre-summer (0.1%) and mid-summer

(3.8%) plantings (Fig. 2.7c). Lehmann lovegrass had the highest seedling establishment

for the pre-summer plantings (9.9%), and green sprangletop had the highest seedling

establishment for the mid-summer plantings (15.3%) (Fig. 2.7c). In general, the number

of established seedlings for the mid-summer plantings was either greater or not different

than the pre-summer plantings for any species except Lehmann lovegrass (Fig. 2.7c).

Table 2.1. Common and scientific names of species used in germination and establishment studies.

Common Name	Scientific Name	Seed Source
Native:		
Sideoats grama	*Bouteloua curtipendula* (Michx.) Torr.	Native Plants, Inc., Arizona
Green sprangletop	*Leptochloa dubia* (H.B.K.) Nees	Granite Seed Co.,Utah; Texas origin
Cane beardgrass	*Bothriochloa barbinodis* (Lag.) Herter	Tucson Plant Materials Center, Arizona, Natural Resource Conservation Service
Arizona cottontop	*Digitaria californica* (Benth.) Chase	Granite Seed Co.,Utah; Arizona origin
Plains bristlegrass	*Setaria machrostachya* H. B. K.	Granite Seed Co., Utah; Texas origin
Bush muhly	*Muhlenbergia porteri* Scribn.	Collected Jornada Expt. Range, New Mexico
Plains lovegrass	*Eragrostis intermedia* Hitchc.	Native Plants, Inc., Arizona
Non-native:		
Lehmann lovegrass	*Eragrostis lehmanniana* Nees	Native Plants, Inc., Arizona
Cochise lovegrass	*Eragrostis lehmanniana* Nees X *E. tricophera* Coss and Dur.	Native Plants, Inc., Arizona

Table 2.2. Likelihood tests of main effects and interactions of year, planting date, species, and retrieval for field germination of warm-season grasses during the summer rainy season in southeastern Arizona.

Variable	Source	d.f.	F	P
Field Germination				
Full model				
	Year	1	14.24	0.0002
	Planting Date	1	105.72	0.0001
	Species	7	99.08	0.0001
	Retrieval	1	393.66	0.0001
	Year X Planting Date	1	157.29	0.0001
	Year X Species	7	4.24	0.0003
	Year X Retrieval	1	9.73	0.0022
	Planting Date X Species	7	6.38	0.0001
	Planting Date X Retrieval	1	111.93	0.0001
	Species X Retrieval	7	5.18	0.0001
	Year X Planting Date X Species	7	3.11	0.0047
	Year X Planting Date X Retrieval	1	69.95	0.0001
	Year X Species X Retrieval	7	1.20	0.3093
	Planting Date X Species X Retrieval	7	5.73	0.0001
	Year X Planting Date X Species X Retrieval	7	4.05	0.0005
Reduced Model by Planting Date, Year 16 June 1992				
	Species	7	13.23	0.0001
	Retrieval	1	11.19	0.0021
	Species X Retrieval	7	0.93	0.4968
30 July 1992				
	Species	7	15.95	0.0001
	Retrieval	1	0.89	0.3541
	Species X Retrieval	7	1.70	0.1478
15 June 1993				
	Species	7	6.00	0.0002
	Retrieval	1	151.95	0.0001
	Species X Retrieval	7	3.05	0.0151
2 August 1993				
	Species	7	35.27	0.0001
	Retrieval	1	3.04	0.1004
	Species X Retrieval	7	4.03	0.0099

Table 2.3. Likelihood tests of main effects and interactions of year, planting date, species, and retrieval for residual germinability of warm-season grasses during the summer rainy season in southeastern Arizona.

Source	d.f.	F	P
Residual Germinability			
Full model			
Year	1	13.14	0.0006
Planting Date	1	97.32	0.0001
Species	7	91.36	0.0001
Retrieval	1	432.58	0.0001
Year X Planting Date	1	145.08	0.0001
Year X Species	7	3.91	0.0013
Year X Retrieval	1	10.63	0.0018
Planting Date X Species	7	5.88	0.0001
Planting Date X Retrieval	1	123.01	0.0001
Species X Retrieval	7	5.68	0.0001
Year X Planting Date X Species	7	2.86	0.0117
Year X Planting Date X Retrieval	1	76.70	0.0001
Year X Species X Retrieval	7	1.31	0.2594
Planting Date X Species X Retrieval	7	6.30	0.0001
Year X Planting Date X Species X Retrieval	7	4.46	0.0004
Reduced Model			
by Planting Date, Year			
16 June 1992			
Species	7	15.14	0.0001
Retrieval	1	68.13	0.0001
Species X Retrieval	7	1.71	0.1757
30 July 1992			
Species	7	16.47	0.0001
Retrieval	1	51.54	0.0001
Species X Retrieval	7	3.81	0.0009
15 June 1993			
Species	7	9.66	0.0001
Retrieval	1	319.74	0.0001
Species X Retrieval	7	3.09	0.0142
2 August 1993			
Species	7	57.31	0.0001
Retrieval	1	5.97	0.0168
Species X Retrieval	7	3.37	0.0034

Table 2.4. Likelihood tests of main effects and interactions of year, planting date, and species for establishment of warm-season grasses during the summer rainy season in southeastern Arizona.

Variable	Source	d.f.	F	P
Establishment				
	Year	1	203.40	0.0001
	Planting Date	1	0.34	0.5768
	Species	7	12.48	0.0001
	Year X Planting Date	1	41.46	0.0002
	Year X Species	7	3.86	0.0017
	Planting Date X Species	7	4.82	0.0003
	Year X Planting Date X Species	7	1.18	0.3314
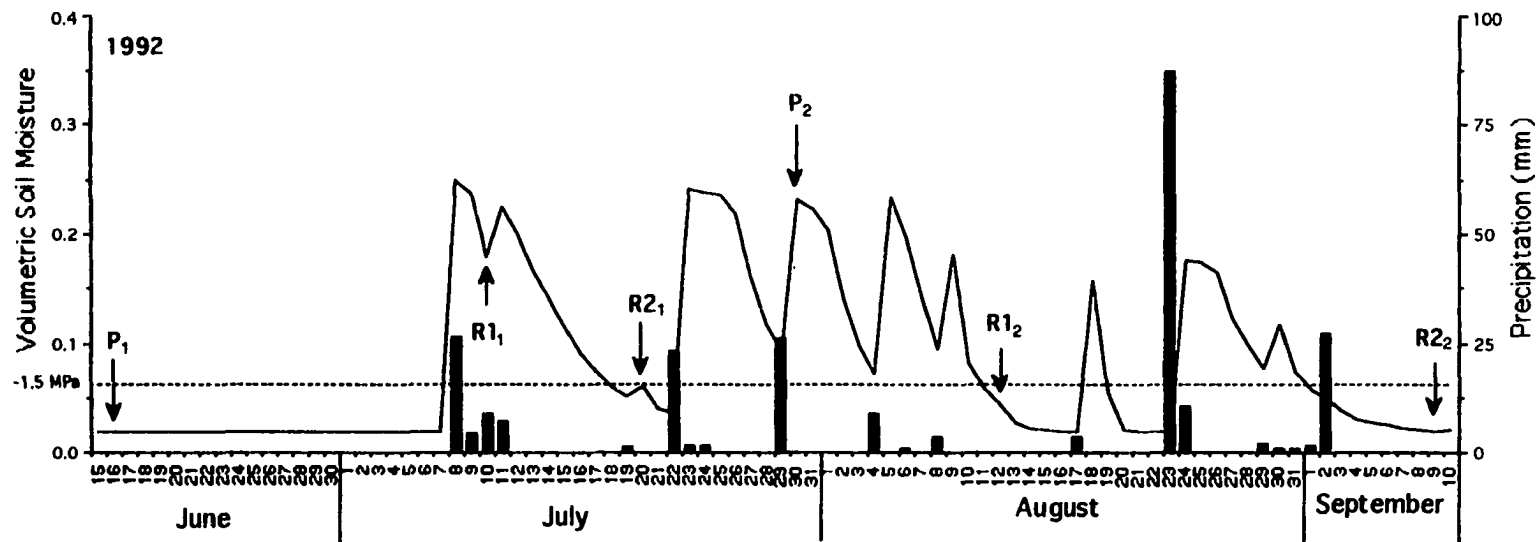
Figure 2.1. Daily total precipitation (solid vertical bars) and soil moisture availability (volumetric soil moisture at 1-3 cm; solid line) at the Santa Rita Experimental Station field site between 15 June and 10 September 1992. Arrows indicate the day on which planting (P₁), first retrieval (R1₁), and second retrieval (R2₁) occurred for the 16 June 1992 planting, and the day on which planting (P₂), first retrieval (R1₂), and second retrieval (R2₂) occurred for the 30 July 1992 planting.
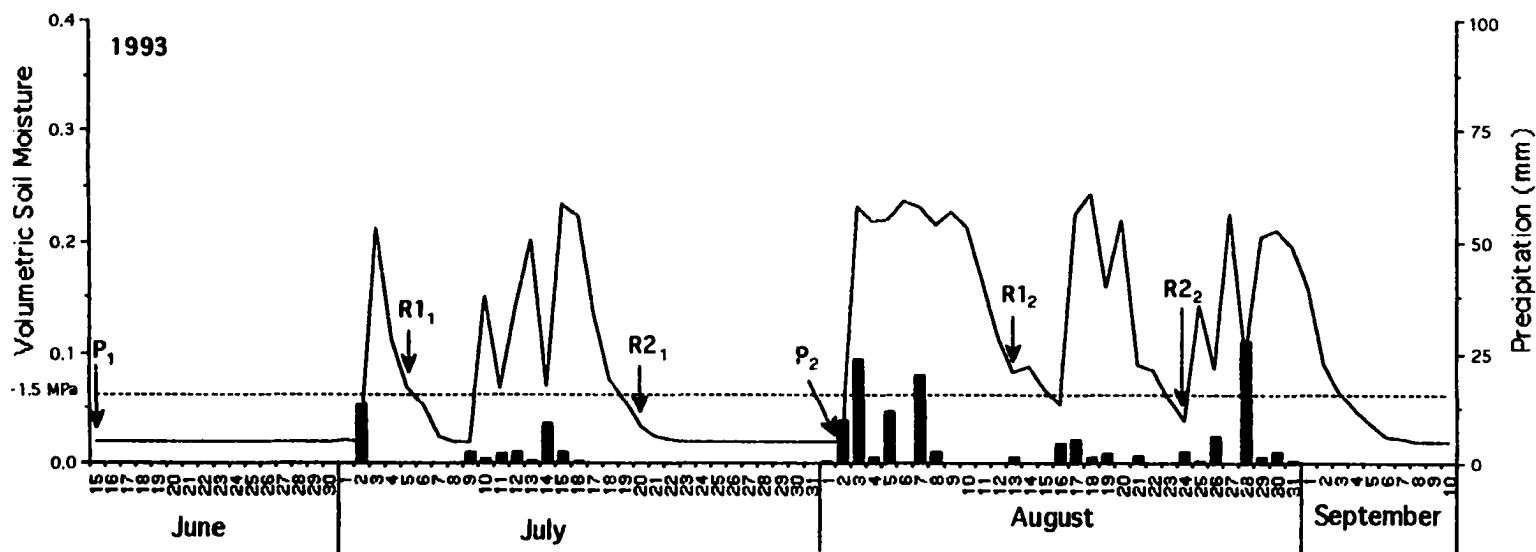
Figure 2.2. Daily total precipitation (solid vertical bars) and soil moisture availability (volumetric soil moisture at 1-3 cm; solid line) at the Santa Rita Experimental Station field site between 15 June and 10 September 1992. Arrows indicate the day on which planting (P1), first retrieval (R1 1), and second retrieval (R21) occurred for the 15 June 1993 planting, and the day on which planting (P2), first retrieval (R12), and second retrieval (R22) occurred for the 2 August 1993 planting.
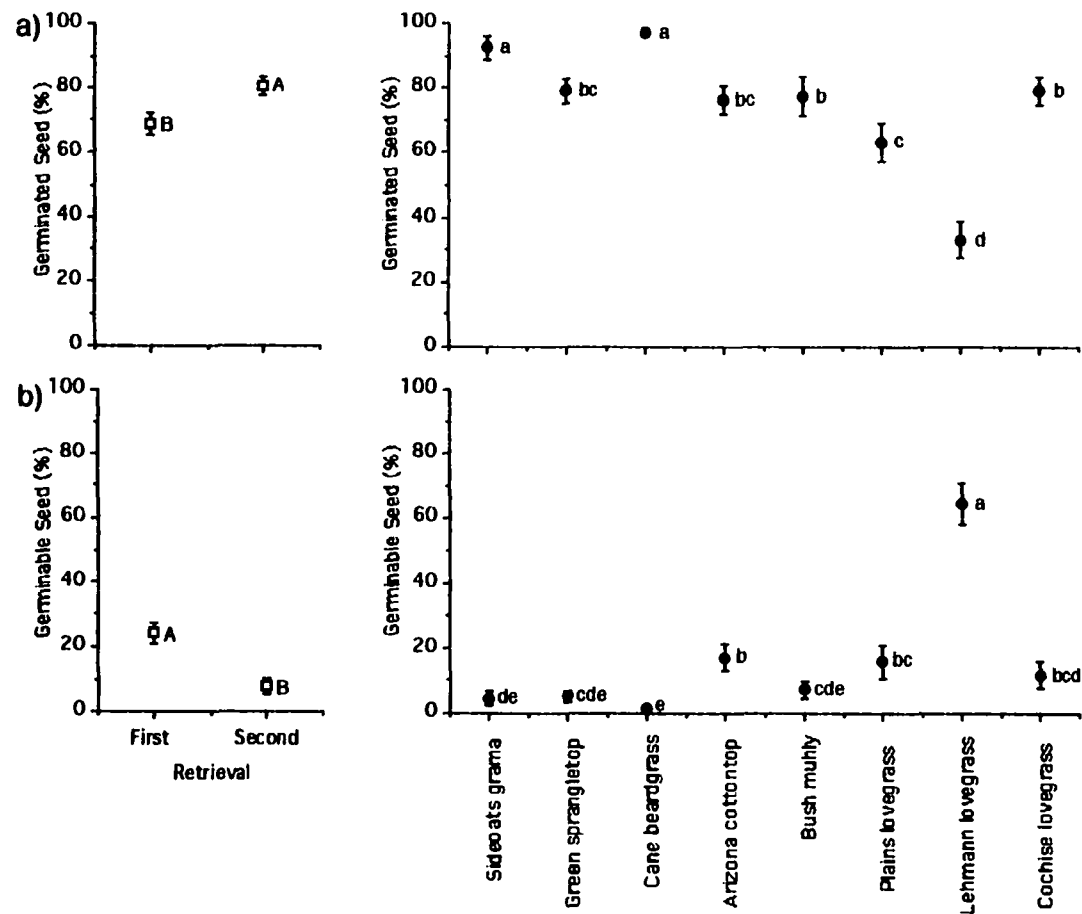
Figure 2.3. Mean total germination (a) and residual germinability (b) as a percent of number of seeds sown for warm-season grass species seeded on 16 June 1992 on a sandy loam upland site in southeastern Arizona. Main effects of retrieval date (open squares) and species (closed circles) are shown on the left and right of the graph, respectively. Error bars represent standard errors of the means. Means identified with the same uppercase letter do not differ between retrieval dates (P> 0.05). Means identified with the same lowercase letter do not differ between species (P > 0.05).
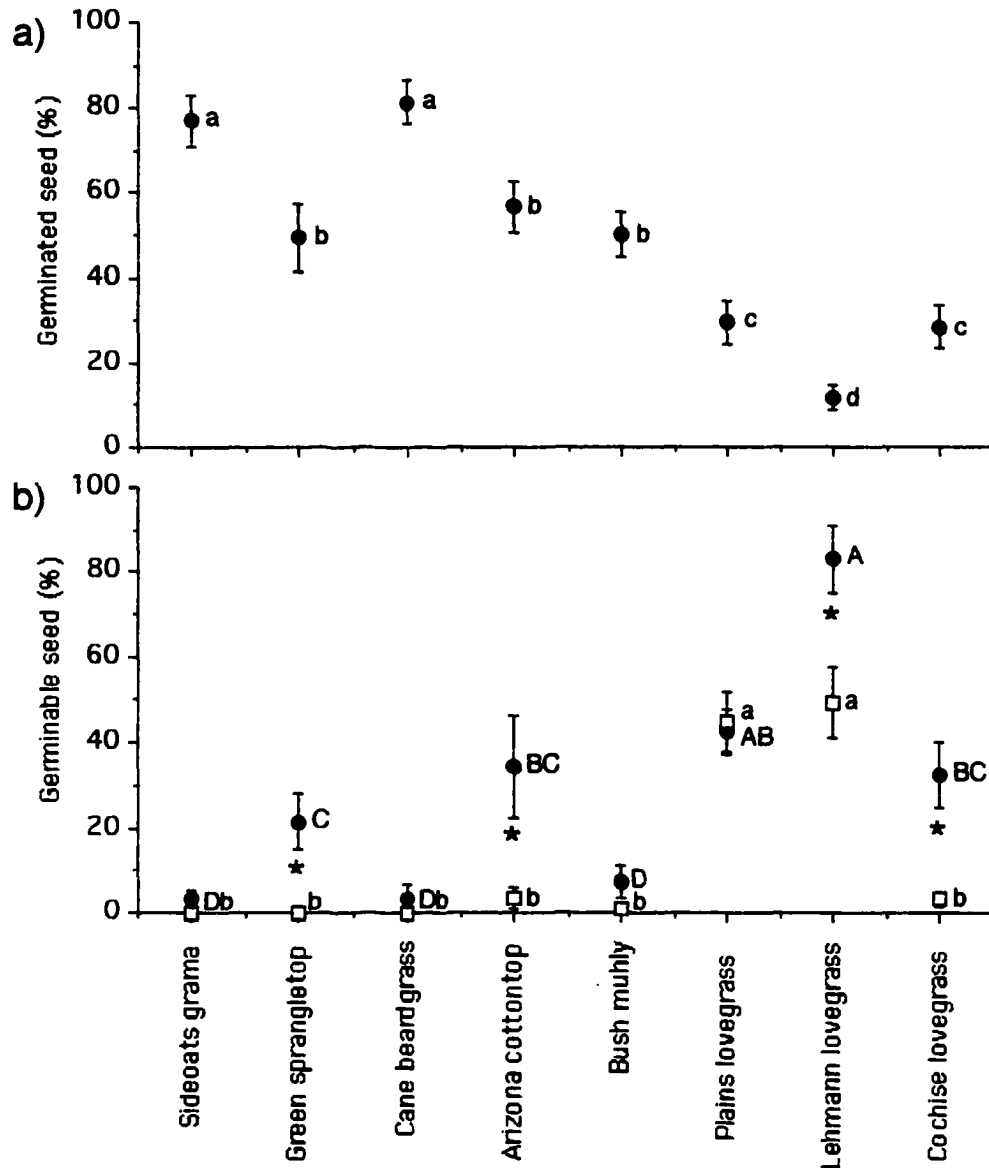
Figure 2.4. Mean total germination (a) and residual germinability (b) as a percent of number of seeds sown for warm-season grass species seeded on 30 July 1992 on a sandy loam upland site in southeastern Arizona. Error bars represent standard errors of the means. a) Main effects of species: means identified with the same lowercase letter do not differ between species (P > 0.05). b) Interaction of species with first retrieval date (closed circles) and second retrieval date (open squares): means identified with the same uppercase letter do not differ within the first retrieval (P > 0.05); means identified with the same lowercase letter do not differ within the second retrieval (P > 0.05). An asterisk (*) indicates differences (P < 0.05) between retrieval means within a species.
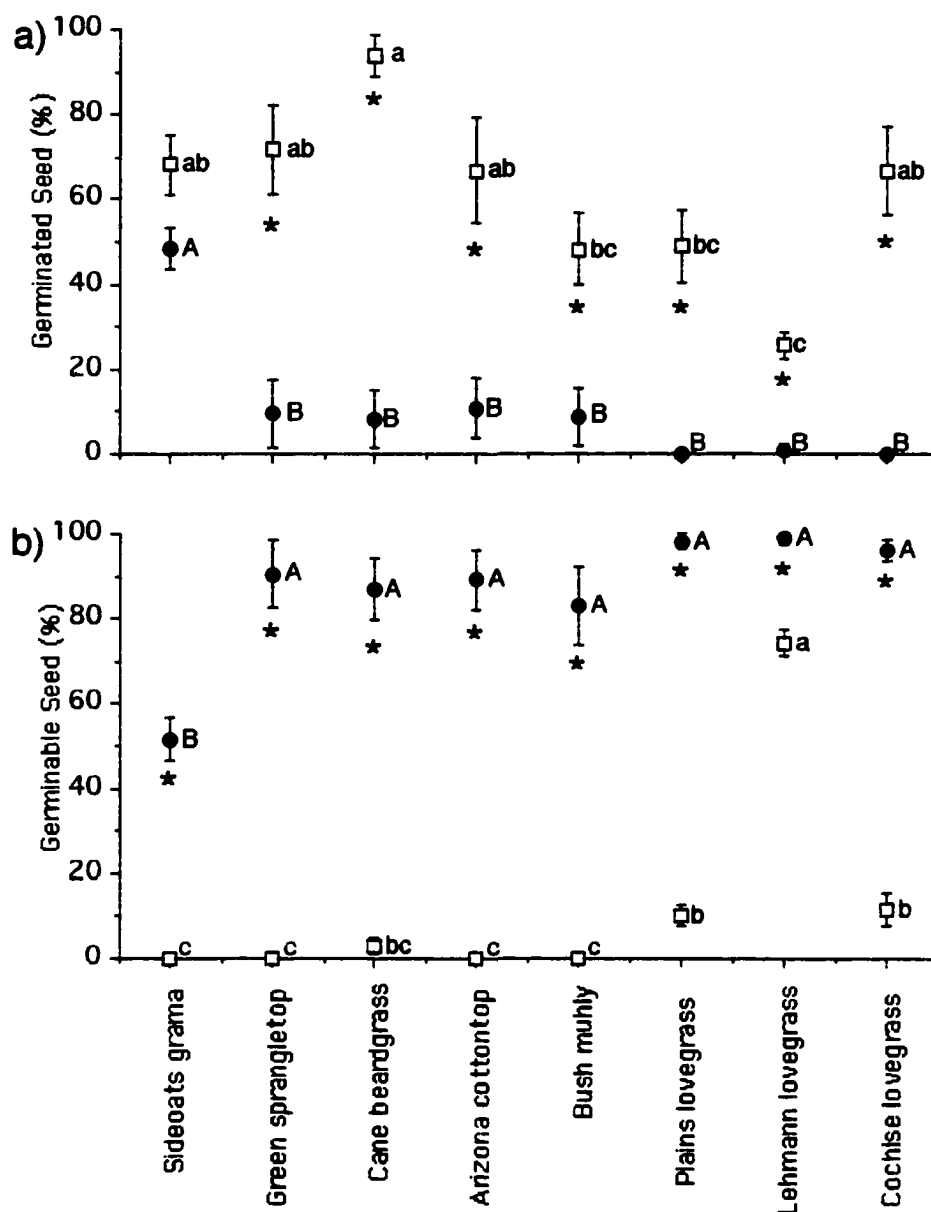
Figure 2.5. Mean total germination (a) and residual germinability (b) as a percent of number of seeds sown for warm-season grass species seeded on 15 June 1993 on a sandy loam upland site in southeastern Arizona. Error bars represent standard errors of the means. Interaction of species with first retrieval date (closed circles) and second retrieval date (open squares): means identified with the same uppercase letter do not differ within the first retrieval (P > 0.05); means identified with the same lowercase letter do not differ within the second retrieval (P > 0.05). An asterisk (*) indicates differences (P < 0.05) between retrieval means within a species.
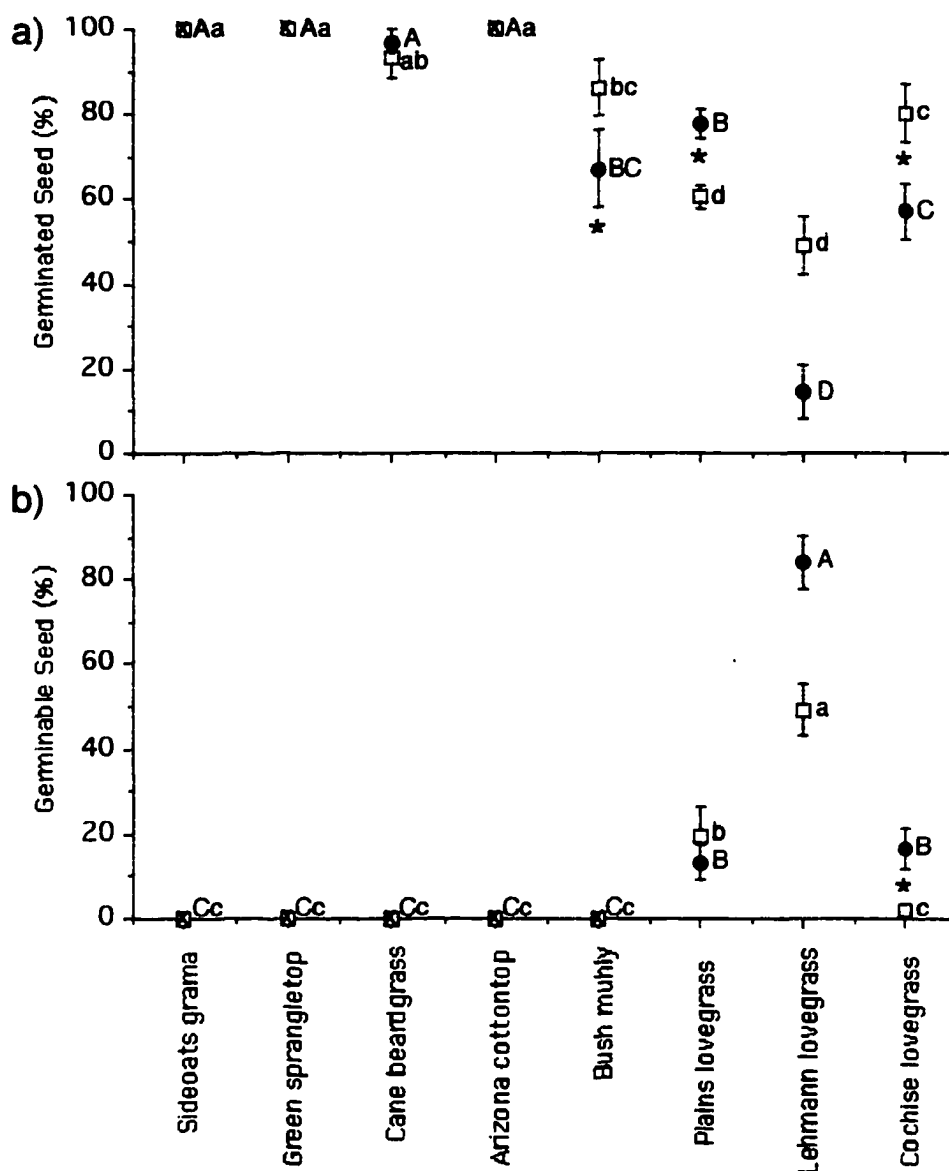
Figure 2.6. Mean total germination (a) and residual germinability (b) as a percent of number of seeds sown for warm-season grass species seeded on 2 August 1993 on a sandy loam upland site in southeastern Arizona. Error bars represent standard errors of the means. Interaction of species with first retrieval (closed circles) and second retrieval (open squares): means identified with the same uppercase letter do not differ within the first retrieval (P > 0.05); means identified with the same lowercase letter do not differ within the second retrieval (P > 0.05). An asterisk (*) indicates differences (P < 0.05) between retrieval means within a species. Open squares with an x indicate identical values for first and second retrievals within a species.
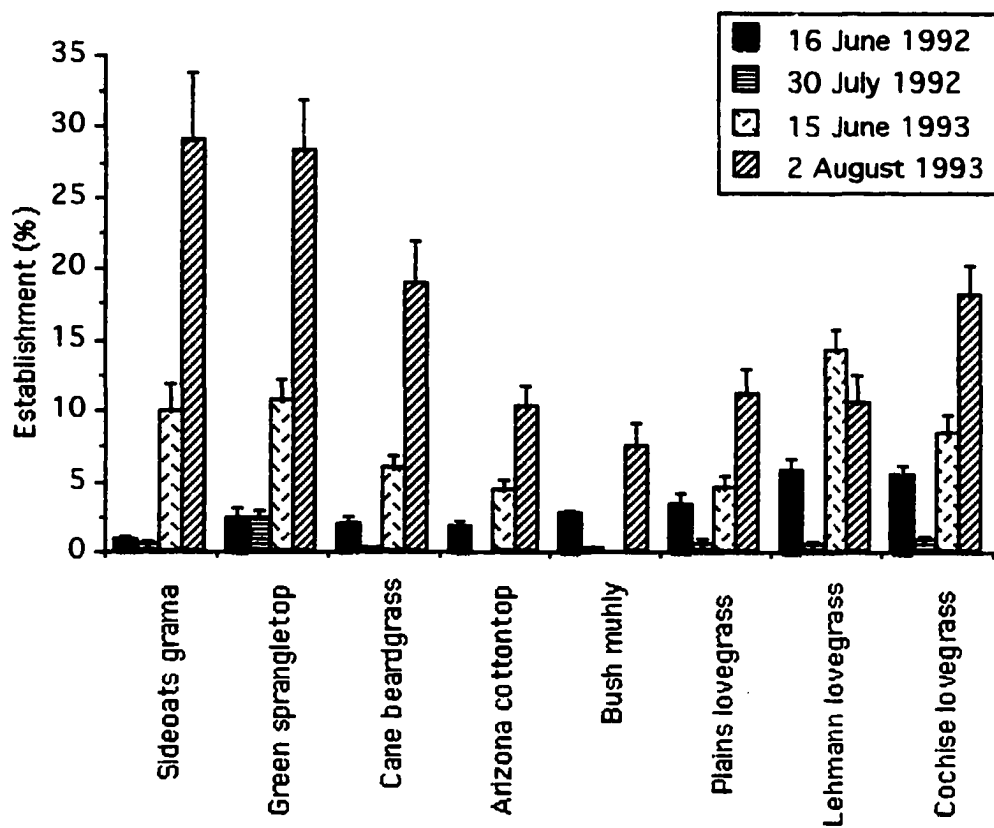
Figure 2.7. Mean establishment as a percentage of number of seeds sown for warm-season grass species seeded on four dates on a sandy loam upland site in southeastern Arizona. Error bars represent standard errors of the means.

DISCUSSION

Germination Response

Differences in germination response should be considered in terms of the germination process and species responses to soil moisture availability. The first stage of germination is imbibition, or water uptake; the process of imbibition is driven by a water potential gradient between the seed and the soil substrate, generally proceeding as long as the water potential of the seed is lower than that of the soil substrate (Wester 1995). Imbibition is a triphasic process, characterized by an initial phase of rapid water uptake, a lag phase during which water content is relatively constant, and a final phase in which water uptake resumes, coincident with radicle emergence (Bewley and Black 1994). Differences in germination rates among species are primarily attributed to differences in the rate of initial water uptake and the length of the lag phase. Seed requirements for a critical minimum level of hydration necessary for germination are species-specific and vary widely (Collis-George and Sands 1959, Hegarty 1978). In general, water uptake may be disrupted during the initial phase of imbibition until the initiation of cell division without detrimental effects on subsequent germination; the response of seeds to hydration/dehydration cycles varies among species (Bewley and Black 1982). Germination models that incorporate dynamic seed water potentials are especially useful for understanding germination and emergence under conditions of variable soil moisture availability (Bradford 1990). The relationship between a seed's critical base water potential, hydrotime (defined as the accumulated time [MPa-hour] that seed water potential is above the threshold base minimum), and germination is the basis for models that consider the effect of variable soil water potential on germination (Gummerson 1986, Bradford 1990). Adams (1997) empirically determined hydrotime constants and base water potentials for several species common to

the present study; these species exhibited a wide range of hydrotime constants and base water potentials. For example, base water potentials were lowest for sideoats grama and Lehmann lovegrass (-1.68 and -1.09 MPa, respectively), intermediate for bush muhly and Arizona cottontop (-0.45 and -0.42 MPa, respectively), and highest for Cochise lovegrass and cane beardgrass (-0.09 and -0.06 MPa, respectively), indicating that sideoats grama and Lehmann lovegrass are capable of germinating at a wider range of water potentials than the other species (Adams 1997). The hydrotime constants were lowest for Cochise lovegrass and sideoats grama (38.4 and 39.1 MPa-hour, respectively), intermediate for bush muhly, cane beardgrass, and Arizona cottontop (50.4, 55.2, and 67.2 MPa-hour, respectively), and highest for Lehmann lovegrass (130.8 MPa-hour) (Adams 1997). Thus, sideoats grama and Cochise lovegrass require relatively short exposure to base water potentials to germinate, but Cochise lovegrass requires more available water than sideoats grama; Lehmann lovegrass and sideoats grama are capable of initiating germination at relatively low water potentials, but time required to complete germination is much longer for Lehmann lovegrass.

Consistent differences in germination responses of certain species likely reflect inherent differences in species-specific moisture requirements for the initiation and completion of germination. For example, sideoats grama and cane beardgrass exhibited consistently high germination (> 79%) following initial rain events for all but the 15 June 1993 planting trial; other native species (green sprangletop, Arizona cottontop, and bush muhly) also exhibited relatively high germination (> 47%) following the initial rain event for the same planting trials. By the second retrieval date, seeds of most native species and Cochise lovegrass had either germinated or were no longer germinable. In sharp contrast to these patterns, Lehmann lovegrass exhibited lower germination and higher residual germinability for seven of the eight retrievals. These germination response patterns generally mirror relative

germination rates determined for the same seed lots exposed to gradually alternating summer temperatures in growth chamber studies; time to 50% germination was 1.4, 1.4, 1.6, 1.7, 2.3, 2.3, 3.1, and 3.7 days for sideoats grama, cane beardgrass, bush muhly, Cochise lovegrass, Arizona cottontop, plains lovegrass, green sprangletop, and Lehmann lovegrass, respectively (Roundy and Biedenbender 1996). The above germination rates are in general agreement with germination rates predicted by the hydrotime model within 0.5 days for all species except cane beardgrass and Lehmann lovegrass, which tend to germinate faster under laboratory conditions than would be predicted by the hydrotime model (Adams 1997). The presence or absence of seed appendages may potentially influence rates of germination for these species but was not addressed in this study; further investigation is needed to determine the relative effects of seed appendages on germination under field conditions.

Field germination tended to lag behind that predicted by germination evaluated in controlled environments. This is most clearly demonstrated by examination of the first retrieval from the 15 June 1993 planting; the first rainfall event after that planting was relatively small and seeds were retrieved after approximately two days from a drying soil (matric potential at 1-3 cm above -1.5 MPa). Germination for the first retrieval date of that planting was relatively low (0-11%) for all species except sideoats grama (48%). Time to 50% germination for cane beardgrass, bush muhly, and Cochise lovegrass in a growth chamber was 1.7 days or less (Roundy and Biedenbender 1996); therefore, observed germination after two days in the field was far less than expected based on laboratory results. However, low germination would be expected if soil matric potentials at the depth of seeds were lower than the critical base water potentials for those species. Seeds were planted no deeper than 0.5 cm, and it is likely that soil drying occurred more quickly at that depth compared to the depth of the soil moisture sensor (1-3 cm). Under drying soil conditions,

species with high critical base water potentials probably did not have sufficient time to complete germination, whereas sideoats grama could germinate as long as the soil matric potential did not drop below that species' critical base water potential (-1.68 MPa). Residual germinability following the first retrieval date was generally high (> 83%) for all species except sideoats grama. The second period of favorable moisture conditions (matric potential above -1.5 MPa at 1-3 cm) lasted for approximately eight days, and by the second retrieval date 48-94% of seeds for all species except Lehmann lovegrass had germinated. Thus, expected species-specific germination responses as predicted by soil moisture availability models were exhibited when favorable soil moisture conditions occurred.

Lehmann lovegrass germination was consistently lower than would be expected based on germination rates and moisture requirements determined in laboratory studies. Lehmann lovegrass total germination and germination rate vary widely within and among seed lots (Hardegree and Emmerich 1991), and germination response varies with temperature, water stress, light, seed priming, seed age, and wet-dry sequences (Knipe and Herbel 1960, Wilhelm 1969, Tapia and Schmutz 1971, Frasier 1989, Jordan and Haferkamp 1989, Hardegree and Emmerich 1992b, Roundy et al. 1992a, 1992b). Lehmann lovegrass germination was low in constant darkness, but increased with exposure to red light and with exposure to fluorescent light and alternating temperature (Tapia and Schmutz 1971, Roundy et al. 1992a). It is possible that Lehmann lovegrass germination in the field was limited by conditions of low light associated with burial of the seed bags, and observed high residual germinability was expressed after exposure to light in the laboratory. However, Lehmann lovegrass is capable of germinating and emerging after burial at a depth of 0.6 cm (Winkel et al. 1991). Given the high variability of germination responses exhibited by Lehmann lovegrass, it is likely that subpopulations of seeds are capable of germinating under a variety of conditions (Hardegree and Emmerich 1991). This

hypothesis is supported by the observation that Lehmann lovegrass produced multiple

cohorts of emerged seedlings after planting directly into soil at this field site (see Chapter

3).

Relative rates of germination under field conditions are in general agreement with previous

studies of emergence, which is commonly used as a proxy for germination. For example,

rapid germination of sideoats grama in the field agrees with earlier greenhouse and growth

chamber studies in which maximum emergence was reached in 2-3 days (Olmsted 1941,

Frasier et al. 1984, 1985; Adams 1997); this pattern is expected for a species that has a

short hydrotime requirement and the potential to germinate at a wide range of soil water

potentials. Similarly, delayed emergence of Lehmann lovegrass has been observed in

previous greenhouse and growth-chamber studies of emergence (Frasier et al. 1985, 1987;

Adams 1997), and would be predicted for a species that is capable of germinating at a wide

range of soil water potentials but has a long hydrotime requirement.

Establishment

Successful establishment requires environmental conditions that promote germination and

support continued seedling growth. Thus, seedling establishment likely was affected by

the timing and duration of soil moisture availability through its combined effect on

germination and seedling growth. Once soil drying has begun, seedling survival is

compromised if the soil drying front surpasses the rooting depth of the seedling (Roundy et

al. 1997). The amount of precipitation, duration of the initial rainy period, and ambient

weather conditions affect the length of the initial wet period; however, once the soil at 2 cm

depth has dried to -1.5 MPa in soil from this site, the drying front proceeds at

approximately 3.6 cm day^{-1} (Roundy et al. 1997). Based on this model, soil drying rates

following the initial rainy period were slow (i.e., soil matric potential of -1.5 MPa at 1-3 cm depth occurs 5.9 ± 1.4 days after the start of the drying period) for the 16 June 1992, 30 July 1992, and 2 August 1993 planting trials. Moderate soil drying rates (i.e., soil matric potential of -1.5 MPa at 1-3 cm depth occurs 2.6 ± 0.9 days after the start of the drying period) followed the first and second rainy periods for the 15 June 1993 planting trial.

In 1992, the pre-summer planting resulted in more established seedlings than the mid-summer planting, although initial rains following both the 16 June and 30 July planting dates resulted in periods of soil moisture availability (10 and 6 days, respectively) that were sufficient to induce germination in most species. However, timing and duration of subsequent dry periods likely affected the ability of seedlings to grow and survive. For the 16 June planting, soil drying proceeded for approximately 10 days between the end of the initial rainy period and the beginning of a subsequent rainy period. The rate at which seminal roots lengthen varies with species, soil moisture, and ambient conditions (Olmsted 1941, Sosebee and Herbel 1969, Simanton and Jordan 1986, Roundy et al. 1993, see Chapter 4). However, assuming a conservative seminal root growth rate of 1 cm day^{-1} and a slow drying rate at the soil surface (Roundy et al. 1997), the soil drying front would exceed the depth of the seminal roots in 11-12 days. Thus, seedlings from the 16 June planting that germinated in response to the initial rain event were likely to survive the first drying period until the second rainy period. In contrast, seedlings from the 30 July planting that had germinated in response to the initial rain event were exposed to soil drying conditions for approximately 8-10 days, 1 day of moist soil conditions, and a subsequent 5-day period of drying soil conditions. Assuming a slow drying rate of the soil surface, the depth of the drying front would have exceeded that of seminal roots within eight days, and seedling mortality was likely high during this lengthy dry period. The next wet period

(8-day duration) would then only benefit seedlings that survived the previous 12 days of dry soil conditions or those seeds that remained ungerminated yet germinable. Germinability after the first retrieval date of the mid-summer planting varied from 3.3 to 42.5% for all species except Lehmann lovegrass, which retained 83.0% germinability. Therefore, less than half of the planted seeds for all species except Lehmann lovegrass had the potential to germinate during that second, 8-day moist period. Furthermore, the next subsequent dry period lasted 13 days, during which the growth and survival of recently emerged seedlings was likely challenged.

Similar relationships between establishment and patterns of soil moisture availability can be detected in the 1993 plantings; establishment from the mid-summer planting was over twice as great as establishment from the pre-summer planting. As previously described, moisture conditions following the 15 June 1993 planting resulted in low initial germination, but relatively high germination of all species except Lehmann lovegrass occurred by the second retrieval date. However, the second retrieval date was followed by a subsequent 15-day dry period, which presumably constrained the growth and survival of emerged seedlings; based on root growth and soil drying rates predictions (Roundy et al. 1997), the depth of the soil drying front would have surpassed the depth of seminal roots after approximately 12 days. In contrast, in the 32 days following the 2 August planting, only two short drying periods occurred, and seedling establishment was high. Thus, the length of dry periods and their timing relative to seedling age apparently affected establishment in all four planting trials. In general, moisture patterns in 1992 resulted in a greater number of lengthy dry periods, and seedling establishment from either planting date in 1992 was low (<3%) relative to either planting date in 1993, which was characterized by fewer periods of low soil moisture conditions.

Seedling establishment followed the same pattern in a concomitant study in which seeds were sown into burned plots at this study site. In 1992, establishment from the pre-summer planting varied between 0 to 7.0 seedlings m^{-2} for native species and produced 34.0 seedlings m^{-2} for Lehmann lovegrass, whereas establishment following the mid-summer planting produced zero seedlings m^{-2} for native species and 24.0 seedlings m^{-2} for Lehmann lovegrass (Biedenbender and Roundy 1996). In 1993, establishment from the pre-summer planting varied between 0 to 5.8 seedlings m^{-2} for native species and produced 44.0 seedlings m^{-2} for Lehmann lovegrass, whereas establishment following the mid-summer planting varied between 0.8 to 57.0 seedlings m^{-2} for native species and 26.0 seedlings m^{-2} for Lehmann lovegrass (Biedenbender and Roundy 1996). Thus, for fast-germinating species that likely germinated in response to the initial wet period, subsequent establishment decreased as the length of ensuing dry periods increased. Lehmann lovegrass, a relatively slow-germinating species, exhibited moderate- to high-establishment in all planting trials. It is unclear from these studies whether successful establishment of Lehmann lovegrass was due to germination response, seedling growth and development patterns, or seedling stress tolerance. Further investigation is required to partition the relative contribution of these factors to successful establishment of native and non-native species in reseeding efforts.

CONCLUSIONS

The probability of successful establishment is increased when the timing and duration of favorable soil moisture conditions promote both seed germination and seedling growth. Our investigation of germination response under field conditions clearly revealed species-specific response patterns to dynamic soil moisture conditions. Many native grass species exhibit high percentages and rates of germination, and thus would be favored by rainfall patterns that result in conditions that support seedling growth subsequent to initial rains. For these species, the planted seedbank is often depleted after the initial rain event and therefore the risk of seeding failure associated with the occurrence of lengthy dry periods after the initial rain event depends on the ability of seedlings to tolerate dry soil conditions. The seedbanks of slower-germinating species such as Lehmann lovegrass are generally not depleted by initial rain events, and thus the occurrence of lengthy dry periods following initial rains imposes less risk to reseeding success due to the potential for subsequent rain events to promote germination and growth of remaining germinable seeds.

Successful establishment requires germination, seedling growth, and survival. Although establishment patterns revealed by these studies reflect germination responses of the seeded species, no specific information is available concerning the growth and survival of seedlings after germination. Insight concerning the timing of emergence and subsequent survival or mortality requires frequent evaluation of individual seedlings throughout the growing season. Once germinated, seedling survival depends on growth and development patterns under conditions of high and low soil moisture availability; seedling development under variable environmental conditions likely differs among species. Additional studies focusing on emergence, mortality, and survival patterns could help to identify environmental conditions that promote survival of individual species. Studies of seedling

growth and development could suggest mechanisms that contribute to seedling survival under a variety of environmental conditions.

Rainfall and soil moisture patterns widely vary between and within years. Environmental conditions during one growing season may favor establishment of one or more species, whereas different environmental conditions may favor the establishment of a different suite of species. Thus, years in which summer soil moisture conditions are highly variable would tend to favor Lehmann lovegrass over faster-germinating native species. The tendency for Lehmann lovegrass to germinate a small proportion of seeds in response to individual rainfall events, yet retain a residual seedbank typifies a bet-hedging strategy that is favorable in variable environments (Venable 1989), and may partly explain the relative success of Lehmann lovegrass reseedings in regions characterized by low precipitation (Cable 1971, Cox et al. 1982). Studies of long-term summer precipitation records in southeastern Arizona indicate that the probability of rain sequences in which the initial rain event is followed by dry periods lasting five days or less is maximized between the third week of July and the first week of August (Frasier and Lopez 1990, Roundy et al. 1996, 1997). Given the rapid germination response and concomitant depletion of seedbank reserves exhibited by native species in this study, chances for successful establishment of native grass species in revegetation projects in southeastern Arizona could be increased by delaying planting until at least the third week of July.

CHAPTER 3

EFFECTS OF PLANTING DATE ON
EMERGENCE AND SURVIVAL OF WARM-SEASON PERENNIAL GRASSES:
IMPLICATIONS FOR REVEGETATION

SUMMARY

Successful multi-species reseeding of native warm-season perennial grasses on rangeland depends on the ability of individuals to germinate, emerge, and survive. Infrequent rainstorms in semi-arid regions result in variable soil moisture patterns that may contribute to differential survival of seeded species. Revegetation efforts are commonly evaluated several months after planting, resulting in a lack of information about emergence patterns of planted species, or the subsequent mortality and survival of those seeded populations. This demographic study investigated the influence of two planting dates (28 June and 10 August) on patterns of emergence, mortality, survival and recruitment for seven native and two non-native grass species commonly reseeded in southeastern Arizona. Plots were monitored every two or three days throughout the summer rainy season to determine emergence, mortality and survival of individual seedlings. Two wet-dry cycles occurred in the first two weeks after the first rain after the 28 June planting, whereas soil moisture availability was high for two weeks following the first rain after the 10 August planting. Some species (e.g., sideoats grama, Arizona cottontop, and green sprangletop) emerged most seedlings in early cohorts, while other species (e.g., plains lovegrass, Lehmann lovegrass, and Cochise lovegrass) tended to produce more cohorts throughout the growing season. Overall, emergence and recruitment were higher from the early planting date, but survival was greater in the later planting date. Mortality generally occurred in the first week

after planting, and was affected by soil moisture availability at shallow depths (1-3 and 4-6 cm) throughout the lifespan of individual seedlings. Cohort influenced survival of individuals in the 28 June planting, when multiple wet-dry cycles occurred in the first 14 days following the initial rain. The relationship between emergence patterns, soil moisture availability patterns, and survival suggests that successful establishment of native warm-season perennial grass species may be favored by delaying the planting date until at least late July, when there is a decreased probability of intermittent dry periods following reseeding.

INTRODUCTION

Establishment of native plants has become a common goal for revegetation projects in recent years. However, in semidesert grasslands, seedings of native warm-season perennial grasses often fail while plantings of non-native species are successful (Cox et al. 1982, Roundy and Biedenbender 1995). For example, Lehmann lovegrass (*Eragrostis lehmanniana* Nees), a warm-season perennial bunchgrass introduced from South Africa, has been commonly used in rangeland revegetation in southern Arizona because of its reliable establishment.

The reasons for differences in establishment between native and non-native grasses are unclear. Natural populations of native grasses in the southwestern United States exhibit an episodic recruitment pattern (Canfield 1957). Summer precipitation in this region is sporadic, which results in variable distribution and amount of rain throughout the growing season (Humphrey 1958, McClaran 1995). The duration and frequency of rainfall directly affects the availability of soil moisture and therefore germination of seeds and growth and

development of seedlings (Beatley 1974, Cox and Jordan 1983, Elberse and Breman

1990). Differences in recruitment of some native grasses and non-native lovegrasses after

reseeding suggest that these species may respond differently to patterns of soil moisture

availability (Roundy et al. 1997). Long-term reseeding success has been linked to the

amount and distribution of precipitation during the initial growing season (Cox and Jordan

1983). Differences in survival and recruitment may be related to differences in patterns of

germination and emergence (Cox 1984; Frasier et al. 1984, 1985; Adams 1997). Species

establishment may vary with the ability of different species to tolerate periods of low soil

moisture availability during germination and seedling growth (Wright 1975, Roundy et al.

1997). Furthermore, species may be differentially vulnerable to environmental stress at

different developmental growth stages between germination and establishment, resulting in

differential survivorship among species (McGuinnies 1960, Wright 1971, Roundy et al.

1997). A better understanding of the patterns and processes underlying establishment

could facilitate planning and implementation of revegetation strategies in this region.

Careful species selection and choice of planting dates are two strategies that land managers

may use to improve the chances of successful reseeding efforts (Roundy and Call 1988,

Wester 1995). Revegetation of arid and semiarid rangelands generally focuses on selection

of species that tolerate conditions of low soil moisture. Historically, species used in

revegetation have been selected based on reseeding trials initiated before the onset of

summer rains and then evaluated at the end of the growing season. However, this practice

reveals little about relationships between patterns of moisture availability and germination,

emergence, and survival. The ability of seeds to tolerate hydration and dehydration prior to

germination varies among species, and is sensitive to the water potential of the soil as well

as the duration of wet and dry soil moisture conditions (Hegarty 1978, Bewley and Black

1982, Bradford 1990, Hardegree and Emmerich 1992a, Adams 1997). Furthermore,

species that tolerate drought as mature plants may not necessarily tolerate dry periods in the seedling stage, and vice versa (Fulbright et al. 1984, McGuinnies 1960). Therefore, survival of individual plants likely depends on the interactive effects of species-specific patterns of germination, growth and development, and variable patterns of soil moisture availability throughout the growing season.

Arizona is characterized by large inter-annual variability in summer precipitation patterns (Sellers and Hill 1974). Long-term records from southeastern Arizona indicate that storms are generally less common in the beginning of the summer rainy season, but that by the third week of July the frequency of storms has usually increased (Smith and Schreiber 1973, Frasier and Lopez 1990). However, in southeastern Arizona the recommended time to reseed warm-season grasses is in May or June, prior to the beginning of the summer rainy season (Jordan 1981). Therefore, the high failure rate of reseeding efforts may result, at least in part, from the tradition of early planting dates that expose seeds and seedlings to fluctuating and variable soil moisture conditions during the period of infrequent storms early in the summer rainy season (Frasier et al. 1987, Roundy et al. 1996).

One of the challenges of revegetation is to intentionally establish plant communities in order to return ecosystems to acceptable levels of structure and function. Harper (1977) notes that one of the fundamental characteristics of natural populations of perennial plants is that generations overlap, and that these different-aged individuals represent survivors from slightly different selective processes. In contrast, communities that are recovering from large-scale disturbances consist of even-aged populations, which are generally considered to have been subjected to identical selective processes; ultimately, such identical selective processes may potentially weaken the resistance and resilience of the community to further perturbation. However, in the case of artificial reseeding, the perception that the resulting

populations of surviving plants are even-aged, and that uniform selective forces shape the genetic integrity of those populations depends on perspective and is scale-dependent. The population of survivors may consist of individuals that emerged as different cohorts and survived through distinct environmental events and selective forces.

Successful rangeland reseedings can be expected in about 1 of 10 years in regions characterized by low and highly variable precipitation (Cox and Jordan 1983). Better understanding of the biological responses of species to different soil moisture conditions has direct implications for rangeland revegetation in southern Arizona (Roundy 1994). The most practical way to control soil moisture conditions without using irrigation is to adjust planting date. The purpose of this experiment was to determine the effect of planting date and species on emergence, mortality, survival, and recruitment of individual seedlings. Increased understanding of the conditions under which survivors emerge and persist may provide valuable insights into species selection and the timing of planting.

METHODS

Study Site

These studies were conducted in a semidesert grassland site at the Santa Rita Experimental Range, approximately 40 km southwest of Tucson, Arizona. A detailed description of the study site is provided elsewhere (see Chapter 2).

Before initiation of research, experimental plots were mowed, raked, and sprayed with glyphosate (N-[phosphonomethyl] glycine, a non-selective herbicide) to reduce the

influence of vegetation on the site. Throughout the study, plots were maintained relatively free of non-target vegetation by mowing, hoeing, and raking.

Experimental Design

The experiment employed a randomized complete block design in a split-plot arrangement, in which planting date was the main plot and species was the sub-plot factor. The experiment was replicated in three blocks. Within each planting date/species treatment combination there were three circular sub-plots (rings), each of which was approximately 38 cm in diameter. The rings were constructed by excavating 40 X 40 cm pits to a depth of approximately 10 cm, placing a 38-cm ring formed from 11.5-cm wide lawn edging material into the pit, and backfilling around the outside of the ring. A rim of lawn edging material approximately 2.5 cm high protruded above the soil to reduce the risk of seedbank contamination due to overland flow. Each ring was then filled with sandy loam soil. Rings were filled with off-site soil to reduce the potential for contamination of the rings with Lehmann lovegrass seeds from the on-site seedbank. The source site for the soil was selected because it was nearby, it had a deep layer of sandy loam very similar to the soil at the study site (D. Post, *pers. comm.*), and because Lehmann lovegrass density at that site was low. To further reduce the risk of contamination from Lehmann lovegrass, the top 10 cm of soil was removed and discarded before harvesting the deeper soil.

Planting dates were 28 June and 10 August 1994, and were selected to compare an early planting date (before the onset of summer rains) with a later planting date (after the onset of summer rains). To ensure that germination occurred in response to subsequent rain events rather than favorable soil conditions at the time of planting, the top 3 cm of soil within the rings was dry at the time of planting. Cleaned seed is commonly used in revegetation to

facilitate flow of seed through mechanical equipment (Vallentine 1989); therefore, prior to planting all seeds were mechanically cleaned to remove appendages from caryopses. Each ring was sown with 25 pure live seeds of one of nine study species (Table 3.1). Planting rates for all species were based on percentages of pure live seed (PLS) determined by germinating the seeds on moist filter paper in petri dishes inside a constant temperature (25° C) germination chamber. Consistent with typical recommendations for the species (Jordan 1981), small-seeded species (lovegrasses) were covered with approximately 0.5 cm of soil, and larger-seeded species were covered with approximately 1 cm of soil.

Patterns of emergence, the timing of mortality and the ultimate survival of different cohorts could remain undetected if observations are made infrequently. Indeed, decreasing the frequency of observations from several times each week to once per week can effectively bias estimations of emergence and mortality, resulting in low estimates of emergence and high estimates of survival (Eggleston and McPherson 1995). The frequency with which observations are made must also allow the researcher the ability to gather information at a scale that will address research questions in a meaningful way (Sarukhan and Harper 1973). The research questions in this study focus on the timing of emergence relative to long-term survival, and require documentation of seedling fate at the level of individual plants. Therefore, after the first planting on 28 June, rings were inspected for emerged seedlings every two to four days until the end of the observation period on 15 October. Every seedling was given an identification number, mapped to aid in re-identification, and its location was marked in the ring by placing a wire flag near the seedling. Each flag was placed within 2 cm of the seedling, but wire flags did not touch the young seedlings. Emergence date was defined as the first date the seedling was observed. A cohort is defined as a group of individuals that shares a particular demographic characteristic; all of the emerged individuals from one species/planting date treatment combination that were

first observed on a particular day comprised a cohort. On each subsequent inspection, surveys were conducted for new seedlings, and the status of emerged seedlings was checked for subsequent mortality. A seedling was considered dead if it was yellowed or brown, dry and brittle to the touch, and if the seedling was easily removed from the soil with a slight pull on the shoot. The mortality date was defined as the inspection day on which death was noted. Thus, the dates of emergence and mortality were accurate within two to four days.

At the end of the observation period, surviving seedlings were classified according to lifestage. Seedling classes were pre-tillered (no tillers had formed), tillered (tillers present, reproductive structures absent), or reproductive (reproductive structures present). Recruitment at the end of the growing season was calculated as the percentage of seeds sown that produced surviving seedlings.

Throughout the observation period, soil moisture and temperature were recorded in each block, as described by Roundy et al. (1997). Soil moisture was estimated with calibrated Colman fiberglass soil cells (Colman and Hendrix 1949) at five depths in the soil: 1-3, 4-6, 8-10, 12-14, and 18-20 cm. Temperature was estimated with calibrated copper-constantan thermocouples buried at 1, 2, 5, 9, 13, and 19 cm. At each depth, soil moisture measurements were replicated with five soil cells, and temperature measurements were replicated using three thermocouples. Moisture and temperature were measured every minute and recorded as hourly averages using Campbell Scientific Inc. CR-10 microloggers.

Data Analysis

With the exception of survival data, the data were analyzed using likelihood-based methods appropriate for general linear mixed models (MIXED procedure in SAS; Littel et al. 1996). Blocks were considered random effects, whereas planting date and species were treated as fixed effects. The data were not normally distributed, and consequently were rank-transformed prior to analysis (Conover and Iman 1981). When appropriate, means were separated with Fisher's LSD mean separation test. Analyses that focused on individual-level phenomena (survival, lifespan of non-survivors, and time to emergence) were conducted using individual seedlings as experimental units. Rings served as the replicates in all population-level analyses (percent emergence and percent recruitment).

Cox's regression (Cox 1972) was used to analyze survival patterns and to detect parameters that influenced survival. Cox's regression is a semiparametric method of survival analysis that combines a maximum partial likelihood estimation method with a proportional hazards model. Like other survival analysis methods, Cox's regression relies on a probabilistic approach that incorporates the timing of mortality into model construction and therefore allows estimates of survival patterns over time. Cox regression models were used to analyze the effect of planting date, species, and cohort on survival. In addition, the relationship between soil moisture availability and survival was assessed with post-hoc tests using Cox regression models. Soil moisture content at each of five depths was incorporated into models as a time-dependent covariate using a cumulative index of soil moisture evaluated throughout the lifespan of the seedlings. The cumulative soil moisture index was constructed by sequentially adding the daily 6:00 a.m. volumetric soil moisture content values for each of the five depths. Subsequently, Cox regression models evaluated the effect of soil moisture availability on the survival of individual seedlings.

Planting date was randomly assigned within each block, and species were randomly assigned to a row within each planting date plot. Each species row contained three rings that had identical species/planting date treatment combinations. Therefore, although the locations of planting date and species were randomized, the location of the individual rings was not assigned at random. As such, caution must be exercised in the extension of these results to other sites due to the potential confounding effects of pseudoreplication.

RESULTS

A total of 762 seedlings emerged during the period between 28 June 1994 and 15 October 1994. Two of the nine species planted (plains bristlegrass and bush muhly) produced a total of five seedlings each, and were excluded from further analysis due to insufficient sample sizes. Therefore, 752 seedlings were retained for statistical analyses.

Rainfall and Soil Moisture Patterns

Soil moisture patterns detected at the 1-3 cm depth were used as a proxy for rainfall patterns. The soil water potential of the sandy loam at this site is -1.5 megapascals (MPa) at a volumetric soil moisture content of 0.0627 (Roundy et al. 1997). This value was considered a threshold value, below which the soil was considered dry, and above which the soil was considered wet. Seeds planted on 28 June experienced soil water potentials below -1.5 MPa for 25 days before sufficient rain fell to raise soil water potential above -1.5 MPa (Fig. 3.1). At the 1-3 cm depth, the wet-dry pattern for four weeks following the initial rain event was 3 days wet, 2 days dry, 5 days wet, 6 days dry, 2 days wet, 3

days dry, and 14 days wet. Seeds planted on 10 August experienced a very different soil water availability pattern. Seeds were in dry soil for only three days before sufficient rain fell to raise soil water potentials above -1.5 MPa. At the 1-3 cm depth, the wet-dry pattern for four weeks following the initial rain event was 14 days wet, 5 days dry, 5 days wet, 3 days dry, 5 days wet. Thus, in the first two weeks following the initial rain event, seeds from the 28 June planting were exposed to two wet-dry cycles, whereas seeds from the 10 August planting were exposed to 14 consecutive days with soil moisture above the threshold level.

Emergence

Seedling emergence varied among species and with planting date (P = 0.06), but did not vary with the interaction of planting date and species (Table 3.2). Emergence of sideoats grama (mean = 71.3%) was greater than that of all other species, which varied between 11.1 and 19.1% for Arizona cottontop and plains lovegrass, respectively (Fig. 3.2). Mean emergence from the 28 June planting was more than twice the percent emergence from the 10 August planting (31.6 and 15.2%, respectively) (Fig. 3.2).

Time to emergence following initial rainfall varied among species, but did not vary with planting date or the interaction of planting date and species (Table 3.2). Time to emergence varied between 7.2 and 24.4 days for sideoats grama and plains lovegrass, respectively (Fig. 3.3). Time to emergence following the 28 June planting did not differ from that of the 10 August planting (16.2 and 10.9 days, respectively) (Fig. 3.3).

The number, size, and timing of emergent cohorts varied among species on both the 28 June planting (Fig. 3.4) and the 10 August planting (Fig 3.5). For example, most sideoats

grama seedlings emerged in the first few cohorts following the first rainfall, whereas more but smaller cohorts of Lehmann lovegrass seedlings emerged over a longer period of time after initiation of precipitation.

Mortality

Lifespan of seedlings that died during the observation period (non-survivors) did not vary with planting date or species (Table 3.2). Lifespan of non-survivors (11.4 days) varied between 2 and 80 days (Fig. 3.6). However, mean values are sensitive to outliers, whereas median values are relatively robust measures of central tendency when distributions are skewed. The median lifespan of all non-surviving seedlings was five days, and nearly 70% of non-surviving seedlings died within 10 days of emergence, confirming the influence of long-lived individuals on the mean values (Fig. 3.6).

Survival

Planting date, species, emergence cohort, and block affected survival of emerged seedlings (Table 3.3). Survival of emerged seedlings was 50 and 65% for the 28 June and 10 August plantings, respectively. Among species, survival of emerged seedlings varied between 20.7 to 77.5% for Cochise lovegrass and cane beardgrass, respectively. Cohort and planting date were necessarily auto-correlated, and were therefore incorporated into separate survival models. When data from different planting dates were analyzed separately, survival differed among species on both planting dates. Survival of emerged seedlings varied between 12.2 and 79.2% in the 28 June planting for Cochise lovegrass and cane beardgrass, respectively; following the 10 August planting, survival of emerged seedlings varied between 29.4 and 88.9% for Arizona cottontop and green sprangletop,

respectively (Fig. 3.7). Furthermore, when the data were analyzed separately by planting dates, emergence cohort affected survival in the 28 June planting, but not in the 10 August planting. When species were considered independently in the 28 June planting, cohort affected survival of Lehmann lovegrass and Cochise lovegrass (Table 3.4). Survival function estimates for the largest cohorts of each species in the 28 June planting illustrate differences in mortality rates among the species and cohorts (Figs. 3.8 and 3.9).

Post-hoc tests of the effects of cumulative soil moisture evaluated throughout the lifespan of individual seedlings were conducted using three models: a single model in which the planting dates were combined, and two subsequent models in which planting dates were considered separately (Table 3.5). When planting dates were considered in a single model, effects of soil moisture on survival were evident at 1-3, 4-6, 8-10, and 12-14 cm; soil moisture at 18-20 cm did not affect survival. When planting dates were assessed with separate models, soil moisture effects on survival were found at 1-3, 4-6, 8-10, and 12-14 cm in the 28 June planting. Cumulative soil moisture at the 18-20 cm depth did not affect survival of seedlings in the 28 June planting; in the 10 August planting soil moisture effects were not evident at any depth.

Recruitment

Recruitment of individuals that produced tillers (with or without reproductive structures) varied among species, but did not vary with planting date or the interaction of planting date and species (Table 3.2). Recruitment varied between 2.4 and 43.6% for Cochise lovegrass and sideoats grama, respectively (Fig. 3.10). Mean recruitment from the 28 June planting was nearly twice that of the 10 August planting (14.3 and 8.8%, respectively) (Fig 3.6).

Recruitment of individuals with reproductive structures may have important implications for future plant population dynamics due to the influx of seed to the existing seedbank. Recruitment of reproductive individuals varied among species, but did not vary with planting date or the interaction of planting date and species (Table 3.2). Green sprangletop exhibited higher recruitment of reproductive individuals than other species (8.2%), while plains lovegrass exhibited the lowest recruitment (0.4%) (Fig. 3.11). Mean recruitment of reproductive individuals from the 28 June planting was more than three-fold greater than that of the 10 August planting (5.4 and 1.6%, respectively) (Fig 3.11).

Block Effects

Blocks represented a large source of variation for survival (Table 3.3). Rings were backfilled with off-site soil to a depth of 10 cm, yet inherent soil differences among blocks may have been present below 10 cm. Post-hoc analyses of soil particle-size distribution at 5-, 15-, and 25-cm depths were conducted by the hydrometer method of mechanical analysis (Gee and Bauder 1986) to determine the relative uniformity of soil among the three blocks. These analyses revealed that percent sand, silt, and clay varied between blocks and that clay increased with depth (Table 3.6). One block had greater clay and silt and less sand than the other two blocks; the particle-size distribution of soil in the remaining two blocks were similar (Fig. 3.12). The soil profile in the clay-rich block is typical of the Baboquivari series, which is a common inclusion of the Combate-Diaspar association (Breckenfeld and Robinett 1997). Seedling emergence, mean time to emergence, lifespan of non-surviving seedlings, survival, and recruitment from the block with relatively greater clay exceeded that of the other two blocks (data not shown). Relative differences in clay content may have pronounced effects on water holding capacity and the availability of soil water. Thus, differences in life history characteristics detected among blocks may be

explained, at least in part, by differences in soil particle-size distribution between the blocks.

Table 3.1. Common and scientific names of species used in emergence and survival analysis study.

Common Name	Scientific Name	Seed Source
Native:		
Sideoats grama	*Bouteloua curtipendula* (Michx.) Torr.	Native Plants, Inc., Arizona
Green sprangletop	*Leptochloa dubia* (H.B.K.) Nees	Granite Seed Co.,Utah; Texas origin
Cane beardgrass	*Bothriochloa barbinodis* (Lag.) Herter	Tucson Plant Materials Center, Arizona, Natural Resource Conservation Service
Arizona cottontop	*Digitaria californica* (Benth.) Chase	Granite Seed Co.,Utah; Arizona origin
Plains bristlegrass	*Setaria machrostachya* H. B. K.	Granite Seed Co., Utah; Texas origin
Bush muhly	*Muhlenbergia porteri* Scribn.	Collected Jornada Expt. Range, New Mexico
Plains lovegrass	*Eragrostis intermedia* Hitchc.	Native Plants, Inc., Arizona
Non-native:		
Lehmann lovegrass	*Eragrostis lehmanniana* Nees	Native Plants, Inc., Arizona
Cochise lovegrass	*Eragrostis lehmanniana* Nees X *E. tricophera* Coss and Dur.	Native Plants, Inc., Arizona

Table 3.2. Likelihood tests of main effects and interactions of planting date and species for emergence, time to emergence, lifespan of non-survivors, recruitment of all tillered individuals, and recruitment of reproductive individuals of warm-season grasses during the summer rainy season in southeastern Arizona.

Variable	Source	d.f.	F	P
Emergence				
	Planting Date	1	6.64	0.0615
	Species	6	8.86	0.0001
	Planting Date X Species	6	0.90	0.5142
Time to Emergence				
	Planting Date	1	0.26	0.6613
	Species	6	8.22	0.0001
	Planting Date X Species	6	1.90	0.1257
Recruitment **(Tillered and Reproductive)**				
	Planting Date	1	1.74	0.3179
	Species	6	7.10	0.0002
	Planting Date X Species	6	0.10	0.9960
Recruitment **(Reproductive only)**				
	Planting Date	1	7.51	0.1113
	Species	6	2.53	0.0484
	Planting Date X Species	6	0.56	0.7606
Lifespan of Non-Survivors				
	Planting Date	1	2.95	0.1613
	Species	6	0.87	0.5387
	Planting Date X Species	6	1.74	0.1694

Table 3.3. Summary of Cox regression models of the effects of block, planting date, species, and emergence cohort on seedling survival of warm-season grasses during the summer rainy season in southeastern Arizona. Both planting dates were incorporated into a single model, and subsequent models considered the 28 June and 10 August planting dates separately.

Model	Depth	df	χ^2	P
28 June and 10 August **Planting Dates in Full Model**				
	Block	1	4.36	0.0367
	Planting Date	1	9.81	0.0017
	Species	1	68.52	0.0001
	Emergence Cohort	1	35.76	0.0001
28 June Planting Date **in Reduced Model**				
	Block	1	0.20	0.6508
	Species	1	69.75	0.0001
	Emergence Cohort	1	22.11	0.0001
10 August Planting Date **in Reduced Model**				
	Block	1	0.23	0.6322
	Species	1	27.72	0.0001
	Emergence Cohort	1	2.00	0.1571

TABLE 3.4. Emergence date, number of emerged seedlings, and percent survival[1] of emergence cohort within species from the 28 June planting for warm-season grasses seeded during the summer rainy season in southeastern Arizona.

EMERGENCE DATE	SIDEOATS GRAMA		GREEN SPRANGLETOP		CANE BEARDGRASS		ARIZONA COTTONTOP		PLAINS LOVEGRASS		LEHMANN LOVEGRASS*		COCHISE LOVEGRASS*		TOTAL*	
	NUMBER	PERCENT SURVIVAL	NUMBER	PERCENT SURVIVAL	NUMBER	PERCENT SURVIVAL	NUMBER	PERCENT SURVIVAL	NUMBER	PERCENT SURVIVAL	NUMBER	PERCENT SURVIVAL	NUMBER	PERCENT SURVIVAL	NUMBER	PERCENT SURVIVAL
25 JUL	5	40.0	0	-	0	-	0	-	0	-	0	-	0	-	5	40.0
27 JUL	77	71.4	0	-	0	-	9	55.6	5	0	1	0	0	-	92	65.2
29 JUL	8	75.0	0	-	0	-	5	40.0	0	-	3	66.7	0	-	16	62.5
1 AUG	67	47.8	18	22.2	0	-	10	20.0	15	0	16	25.0	17	5.9	143	30.1
3 AUG	27	48.2	8	75.0	0	-	1	0	1	0	7	14.3	0	-	44	45.5
5 AUG	2	50.0	0	-	0	-	0	-	3	66.7	0	-	1	0	6	50.0
8 AUG	1	0	0	-	0	-	0	-	0	-	0	-	0	-	1	0
10 AUG	0	-	0	-	0	-	0	-	0	-	1	100	0	-	1	100
15 AUG	0	-	1	0	0	-	0	-	0	-	0	-	0	-	1	0
17 AUG	3	100	20	60.0	0	-	0	-	14	35.7	1	0	7	28.6	45	48.9
20 AUG	0	-	5	80.0	40	82.5	4	50.0	0	-	2	100	1	0	52	78.9
23 AUG	8	100	2	0	11	81.8	2	50.0	15	20.0	2	50.0	14	14.3	54	44.4
27 AUG	4	50.0	0	-	2	0	2	50.0	13	53.9	8	87.5	0	-	29	58.6
30 AUG	0	-	0	-	0	-	0	-	5	60.0	2	100	1	0	8	62.5
4 SEP	0	-	1	100	0	-	0	-	1	0	0	-	0	-	2	50.0
17 SEP	0	-	0	-	0	-	0	-	0	-	6	66.7	0	-	6	66.7
20 SEP	0	-	0	-	0	-	0	-	1	0	4	50.0	0	-	5	40.0
24 SEP	0	-	0	-	0	-	0	-	1	100	0	-	0	-	1	100
2 OCT	0	-	0	-	0	-	0	-	0	-	1	0	0	-	1	0
MEAN SURVIVAL	60.4		49.1		79.3		39.4		28.4		48.2		12.2		50.0	
TOTAL EMERGENCE	202		55		53		33		74		54		41		512	
TOTAL NUMBER OF COHORTS	10		7		3		7		11		13		6		19	
COHORTS WITH >1 SEEDLING	9		5		3		6		7		9		3		14	

* denotes significant effect of emergence date on survival at P < 0.05 level.

[1] percent survival to end of observation period

Table 3.5. Summary of Cox regression models of the effects of cumulative soil moisture at five depths (1-3, 4-6, 8-10, 12-14, and 18-20 cm) on seedling survival of warm-season grasses during the summer rainy season in southeastern Arizona. Cumulative soil moisture was evaluated throughout the lifespan of the individual seedlings. Both planting dates were incorporated into a single model, and subsequent models considered the 28 June and 10 August planting dates separately.

Model	Depth	df	χ^2	P
28 June and 10 August				
Planting Dates in Full Model				
	1 - 3 cm	1	37.44	0.0001
	4 - 6 cm	1	24.88	0.0001
	8-10 cm	1	17.86	0.0001
	12-14 cm	1	11.54	0.0007
	18-20 cm	1	2.30	0.1297
28 June Planting Date				
in Reduced Model				
	1 - 3 cm	1	35.64	0.0001
	4 - 6 cm	1	20.87	0.0001
	8-10 cm	1	17.53	0.0001
	12-14 cm	1	10.41	0.0013
	18-20 cm	1	1.99	0.1582
10 August Planting Date				
in Reduced Model				
	1 - 3 cm	1	0.45	0.5039
	4 - 6 cm	1	1.44	0.2304
	8-10 cm	1	0.16	0.6884
	12-14 cm	1	0.32	0.5711
	18-20 cm	1	0.003	0.9542

Table 3.6. Analysis of variance of main effects and interactions of block and depth on percent sand, percent silt, and percent clay fractions of the soil at the site into which warm-season grasses were seeded during the summer rainy season in southeastern Arizona.

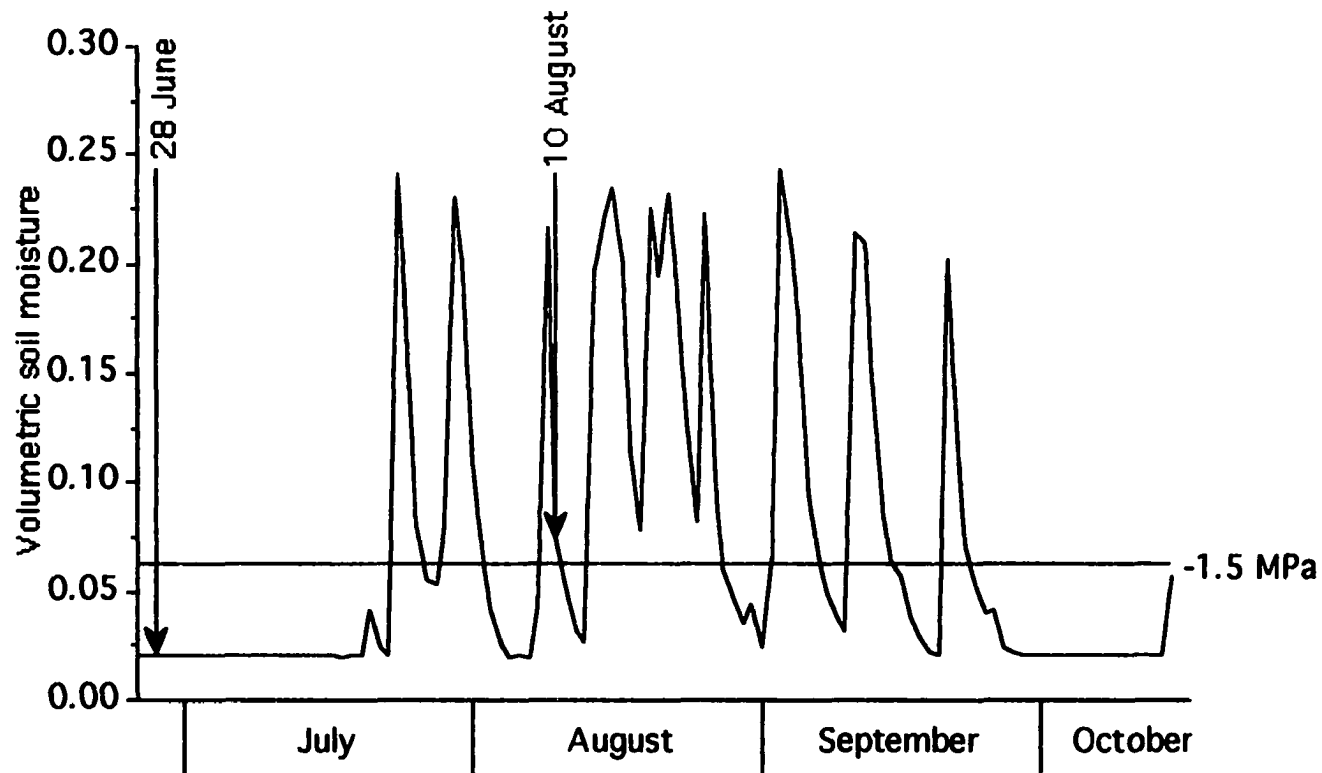| Variable	Source	df	F	P
Sand (%)				
	Block	2	25.00	0.0001
	Depth	2	3.39	0.0563
	Block X Depth	4	0.42	0.7934
Silt (%)				
	Block	2	23.05	0.0001
	Depth	2	1.01	0.3840
	Block X Depth	4	0.95	0.4560
Clay (%)				
	Block	2	29.78	0.0001
	Depth	2	5.81	0.0113
	Block X Depth	4	0.90	0.4833

Figure 3.1. Soil moisture availability at 1-3 cm from Santa Rita Experimental Station field site between 26 June and 15 October 1994. Volumetric soil moisture (Vol/Vol) is reported. Arrows along horizontal axis delineate monthly increments. Arrows pointing to soil moisture line indicate the soil moisture values at the time of the 28 June and 10 August plantings. Horizontal line across graph indicates volumetric soil moisture (0.0627) at which soil water potential is -1.5 MPa.
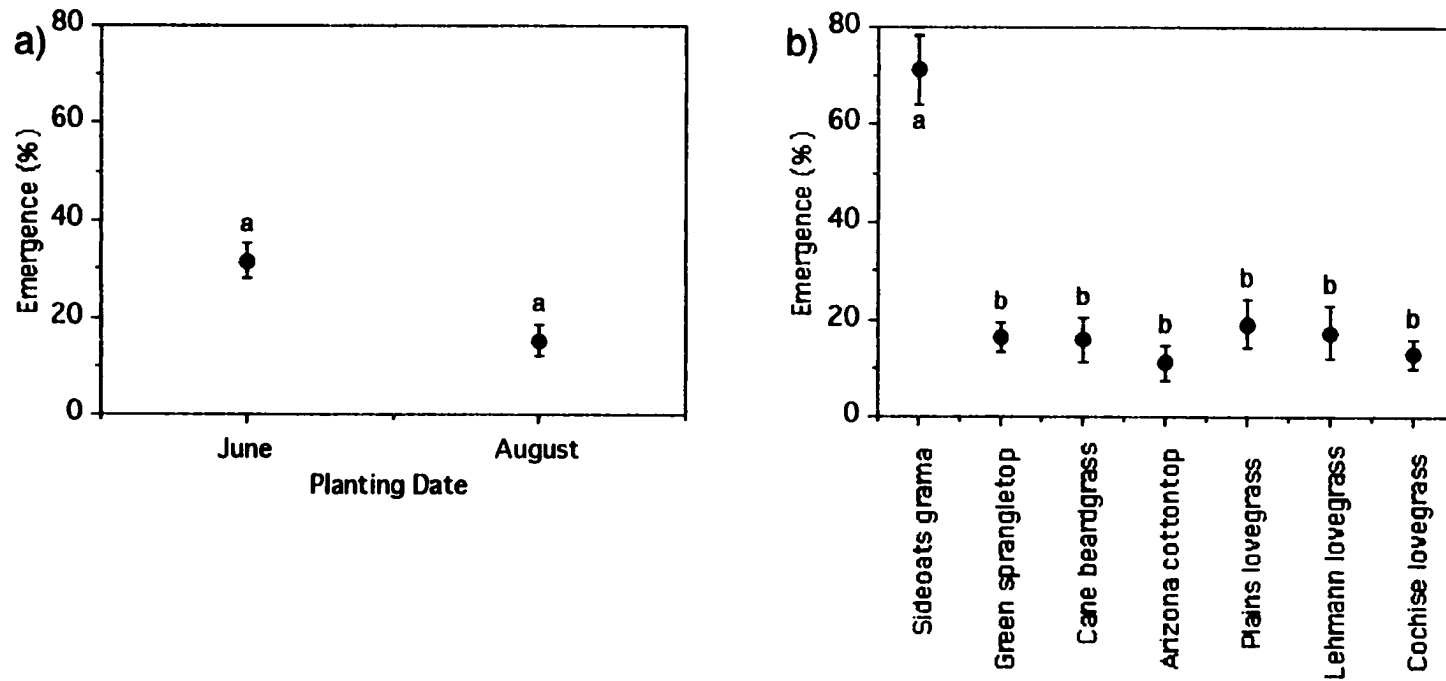
74

Figure 3.2. Mean total seedling emergence by planting date (a) and species (b), as a percentage of number of seeds sown for warm-season grass species seeded on two dates during the summer rainy season in southeastern Arizona. Error bars represent standard errors of the means. Means identified with the same lowercase letter are not different (P > 0.05).
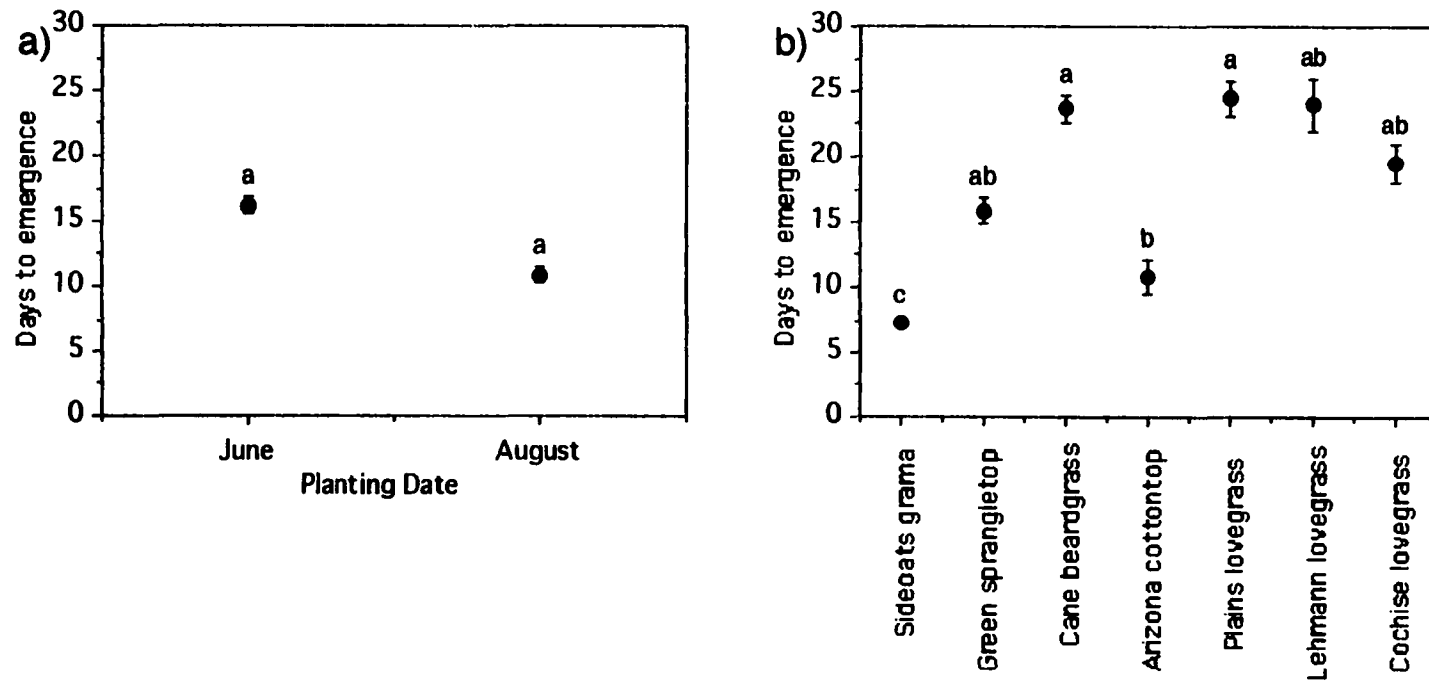
Figure 3.3. Mean time to seedling emergence from initial rainfall event to emergence event for warm-season grass species seeded on two dates during the summer rainy season in southeastern Arizona. Error bars represent standard errors of the means. Means identified with the same lowercase letter are not different (P > 0.05).

Figure 3.4. Emergence patterns of warm-season grass species seeded on 28 June in southeastern Arizona. Bars represent the percent of total emergence for each species that emerged on a specific day. The total number of seedlings that emerged for each species is shown in the upper left corner of each graph. Time is shown on the horizontal axis; zero indicates the initial rain event on 24 July.

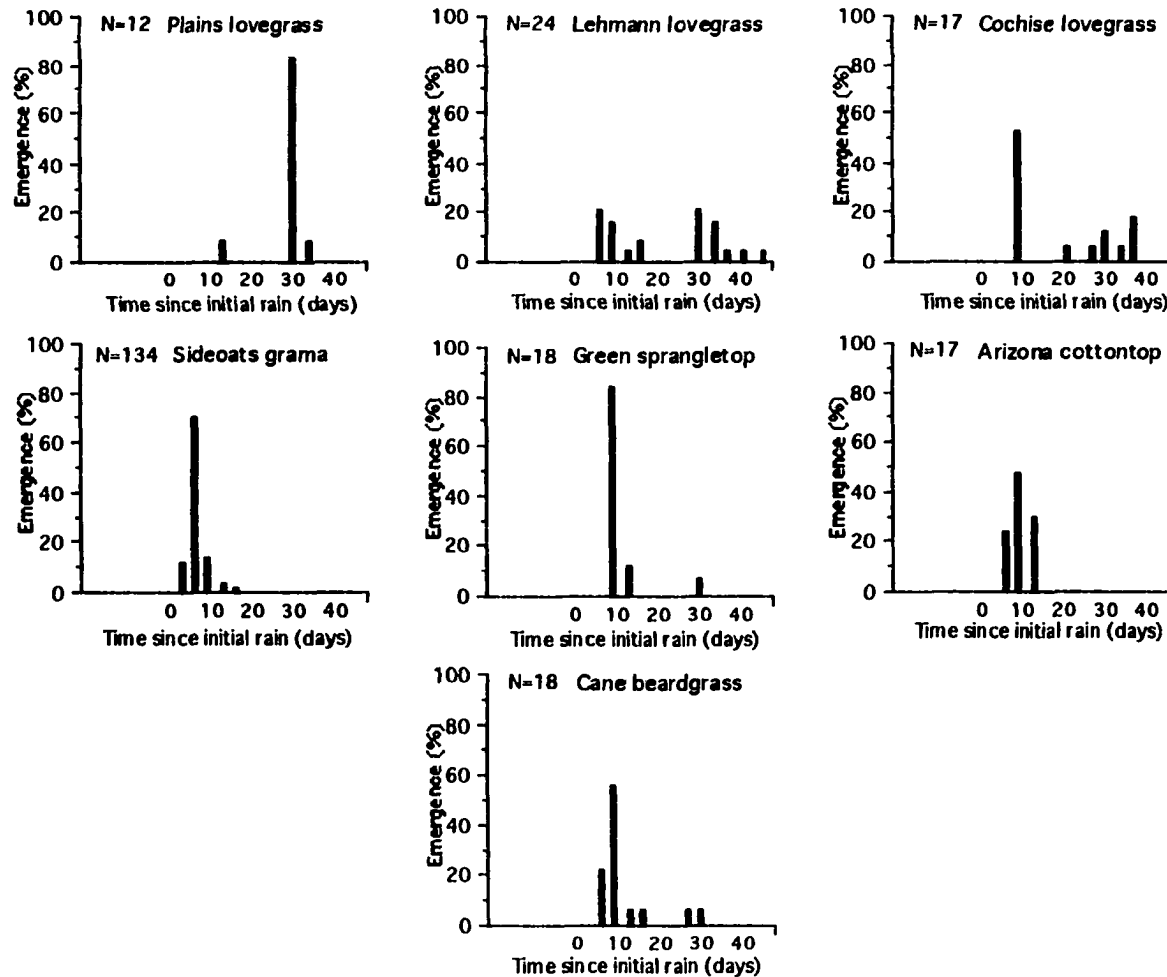Figure 3.5. Emergence patterns of warm-season grass species seeded on 10 August in southeastern Arizona. Bars represent the percent of total emergence for each species that emerged on a specific day. The total number of seedlings that emerged for each species is shown in the upper left corner of each graph. Time is shown on the horizontal axis; zero indicates the initial rain event on 14 August.
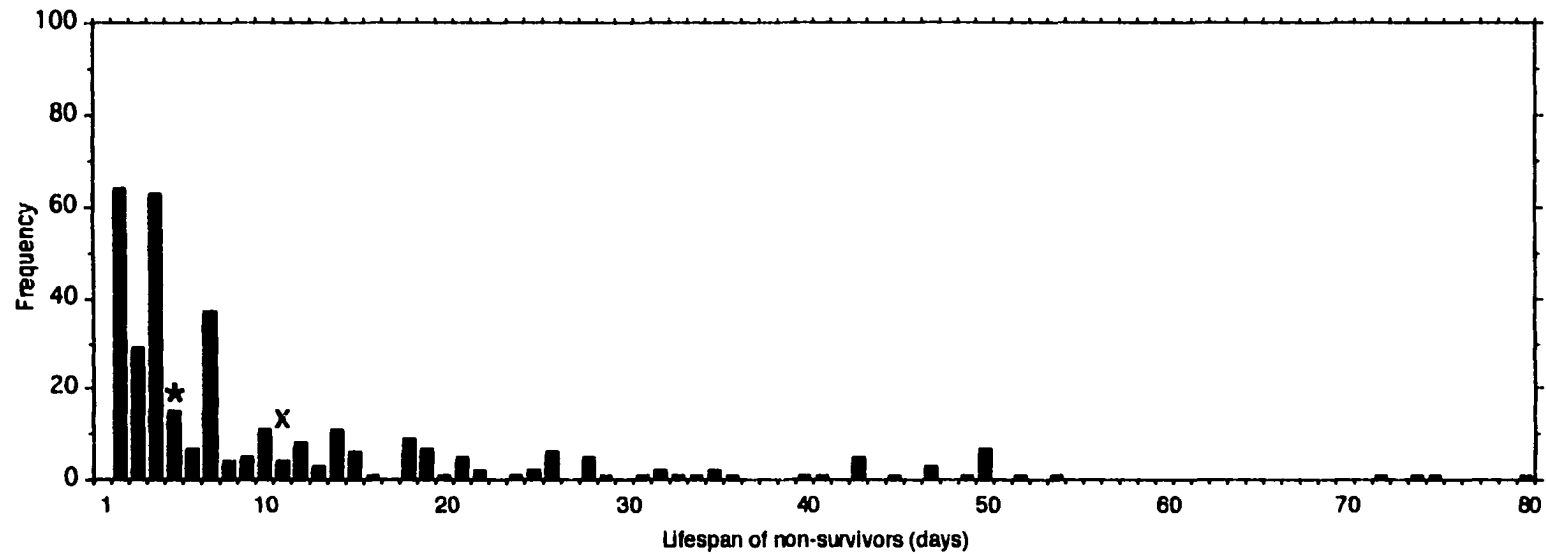
Figure 3.6. Lifespan of non-surviving seedlings of warm-season grasses seeded during the summer rainy season in southestern Arizona. Vertical bars represent the number of seedlings exhibiting a specific lifespan after emergence. Mean (x) and median (*) values indicated.
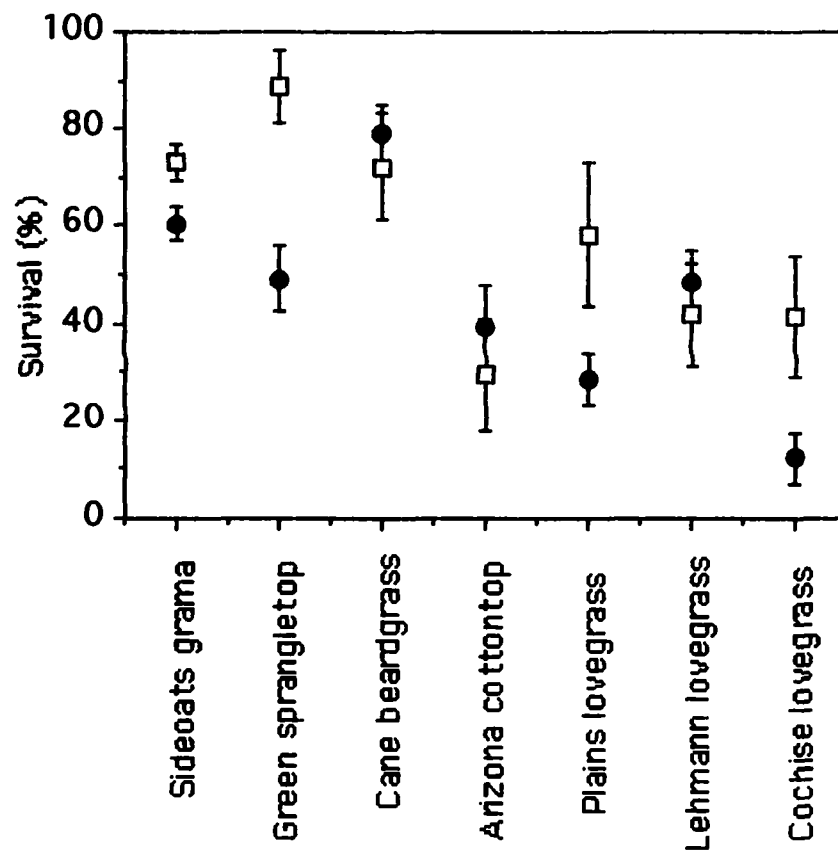
Figure 3.7. Mean survival of seedlings for the 28 June planting (solid circles) and the 10 August planting (open squares), as a percentage of emerged seedlings for warm-season grass species seeded on two dates during the summer rainy season in southeastern Arizona. Error bars represent standard errors of the means.
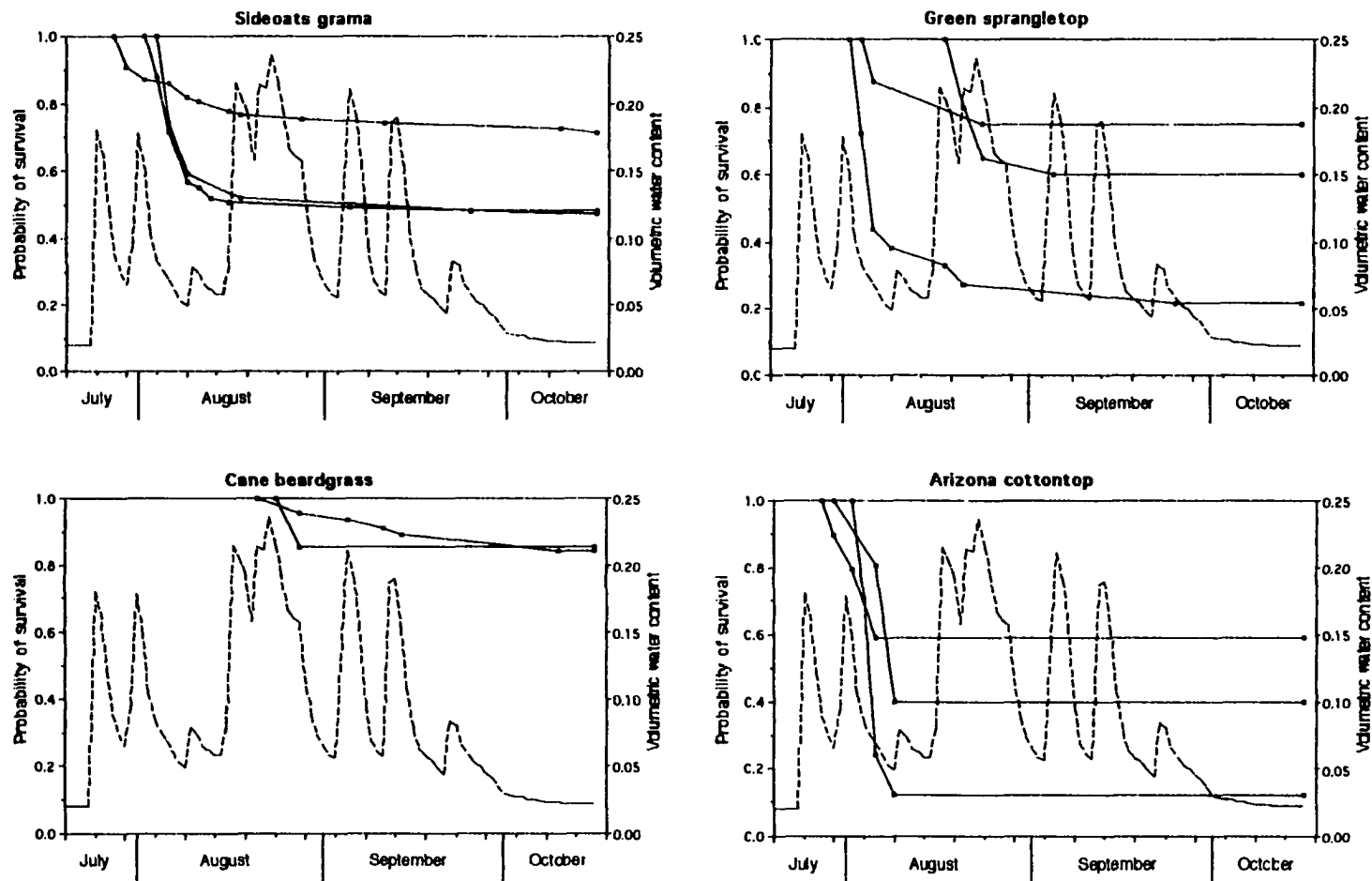
Figure 3.8. Survivor function estimates of the largest cohorts of four native warm-season grass species seeded on 28 June. Each cohort represents at least 10% of the total number of seedlings emerged for each species. Volumetric soil moisture content at 8-10 cm is represented by dashed line (no plot symbol).
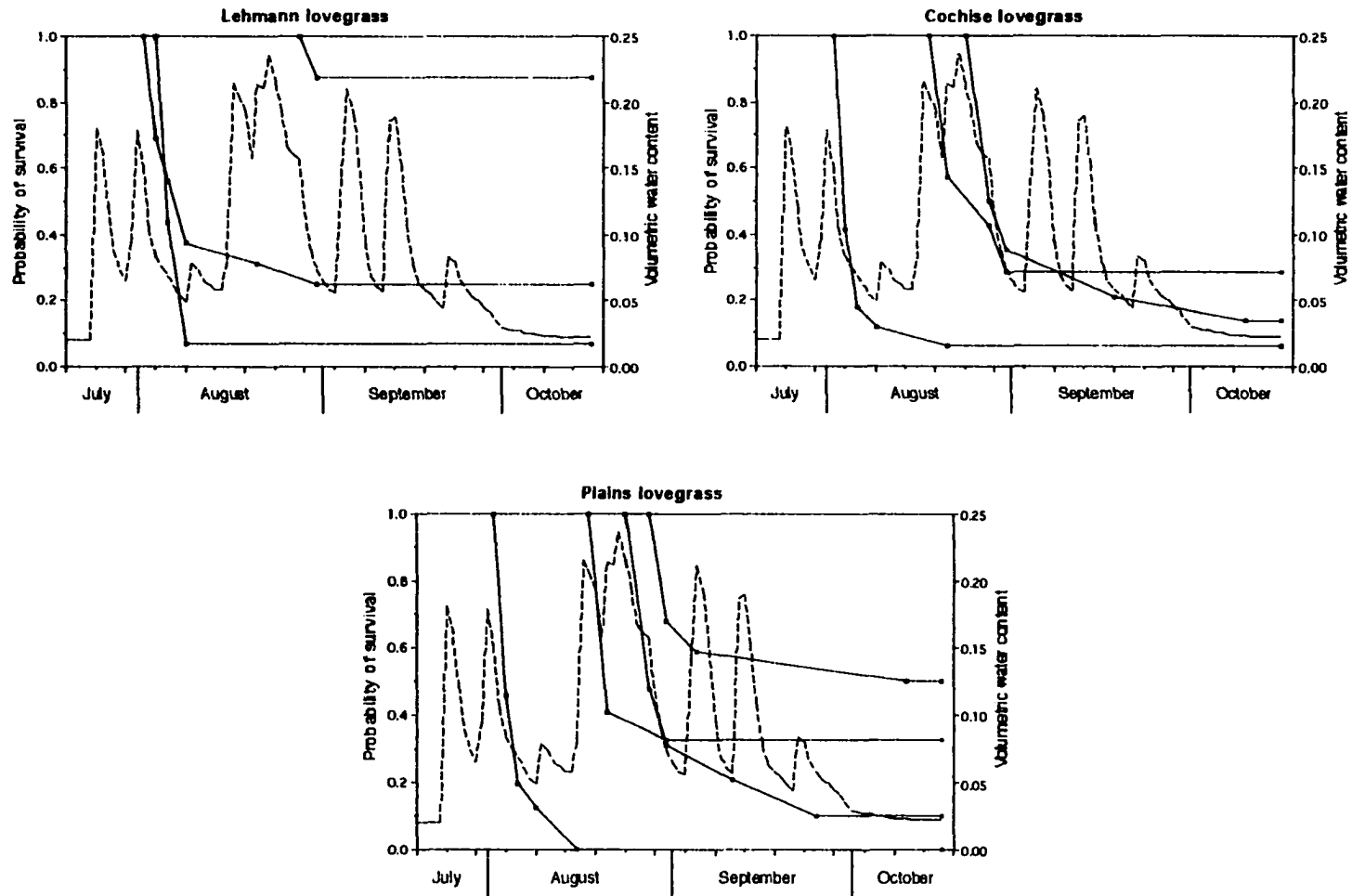
Figure 3.9. Survivor function estimates of the largest cohorts of three warm-season grass species (*Eragrostis* spp.) seeded on 28 June. Each cohort represents at least 10% of the total number of seedlings emerged for each species. Volumetric soil moisture content at 8-10 cm is represented by dashed line (no plot symbol).
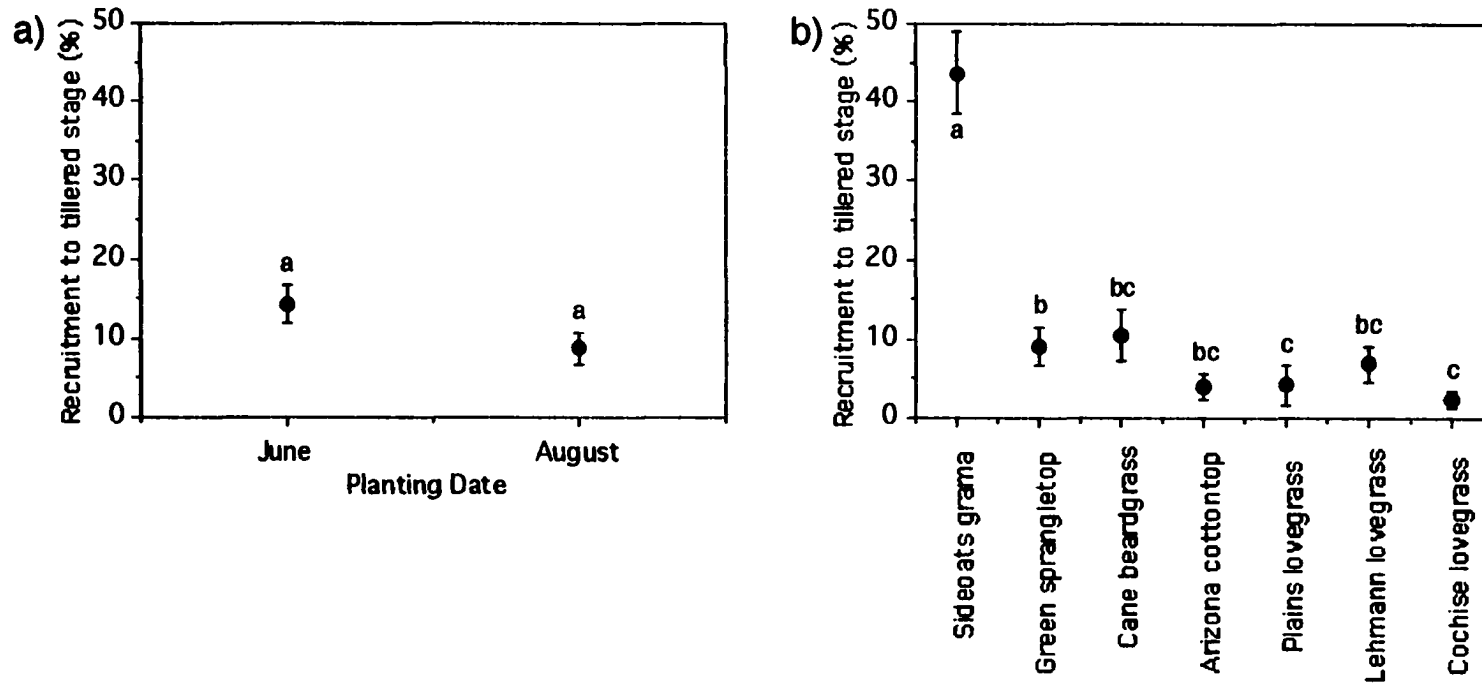
Figure 3.10. Mean recruitment of all tillered individuals (non-reproductive and reproductive) for different planting dates (a) and species (b), as a percentage of number of seeds sown for warm-season grass species seeded on two dates during the summer rainy season in southeastern Arizona. Error bars represent standard errors of the means. Means identified by the same lowercase letter are not different (P > 0.05).
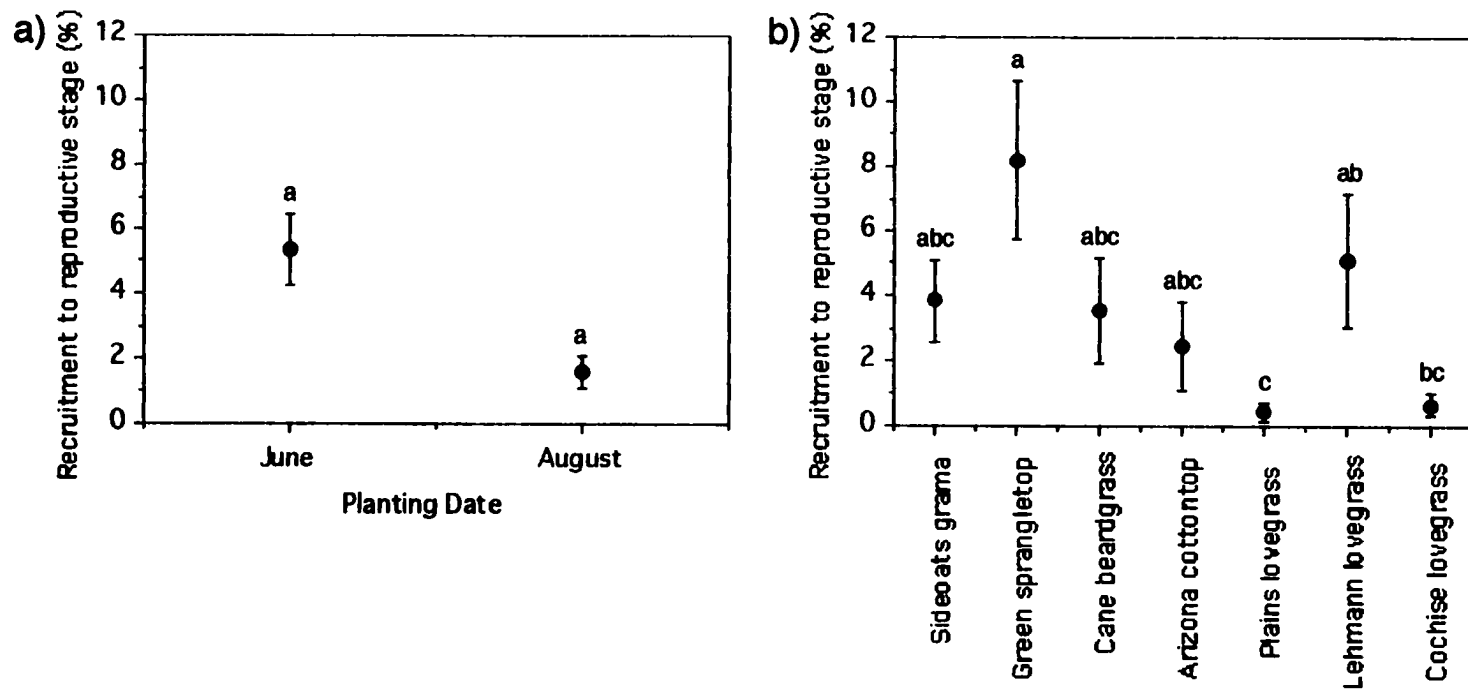
Figure 3.11. Mean recruitment of reproductive individuals for different planting dates (a) and species (b), as a percent of number of seeds sown for warm-season grass species seeded on two dates during the summer rainy season in southeastern Arizona. Error bars represent standard errors of the means. Means identified by the same lowercase letter are not different (P > 0.05).

Figure 3.12. Mean particle-size distribution of sand, silt, and clay fractions of the soil in three blocks at the site into which warm-season grasses were seeded during the summer rainy season in southeastern Arizona. Error bars represent standard error of the means. Means within particle size class with the same letter are not different (P > 0.05).

DISCUSSION

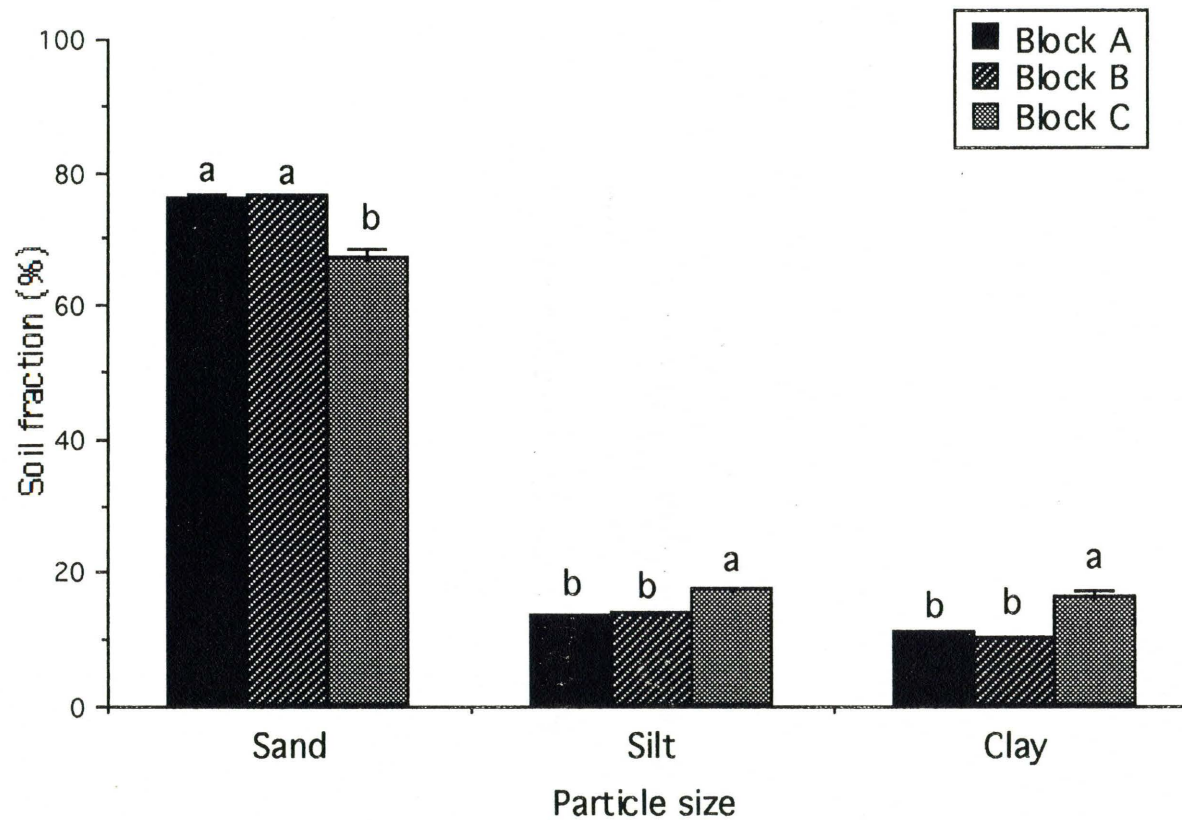Relationships between patterns of emergence, recruitment, and survival were apparent in many cases. Patterns of emergence varied among species and were affected by planting date for some species. In addition, survival of early cohorts was high for some species whereas later cohorts had greater survival for other species. Thus, differences among species and their response to environmental conditions have the potential to greatly affect the success of revegetation efforts.

Statistical analyses provide a framework for objective decision-making, but interpretation of results remains subjective and discretionary (Warren 1986). For emergence, the effect of planting date was large but not significant at the 0.05 level (P = 0.06). The lack of significance may be due, at least in part, to the split plot arrangement of the experimental design, which tends to provide more precise information on the subplot factor at the expense of the whole plot factor (Sokal and Rohlf 1981). The ability to detect effects of planting date may be further diminished by the ranking procedure. A lack of statistical significance does not preclude biological significance (Warren 1986), and failure to recognize the effects of experimental design and data manipulation could result in a failure to acknowledge that for some response variables, the effect of planting date may have biological significance and substantial implications for revegetation practices.

Emergence

Differences in patterns of emergence and cumulative emergence should be considered in terms of the germination process and species responses to soil moisture availability. Water uptake processes and species-specific requirements for exposure to threshold water

potentials (base water potential) for a minimum time period (hydrotime) affect emergence as well as germination (see Chapter 2). Emergence response is inextricably linked to germination response due to the natural sequential order of these events; germination must precede seedling emergence, and therefore patterns of emergence likely reflect germination patterns. Successful emergence may only occur if previous soil moisture conditions promoted seed germination and subsequent growth of the heterotrophic seedling. Therefore, it is a reasonable assumption that seedling emergence indicates species-specific requirements for germination were met (see Chapter 2).

Time to emergence and patterns of emergence reveal differences between species that have important consequences for recruitment and survival. Seeds from the 28 June planting experienced more wet-dry cycles in the first four weeks than did seeds from the 10 August planting. In general, species produced more cohorts in the 28 June planting relative to the 10 August planting. Overall, sideoats grama exhibited the shortest mean time to emergence and produced few, relatively large cohorts. Arizona cottontop and green sprangletop also had relatively rapid emergence times, with the largest cohorts emerging within the first 10 days following the initial rain; this pattern was also observed for cane beardgrass in the 10 August planting only. In contrast to these rapidly emerging species, time to emergence of the lovegrasses was relatively long. The observed emergence times for these species generally reflect relative germination rates determined in growth chamber studies (Roundy and Biedenbender 1996, Adams 1997), in which sideoats grama, green sprangletop, and Arizona cottontop germinated faster than plains lovegrass or Lehmann lovegrass. Furthermore, the rapid, early emergence of sideoats grama in the field agrees with earlier greenhouse and growth chamber studies in which maximum emergence was reached in 2-3 days (Olmsted 1941, Frasier et al. 1984, 1985; Adams 1997) and would be predicted for a species that has a short hydrotime requirement and the potential to germinate at a wide

range of soil water potentials (Adams 1997). Similarly, delayed emergence of Lehmann lovegrass has been observed in previous greenhouse and growth chamber emergence studies (Frasier et al. 1985, 1987; Adams 1997), and is expected for a species that is capable of germinating at a wide range of soil water potentials but has a long hydrotime requirement (Adams 1997). The presence or absence of seed appendages may potentially influence rates of germination and emergence for these species but was not addressed in this study; further investigation is needed to determine the relative effects of seed appendages on these processes under field conditions.

Delayed emergence of Cochise lovegrass (both plantings) and cane beardgrass (early planting only) does not reflect the findings of previous germination rate studies, which indicated that both species germinate quickly under conditions of high water potential (Roundy and Biedenbender 1996, Adams 1997). Cochise lovegrass and cane beardgrass have high base water potential requirements (-0.09 and -0.06 MPa, respectively; Adams 1997) and thus delayed emergence may reflect delayed germination if moisture availability at the depth of the seeds became limiting. In addition, Cochise lovegrass has exhibited delayed emergence in previous studies (Frasier et al. 1984, 1985, 1987; Adams 1997), which suggests that the lag period between germination and emergence is often longer than the lag period of other species. Cane beardgrass emergence patterns varied widely between the two planting dates, resulting in a large difference in mean time to emergence for the early and late planting dates (27.9 and 11.1 days, respectively). After the 10 August planting the first cohort of cane beardgrass emerged within six days of the first rain, but in the 28 June planting, the first seedlings of cane beardgrass emerged 27 days following the first rain (the first seedlings of cane beardgrass from both plantings emerged on the same day). This pattern of delayed emergence for cane beardgrass observed in the early planting is in direct contrast with germination patterns detected in earlier studies of seed fate, in

which nearly all cane beardgrass seeds germinated following the initial rain event, and the species did not display increased germination following a drying sequence (see Chapter 2). However, after the initial rain event of the 28 June planting, I observed several cane beardgrass seeds that had germinated and produced 15 cm-long roots without producing shoots in a separate, concurrent field study. Therefore, it is likely that the first cohort of cane beardgrass seedlings from the 28 June planting actually germinated in response to initial rain events, but did not produce shoots and emerge until wet soil conditions returned in mid-August. Thus, a well-developed root system at the time of emergence may help explain the relatively low mortality of cane beardgrass associated with the 28 June planting.

Lovegrasses produced numerous cohorts, but each cohort was relatively small. Lehmann lovegrass seeds tolerate multiple wetting/drying cycles without detrimental effects on subsequent germination (Wilhelm 1969). Greenhouse studies on the effects of wet-dry-wet cycles showed that Lehmann lovegrass and Cochise lovegrass emergence is frequently greater during the second wet period than during the first wet period (Frasier et al. 1985). Field emergence patterns of Lehmann lovegrass, Cochise lovegrass, and plains lovegrass described here show not only a tendency for substantial emergence following the first wet-dry cycle, but the ability of these species to produce multiple cohorts following multiple wet-dry cycles. This tendency to produce several cohorts over a relatively long period may affect survival of these species by spreading their risk of mortality through time. Indeed, species that produce both early- and late-germinating seeds tend to be favored in variable environments (Venable 1989).

Given the long initial period of moist soil conditions following the 10 August planting, it was unexpected that the total emergence from the 28 June planting was more than twice the total emergence from the 10 August planting. Exposure to high soil temperatures and the

influence of alternating temperature and moisture conditions provide potential explanations

for this pattern. In the 26 days between the 28 June planting and the first rainfall, the

maximum soil temperature at 1 cm depth averaged 48.9 ° C and the difference between

diurnal maximum and minimum temperatures averaged 23.9 ° C (data not shown); in 17 of

the first 20 days after planting the maximum temperature at that depth exceeded 50 ° C.

Exposure to high temperatures and high fluctuations in temperature under dry soil

conditions effectively breaks dormancy, and subsequently increases germination and often

germination rate in a several species (Weaver and Jordan 1985, Baskin and Baskin 1989,

Simpson 1990); however, exposure to excessively high temperatures also may induce

secondary dormancy in some grass species (Simpson 1990). Increased germination has

been attributed to increased seed coat permeability following dry heat treatments for some

grasses and legumes (Haferkamp and Jordan 1977, Simpson 1990, Williams and Elliott

1960, Quinlivan 1966, McKeon and Mott 1982). In addition to temperature effects in dry

soil, exposure to alternate wetting and drying at high temperatures has also been associated

with increased seed coat permeability (Baskin and Baskin 1974, 1989). Furthermore,

temperature fluctuations under moist soil conditions have resulted in greater germination for

both warm- and cool-season grasses (Roundy et al. 1992b, Young et al. 1987, Probert et

al. 1986). In contrast to conditions following the 28 June planting, seeds planted on 10

August were exposed to dry soil for only four days before the initial rain event, during

which time the maximum soil temperature at 1 cm depth averaged 43.3 ° C, while the

difference between maximum and minimum temperatures in a 24-hr period averaged 19.9°

C (data not shown). In addition, the initial period of wet soil conditions persisted for 14

consecutive days before the first dry period occurred. Thus, a combination of prolonged

exposure to high soil temperatures and alternate wetting and drying may have enhanced

germination and therefore emergence following the 28 June planting relative to the 10

August planting.

Total emergence also varied among species. Emergence of sideoats grama (71%) was at least 3.5 times greater than that of the other species. Seed age potentially affects emergence; seeds of all species varied in age, yet with the exception of sideoats grama, this variability was not obviously correlated with emergence. The sideoats grama seed used in this study had been recently purchased from a commercial seed supplier; it is possible that the seed had not completed its after-ripening period at the time PLS percentage was determined in the germination chamber. For example, exposure to high temperatures such as those experienced by the seeds planted in June shortens the after-ripening period for sideoats grama seeds (Coukos 1944, Sumner and Cobb 1962). Furthermore, Major and Wright (1974) demonstrated that adding soil to sideoats grama seeds during germination experiments broke seed dormancy and increased total germination. Therefore, the estimation of sideoats grama PLS percentage may have been low, resulting in relatively more germinable sideoats grama seeds planted relative to the other species. However, although there were large differences in emergence within and among species, the general trend of higher emergence in the first planting than the second planting was seen in all species. Thus, while not dispelling the relative importance of dormancy and seed age on emergence, this trend supports the suggestion that planting date effects are largely due to environmental differences experienced by the seeds after planting.

Mortality

In general, the majority of seedling mortality occurred in the first week after emergence: the median lifespan of non-survivors was five days. All species exhibited high rates of mortality within the first few days after emergence, as evidenced by cohort survival curves that were very steeply sloped in the first few days after emergence (Figs. 3.8 and 3.9).

Survival decreased as the availability of soil moisture at 0-14 cm decreased. Thus, seedling mortality occurred primarily when seedlings were very young, which is consistent with results of other studies in which seedling mortality occurred during dry periods immediately following emergence (Olmsted 1941, Frasier 1989, Frasier et al. 1984, 1985, 1987; Elberse and Breman 1990). Differential survival among species is commonly attributed to differences in physiological tolerance or rates of seedling growth and development (Wright and Dobrenz 1973, Wright 1975, Simanton and Jordan 1986, Roundy et al. 1993). The lifespan of non-surviving seedlings did not vary among species, which suggests that seedlings are most vulnerable to mortality within the first week after emergence despite species-specific differences in development or physiology. Before development of adventitious roots seedlings rely exclusively on seminal roots for water delivery to the plant (Wilson et al. 1976, Simanton and Jordan 1986); if root growth rates are slower than the rate at which soil dries, the seedling is vulnerable to mortality through desiccation (Frasier and Simanton 1987, Roundy et al. 1997). Further studies under field conditions are required to determine the relationship between seedling root growth, rates of water loss from the soil surface, and seedling mortality (Roundy et al. 1997).

Survival and Recruitment

A comprehensive discussion of survival must consider recruitment at the end of the observation period and differences in patterns of survival. Considered in the form of a simplified, conceptual model, recruitment is the product of germination and survival. Survival analysis indicated that planting date, species, and emergence cohort affected patterns of survival. Differential survival and recruitment patterns among species may be related to species-specific differences in emergence patterns that reflect emergence rate, the tendency to produce few or many cohorts, and differences in seedling growth and

development. Furthermore, survival of individuals through the first growing season may depend on these species-specific characteristics within the context of environmental variability. Thus, both environmental conditions and early life history strategies that result in different germination, emergence, and seedling growth patterns have the potential to affect survival and recruitment.

The overall greater survival from the 10 August planting can be explained by the relatively long period of soil moisture available to seedlings after emergence. Of the 240 seedlings that emerged from the 10 August planting, nearly 85% emerged during the initial 14-day period of wet soil conditions, and 70% of that initial group of seedlings survived to the end of the observation period. Of the 512 seedlings that emerged from the 28 June planting, 60% emerged in the first 14 days following the first rain. This 14-day period included two wet-dry cycles, and only 45% of the seedlings that emerged during that period survived to the end of the observation period. However, seedlings that emerged in the first three cohorts (25 July, 27 July, and 29 July) had 64% survival, whereas seedlings that emerged just prior to or during the 6-day dry period (emergence dates 1 August, 3 August, 5 August, and 8 August) exhibited 34% survival. Cohort identity and cumulative effects of soil moisture influenced seedling survival only for the first planting. It is likely that reduced availability of soil moisture during the 6-day dry period was a factor in the low survival of these cohorts. In contrast, a more continuous period of high soil moisture would allow seedlings to develop root and shoot systems with minimal moisture or temperature stress. Such a period of high soil moisture would be most beneficial to those species that emerge primarily in early cohorts (e.g., sideoats grama, green sprangletop, cane beardgrass, and Arizona cottontop), and provides a reasonable explanation for high survival of those species characterized by relatively large cohorts shortly after the initial rain in both plantings. However, species that emerged large cohorts immediately after the first

rain probably would have experienced greater mortality if the first dry period had been longer than two days.

Frasier et al. (1985) proposed two scenarios of soil moisture that may favor grass seedling survival following planting: 1) an initial wet period of short duration which results in low germination and emergence enables ungerminated seeds to survive the following dry period and then germinate in response to subsequent rains; or 2) an initial wet period of sufficient duration such that seedlings develop adequate root systems and vigor thus enabling them to survive subsequent dry periods. Recently germinated sideoats grama survived short periods of desiccation to a greater extent than Lehmann lovegrass or Cochise lovegrass, but differences in survival between these species were not detected after approximately three days of desiccation in growth chamber studies (Frasier 1987, Adams 1997). Thus, a species that germinates quickly has a decreased ability to survive unless initial conditions of limited moisture availability are relatively brief. For example, emergence of sideoats grama was lower than that of Lehmann lovegrass and Cochise lovegrass after a growing season characterized by high rainfall; the low establishment of sideoats grama was attributed to a 12-day dry period following the initial rain event, which likely resulted in mortality of germinated, unemerged sideoats grama seeds (Winkel and Roundy 1991). Therefore, the interactive effects of moisture availability patterns and germination rates apparently account for some of the observed differences in recruitment among species.

Depending on the timing and frequency of rain events, species that tend to produce multiple cohorts of seedlings may have an advantage in certain years. Over the course of a growing season, episodic rain events that produce variable soil moisture conditions may result in high mortality for some cohorts but not others. For example, in a greenhouse study on the effects of initial wet-dry sequences (Frasier et al. 1985), early cohorts of sideoats grama

experienced 34 to 60% mortality after the initial wet period and later cohorts accounted for 6 to 10% of surviving seedlings. In contrast, early wet periods of two days or less produced no Lehmann lovegrass seedlings, and later cohorts that emerged after the dry period accounted for 95 to 100% of surviving Lehmann lovegrass seedlings (Frasier et al. 1985). Similarly, precipitation patterns that result in intermittent dry periods in Sahelian rangelands favor the establishment of species that produce later cohorts because the early cohorts of fast-emerging species experience high rates of mortality during dry periods (Elberse and Breman 1990). Thus, regardless of seedling growth characteristics, species that produce several cohorts may have an advantage over other species when availability of soil moisture is sporadic and infrequent. Species that tend to produce many cohorts over an extended period of time (e.g., lovegrasses) would have an increased potential for survival because the risk of mortality is spread over time.

In addition to the interactive effects of the timing of emergence and the timing of wet and dry periods, it is important to consider the potential impact of species-specific differences in growth and development on survival. Species that are capable of rapid seminal root growth and production of adventitious roots are likely to have an advantage during the establishment phase over species that develop root systems more slowly. A well-developed root system may leave seedlings less vulnerable to erratic soil moisture availability that results from rapid drying of the soil surface (Plummer 1943). In general, the development of adventitious roots capable of delivering water and nutrients to the seedling is considered requisite for grass seedling establishment (Hyder et al. 1971, Ries and Svecjar 1991). Under greenhouse conditions, adventitious root initiation occurs within 9 to 14 days of emergence for a variety of warm-season grasses given a 2- to 4-day period of available soil moisture at the time of initiation (Olmsted 1941, Wilson and Briske 1979, Roundy et al. 1993). In the absence of frequently repeated rainfall events, the loss of

surface soil moisture from sandy loam soils occurs at a rate that could prevent or severely inhibit the development of adventitious roots (Roundy et al. 1997). Thus, the extended initial period of moist soil conditions following the 10 August planting very likely favored sufficient root development that enabled seedlings to survive subsequent dry periods, whereas the first relatively long dry period following the 28 June planting probably impaired seedling development and ultimately affected survival.

It is difficult to identify any single life-history characteristic that confers survival advantages on a particular species. Rather, it is probable that several characteristics combine to confer advantages under certain environmental circumstances. For example, differences in survival patterns were evident between cohorts, even within a species. In the 28 June planting, the early cohorts of sideoats grama tended to have greater survival, whereas greater survival was observed in the later cohorts of the lovegrasses. It is unclear to what degree these differences in survival patterns were due to differences in growth and development, cohort production, or to stochastic factors. Thus, although roots of sideoats grama grow faster than those of Cochise lovegrass, Cochise lovegrass frequently establishes better than sideoats grama in reseeding trials; therefore, root morphology alone cannot explain the greater relative reseeding success of this species (Simanton and Jordan 1986, Roundy et al. 1993). It is possible that the greater establishment of Cochise lovegrass is related in part to its ability to produce multiple cohorts throughout the growing season. Ironically, survival of sideoats grama was greater than that of Cochise lovegrass for both planting dates in the current study. This fast-germinating species probably avoided major mortality because the initial dry period following the 28 June planting was short (two days) and the initial rain event for the 10 August planting was followed by 14 days of favorable soil moisture conditions.

Recruitment is inextricably linked to emergence and survival. In a 17-year study of natural recruitment and longevity of range grasses, Canfield (1957) observed that seedling mortality is highest in the first year; on average, approximately one-third of all seedlings survived the first growing season. The 28 June planting produced survivors that were older and generally further developed than those produced from the 10 August planting. The presence of tillers has been used as one criterion for establishment, and may indicate a high probability of survival to the next growing season (Ries and Svecjar 1991); between 85 and 100% of surviving individuals other than plains lovegrass were either reproductive or tillered. The population of surviving plains lovegrass plants included 32% pre-tillered individuals. For this species, the large but late cohort that emerged on 13 September following the 10 August planting accounted for 67% of the pre-tillered individuals.

The ability of plants to produce seed in the first growing season may have significant ramifications for stand renewal and the long-term success of reseeding projects. Green sprangletop, Lehmann lovegrass, and sideoats grama produced the greatest percentages of surviving reproductive plants, whereas Cochise lovegrass and plains lovegrass produced far fewer reproductive survivors. Furthermore, the 28 June planting produced three-fold more reproductive plants than the 10 August planting. The effect of planting date on the age and lifestage of survivors supports the general belief that longer growing seasons produce more robust plants. While this effect is not surprising, there is a potential trade-off between producing a stand of fewer but larger plants or a stand with greater numbers of smaller plants. Adjustments in planting date must consider potential effects on both survival and plant growth.

CONCLUSIONS

Relationships between emergence patterns, soil moisture availability patterns, and survival suggests that successful establishment of native warm-season perennial grass species may be favored by delaying the planting date until there is an increased probability of frequent rain events. Several native species (e.g., sideoats grama, Arizona cottontop, and green sprangletop) emerged primarily in early cohorts shortly after the initial rain event following planting. Subsequent mortality was high when seedlings were exposed to dry periods in the first two weeks after emergence. In southeastern Arizona, the probability of intermittent dry periods decreases as rainstorm frequency increases near the end of July. Thus, adjusting the planting date to late July or early August may improve the potential for successful revegetation projects in which the goal is to establish those native species that primarily produce early cohorts of seedlings.

The reliability with which non-native lovegrasses establish may be due, at least in part, to their tendency to produce multiple cohorts. The emergence of multiple cohorts spreads the risk of mortality over time, thus increasing the potential to produce at least one successful cohort during a season in which environmental variability is high. Furthermore, species-specific differences in seedling growth and development within the context of environmental variability may also contribute to differential survival among species in different years. Additional research is needed to investigate early seedling growth and development in response to variable soil moisture. Such studies may elucidate the relative importance of different life-history strategies (e.g., emergence patterns, seedling development) as processes responsible for differential establishment of grass species used for revegetation in southeastern Arizona.

CHAPTER 4

EARLY GROWTH AND DEVELOPMENT OF THREE WARM-SEASON PERENNIAL
GRASS SPECIES IN RESPONSE TO VARIABLE MOISTURE AND
ENVIRONMENTAL CONDITIONS

SUMMARY

Successful revegetation of native warm-season perennial grasses on rangeland depends on

the ability of individuals to germinate, grow, and establish. Sporadic rainstorms in semi-

arid regions of southeastern Arizona result in variable soil moisture patterns that may

contribute to differential growth and survival of seeded species. This study examined the

growth and development of two native species, cane beardgrass (*Bothriochloa barbinodis*

(Lag.) Herter) and sideoats grama (*Bouteloua curtipendula* (Michx.) Torr.); and one non-

native species, Lehmann lovegrass (*Eragrostis lehmanniana* Nees) grown outdoors in

buried pots under field conditions. Seedlings planted on two dates were exposed to

different temperature and humidity conditions in addition to different watering frequencies.

Development of seedling root and shoot systems was examined 9, 18, and 29 days after

planting. The effect of a 22-day drought imposed on 9- and 21-day-old seedlings was also

examined. Lehmann lovegrass seedlings initiated adventitious roots at an earlier age,

produced more adventitious roots, and greater adventitious root biomass than sideoats

grama or cane beardgrass. Lehmann lovegrass tended to produce longer adventitious roots

and shorter seminal roots relative to cane beardgrass, whereas sideoats grama roots were

generally intermediate between the other species. Timing of drought initiation affected root

system development and biomass production; plants exposed to drought at 9 days

developed seminal root systems in lieu of adventitious roots and produced less biomass than plants exposed to drought at 21 days, which developed adventitious roots. Drought-affected Lehmann lovegrass seedlings produced more biomass than native species. Lehmann lovegrass seedlings produced reproductive structures when exposed to drought, and root-to-shoot ratios decreased from 0.30 to 0.05. Increased seed production and relative allocation to shoot are strategies characteristic of annual plants, indicating that Lehmann lovegrass is capable of expressing substantial phenotypic plasticity in life history traits in response to drought.

INTRODUCTION

Low moisture conditions typical of arid and semiarid rangelands present challenges for successful reseeding and establishment of perennial grasses. Differential establishment of native and non-native grasses seeded in revegetation projects in southeastern Arizona is well-documented (Cox et al. 1982, Cox and Jordan 1983, Roundy and Biedenbender 1995). Successful establishment of native species remains a common goal although it is often difficult to achieve, and reasons for the failure of native grass seedings are unclear.

Summer precipitation in southeastern Arizona is sporadic, resulting in variable total precipitation and distribution of rain throughout the growing season (Humphrey 1958, McClaran 1995). The duration and frequency of rainfall events directly affects the availability of soil moisture and therefore germination of seeds and growth and development of seedlings (Beatley 1974, Cox and Jordan 1983, Elberse and Breman 1990). Differences in native and non-native grass establishment after reseeding suggest that species may respond differently to patterns of soil moisture availability (Roundy et al. 1996). Differential establishment may result from species-specific differences in total

germination, germination rate, and seedling growth and development during periods when soil moisture availability is not limiting (Cox 1984, Frasier et al. 1984, 1985; Adams 1997). Furthermore, species may differ in their ability to tolerate periods of limited soil moisture availability during these stages, which ultimately affects survival and recruitment (McGinnies 1960, Wright 1971, 1975; Roundy et al. 1996). Increased understanding of the patterns and processes underlying species establishment may facilitate planning and implementation of revegetation strategies in this region.

Grasses typically produce two types of root systems; the primary seminal root is the first seedling root system, and the adventitious root system develops later. The fibrous root system characteristic of grasses is comprised primarily of adventitious roots, and development of the adventitious root system is necessary for successful grass establishment (Ries and Svecjar 1991). Rates at which seedlings grow and develop root and shoot systems may be affected by patterns of moisture availability and may vary among species. Species that tolerate drought conditions in the seedling stage may not necessarily tolerate drought as mature plants, and vice versa (Fulbright et al. 1984, McGinnies 1960, Qi and Redmann 1993). Time to initiation of adventitious roots varies with species and moisture availability, but generally occurs one to eight weeks after germination (Olmsted 1941, Roundy et al. 1993, Wilson and Briske 1979). For example, depending on the interaction of biological and environmental factors, sideoats grama may initiate adventitious roots as early as nine days after germination (Roundy et al. 1993), whereas blue grama (*Bouteloua gracilis* (H.B.K.) Lag. ex Griffiths) adventitious roots may not form until two to eight weeks after germination (Wilson and Briske 1979). Furthermore, initiation of adventitious roots may be constrained to periods of adequate soil moisture availability (Olmsted 1941, Roundy et al. 1993, Wilson and Briske 1979), potentially delaying or prohibiting the formation of these roots. Thus, the survival of young seedlings may depend on the ability

of the seminal root to grow and supply water and nutrients to the plant (Simanton and Jordan 1986). Seedlings may be vulnerable to desiccation and mortality if rainfall patterns produce sufficient soil moisture to germinate seeds, but insufficient moisture to support the growing seedling (Roundy et al. 1997). Once a period of soil drying begins, the rate at which seminal roots lengthen must exceed the rate at which the soil drying front proceeds, or survival of the seedling is compromised (Roundy et al. 1997).

Careful selection of species and planting date are two strategies that land managers may use to improve reseeding efforts (Roundy and Call 1988, Wester 1995). Revegetation of arid and semiarid rangelands generally focuses on species that tolerate drought. Historically, species used in revegetation have been selected based on reseeding trials initiated before the onset of summer rains. Large inter-annual variability in summer precipitation patterns has been documented in Arizona (Sellers and Hill 1974). Long-term records from southeastern Arizona indicate that storms are generally less common in the beginning of the summer rainy season, but the frequency of storms usually increases by the third week of July (Smith and Schreiber 1973, Frasier and Lopez 1990, Roundy et al. 1996). However, in southeastern Arizona, the recommended time to reseed warm-season grasses is in May or June, prior to the beginning of the summer rainy season (Jordan 1981). Utilizing these seeding practices, successful rangeland reseedings can be expected in about 1 of 10 years in this environment (Cox and Jordan 1983). Therefore, the high failure rate of reseedings may result, at least in part, from the tradition of early planting dates that expose seeds and seedlings to fluctuating and variable soil moisture conditions during the period of infrequent storms early in the summer rainy season (Frasier et al. 1987, Roundy et al. 1996).

Better understanding of the biological responses of species to different soil moisture conditions has direct implications for rangeland revegetation in southern Arizona (see Chapters 2 and 3). The most practical way to accommodate soil moisture conditions without using irrigation is to adjust planting date. The purpose of these experiments was to determine effects of moisture availability and species on the development of roots and shoots of seedlings grown under field conditions. Differences in the timing of adventitious root initiation and relative rates of seminal and adventitious roots growth could prove advantageous to young seedlings given certain conditions of soil moisture availability. For example, rapid extension of roots would be an advantage if soil moisture becomes limiting at shallow depths. Early establishment of adventitious roots could allow seedlings to maintain higher transpiration and photosynthetic rates than would be possible if water delivery was provided exclusively by seminal roots. Increased understanding of the relationship between moisture stress and seedling development and growth may provide valuable insights into species selection and the timing of planting.

METHODS

This study was comprised of three experiments; two experiments examined the effects of watering frequency and species on seedling development and a third experiment examined how seedling development was affected by drought on different-aged seedlings. Each experiment employed a completely randomized design in a 2 X 3 X 3 factorial arrangement, in which watering frequency, species, and seedling age were the main factors. Watering frequency and seedling age varied by experiment as described below. All pots received equivalent total volumes of water (100 ml/day) during the experiments, although the frequency at which water was applied varied. The species studied in these experiments

included the native species cane beardgrass (*Bothriochloa barbinodis* (Lag.) Herter) and sideoats grama (*Bouteloua curtipendula* (Michx.) Torr.), and the non-native species Lehmann lovegrass (*Eragrostis lehmanniana* Nees). To simultaneously accommodate the need to grow plants under ambient environmental conditions, yet allow the removal of intact root systems, plants were grown outdoors in buried pots. Burial of the pots ensured that root systems were exposed to nearly normal soil temperature dynamics.

Seedling development experiments were conducted in a cleared agricultural field at the Tucson Plant Materials Center of the USDA Natural Resource Conservation Service during summer 1995. Air temperature, relative humidity, and precipitation data were recorded daily on site. Soil water potential was measured with gypsum blocks buried at depths of 2-4, 5-7, and 12-14 cm in Experiments 1 and 2; in Experiment 3, gypsum blocks were buried at the 12-14 cm depth only. At each depth, soil moisture measurements were replicated in three unharvested pots for each watering regime-, species-, and drought-treatment. Soil moisture measurements were recorded every minute using Campbell Scientific Inc. CR-10 microloggers, and stored as hourly averages.

An open-sided precipitation shelter was erected on site to prevent the interception of rainfall by the plants. The 4-m X 8-m structure was constructed from four sections of chain link fence supported by fence posts. The ridgeline of the pitched roof was parallel to the long axis of the structure, and was 1.75-m above ground level at the apex; the lower edge of the roof was 0.85-m above ground level. Clear polyethylene film fastened over the top and sides of the frame created a waterproof barrier with open sides below 0.85-m. Thus, the open-sided structure had minimal effects on ambient temperature, wind-flow, and relative humidity; reduction of photosynthetically active photon flux density under similarly-constructed shelters was $29 \pm 10\%$ (mean $\pm$ se) at solar noon on a clear, midsummer day

(Weltzin and McPherson *in press*). A 50-cm high vertebrate exclosure was constructed by fastening poultry netting around the perimeter of the structure.

Pots were constructed from 38-cm long segments of 15-cm diameter PVC pipe to which a 15-cm X 15-cm wire mesh screen (3.18-mm openings) was attached at one end. Pots were placed, screened-end down, into a 36-cm-deep trench located under the precipitation shelter; trenches were subsequently backfilled with soil. Sandy loam soil transported from the Santa Rita Experimental Range (*see Chapter 2*) was used to fill pots. The soil surface within pots was level with the soil surface of the backfilled trenches; the rim of each pot protruded approximately 2.5 cm from the soil surface. Pots were filled with incremental additions of 700 g of soil into sequential 2.5-cm deep layers of the pots; thus, the bulk density of soil in all pots was roughly equivalent throughout the soil core (approximately 1.5 g/cm^3). Approximately 15-20 seeds of a single species were sown on the surface of each pot, and covered with approximately 5 mm of soil, the surface of which was lightly tamped. After watering was initiated, the first five emerged seedlings per pot were retained for study; any subsequently emerged seedlings were removed from the pots.

Harvest dates were selected so that all pots had received equivalent total volumes of water at the time of harvest. In each experiment, five pots of each watering frequency/species treatment combination were harvested on each harvest date.

Pots were removed intact from the plot on harvest dates; following removal of the pots, the resulting holes in the trench were refilled with soil to maintain stable soil temperature dynamics for remaining pots. Immediately prior to removal, pots were watered to reduce potential root breakage caused by cracking of the soil core. After removing the wire mesh screen from the bottom of the pot, the soil core with intact plants was pushed out of the pot

into a supporting cradle that reduced potential cleavage of the soil core. Soil was washed from the roots, taking care to minimize root damage. Intact plant groups from each pot were then subjected to a second washing, at which time individual plants were separated and any residual soil was removed. Plants that incurred obvious root breakage at any time during the washing procedure were discarded; only intact plants were used for analysis. Each plant was separated into components of shoot, seminal root, and adventitious roots. The following measurements were made on individual plants: maximum seminal root length; number of adventitious roots; maximum length of adventitious roots; biomass of shoots and roots. All biomass measurements were made after plant materials had been dried at 70° C for 40 hours. Prior to drying, seminal and adventitious root systems were divided into 10-cm increments, thus allowing analysis of biomass allocation at different depths.

Experiment 1

Two watering treatments were applied in this experiment: pots received 200 ml of water every two days or 400 ml of water every four days. Plants were harvested 9, 18, or 29 days after the initial watering. This experiment was conducted between 8 July and 6 August 1995.

Experiment 2

Two watering treatments were applied in this experiment: pots received 300 ml of water every three days or 600 ml of water every six days. As in the previous experiment, plants were harvested 9, 18, or 29 days after the initial watering. This experiment was conducted between 22 August and 20 September 1995.

Experiment 3

This experiment was conducted concurrent with Experiment 2; before the initiation of

drought, pots received the watering treatments applied in Experiment 2. Drought

treatments varied by the timing of the initiation of drought; water application ceased on day

9 or day 21 after the initial watering. Each pot was watered with 300 ml of water 21 days

after the initiation of drought, and harvested on the following day. Thus, pots exposed to

drought on day 9 were harvested on day 31, and pots exposed to drought on day 21 were

harvested on day 43 after the initial watering. The 29-day-old seedlings from Experiment 2

served as a control, and were compared with the drought-affected seedlings from this

experiment. This experiment was conducted between 22 August and 4 October 1995.

Data Analysis

Data were analyzed with analysis of variance; the distribution of root biomass at depth was

analyzed with repeated measures analysis of variance. All factors (watering treatment,

species, and seedling age) were treated as fixed effects. Data did not meet the assumptions

of analysis of variance, and were therefore rank-transformed prior to analysis of variance

(Conover and Iman 1981). In all analyses, effects were considered significant at the 0.05

level; when significant effects were detected, means were separated with Fisher's LSD

mean-separation test. Individual pots served as replicates in all analyses. Data from the

three experiments were analyzed separately. However, the 29-day-old seedlings from

Experiment 2 were included in statistical analyses for Experiments 2 and 3; the 29-day-old

seedlings were included in the Experiment 3 analysis as an non-drought-affected control.

RESULTS

Seedlings emerged in all pots in one to four days after the initial watering in all experiments, and the first five seedlings to emerge in each pot were retained for use in these studies. However, due to uncontrolled variation in the timing of seedling emergence, seedlings within each age class are the same age within three days. Therefore, comparisons made within age classes do not necessarily reflect effects due to seedling age per se, but the average stage of development achieved by a particular harvest date.

Environmental Conditions

Ambient environmental conditions were generally hotter and drier during the first experiment relative to conditions during the second and third experiment (Table 4.1) (USDA 1995). Soil moisture was more variable at 2-4 cm than at deeper depths throughout Experiments 1 (Fig. 4.1) and 2 (Fig. 4.2). In Experiment 3, soil moisture at 12-14 cm decreased more quickly after drought initiation in pots exposed to drought at 21 days than in pots exposed to drought 9 days after planting (Fig. 4.3).

Experiment 1

Length and number of roots

Seminal root length varied with main effects of watering regime (P = 0.01) and the interaction of species and seedling age (P < 0.01), but did not vary with any other first- or second-order interactions (0.25 ≥ P ≤ 0.91) (Table 4.2). The four-day watering regime produced longer seminal roots (mean ± se = 16.4 ± 2.1 cm) than the two-day watering regime (14.1 ± 2.2 cm). Seminal root length tended to increase with seedling age for all species, although the rate of increase varied among species (Fig. 4.4a). Within seedling

age, seminal root length varied among species. For example, seminal roots of sideoats grama were longer in 9-day-old and 18-day-old seedlings than seminal roots of cane beardgrass or Lehmann lovegrass at the same ages; at 29 days of age, seminal root length did not differ among species (Fig. 4.4a).

Adventitious root length varied with the interaction of species and seedling age ($P < 0.01$), but did not vary with any other first- or second-order interaction ($0.31 \geq P \leq 0.88$) (Table 4.2). Adventitious root length of sideoats grama and Lehmann lovegrass increased with increasing age; adventitious root length of cane beardgrass did not differ between 9-day-old and 18-day-old seedlings, but increased by day 29 (Fig. 4.4b). Within age classes, differences in adventitious root length among species were not evident for 9-day-old seedlings; however, adventitious roots of 18-day-old and 29-day-old cane beardgrass seedlings were shorter than those of sideoats grama and Lehmann lovegrass, which did not differ from each other (Fig. 4.4b).

The number of adventitious roots varied with the interaction of species and seedling age ($P < 0.01$) but did not vary with any other first- or second-order interaction ($0.09 \geq P \leq 0.66$) (Table 4.2). The number of adventitious roots of sideoats grama and Lehmann lovegrass increased with increasing age, whereas cane beardgrass adventitious root number did not differ between 9-day-old and 18-day-old seedlings, but increased by day 29 (Fig. 4.4c). Within age classes, differences among species in number of adventitious root were not evident for 9-day-old seedlings; however, 18-day-old and 29-day-old cane beardgrass seedlings had fewer adventitious roots than sideoats grama and Lehmann lovegrass, which did not differ from each other (Fig. 4.4c).

Biomass of shoot and root systems

Shoot, adventitious root, and seminal root biomass varied with the interaction of species and seedling age (P < 0.01, P < 0.01, and P < 0.03, respectively), but did not vary with any other first- or second-order interactions (0.19 ≥ P ≤ 0.50, 0.08 ≥ P ≤ 0.95, and 0.36 ≥ P ≤ 0.85, respectively) (Table 4.2). Within seedling age, shoot, adventitious root, and seminal root biomass did not differ among species for 9-day-old seedlings (Fig. 4.5a). However, shoot biomass of 18-day-old sideoats grama was greater than that of cane beardgrass or Lehmann lovegrass; adventitious root biomass of 18-day-old sideoats grama and Lehmann lovegrass was greater than cane beardgrass. Seminal root biomass of 18-day-old sideoats grama was greater than Lehmann lovegrass, but neither was different from cane beardgrass (Fig. 4.5b). Shoot biomass of 29-day-old cane beardgrass was less than Lehmann lovegrass, but neither differed from sideoats grama. Adventitious root biomass of 29-day-old cane beardgrass was less than either Lehmann lovegrass or sideoats grama ; seminal root biomass did not differ among species for 29-day-old seedlings (Fig. 4.5c).

Experiment 2

Length and number of roots

Seminal root length varied with main effects of watering regime (P = 0.03), species (P < 0.01), and age class (P < 0.01), but did not vary with any first- or second-order interactions (0.16 ≥ P ≤ 0.91) (Table 4.3). The six-day watering regime produced longer seminal roots (17.7 ± 1.8 cm) than the three-day watering regime (13.3 ± 1.5 cm). Seminal root lengths of cane beardgrass and sideoats grama were greater than Lehmann lovegrass, but did not differ from each other (Fig. 4.6a). Seminal root length of 18-day-old seedlings was greater than that of either 9-day-old or 29-day-old seedlings (Fig. 4.6b).

Adventitious root length varied with main effects of species (P < 0.01) and age class (P < 0.01), but did not vary with any first- or second-order interactions (0.25 ≥ P ≤ 0.96) (Table 4.3). Adventitious root length of Lehmann lovegrass was greater than that of either cane beardgrass or sideoats grama, which did not differ from each other (Fig. 4.6a). The length of adventitious roots differed among each of the three age classes; adventitious root length increased with increased seedling age (Fig. 4.6b).

Number of adventitious roots varied with main effects of species (P < 0.01) and age class (P < 0.01), but did not vary with first- or second-order interactions (0.06 ≥ P ≤ 0.99) (Table 4.3). The number of adventitious roots differed among all species and age classes. Lehmann lovegrass had more adventitious roots than sideoats grama; both species had more adventitious roots than cane beardgrass (Fig. 4.7a). The number of adventitious roots increased with increased seedling age (Fig. 4.7b).

Biomass of shoot and root systems

Shoot and adventitious root biomass varied with the interaction of species and seedling age (P < 0.01, and P < 0.02, respectively), but did not vary with any other first- or second-order interactions (0.14 ≥ P ≤ 0.37, and 0.47 ≥ P ≤ 0.82, respectively) (Table 4.3). Within the 9-day-old seedlings, shoot biomass of cane beardgrass and sideoats grama were greater than that of Lehmann lovegrass, but did not differ from each other (Fig. 4.8a). Within the 18-day-old age class, shoot biomass of cane beardgrass was greater than that of sideoats grama; Lehmann lovegrass shoot biomass did not differ from either species (Fig. 4.8b). Within the 29-day-old age class, Lehmann lovegrass shoot biomass was greater than that of cane beardgrass; shoot biomass of sideoats grama was less than either other species (Fig. 4.8c). Adventitious root biomass of 9-day-old Lehmann lovegrass was greater than that of cane beardgrass and sideoats grama, which did not differ from each

other (Fig. 4.8a). Adventitious root biomass of 18-day-old cane beardgrass, sideoats grama, and Lehmann lovegrass did not differ from each other (Fig. 4.8b). Adventitious root biomass of 29-day-old cane beardgrass and Lehmann lovegrass were greater than that of sideoats grama, but did not differ from each other (Fig. 4.8c).

Seminal root biomass varied with main effects of watering regime ($P < 0.03$), species ($P < 0.01$), and seedling age ($P < 0.01$), but did not vary with any first- or second-order interactions ($0.30 \geq P \leq 0.94$) (Table 4.3). Seminal root biomass of seedlings watered every six days ($3.7 \pm 0.5 \times 10^{-3}$ g) was greater than that of seedlings watered every three days ($3.1 \pm 0.5 \times 10^{-3}$ g). Cane beardgrass seminal root biomass was greater than that of sideoats grama; Lehmann lovegrass seminal root biomass was less than that of either species. Seminal root biomass of 18-day-old seedlings was greater than either 9-day-old or 29-day-old seedlings, which did not differ from each other.

Experiment 3

Length and number of roots

Seminal root length varied with main effects of species ($P < 0.01$) and drought treatment ($P < 0.01$), but did not vary with any first- or second-order interactions ($0.32 \geq P \leq 0.89$) (Table 4.4). Seminal roots of cane beardgrass and sideoats grama were longer than those of Lehmann lovegrass, but did not differ from each other (Fig. 4.9a). Seminal roots of seedlings exposed to drought at 9 days were longer than either those exposed to drought at 21 days or control seedlings (Fig. 4.9b).

Adventitious root length varied with the interaction of species and drought treatment ($P < 0.01$), but did not vary with any other first- or second-order interactions ($0.16 \geq P \leq 0.47$) (Table 4.4). Adventitious roots of all species were shorter when drought was initiated at 9

days compared with those exposed to drought at 21 days or control plants; however, no differences were detected among species for those seedlings exposed to drought at 9 days (Fig. 4.10). Adventitious roots of cane beardgrass and sideoats grama seedlings exposed to drought at age 21 days were than those of Lehmann lovegrass, but did not differ from each other (Fig. 4.10). Adventitious roots of control Lehmann lovegrass seedlings were longer than those of sideoats grama, although neither species differed from cane beardgrass (Fig. 4.10).

Number of adventitious roots varied with main effects of species (P < 0.01) and drought treatment (P < 0.01), but did not vary with any first- or second-order interactions (0.15 ≥ P ≤ 0.87) (Table 4.4). Lehmann lovegrass had more adventitious roots than either cane beardgrass or sideoats grama, which did not differ from each other (Fig. 4.11a). Control seedlings had more adventitious roots than those exposed to drought at 9 or 21 days; the drought-affected seedlings did not differ from each other (Fig. 4.11b).

Biomass of shoot and root systems

Shoot and seminal root biomass varied with main effects of species (P < 0.01; P < 0.01, respectively) and drought treatment (P < 0.01; P < 0.01, respectively), but did not vary with any first- or second-order interactions (0.23 ≥ P ≤ 0.92, and 0.74 ≥ P ≤ 0.94, respectively) (Table 4.4). Shoot biomass of Lehmann lovegrass was greater than that of cane beardgrass, which were both greater than sideoats grama (Fig. 4.12). Shoot biomass of seedlings exposed to drought at 21 days was greater than control seedlings; seedlings exposed to drought at 9 days had less shoot biomass than either other drought treatment (Fig. 4.12). Seminal root biomass of cane beardgrass and sideoats grama were greater than Lehmann lovegrass, but did not differ from each other (Fig. 4.12). Seminal root biomass of seedlings exposed to drought at 9 days was greater than that of seedlings

exposed to drought at 21 days or control seedlings, which did not differ from each other (Fig. 4.12).

Adventitious root biomass varied with the interaction of species and drought treatment (P < 0.01), but did not vary with any other first- or second-order interactions (0.18 ≥ P ≤ 0.73) (Table 4.4). Each species produced less adventitious root biomass when drought was initiated at 9 days compared with those exposed to drought at 21 days or control plants; no differences were detected among species for those seedlings exposed to drought at 9 days (Fig. 4.12b). Adventitious roots biomass of control Lehmann lovegrass was greater than that of drought-affected at 21 days, whereas cane beardgrass and sideoats grama seedlings exposed to drought at 21 days had greater adventitious root biomass than control plants. Adventitious root biomass of cane beardgrass and sideoats grama seedlings drought-affected at 21 days was greater than Lehmann lovegrass, but did not differ from each other (Fig. 4.12c). Adventitious root biomass of control cane beardgrass and Lehmann lovegrass seedlings were greater than sideoats grama, but did not differ from each other (Fig. 4.12a).

Root Biomass Allocation at Depths

Repeated measures analysis of the allocation of seminal root and adventitious root biomass at sequential depth increments for all experiments indicated that biomass increased over time, decreased with increased depth, and exhibited minor variability among species within an age class (data not shown). These results are expected and consistent with other analyses; details are omitted here (see Appendix A).

Table 4.1. Maximum and minimum ambient temperature and relative humidity at the Tucson Plant Materials Center of the USDA Natural Resource Conservation Service during three time periods in summer 1995. Values given are mean, standard error of the mean, and range.

Variable	Experiment 1			Experiment 2			Experiment 3		
	8 July - 6 August 1995			22 August - 20 September 1995			22 August - 4 October 1995		
	Mean	s.e.	Range	Mean	s.e.	Range	Mean	s.e.	Range
Temperature (°C)									
Maximum	41.2	0.6	33.4 - 41.7	37.3	0.5	30.0 - 41.7	36.6	0.4	30.0 - 41.7
Minimum	24.3	0.4	18.9 - 27.8	22.2	0.4	17.2 - 26.7	21.3	0.4	14.5 - 26.7
Relative Humidity (%)									
Maximum	70.0	2.9	46 - 98	87.7	2.8	48 - 100	86.3	2.3	48 - 100
Minimum	31.4	1.5	20 - 50	32.2	1.3	20 - 52	31.4	1.1	20 - 52

Table 4.2. Seedling attributes of three perennial grass species grown under field conditions in Tucson, Arizona. Seedlings grown between 8 July and 6 August 1995 were evaluated at three ages.

Experiment 1	Seedling age		
	9 day	18 day	29 day
	mean ± s.e. [1,2]	mean ± s.e.	mean ± s.e.
Maximum seminal root length (cm)			
Cane beardgrass	2.27 ± 0.63	9.24 ± 2.93	32.84 ± 3.31
Sideoats grama	6.61 ± 0.64	20.99 ± 2.23	25.98 ± 3.84
Lehmann lovegrass	2.89 ± 0.63	4.85 ± 1.23	25.20 ± 2.92
Maximum adventitious root length (cm)			
Cane beardgrass	0 ± 0	0.03 ± 0.03	17.34 ± 4.40
Sideoats grama	0 ± 0	7.68 ± 2.07	32.58 ± 1.91
Lehmann lovegrass	0 ± 0	3.13 ± 0.82	36.38 ± 2.25
Number of adventitious roots			
Cane beardgrass	0 ± 0	0.1 ± 0.1	2.4 ± 0.6
Sideoats grama	0 ± 0	1.8 ± 0.2	4.6 ± 0.6
Lehmann lovegrass	0 ± 0	1.8 ± 0.4	6.6 ± 0.9
Seminal root biomass (g)			
Cane beardgrass	$0.98 \times 10^{-3} \pm 0.08 \times 10^{-3}$	$2.70 \times 10^{-3} \pm 1.0 \times 10^{-3}$	$1.39 \times 10^{-2} \pm 0.26 \times 10^{-2}$
Sideoats grama	$1.26 \times 10^{-3} \pm 0.17 \times 10^{-3}$	$4.77 \times 10^{-3} \pm 0.52 \times 10^{-3}$	$8.15 \times 10^{-3} \pm 1.39 \times 10^{-3}$
Lehmann lovegrass	$0.85 \times 10^{-3} \pm 0.09 \times 10^{-3}$	$1.35 \times 10^{-3} \pm 0.38 \times 10^{-3}$	$6.39 \times 10^{-3} \pm 1.16 \times 10^{-3}$
Adventitious root biomass (g)			
Cane beardgrass	0 ± 0	$0.2 \times 10^{-4} \pm 0.2 \times 10^{-4}$	$1.79 \times 10^{-2} \pm 0.62 \times 10^{-2}$
Sideoats grama	0 ± 0	$2.44 \times 10^{-3} \pm 1.0 \times 10^{-3}$	$3.06 \times 10^{-2} \pm 0.58 \times 10^{-2}$
Lehmann lovegrass	0 ± 0	$1.13 \times 10^{-3} \pm 0.3 \times 10^{-3}$	$4.33 \times 10^{-2} \pm 0.71 \times 10^{-2}$
Shoot biomass (g)			
Cane beardgrass	$1.04 \times 10^{-3} \pm 0.11 \times 10^{-3}$	$2.54 \times 10^{-3} \pm 0.70 \times 10^{-3}$	$3.88 \times 10^{-2} \pm 0.74 \times 10^{-2}$
Sideoats grama	$1.33 \times 10^{-3} \pm 0.09 \times 10^{-3}$	$9.66 \times 10^{-3} \pm 1.30 \times 10^{-3}$	$7.03 \times 10^{-2} \pm 1.2 \times 10^{-2}$
Lehmann lovegrass	$0.94 \times 10^{-3} \pm 0.10 \times 10^{-3}$	$3.54 \times 10^{-3} \pm 0.82 \times 10^{-3}$	$1.29 \times 10^{-1} \pm 0.30 \times 10^{-2}$

[1] Values are mean and standard error of the mean.

[2] Values are averaged across watering treatments.

Table 4.3. Seedling attributes of three perennial grass species grown under field conditions in Tucson, Arizona. Seedlings grown between 22 August and 20 September 1995 were evaluated at three ages.

Experiment 2	Seedling age		
	9 day	18 day	29 day
	mean ± s.e. [1,2]	mean ± s.e.	mean ± s.e.
Maximum seminal root length (cm)			
Cane beardgrass	14.21 ± 1.35	29.26 ± 1.40	20.82 ± 4.35
Sideoats grama	12.16 ± 1.18	23.88 ± 2.95	19.22 ± 3.71
Lehmann lovegrass	6.30 ± 1.22	7.84 ± 2.55	4.18 ± 2.69
Maximum adventitious root length (cm)			
Cane beardgrass	0 ± 0	12.79 ± 2.01	41.08 ± 1.11
Sideoats grama	0.03 ± 0.01	15.17 ± 3.38	38.19 ± 1.42
Lehmann lovegrass	0.87 ± 0.44	23.24 ± 3.12	43.93 ± 1.63
Number of adventitious roots			
Cane beardgrass	0 ± 0	2.0 ± 0.3	6.4 ± 0.2
Sideoats grama	0.2 ± 0.1	2.3 ± 0.3	8.3 ± 1.0
Lehmann lovegrass	0.9 ± 0.2	3.5 ± 0.5	11.3 ± 1.3
Seminal root biomass (g)			
Cane beardgrass	$4.38 \times 10^{-3} \pm 0.34 \times 10^{-3}$	$9.80 \times 10^{-3} \pm 0.92 \times 10^{-3}$	$3.75 \times 10^{-3} \pm 0.93 \times 10^{-3}$
Sideoats grama	$2.20 \times 10^{-3} \pm 0.29 \times 10^{-3}$	$4.45 \times 10^{-3} \pm 0.62 \times 10^{-3}$	$2.45 \times 10^{-3} \pm 0.44 \times 10^{-3}$
Lehmann lovegrass	$1.10 \times 10^{-3} \pm 0.14 \times 10^{-3}$	$1.93 \times 10^{-3} \pm 0.71 \times 10^{-3}$	$0.44 \times 10^{-3} \pm 0.26 \times 10^{-3}$
Adventitious root biomass (g)			
Cane beardgrass	0 ± 0	$7.05 \times 10^{-3} \pm 1.69 \times 10^{-3}$	$1.16 \times 10^{-1} \pm 0.16 \times 10^{-1}$
Sideoats grama	$0.10 \times 10^{-3} \pm 0.06 \times 10^{-3}$	$7.85 \times 10^{-3} \pm 2.00 \times 10^{-3}$	$7.55 \times 10^{-2} \pm 1.35 \times 10^{-2}$
Lehmann lovegrass	$0.73 \times 10^{-3} \pm 0.21 \times 10^{-3}$	$8.53 \times 10^{-3} \pm 1.48 \times 10^{-3}$	$1.75 \times 10^{-1} \pm 0.38 \times 10^{-1}$
Shoot biomass (g)			
Cane beardgrass	$3.60 \times 10^{-3} \pm 0.43 \times 10^{-3}$	$2.65 \times 10^{-2} \pm 0.25 \times 10^{-2}$	$2.30 \times 10^{-1} \pm 0.29 \times 10^{-1}$
Sideoats grama	$2.90 \times 10^{-3} \pm 0.23 \times 10^{-3}$	$2.15 \times 10^{-2} \pm 0.43 \times 10^{-2}$	$1.32 \times 10^{-1} \pm 0.19 \times 10^{-1}$
Lehmann lovegrass	$1.58 \times 10^{-3} \pm 0.29 \times 10^{-3}$	$2.14 \times 10^{-2} \pm 0.50 \times 10^{-2}$	$5.86 \times 10^{-1} \pm 1.29 \times 10^{-1}$

[1] Values are mean and standard error of the mean.

[2] Values are averaged across watering treatments.

Table 4.4. Seedling attributes of three perennial grass species subjected to drought under field conditions in Tucson, Arizona. Drought treatments were initiated 9 and 21 days after planting. Seedlings grown between 22 August and 4 October 1995 were evaluated 22 days initiation of drought. Control seedlings were evaluated 29 days after planting.

Experiment 3	Seedling age at initiation of drought		
	Control	9 day	21 day
	mean ± s.e. [1,2]	mean ± s.e.	mean ± s.e.
Maximum seminal root length (cm)			
Cane beardgrass	20.82 ± 4.35	40.11 ± 2.21	11.66 ± 2.51
Sideoats grama	19.22 ± 3.71	27.72 ± 1.62	14.89 ± 4.28
Lehmann lovegrass	4.18 ± 2.69	19.04 ± 6.11	3.52 ± 2.77
Maximum adventitious root length (cm)			
Cane beardgrass	41.08 ± 1.11	0.17 ± 0.03	42.95 ± 0.82
Sideoats grama	38.19 ± 1.42	4.23 ± 3.97	44.29 ± 1.23
Lehmann lovegrass	43.93 ± 1.63	2.52 ± 2.14	33.64 ± 3.98
Number of adventitious roots			
Cane beardgrass	6.4 ± 0.2	4.4 ± 0.6	5.2 ± 0.8
Sideoats grama	8.3 ± 1.0	6.2 ± 0.5	5.6 ± 0.6
Lehmann lovegrass	11.3 ± 1.3	5.9 ± 1.0	6.6 ± 1.0
Seminal root biomass (g)			
Cane beardgrass	$3.75 \times 10^{-3} \pm 0.93 \times 10^{-3}$	$2.57 \times 10^{-2} \pm 0.43 \times 10^{-2}$	$2.10 \times 10^{-3} \pm 0.41 \times 10^{-3}$
Sideoats grama	$2.45 \times 10^{-3} \pm 0.44 \times 10^{-3}$	$1.39 \times 10^{-2} \pm 0.44 \times 10^{-2}$	$4.40 \times 10^{-3} \pm 1.60 \times 10^{-3}$
Lehmann lovegrass	$0.44 \times 10^{-3} \pm 0.26 \times 10^{-3}$	$1.12 \times 10^{-2} \pm 0.68 \times 10^{-2}$	$1.20 \times 10^{-3} \pm 0.79 \times 10^{-3}$
Adventitious root biomass (g)			
Cane beardgrass	$1.16 \times 10^{-1} \pm 0.16 \times 10^{-1}$	$1.17 \times 10^{-3} \pm 0.19 \times 10^{-3}$	$1.74 \times 10^{-1} \pm 0.23 \times 10^{-1}$
Sideoats grama	$7.55 \times 10^{-2} \pm 1.35 \times 10^{-2}$	$4.90 \times 10^{-3} \pm 3.79 \times 10^{-3}$	$1.44 \times 10^{-1} \pm 0.17 \times 10^{-1}$
Lehmann lovegrass	$1.75 \times 10^{-1} \pm 0.38 \times 10^{-1}$	$1.88 \times 10^{-3} \pm 0.71 \times 10^{-3}$	$6.48 \times 10^{-2} \pm 1.44 \times 10^{-2}$
Shoot biomass (g)			
Cane beardgrass	$2.30 \times 10^{-1} \pm 0.29 \times 10^{-1}$	$1.18 \times 10^{-1} \pm 0.11 \times 10^{-1}$	$9.02 \times 10^{-1} \pm 1.26 \times 10^{-1}$
Sideoats grama	$1.32 \times 10^{-1} \pm 0.19 \times 10^{-1}$	$6.86 \times 10^{-2} \pm 1.63 \times 10^{-2}$	$3.59 \times 10^{-1} \pm 0.44 \times 10^{-1}$
Lehmann lovegrass	$5.86 \times 10^{-1} \pm 1.29 \times 10^{-1}$	$2.66 \times 10^{-1} \pm 1.24 \times 10^{-1}$	1.39 ± 0.26

[1] Values are mean and standard error of the mean.
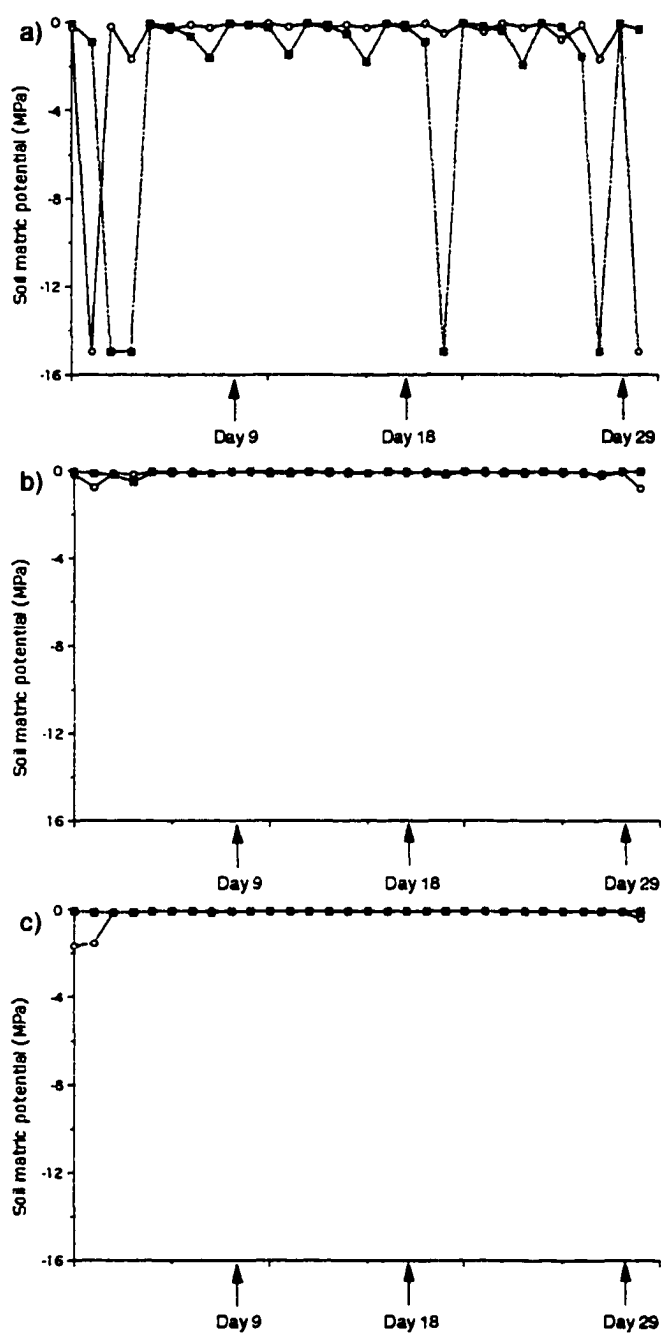[2] Values are averaged across watering treatments.

Figure 4.1. Soil moisture availability (matric potential) in pots seeded to warm-season perennial grasses between 8 July and 6 August 1995. Moisture was evaluated at (a) 2-4, (b) 5-7, and (c) 12-14 cm depths. Pots were watered every 2 (open circles) or 4 (closed squares) days. Arrows indicate harvest dates 9, 18, and 29 days after planting.
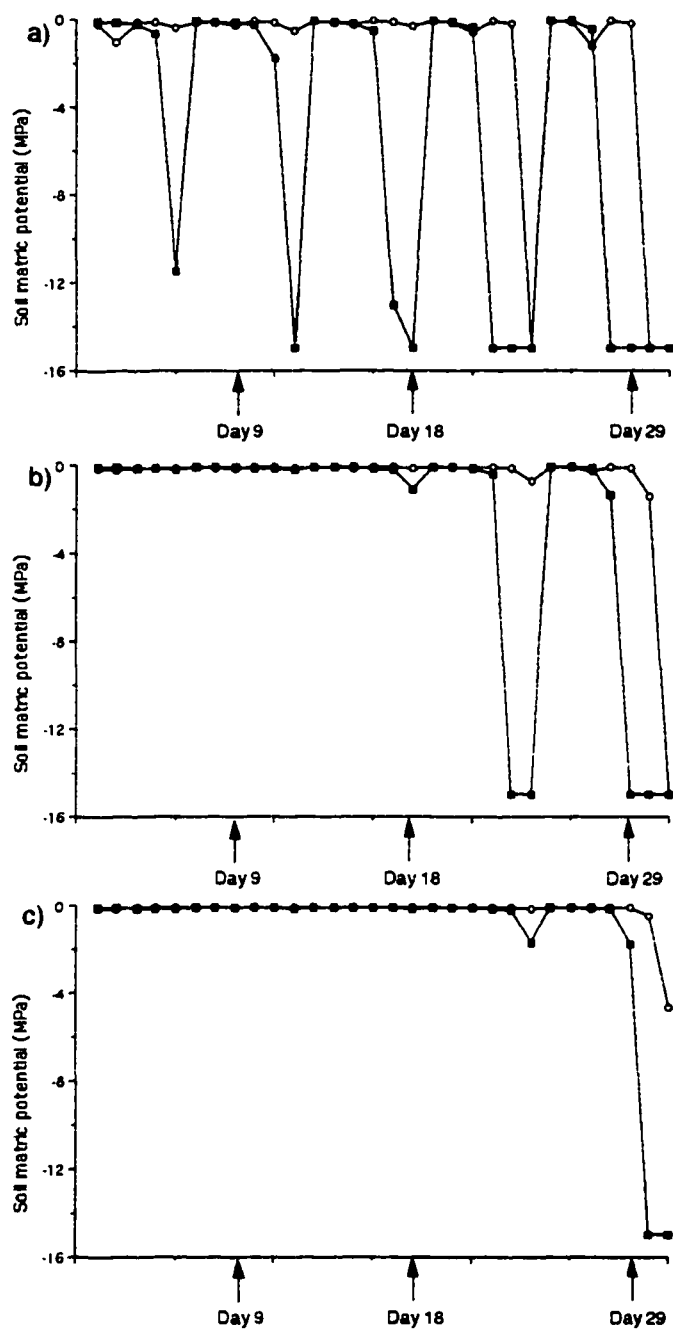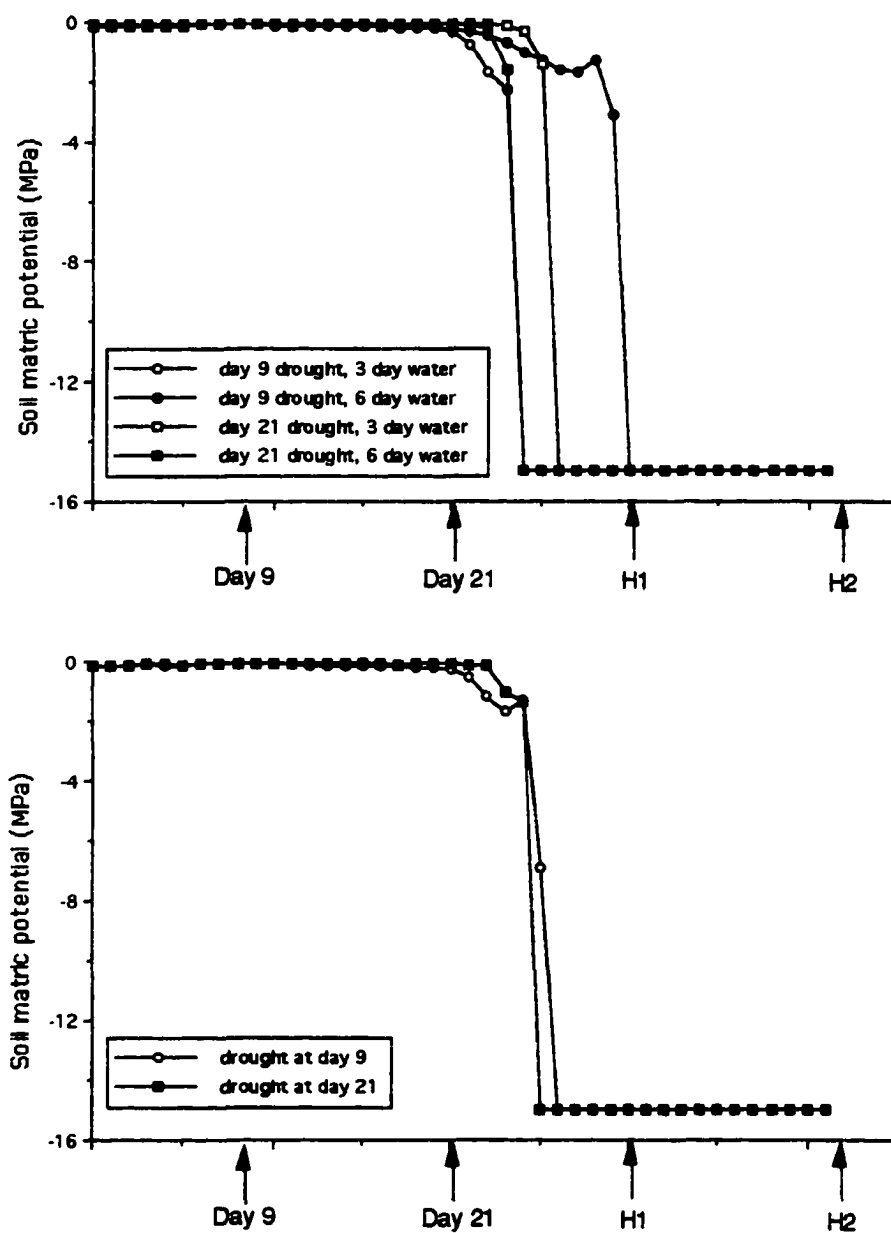
Figure 4.2. Soil moisture availability (matric potential) in pots seeded to warm-season perennial grasses between 22 August and 20 September 1995. Moisture was evaluated at (a) 2-4, (b) 5-7, and (c) 12-14 cm depths. Pots were watered every 3 (open circles) or 6 (closed squares) days. Arrows indicate harvest dates 9, 18, and 29 days after planting.

Figure 4.3. Soil moisture availability (matric potential) in pots seeded to warm-season perennial grasses between 22 August and 4 October 1995. Moisture was evaluated at 12-14 cm depth. Pots were watered every 3 or 6 days prior to initiation of drought 9 or 21 days after planting. Arrows indicate initiation of drought and harvest dates 22 days later (H1 and H2).
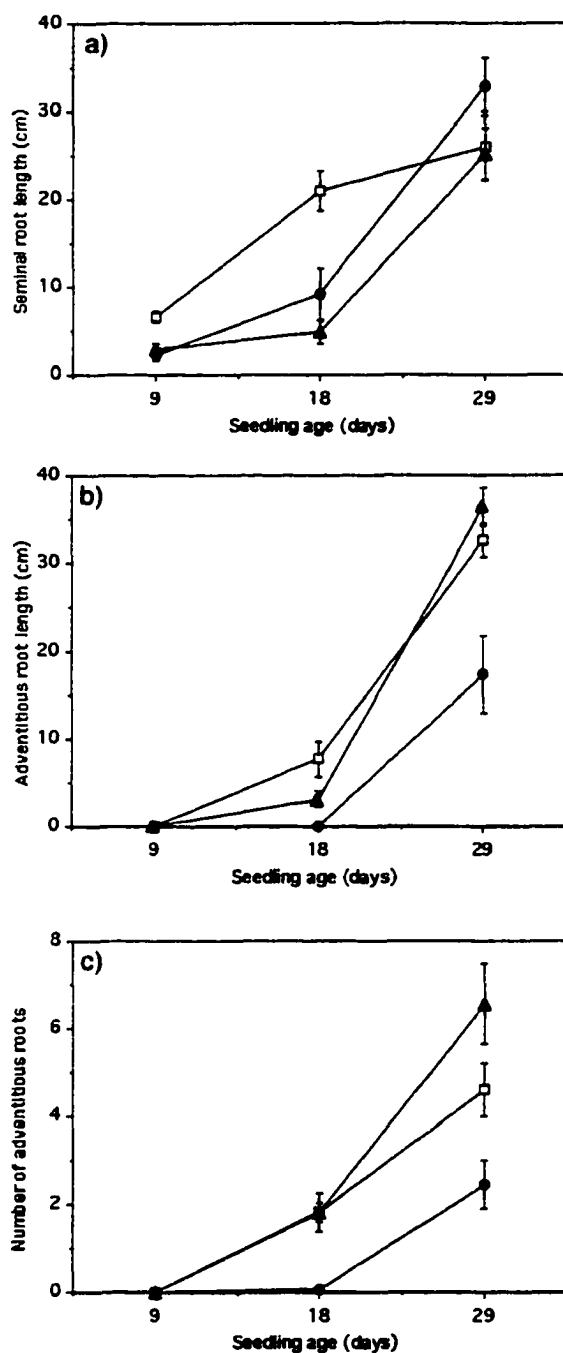
Figure 4.4. Mean maximum seminal root length (a), maximum adventitious root length (b), and number of adventitious roots of cane beardgrass (closed circles), sideoats grama (open squares), and Lehmann lovegrass (closed triangles) seedlings evaluated 9, 18, and 29 days after initial watering. Plants were watered every 2 or 4 days. Error bars represent standard errors of the means.
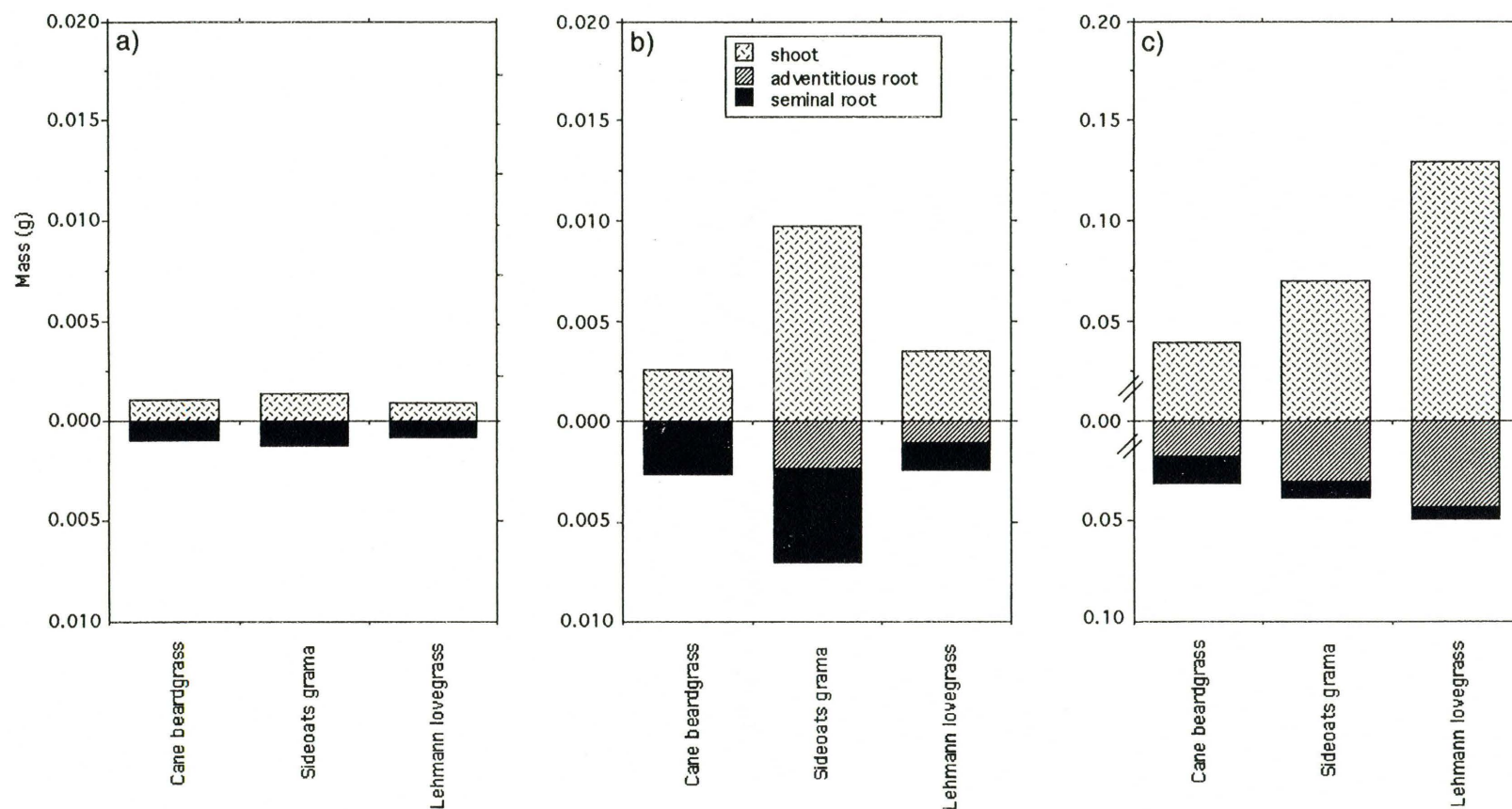
Figure 4.5. Biomass of shoot, adventitious root, and seminal root systems of cane beardgrass, sideoats grama, and Lehmann lovegrass seedlings evaluated 9 (a), 18 (b), and 29 (c) days after initial watering. Plants were watered every 2 or 4 days.
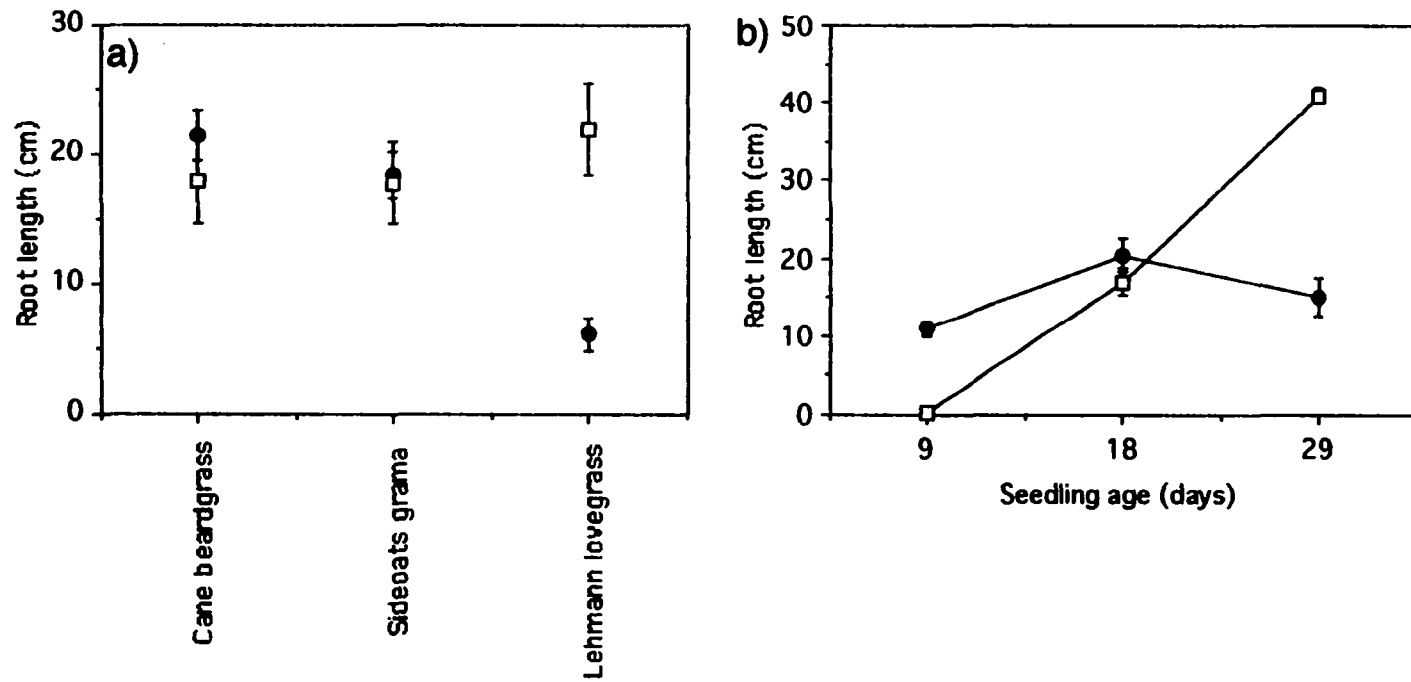
Figure 4.6. Mean maximum seminal root length (closed circles) and maximum adventitious root length (open squares) of seedlings watered every 3 or 6 days. a) Main effects of species. b) Main effects of seedling age. Error bars represent standard errors of the means.
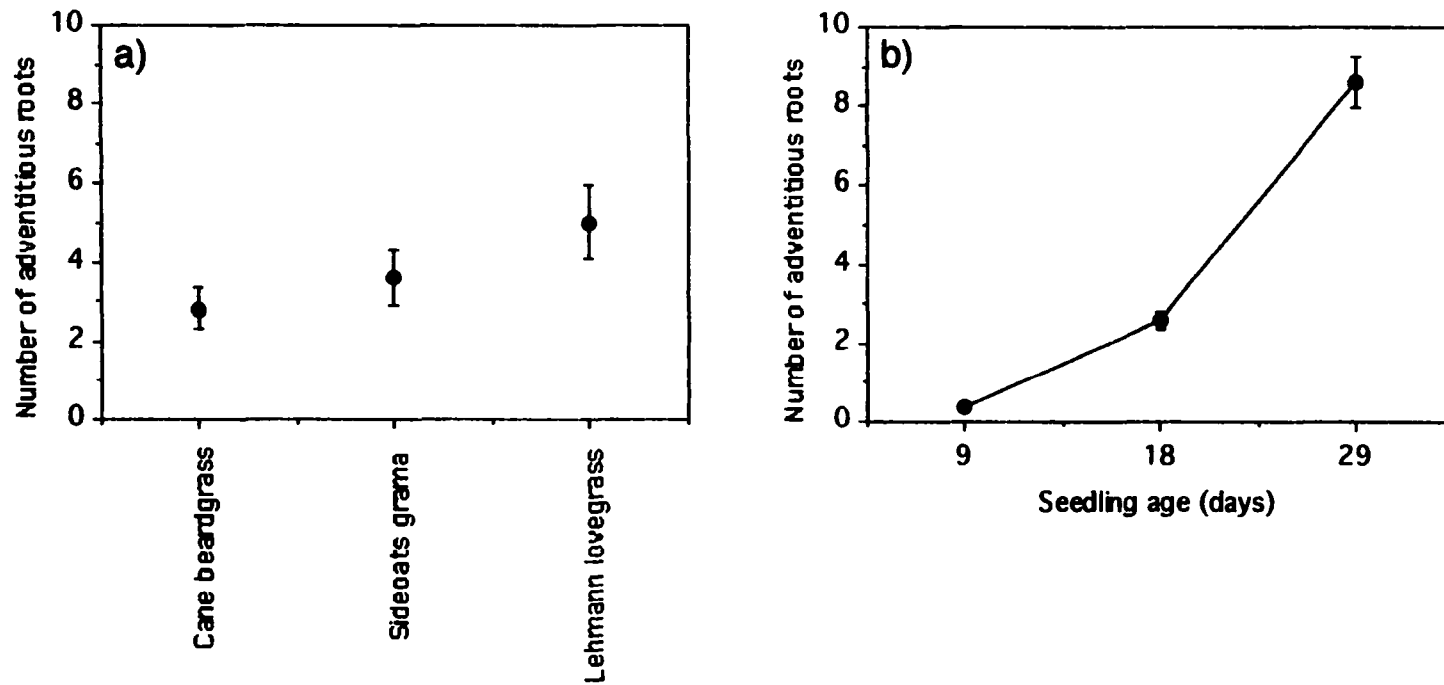
Figure 4.7. Mean number of adventitious roots of seedlings watered every 3 or 6 days. a) Main effects of species. b) Main effects of seedling age. Error bars represent standard errors of the means.
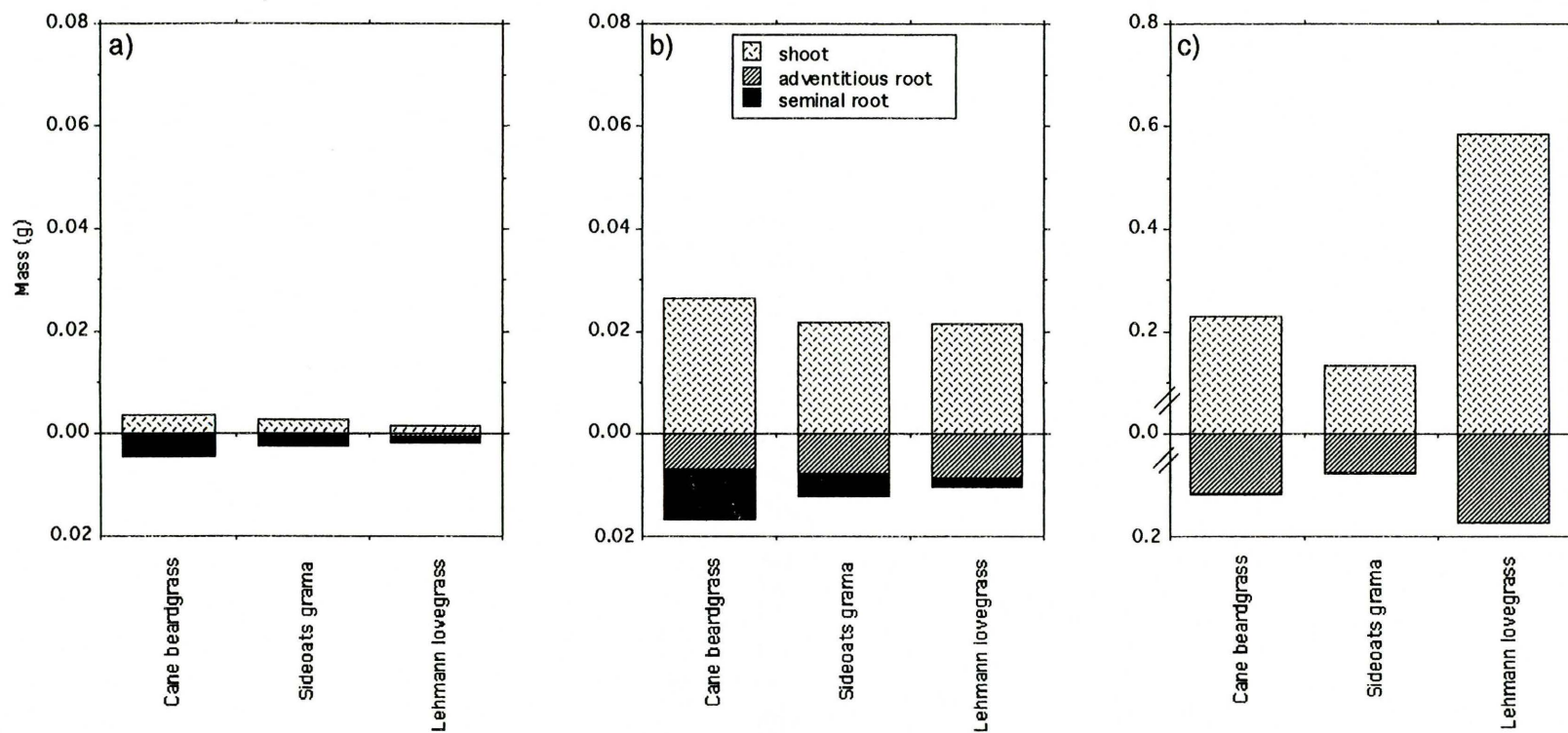
Figure 4.8. Biomass of shoot, adventitious root, and seminal root systems of cane beardgrass, sideoats grama, and Lehmann lovegrass seedlings evaluated 9 (a), 18 (b), and 29 (c) days after initial watering. Plants were watered every 3 or 6 days.
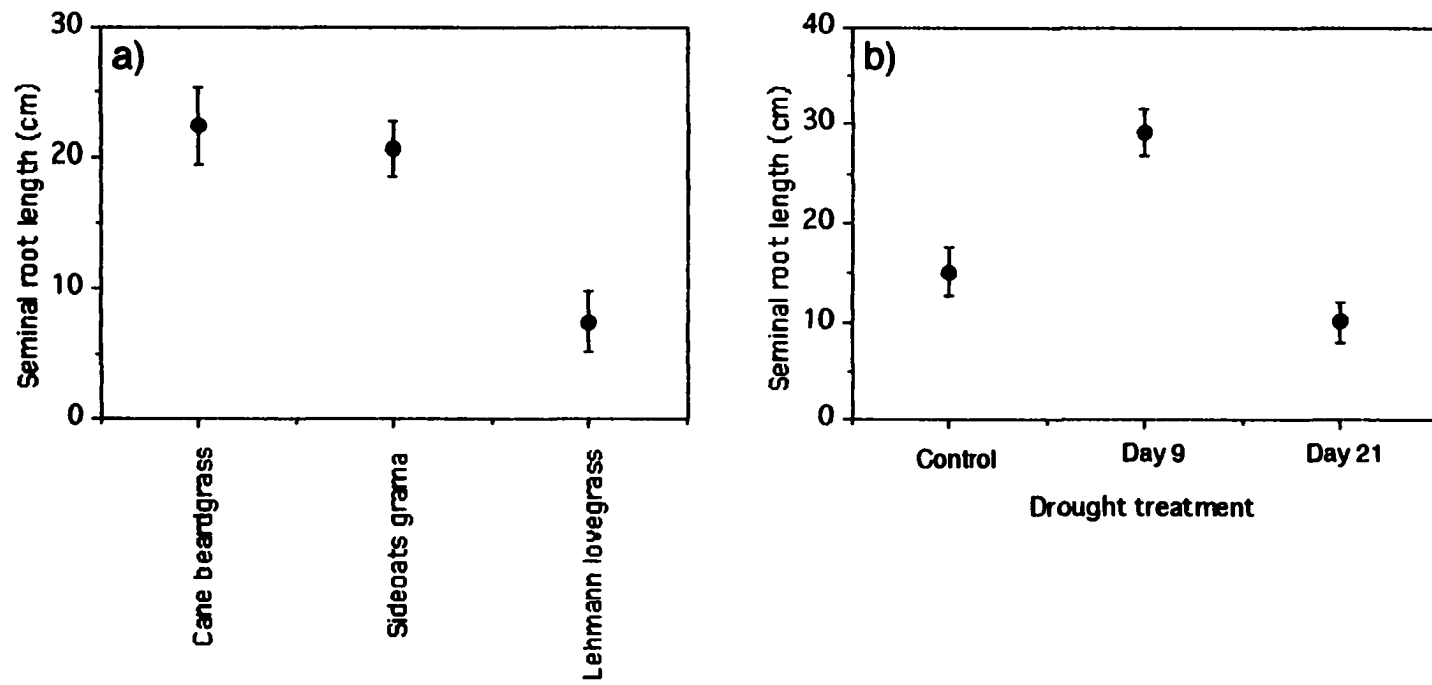
Figure 4.9. Mean maximum seminal root length of drought-affected and control seedlings watered every 3 or 6 days prior to the initiation of drought. a) Main effects of species. b) Main effects of drought treatment: a 22-day drought was imposed on seedlings 9 days or 21 days after initial watering; non-droughted control seedlings were evaluated 29 after initial watering. Error bars represent standard errors of the means.
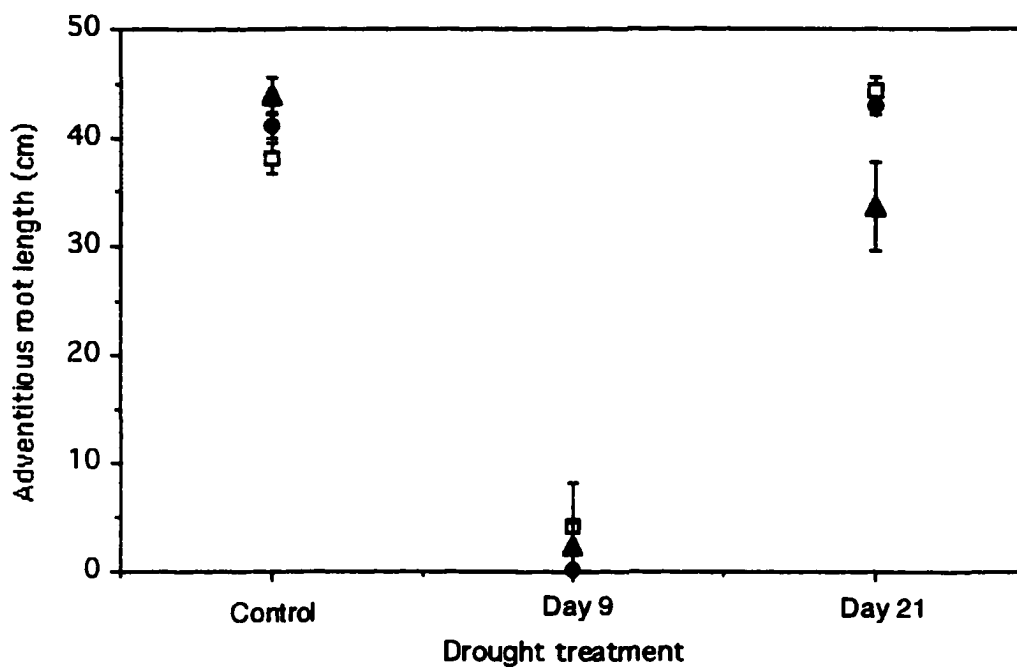
Figure 4.10. Mean maximum adventitious root length of drought-affected and control cane beardgrass (closed circles), sideoats grama (open squares), and Lehmann lovegrass (closed triangles) seedlings watered every 3 or 6 days prior to the initiation of drought. Interaction of species with drought treatment: a 22-day drought was imposed on seedlings 9 days or 21 days after initial watering; non-droughted control seedlings were evaluated 29 after initial watering. Error bars represent standard errors of the means.
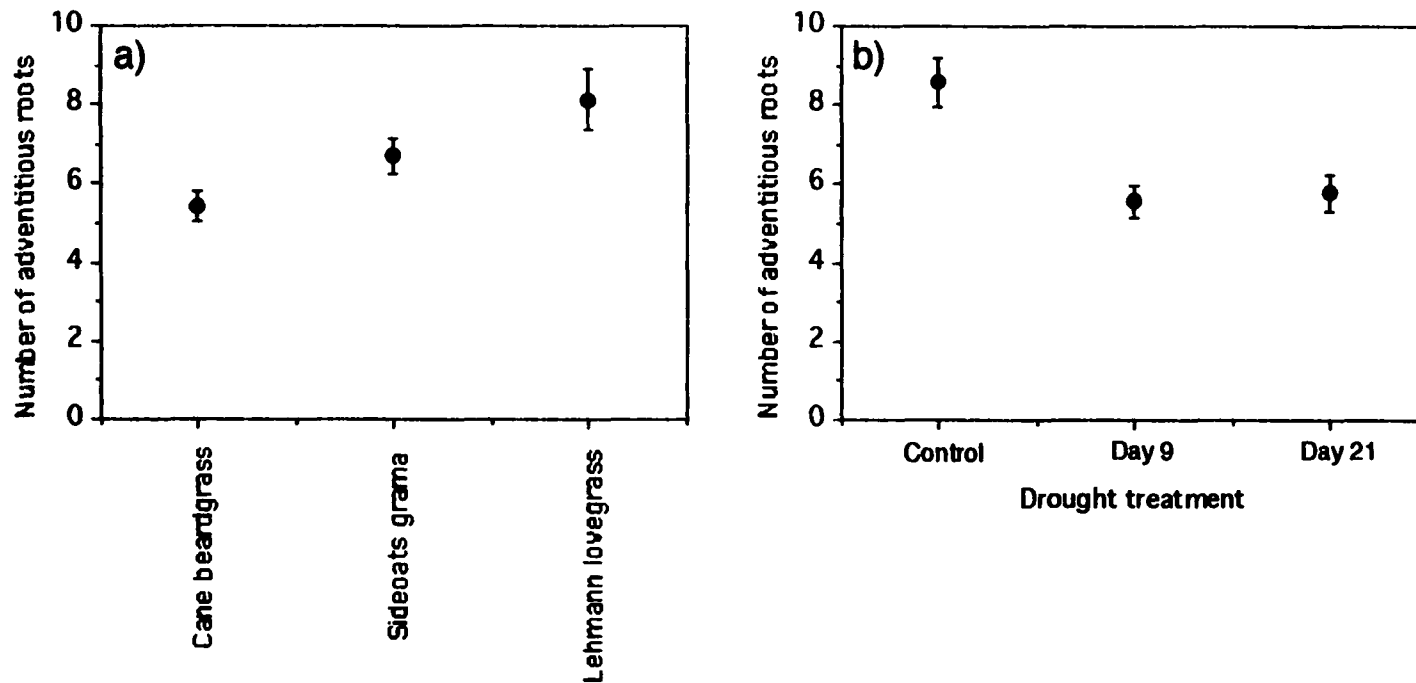
Figure 4.11. Mean number of adventitious roots of drought-affected and control seedlings watered every 3 and 6 days prior to the initiation of drought. a) Main effects of species. b) Main effects of drought treatment: a 22-day drought was imposed on seedlings 9 days or 21 days after initial watering; non-droughted control seedlings were evaluated 29 after initial watering. Error bars represent standard errors of the means.
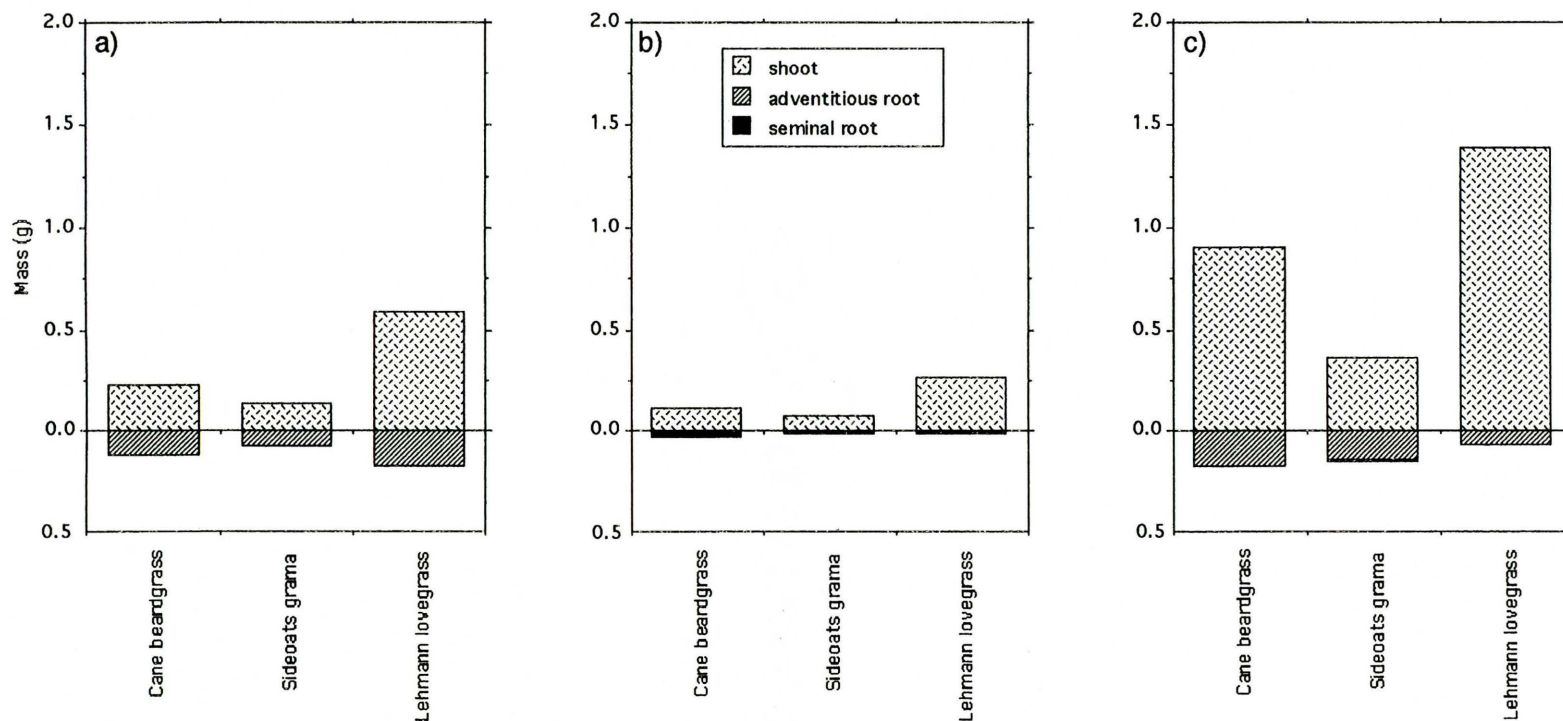
Figure 4.12. Biomass of shoot, adventitious root, and seminal root systems of cane beardgrass, sideoats grama, and Lehmann lovegrass seedlings evaluated after drought treatment. Drought treatment included: a) control seedlings evaluated 29 days after initial watering; b) a 22-day drought imposed on seedlings 9 days after initial watering; c) a 22-day drought imposed on seedlings 21 days after initial watering. Plants were watered every 3 or 6 days prior to the initiation of drought.

DISCUSSION

Differences among species in the development of root systems, allocation of biomass to root and shoot systems, and total biomass production suggest possible explanations for differential survival and establishment of species planted in revegetation projects. The following discussion is organized with respect to these explanations.

Species Effects

In general, Lehmann lovegrass initiated adventitious roots at an earlier age, produced more adventitious roots, and greater adventitious root biomass than sideoats grama or cane beardgrass under non-drought conditions. Lehmann lovegrass tended to produce longer adventitious roots and shorter seminal roots than cane beardgrass, whereas sideoats grama roots was generally intermediate between the other species. Germination of Lehmann lovegrass seeds was probably delayed relative to that of cane beardgrass and sideoats grama (Roundy and Biedenbender 1996, see Chapter 2); thus, it is likely that within an age class, Lehmann lovegrass seedlings were at least one or two days younger than those of the other species. Therefore, given the probable difference in real age of individual seedlings, the timing of adventitious root production exhibited by Lehmann lovegrass is likely somewhat earlier than indicated by these results. Adventitious root development is necessary for establishment of grass seedlings (Esau 1977); due to the greater cross-sectional area of xylem in adventitious roots relative to seminal roots, adventitious roots are better able to meet the transpiration demands of the plant (Hyder et al. 1978, Ries and Svecjar 1991, Wilson et al. 1976). Thus, early and prolific development of adventitious roots would confer an advantage to recently emerged grass seedlings subjected to high transpiration demands that commonly occur during summer in southeastern Arizona.

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Environmental Effects

Development of root systems, most notably seminal and adventitious root length and the timing of adventitious root development, were apparently influenced by environmental conditions. Differences in root length were most apparent when moisture was limiting. Very few effects due to watering treatment were detected indicating that differences between watering regimes were insufficient to elicit a biological response in most cases. However, watering regime affected seminal root length in Experiments 1 and 2; in both experiments, longer seminal roots were produced when seedlings were exposed to less frequent watering. These results are consistent with other studies in which seminal root length increased as watering frequency decreased (Olmsted 1941, Roundy et al. 1993). In addition, relative differences in root growth patterns were apparent between Experiments 1 and 2. Seminal roots of younger seedlings were longer in Experiment 2 than Experiment 1; seminal roots of 9-day-old sideoats grama and Lehmann lovegrass seedlings from Experiment 2 were twice as long as those from Experiment 1, whereas seminal roots of 9-day-old cane beardgrass seedlings from Experiment 2 were over six times longer than those from Experiment 1. Furthermore, seminal roots continued to lengthen with seedling age throughout Experiment 1, whereas in Experiment 2 the maximum depth of seminal roots was attained by the 18-day-old seedlings. Soil moisture at 2-4 cm was quite variable in both experiments, yet hotter, drier environmental conditions prevailed in Experiment 1 relative to Experiment 2; it is likely that higher temperatures and lower relative humidity existed at the soil surface in Experiment 1. Given that panicoid-type grasses initiate adventitious roots at or near the soil surface, the development of these roots was probably delayed by reduced moisture availability at the soil surface in Experiment 1; none of the species had produced adventitious roots by day 9 in Experiment 1. Thus, continued growth of seminal roots exhibited throughout Experiment 1 was needed to ensure adequate water delivery to the shoot. However, lower ambient temperatures and higher relative

humidity predominated throughout Experiment 2, and differences among species in adventitious root initiation were detected; when 9 days-old, Lehmann lovegrass and sideoats grama produced adventitious roots, whereas cane beardgrass had not. Pulses of decreased soil moisture availability occurred at 5-7 and 12-14 cm depths in Experiment 2, and likely reflect depletion of soil water by adventitious roots. Lack of discernible soil water depletion at deeper depths in Experiment 1 probably reflects both the delayed development of adventitious roots and low transpiration demands associated with relatively smaller shoots. Seedlings of all species had developed adequate adventitious root systems for water delivery after 29 days and reliance on the seminal root system to supply water was diminished for all species.

Inconsistencies among results from this and several previous studies must be addressed because they directly affect predictions about root growth rates. Seminal root lengths observed in this study were generally longer than those observed by other researchers. Sideoats grama root growth has been examined in several studies and comparisons involving this species will be used here for illustrative purposes. Seminal root growth rates of sideoats grama from Experiment 1 averaged 0.7-, 1.2-, and 0.9-cm day $^{-1}$ for 9-, 18-, and 29-day-old seedlings, respectively; those from Experiment 2 averaged 1.4- 1.3-, and 0.7-cm day $^{-1}$, respectively. Seminal root growth rates reported in other studies varied between 1.0 cm day $^{-1}$ (Simanton and Jordan 1986), 0.4 cm day $^{-1}$ with frequent watering to 0.6 cm day $^{-1}$ with less frequent watering (Roundy et al. 1993), 0.5 cm day $^{-1}$ under high soil temperatures to 0.6 cm day $^{-1}$ under low soil temperature conditions (Sosebee and Herbel 1969), and 0.8 cm day $^{-1}$ increasing to 0.9 cm day $^{-1}$ (Olmsted 1941). Thus, seminal root extension rates for 9-day-old seedlings from Experiment 1 are nearly in agreement with results obtained by Simanton and Jordan (1986) and Olmsted (1941); otherwise, seminal roots in this study generally grew more rapidly than those of previous

studies. These inconsistencies may reflect differences in cultural techniques; seedlings in all previous studies were grown in containers in a greenhouse or growth chamber. In each of these studies, containers were free-standing, which exposed the container sides to ambient temperatures maintained in the controlled environment. Thus, soil temperatures were likely fairly constant throughout the soil volume, and thus did not reflect soil temperature dynamics typical of field conditions. Root growth is frequently restricted once soil temperatures are elevated beyond an optimum threshold (Sosebee and Herbel 1969), thus it is not surprising that root lengths obtained under field conditions were longer than those obtained from containers in controlled environments. Therefore, estimates of root growth rates based on previous studies may be conservative relative to root growth rates under field conditions, and predictions based on these rates may be skewed. However, root growth is commonly greater in disturbed soils relative to undisturbed soils (Cornish 1993); depending on the nature of seedbed preparations prior to seeding, root growth rates in reseeding projects may differ from those achieved in studies using repacked soils.

Growth of the seminal root prior to development of an adventitious root system is essential for survival. If the rate at which the soil drying front proceeds is faster than the rate at which the seminal root grows, survival is unlikely (Roundy et al. 1993, 1997). The rate at which the soil dries depends on the amount and duration of the initial rainfall event, soil surface characteristics, and subsequent environmental conditions (Roundy et al. 1997). If an initial rainfall event is not followed by subsequent rain events, the soil drying front moves 15 to 36 mm day $^{-1}$ (Roundy et al. 1993, 1997). Seminal root growth rates for sideoats grama estimated 9 days after seeding were 7.3 and 13.5 mm day $^{-1}$ from Experiments 1 and 2 respectively; previous estimates of 8.7 to 10.0 mm day $^{-1}$ have been reported for this species (Roundy et al. 1993, Simanton and Jordan 1986). Sideoats grama and cane beardgrass seminal root growth rates were faster between day 9 and day 18 than

between planting and day 9. Interestingly, Lehmann lovegrass seminal root growth rates were slower between days 9 and 18 relative to the first 9 days, suggesting that early development of adventitious roots may alleviate the need for this species to depend on the seminal root system for water delivery.

Predictive models incorporate estimated rates for seminal root growth and movement of the soil drying front to predict the number of rainless days that seedlings could survive before the depth of the drying front exceeds seminal root depth (Roundy et al. 1997). Clearly, the predicted rainless period preceding seedling mortality would be extended if actual root growth rates exceed estimated rates used in these models. Given that seminal root growth rates for sideoats grama and cane beardgrass were about two and six times greater, respectively, in Experiment 2 than in Experiment 1, it is reasonable to assume that seedling survival may be facilitated if planting occurs when subsequent environmental conditions are likely to produce relatively low evapotranspirational demands. Root growth predictions may be more accurate if they incorporate growth rates that vary with seedling age and environmental conditions rather than static rates. Additional study is needed to assess the dynamic nature of seminal root growth rates and how they are affected by ambient environmental conditions.

Biomass Allocation

Total production and biomass allocation to different root and shoot systems varied with species and varied between plantings. At 9 and 18 days, Lehmann lovegrass total biomass did not differ from, or was less than that of the other two species. However, after 29 days Lehmann lovegrass had produced more total biomass than either sideoats grama or cane beardgrass; the largest gain in biomass occurred primarily between days 18 and 29 in both plantings. Water-use efficiency (WUE) of Lehmann lovegrass seedlings and mature plants

is commonly higher than that of other C4 grasses (Snyman et al. 1997, Wright 1975, Wright and Dobrenz 1973), which provides a physiological mechanism to explain the high productivity of this species. Adventitious root biomass of Lehmann lovegrass after 29 days generally equaled or exceeded that of the other two species. Overall, biomass accumulation after 29 days for all species was about two to five times greater in Experiment 2 relative to Experiment 1, which likely reflects both increased evapotranspirational demand and reduced and delayed growth of adventitious roots during the first experiment. However, relative allocation to root and shoot systems over time varied between the two experiments. In Experiment 1, root-to-shoot ratios at 9 days were roughly equal among the species (0.98, 0.95, and 1.01 for cane beardgrass, sideoats grama, and Lehmann lovegrass, respectively), and had decreased to 0.83, 0.53, and 0.68 for those species by 29 days. In Experiment 2, root-to-shoot ratios at 9 days varied between 0.84 to 1.6; however; after 29 days root-to-shoot ratios were 0.52, 0.60, and 0.30 for cane beardgrass, sideoats grama, and Lehmann lovegrass respectively. Root-to-shoot ratios generally increase with water stress (Roundy et al. 1993) and increased relative allocation to roots confers an advantage to seedlings under drought conditions (Simanton and Jordan 1986). Thus lower root-to-shoot ratios in Experiment 2 provide supporting evidence that seedlings were less stressed for water than in Experiment 1.

Drought Effects

The timing of drought initiation affected root system development and biomass accumulation. The initiation of adventitious roots was apparently arrested by the imposition of drought but was not affected by the time at which drought occurred; the number of adventitious roots was similar for plants droughted at 9 and 21 days. Non-droughted controls had more adventitious roots than droughted plants, although it cannot be determined from these data whether the difference was due to loss of adventitious roots

during the drought treatment, or new root formation on non-droughted plants between days 21 and 29. Development of the adventitious root system was affected by the timing of drought for all species; adventitious root biomass of plants droughted at 21 days was greater than that of plants droughted at 9 days, despite the similarity in root numbers. Adventitious roots on early-droughted plants were generally extremely short and poorly-developed, and appeared to be non-functional. Non-active adventitious roots on droughted blue grama (Van der Sluijs and Hyder 1974) and sideoats grama (Olmsted 1942) seedlings resumed growth shortly after watering resumed. It is unclear from this study whether the adventitious roots present on seedlings droughted at 9 days were quiescent, and thus capable of regrowth, or dead. Nevertheless, seedlings droughted at 21 days had well-developed adventitious root systems, in contrast to seedlings droughted at 9 days, which allocated most of the root biomass to the seminal root system; thus, the seminal root system was singularly responsible for delivering water to those plants. Depletion of soil moisture to -1.5 MPa at 12-14 cm occurred within 3-5 days after drought when plants were droughted at 21 days, but took 14-18 days when plants were droughted at 9 days. Differential rates of soil moisture depletion likely reflect combined differences in transpiration demands (plants droughted at 9 days had smaller shoots) and ability of the different root systems to deliver water to the shoot. Total biomass accumulation of the plants droughted at day 9 was lower than either the undroughted control or the plants droughted on day 21. Greater production of shoot biomass on plants droughted at 21 days relative to the non-droughted controls indicates that the former plants were able to continue photosynthesizing and therefore produce biomass despite the imposition of drought; therefore, adventitious roots present before the initiation of drought were capable of meeting the water demands of the plants by accessing water sources remaining at deeper depths.

The influence of drought on total biomass production and allocation to root and shoot systems was especially notable for Lehmann lovegrass. Under drought conditions, Lehmann lovegrass produced more total biomass than the other species, regardless of the timing of drought initiation. The ability to continue high productivity under water stress is typical for many species that exhibit high WUE. Clearly, biomass production of Lehmann lovegrass droughted at 9 days was low relative to non-droughted controls, and likely reflects limitations of the seminal root system to meet water demands of the plant. However, the effect of drought on relative allocation to root and shoot systems is perhaps more interesting. At harvest, the root-to-shoot ratio of non-droughted Lehmann lovegrass seedlings was 0.30, but this ratio dropped to 0.06 and 0.05 for individuals droughted at 9 and 21 days, respectively. These root-to-shoot ratios are fairly similar to those of annual grasses (Jackson and Roy 1989), yet high root-to-shoot ratios are usually considered advantageous to perennial plants under water stress (Harper 1977, Brown 1995). Lehmann lovegrass commonly produces reproductive structures in response to water stress (Snyman et al. 1997). Indeed, among Lehmann lovegrass plants droughted at 9 and 21 days, 20 and 90% of the individuals had entered the reproductive phase by harvest, respectively (data not shown). Flowering structures were present on 20% of sideoats grama plants droughted at 21 days, but were not present on any other individuals in any of the experiments. Under water stress, Lehmann lovegrass apparently ripens seed while maintaining relatively high, nearly constant transpiration rates (Snyman et al. 1997). Diversion of resources from vegetative to flowering structures and early, indeterminate seed production are common strategies for annual and biennial plants growing in variable environments (Harper 1977, Grime 1979). Lehmann lovegrass populations severely reduced by drought have rapidly re-established from seed in subsequent years (Fourie and Roberts 1977, Cox and Ruyle 1986, Robinett 1992), indicating that at the population level, drought survival for this species incorporates both drought tolerance of individual plants

and reliance on reproduction by seed. The extremely low root-to-shoot ratios and precocious seed production of Lehmann lovegrass suggest that this species is capable of adopting opportunistic life-history strategies and may exhibit several traits common to annual plants when water-stressed.

CONCLUSIONS

Differences among species in root development and plant growth rates suggest mechanisms for the observed success of Lehmann lovegrass in reseeding projects. Lehmann lovegrass seedlings are better able to produce biomass under conditions of water stress than native species, and rapid growth of the adventitious root system provides increased water-delivery capabilities in the non-native species. Under water stress, Lehmann lovegrass adopts strategies that favor reproduction over vegetation biomass production of the individual, thus facilitating population-level success. However, root growth of all species proceeds at a faster rate when lower ambient temperatures and higher relative humidity prevails. Therefore, under favorable environmental conditions, the native species tested here are capable of growth and survival. Judicious choice of planting date may increase the potential for successful reseeding of native species in southeastern Arizona.

CHAPTER 5

CONCLUSIONS

Changes in land management policy often create new priorities which necessitate revised management goals. However, implementation of new goals may be hindered when the biotic components of a system do not respond in ways that allow managers to achieve those goals. Establishment of native grasses has recently become a priority in many revegetation projects, yet efforts to establish native grasses in southeastern Arizona often fail, whereas revegetation of non-native grasses is frequently more successful (Cox et al. 1982). This dilemma led to the basic premise for my research concerning revegetation of native grasses: Why is native grass establishment poor compared to that of non-native grasses when planted in revegetation projects? Furthermore, what can be done to improve the potential for successfully establishing native grasses from seed? To address these questions, I determined the fate of seeds planted under field conditions during summer in southeastern Arizona. Once planted, seeds must successfully negotiate several transitions through transitory stages before becoming an established plant. Differential establishment of seeded species reflects the fate of individual seeds, and likely results from differential vulnerabilities during germination and subsequent seedling growth stages. I examined germination, emergence, mortality, survival, and seedling growth of seeded species exposed to variable soil moisture conditions to elucidate species-specific patterns and processes that affect establishment.

Species exhibited differences in rates and patterns of germination (Chapter 2). Native species, (e.g., sideoats grama, cane beardgrass, green sprangletop, Arizona cottontop, and bush muhly) exhibited high germination percentages and limited residual germinability following initial rain events. Lehmann lovegrass exhibited lower germination and higher

residual germinability in response to initial and subsequent rainfall events, yet retained more residual germinable seeds than all other species studied. Emergence patterns mirrored germination and germinability patterns; fast-germinating species tended to produce a few, early cohorts, whereas those species that germinated more slowly or retained more residual germinable seeds following initial rain events (e.g., lovegrasses) tended to produce many, small cohorts throughout the growing season (Chapter 3). Survival of emerged seedlings varied among emerged cohorts when several wet-dry periods occurred within two weeks of emergence. A strong correlation between seedling survival and soil moisture availability during the lifespan of seedlings provided further evidence that seedling survival was affected by variable moisture availability. Mortality was highest during the first week after emergence, indicating that seedlings are most vulnerable before seedling root systems are well-developed. Indeed, seedling growth studies verified that while the timing and rate of adventitious root development differed among species, the seminal root system predominated nine days after planting (Chapter 4). Under non-drought conditions Lehmann lovegrass produced more above- and belowground biomass than either of the native species. Under drought conditions, Lehmann lovegrass produced more aboveground biomass, but less belowground biomass than native species. Seedlings exposed to drought nine days after planting depended exclusively on seminal roots for water delivery, and seedling biomass was greatly diminished relative to control plants and to plants exposed to drought 21 days after planting, both of which had well-established adventitious roots.

Collectively, species-specific patterns of germination and seedling growth result in differential establishment, and differences are mediated by patterns of soil moisture availability. Establishment of species that rapidly germinate and produce a few, large cohorts are favored by rainfall patterns which result in conditions that support early

seedling growth subsequent to initial rains. For these species, the planted seedbank is often depleted after the initial rainfall event and therefore the risk of seeding failure associated with the occurrence of lengthy dry periods after the initial rainfall depends on the ability of seedlings to tolerate dry soil conditions. The seedbanks of slower-germinating species such as Lehmann lovegrass are generally not depleted by initial rainfall events; the occurrence of lengthy dry periods following initial rains imposes less risk to reseeding success due to the potential for subsequent rainfall events to promote germination and growth of remaining germinable seeds. In addition, Lehmann lovegrass seedlings likely benefit from precocious adventitious root development and relatively high rates of biomass accumulation under a variety of environmental conditions. Combined germination and seedling growth characteristics provide mechanistic explanations for the relative success of Lehmann lovegrass reseedings in regions characterized by highly variable precipitation. However, the nature of germination mechanisms remain largely untested under field conditions. Additional field experiments that control soil moisture availability would provide greater discernment of germination response. These studies would be aided by future technological advances that allow more precise measurement of soil moisture at small scales (e.g., at the soil surface or at the level of a seed). Additional experiments investigating root growth over time at finer scales of resolution would allow more accurate predictions of growth for different-aged seedlings under various environmental conditions. The potential for drought-affected seedlings to resume growth when favorable moisture conditions return needs further investigation to better understand the dynamics of seedling drought tolerance.

Rainfall and soil moisture patterns vary widely between and within years. Environmental conditions during one growing season may favor establishment of one or more species, whereas different environmental conditions may favor the establishment of a different suite

of species. Years in which summer soil moisture conditions are highly variable would tend to favor Lehmann lovegrass over faster-germinating native species. However, the potential for native species establishment is increased if initial rains that induce germination are followed quickly by rainfall events that promote continued seedling growth. For these species, seedling mortality that results in reseeding failures is more likely if lengthy dry periods follow initial rains. Studies of long-term summer precipitation records in southeastern Arizona indicate that the probability of rain sequences in which the initial rainfall event is followed by dry periods lasting five days or less is maximized between the third week of July and the first week of August (Frasier and Lopez 1990, Roundy et al. 1996, 1997). Given the rapid germination response and concomitant depletion of seedbank reserves exhibited by native species in this study, chances for successful establishment of native grass species in revegetation projects in southeastern Arizona could be increased by delaying planting until at least the third week of July.
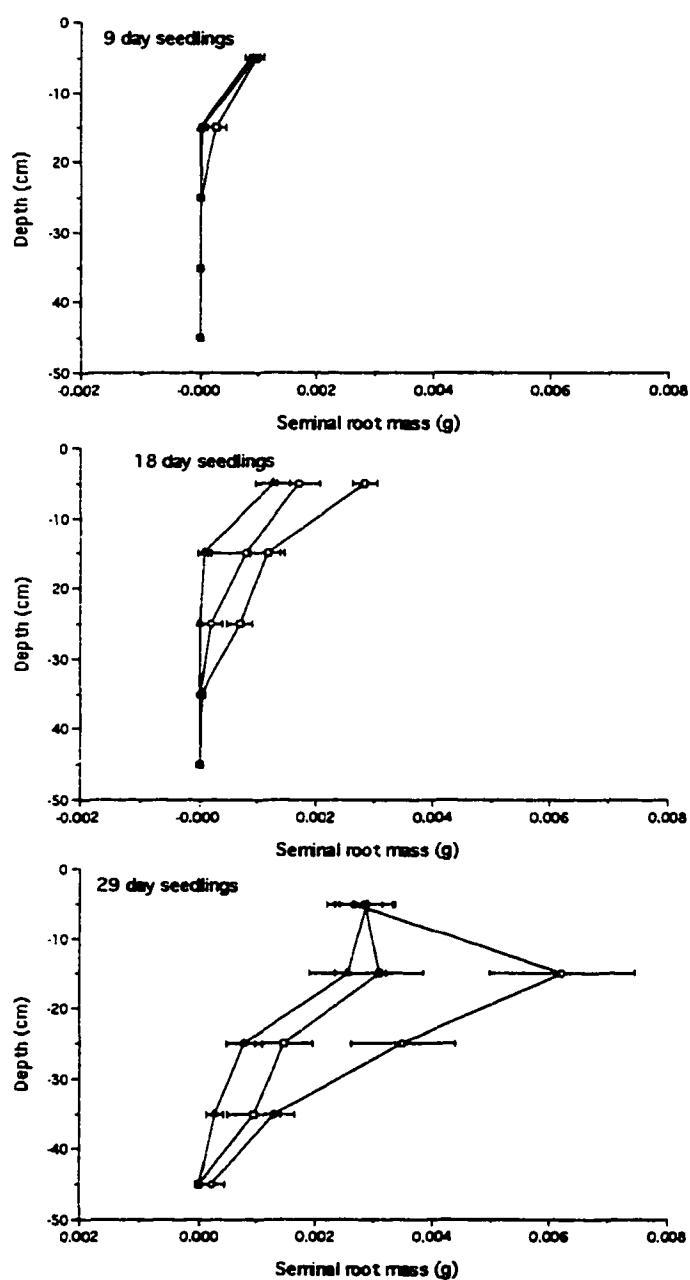
APPENDIX A

ROOT BIOMASS DISTRIBUTION WITH DEPTH

Figure A.1. Mean seminal root biomass distribution of cane beardgrass (open circles), sideoats grama (open squares), and Lehmann lovegrass (closed triangles) seedlings evaluated 9, 18, and 29 days after initial watering. Plants were watered every 2 or 4 days. Biomass was evaluated over 10 cm depth increments; mean values are plotted at the midpoint of each depth increment. Error bars represent standard error of the means.
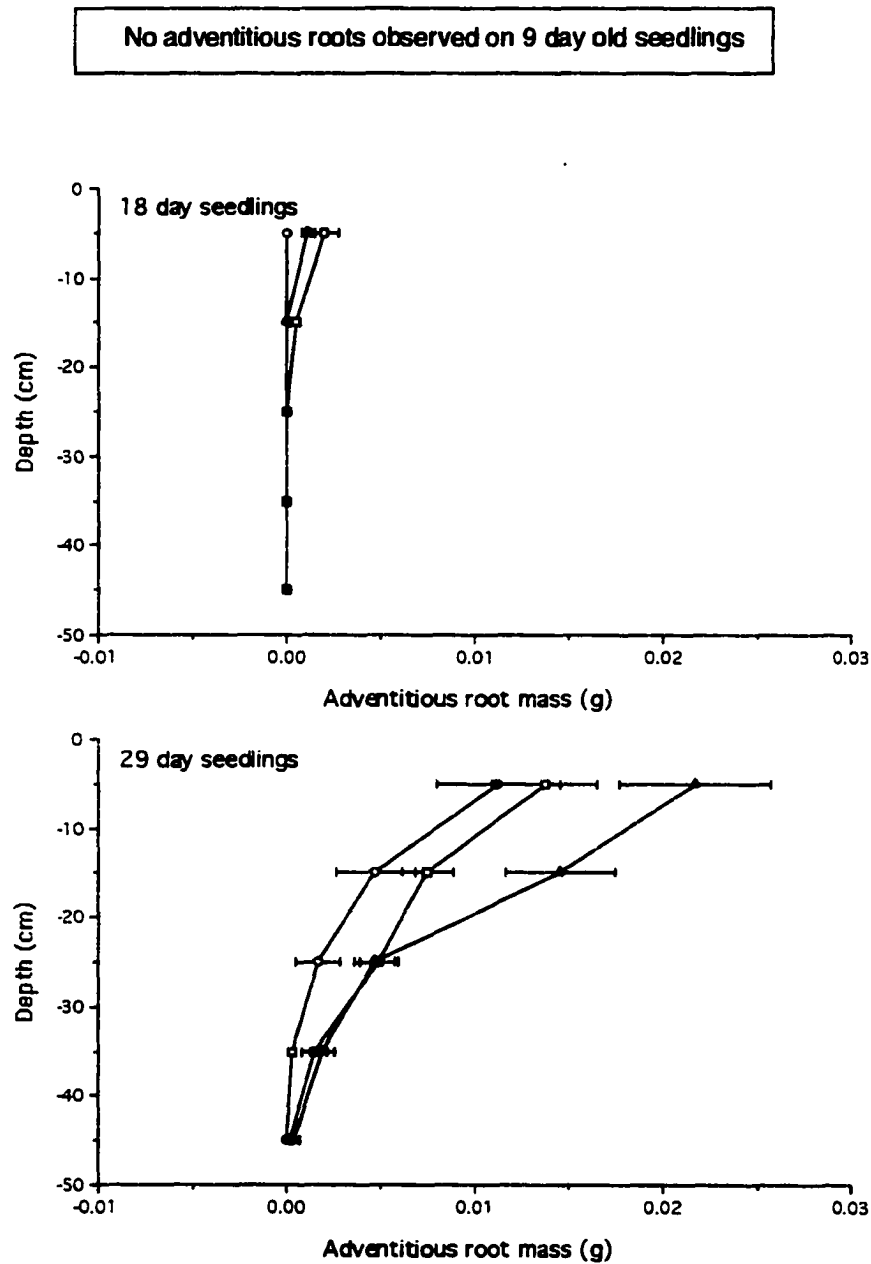
146

Figure A.2. Mean adventitious root biomass distribution of cane beardgrass (open circles), sideoats grama (open squares), and Lehmann lovegrass (closed triangles) seedlings evaluated 9, 18, and 29 days after initial watering. Plants were watered every 2 or 4 days. Biomass was evaluated over 10 cm depth increments; mean values are plotted at the midpoint of each depth increment. Error bars represent standard error of the means.
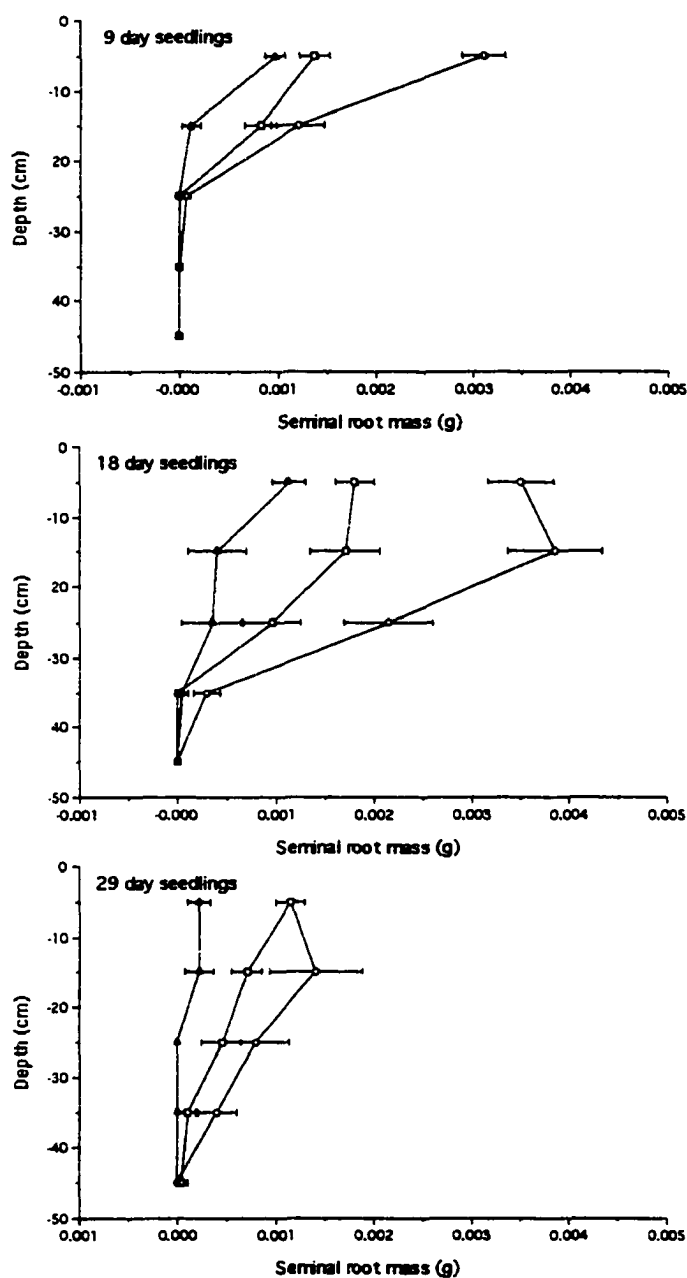
Figure A.3. Mean seminal root biomass distribution of cane beardgrass (open circles), sideoats grama (open squares), and Lehmann lovegrass (closed triangles) seedlings evaluated 9, 18, and 29 days after initial watering. Plants were watered every 3 or 6 days. Biomass was evaluated over 10 cm depth increments; mean values are plotted at the midpoint of each depth increment. Error bars represent standard error of the means.
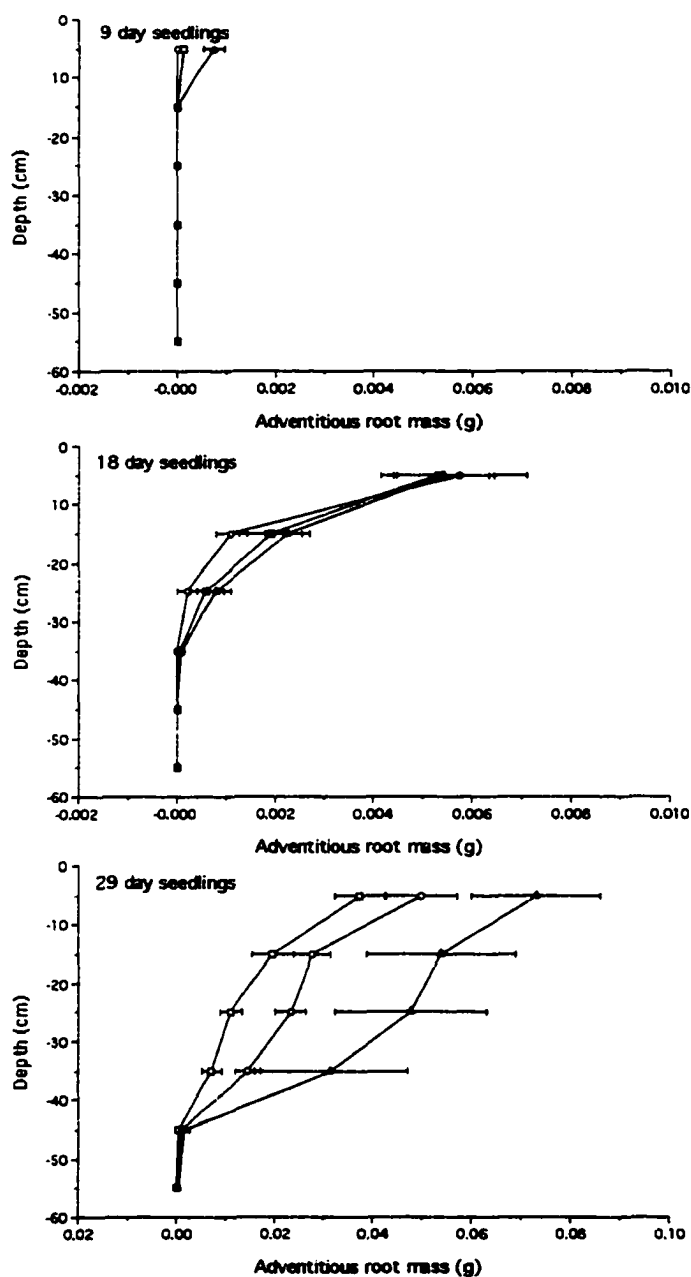
Figure A.4. Mean adventitious root biomass distribution of cane beardgrass (open circles), sideoats grama (open squares), and Lehmann lovegrass (closed triangles) seedlings evaluated 9, 18, and 29 days after initial watering. Plants were watered every 3 or 6 days. Biomass was evaluated over 10 cm depth increments; mean values are plotted at the midpoint of each depth increment. Error bars represent standard error of the means.
NOTE: Horizontal scale for 29 day seedlings differs from those for 9 and 18 day seedlings.
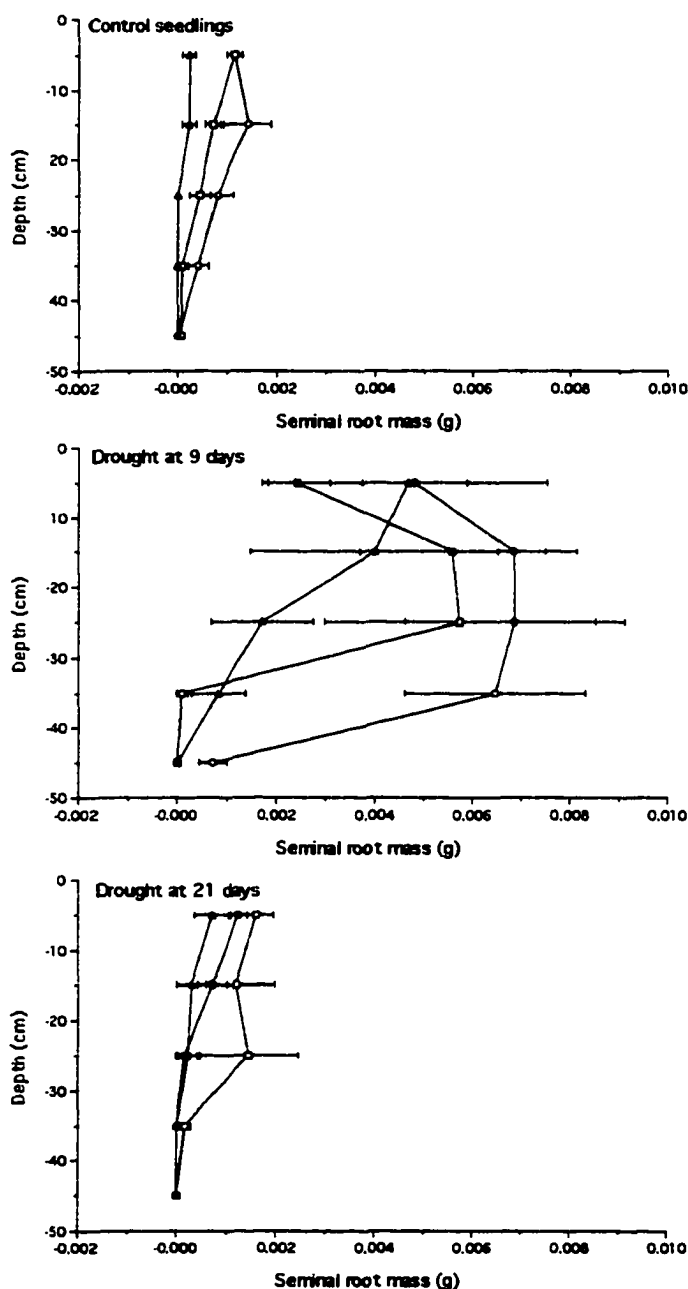
Figure A.5. Mean seminal root biomass distribution of cane beardgrass (open circles), sideoats grama (open squares), and Lehmann lovegrass (closed triangles) seedlings. Seedlings exposed to drought 9 and 21 days after initial watering were evaluated on day 31 and 42, respectively; control seedlings were evaluated 29 days after initial watering. Plants were watered every 3 or 6 days. Biomass was evaluated over 10 cm depth increments; mean values are plotted at the midpoint of each depth increment. Error bars represent standard error of the means.
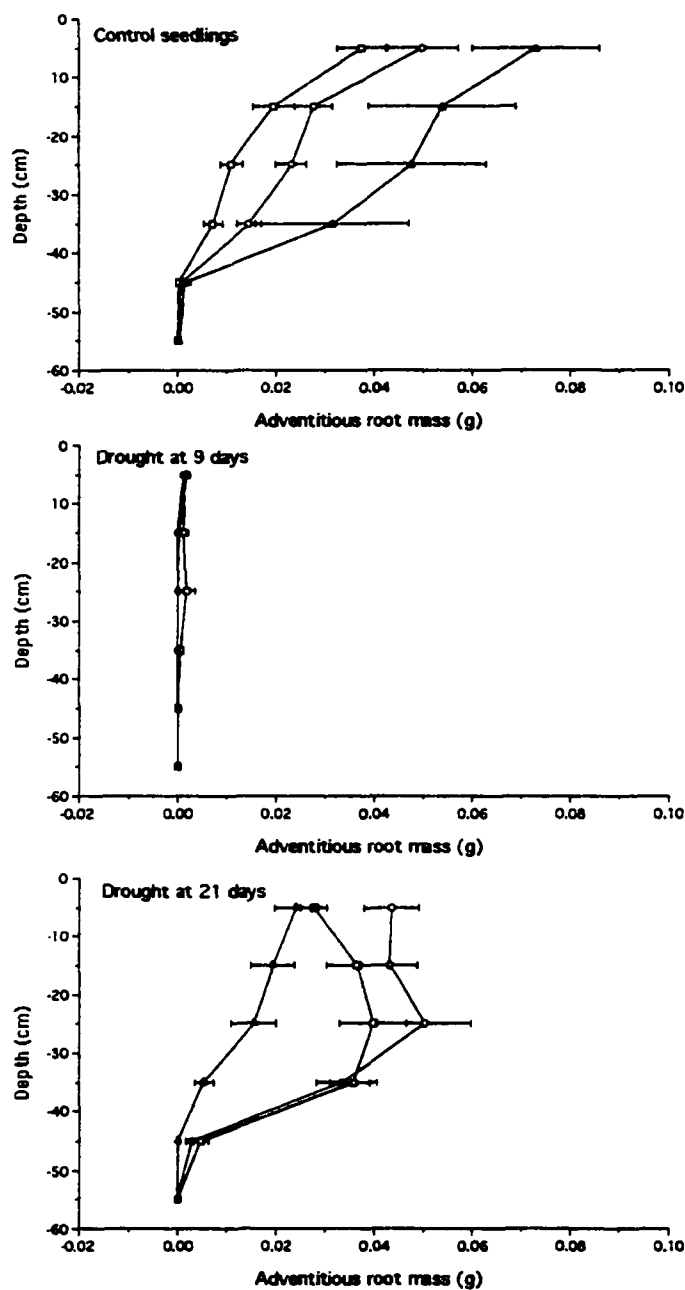
Figure A.6. Mean adventitious root biomass distribution of cane beardgrass (open circles), sideoats grama (open squares), and Lehmann lovegrass (closed triangles) seedlings. Seedlings exposed to drought 9 and 21 days after initial watering were evaluated on day 31 and 42, respectively; control seedlings were evaluated 29 days after initial watering. Plants were watered every 3 or 6 days. Biomass was evaluated over 10 cm depth increments; mean values are plotted at the midpoint of each depth increment. Error bars represent standard error of the means.

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