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Water requirements for emergence of buffelgrass (*Pennisetum ciliare*)

Judy P. Ward
Corresponding author. Jornada Experimental Range, MSC 3JER, New Mexico State University, P.O. Box 30003, Las Cruces, NM 88003–8003; jward@nmsu.edu

Steven E. Smith
Mitchel P. McClaran
School of Natural Resources, 325 Biological Sciences East, University of Arizona, Tucson, AZ 85721

The ability of an invasive species to acquire and use a limiting resource during critical life history stages governs its ability to establish and persist within an environment. Arid environments are generally considered more resistant to invasion and are defined by low and sporadic precipitation. Warm-season grasses are most susceptible to mortality during seedling emergence, but water requirements for emergence are rarely known. We examined the ability of the often invasive warm-season grass, buffelgrass, to emerge given a range of simulated precipitation delivered on 2, 3, and 4 consecutive days with the use of a line-source irrigation system in a glasshouse. The minimum amount of water required for buffelgrass emergence was observed to be 6.3 mm (3.14 mm on 2 consecutive days). With the use of probit analysis, the median emergence response (0.5 emergence probability) was predicted to require 17.4–19.9 mm of water. Emergence was concentrated within the first 5 days following initial simulated precipitation with the probability of new emergence highest on Days 3 and 4. Over the period from 1949–2001 in Tucson, Arizona within the Sonoran Desert, the total number of consecutive rainy-day sequences meeting the minimum per-day precipitation levels for a median and minimum emergence response was 27 and 92, respectively. Precipitation sufficient to result in emergence of 50% of viable buffelgrass caryopses has occurred in Tucson in about 1 of 2 years over this period. We compare the soil water requirements for emergence of buffelgrass to other perennial species in the Sonoran Desert and suggest that the invasion success of buffelgrass is due in part to its ability to emerge following relatively low precipitation levels.

Nomenclature: buffelgrass, *Pennisetum ciliare* (L.) Link PESCI

Key words: invasion, simulated precipitation, line-source irrigation system, limiting resources.

Identifying a general set of invasion predictors has been a major research focus in invasive species biology (Wade 1997). Some of this work attempts to identify plant life history traits associated with invasiveness (e.g., Goodwin et al. 1999; Pyšek 1998); other research focuses on the general environmental properties that confer susceptibility to invasion (e.g., Case 1990; Crawley 1987; Davis et al. 2000; Higgins et al. 1999; Peterson 2003). Results of these efforts suggest that arid wildland environments are relatively resistant to invasion (Usher 1988) due primarily to the infrequent occurrence of conditions when soil water is sufficient to permit seedling emergence and establishment (Rejmánek 1989). More case-specific work has focused on understanding specific traits associated with a species' capability to invade a particular environment (Gerlach and Rice 2003). We suggest that focusing on a taxon's ability to acquire and use limiting resources during critical life stages could further advance this effort and help explain an invasive species' ability to establish and persist in a given environment, and provide crucial information to facilitate control. We adopt this approach and focus on describing water requirements for seedling emergence of buffelgrass, an invasive nonnative warm-season grass in the Sonoran Desert of the United States and Mexico.

Soil water is the primary ecological driver in desert environments due to the low frequency of precipitation and high variability in its occurrence, and to high potential evapotranspiration (Noy-Meir 1973; Reynolds et al. 2004). For warm-season perennial grasses in arid ecosystems, seed germination and seedling emergence and establishment have been identified as the critical life history stage (Call and Roundy 1991). Therefore, we posit that soil water availability for establishment is a critical factor affecting successful invasion of these species in arid wildland environments.

Buffelgrass, a caespitose, apomictic warm-season perennial grass, was first introduced into the United States in the 1940s as part of an effort to stabilize degraded rangelands and provide livestock forage (Cox et al. 1988). Numerous buffelgrass strains from its native range in Africa, southwestern Asia, and India (Bashaw 1985) were evaluated (e.g., Holt 1985; Cox et al. 1988; USDA-SCS, 1943–1983). Early trials in southern Arizona demonstrated that common buffelgrass from the Turkana desert in northern Kenya (Holt 1985) established readily from seed and survived drought (Cox et al. 1988). Based on these results, numerous field plantings of buffelgrass were made in the Sonoran Desert during the period from the 1940s through the 1980s (USDA-SCS, 1943–1983). However, buffelgrass has expanded beyond the original seeding areas to become invasive in numerous natural areas, roadsides, and in urban landscapes (Felger 1990; Rutman and Dickson 2002; Ward 2003). Many observers believe that expansion is likely to continue to affect regions of the Sonoran Desert, where native vegetation is relatively intact (Arriaga et al. 2003), displacing native plants (Burgess et al. 1991), and severely altering ecosystem processes as observed in regions of Australia where buffelgrass was extensively sown (Lonsdale 1994; Smith 1995). In particular, buffelgrass increases the continuity and abundance of fine fuels, which can lead to increased frequency and extent of wildfires in the Sonoran Desert (Búrquez-Montijo et al. 2002), which is one of the few ecosystems in North America where natural fires are rare (Schmid and Rogers 1988). Fire has been shown to increase buffelgrass density and biomass in established stands in Australia (Lazarides et al. 1997). The expansion of buffelgrass in the Sonoran Desert may lead to a grass/fire cycle (D'Antonio and Vitousek 1992) that seriously limits the native vegetation's ability to persist (Búrquez-Montijo et al. 2002; Esque and Schwalbe 2000; Felger 1990; Van Devender et al. 1997; Williams and Baruch 2000).

The climate below about 1000 m near Tucson, Arizona is characteristic of the Sonoran Desert. About 55 to 65% of annual precipitation occurs in a 4-mo summer rainy season (July–October) in which mean temperature is near 25 C. An additional 30–35% of annual precipitation falls in a 5-mo winter to spring rainy season (November through March) when mean temperature at most locations is below 13 C (Smith et al. 2006). Jordan and Haferkamp (1989) established that the minimum temperature for germination of buffelgrass is 12.5 C. This indicates that germination of buffelgrass is most likely to occur during the summer rainy season in the Sonoran Desert. Here, we examine the timing and amount of precipitation required within the summer rainy season to elicit emergence of buffelgrass over a range of simulated precipitation levels that occur in 2, 3, and 4 consecutive days with the use of a glasshouse line-source irrigation system (Smith et al. 2000). Emergence speed and the length of the intervening dry period are primary factors determining seedling survival in warm-season grasses (Frasier et al. 1984). Therefore, we estimate seedling emergence speed by determining the probability of new emergence each day across all simulated precipitation levels. We then quantify the historical likelihood of the median emergence response (0.5 emergence probability) with the use of precipitation records over a 53-yr span from Tucson, located in the northern Sonoran Desert. We suggest that an understanding of the soil water requirements for seedling emergence, the rate of emergence, and the frequency of precipitation events that produce these conditions can be integrated with seed-bank information to develop knowledge-based control efforts for buffelgrass within the Sonoran Desert.

Materials and Methods

Seed collection and storage

Buffelgrass seed fascicles were collected from a population located in Tucson in September 2000. Seed fascicles consist of a cluster of spikelets enclosed by an involucre of bristles and include 1 to 3 caryopses that disperse as a unit (Anderson 1974; Humphreys 1958; Winkworth 1971). Fascicles were stored at ambient conditions in the glasshouse (mean temperature range: 12 to 36 C) for 10 mo until initiation of this experiment in July 2001.

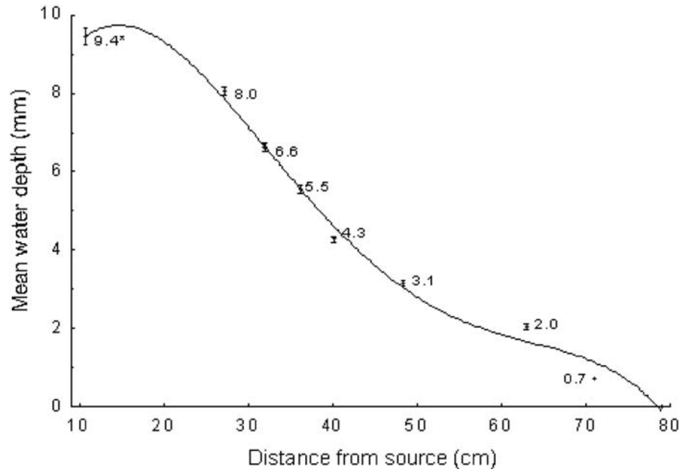

Figure 1. Mean depth of water (mm) per day (± SE) applied across a range of distances (cm) from the line-source irrigation system (LSIS). Positions used in experiments are labeled with mean depth of water (mm). Observations fitted with a fourth-order polynomial; $y = 4.6323 + 0.8094x - 0.0399x^2 + 0.0006x^3 - 3E\text{-}06\ x^4$; $r^2 = 0.9942$).

Simulated precipitation experiment

We used soil from the Combate-Diaspar series (loamy sand, thermic Ustic Torrifluvent; Breckenfeld and Robinett 2003) collected on the Santa Rita Experimental Range located 45 km southeast of Tucson. Soil from the surface 5 cm was passed through a 2.5-mm sieve, autoclaved, and air dried prior to use. Soil was placed in 20-cm-deep tapered plastic containers.[1] The bottom of each container was plugged with a crumpled square of paper (150 cm^2) and filled with 19 ml of pea gravel, followed by 135 ml of soil, which settled to 1 cm below the container rim. We placed four seed fascicles in each container, added 11.4 ml soil that completely covered the fascicles, and smoothed the soil to the container rim with the use of a straight edge.

To simulate a range of precipitation levels, we used a line-source irrigation system (LSIS) in which a single sprinkler nozzle moves along a fixed linear track above the experimental containers in an evaporatively cooled glasshouse. LSIS applies a gradient of water perpendicular to the track in a single irrigation event each day (Johnson et al. 1982; Smith et al. 2000). Prior to initiation of the experiment, we calibrated the LSIS and selected specific distances from the fixed track that received eight water application levels (simulated precipitation) between 0.7 and 9.4 mm per day (Figure 1). Each increment of increasing water application was between 1.1 and 1.4 mm, thus providing nearly equal intervals across the 8.7-mm range.

We conducted three 25-day experimental runs beginning on 20 and 28 July, and 11 August 2001. Each run included six replications with treatments (amount of water applied by number of consecutive days with this application) arranged in a complete factorial design with water applied on 1, 2, 3, or 4 consecutive days. Water was applied using the LSIS on Days 1 to 4 of each run. After the first day of water application, the containers receiving simulated precipitation for 1 day were removed from the LSIS and relocated within the glasshouse to an area where they received no water. Those receiving simulated precipitation on 2 consecutive days were similarly relocated on Day 2, and those receiving simulated precipitation for 3 consecutive days were relocated on Day 3. Simulated precipitation from the LSIS was followed by an irrigation-free period from the day the containers were relocated for 14 days. Following this, containers received daily liberal water application for 10 consecutive days to evenly saturate the soil and allow germination of the remaining viable and non-dormant caryopsis. We recorded emergence on Days 1 to 14 and on the day following the tenth day of liberal water application.

Temperature (mean = 25.7 C, SE = 0.1 C) and relative humidity (mean = 72.1%, SE = 0.4%) within the glasshouse during the experimental period approximated ambient conditions for this time period at elevations between 500 and 1,000 m in the Sonoran Desert (National Oceanic and Atmospheric Administration, National Climate Data Center 2003).

Data analyses

Containers in the line-source position receiving 0.7 mm of water per irrigation (Figure 1) did not exhibit any emergence by Day 14 and were therefore excluded from analyses. Likewise, containers receiving simulated precipitation for only 1 day were excluded because only 1.4% of these containers exhibited any emergence during the initial irrigation and drought period (Days 1 to 14).

We calculated the maximum potential emergence as the mean number of seedlings to emerge per container in the treatment combination (water depth by number of consecutive days irrigated) with the highest total emergence following liberal application of water. We used the value 2.3 as an estimate of the mean number of viable and nondormant caryopsis per each group of four seed fascicles in a container when the experiments began.

We subjected emergence data to probit analysis to determine the amount of water required to illicit the median emergence response (Scott et al. 1984). Probit analysis permits the use of regression to examine binary dependent variables such as seedling emergence whose expression reflect a normally distributed underlying but immeasurable variable. Ordinary least-squares regression is inadequate under such conditions. With the use of SAS (SAS 1999), probit analysis involved transformation of emergence response into the probit scale, which was used to generate percent emergence-water amount curves. The fit of the underlying data to a normal distribution using the probit model is evaluated with the use of a chi-square goodness-of-fit test. If the p-value for the test is too small (< 0.05), variances and covariances are adjusted by a heterogeneity factor (goodness-of-fit chi-square/degrees of freedom) and a critical value from the t distribution is used to compute fiducial limits. Confidence intervals based on fiducial limits provide conservative estimates for likely range of values predicted based on probit analysis under conditions when the underlying distribution is normal or nonnormal and correspond to an approximate 95% confidence interval (Payton et al. 2003).

In predicting the amount of water required to elicit the median emergence response each container was treated as a unique observation and the maximum potential emergence value represented the number of trials per observation (Smith et al. 2000). Each emerged seedling was treated as an event, and the amount of simulated precipitation applied by the line-source irrigation system was the dose (Statistical Analysis Systems, 1999). Initial analyses failed to identify a significant experimental run effect; therefore all three runs were analyzed as a single experiment with 18 replications.

We used the life-table method of survival analysis to compare the speed of seedling emergence across containers receiving simulated precipitation on 2, 3, or 4 consecutive days (Scott et al. 1984). In this case, the response was the day in which emergence occurred, and the total amount of simulated precipitation received by that day was treated as a covariate. We report the probability of new emergence within the time interval (the hazard estimate) for each time interval and test for differences in speed of emergence across irrigation frequencies by comparing responses in containers receiving water on 2, 3, and 4 consecutive days using the Wilcoxon test (Allison 1995). To examine the effect of irrigation frequency with comparable total water application, our first comparison included samples receiving a total of between 16.1 and 17.1 mm of simulated precipitation across the three frequencies. We selected 16.1 to 17.1 mm because it minimized the range in which all three frequencies could be represented.

To characterize the actual frequency of precipitation events likely to result in buffelgrass emergence, we examined precipitation records from Tucson (Station: Campbell Avenue Experimental Farm; NOAA Cooperative ID: 028796) for the period 1949–2001 (National Oceanic and Atmospheric Administration, National Climate Data Center 2003). Specifically, we determined the number of consecutive-day sequences during the warm season (May 1 to September 30) in which daily precipitation was equivalent to or greater than the amount required to elicit the observed minimum and predicted median emergence responses from our experiments. To avoid double-counting rainy-day sequences for the minimum response, the second day of any 2-day sequence was excluded from consideration as the first day of the next 2-day sequence. To avoid double-counting rainy-day sequences for the median response, a sequence of 4 rainy days meeting the per-day precipitation requirements was counted as an event and was not included as a 2- and 3-day precipitation event. Similarly, sequences that met the 3-day requirement were not evaluated against the 2-day criteria, etc. We did not simulate rainy-day sequences longer than 4 days; however, we noted the occurrence of these longer rainy-day sequences in the precipitation records.

Results and Discussion

Chi-square values from probit analyses indicated that the assumption that the underlying distribution for seedling emergence was normal for treatments that received water for 2 and 4 consecutive days. When predicting the median emergence response, fiducial limits were calculated without the use of the heterogeneity factor for these treatments. Chi-square values for the treatment that received water for 3 consecutive days were large enough so that the heterogeneity factor was used to calculate fiducial limits for the predicted median emergence response (Payton et al. 2003). The maximum mean number of seedlings to emerge per container was observed in the containers that initially received 8.05 mm per day on 4 consecutive days, and we used this value (2.3 seedlings) to represent the mean number of viable, nondormant caryopsis per container. Overall, emergence increased with increasing water application per day and the

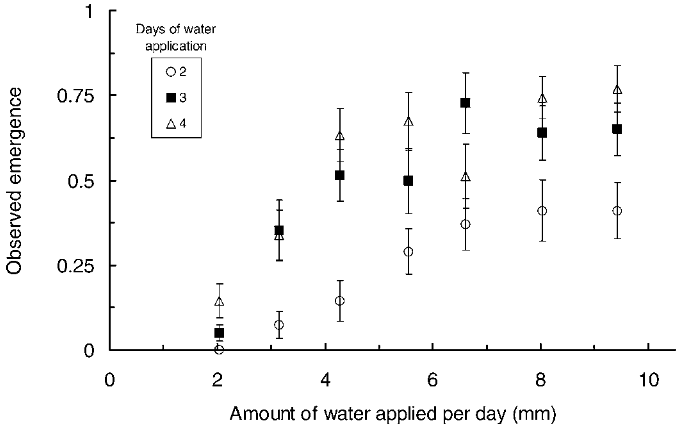

FIGURE 2. Mean (± SE) proportion of viable and nondormant buffelgrass seeds that emerged over seven amounts of water applied for either 2, 3, or 4 consecutive days.

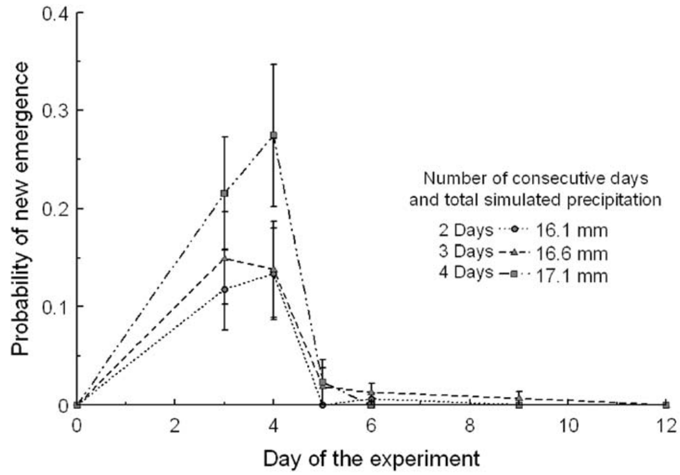

FIGURE 3. Mean (± SE) probability of new buffelgrass seedling emergence on each day of the experiment for containers receiving 16.1–17.1 mm of total water for 2, 3, or 4 consecutive days.

number of consecutive days of irrigation (Figure 2). The minimum amount of water in which we observed buffelgrass emergence was 6.3 mm (3.14 mm on 2 consecutive days). The median emergence response was predicted to require a total of 17.4 to 19.9 mm of water depending on the frequency of irrigation events (Table 1). A sample of common herbaceous and woody perennial species in the Sonoran Desert have been shown to require a minimum of 17.5 to 35.6 mm of precipitation for emergence (Bowers et al. 2004), which places the precipitation requirements for a median emergence response of buffelgrass at the lower end of this range. However, these values are higher than populations of a native caespitose warm-season perennial grass from the Sonoran and adjacent Chihuahuan Desert [*Digitaria californica* (Benth.) Henr.] that exhibited a median emergence water requirement of 9 to 12 mm over 3 consecutive days (Smith et al. 2000).

Buffelgrass emergence was observed to be concentrated within the first 4 days following initial irrigation with the probability of new emergence highest on Days 3 and 4 (Figure 3). Within a given range of total water (16.1 to 17.1 mm), the probability of new emergence (the hazard estimate) was highest (0.27) on Day 4 for containers receiving water on four days (Figure 3). Within this range of total water, the probability of new emergence was not different for containers irrigated on 2 or 3 days throughout the observation period. Across all irrigation frequencies, the probability of new emergence was less than 0.03 by Day 7 (Figure 3). These results indicated that there might be a slightly higher speed of emergence when buffelgrass receives a given amount of water over a longer period, 4 days compared to 2 days. However, this difference may also be due to the slightly higher water applied in the 4-day treatment (17.1 mm) versus 3-day (16.6 mm) and 2-day (16.1 mm).

During the 53-yr period from 1949 to 2001, there were 27 consecutive-day sequences between May 1 and September 30 in Tucson with daily precipitation equal to or greater than that observed to elicit emergence of 50% of the viable, nondormant buffelgrass caryopses (17.4 mm, Table 2). Most of these events were 2-day sequences, with the annual probability of a 2-day sequence of 0.30 and a combined probability across 2-, 3- and 4-day sequences of 0.51. Over the same period, there were 92 sequences that met the minimum precipitation level for at least some buffelgrass emergence of at least 3.14 mm on two consecutive days. Our results indicate that 2, 3, and 4 consecutive rainy-day events equivalent to the level that stimulated emergence of 50% of the viable, nondormant caryopsis occurred in approximately 1 out of 2 years, whereas on average minimum emergence sequences occurred 1.8 times per year. Because we did not simulate rainy-day sequences longer than 4 days, these events did not contribute to the probabilities. However, there were five 5-day sequences that also met the 4-day pre-

TABLE 1. Daily and total amount of water required for 0.50 emergence probability of the viable and nondormant buffelgrass caryopses[a] receiving water on 2, 3, or 4 consecutive days via a line-source irrigation system.

Number of consecutive days with irrigation	Amount of water per day (mm)		Total amount of water (mm)	
	Mean	(95% CI[b])	Mean	(95% CI[b])
2	9.2	(8.2–10.9)	18.4	(16.4–21.8)
3	5.8	(4.9–6.7)	17.4	(14.7–20.2)
4	5.0	(4.1–5.7)	19.9	(16.4–22.9)

[a] Estimate of the number of viable and nondormant caryopsis per container derived from the mean emergence (2.3 seedlings per container) from four seed fascicles in the treatment with the maximum emergence.

[b] 95% confidence interval (CI) estimated with the use of the fiducial limits in probit analysis.

TABLE 2. Number and per annual probability of consecutive rainy-day sequences between 1 May and 30 September in Tucson, Arizona from 1949 to 2001, with daily precipitation levels equivalent or greater than that required for median emergence response of buffelgrass caryopses.

Sequence:	2 days	3 days	4 days	All three sequences
Minimum rain per day:	9.2 mm	5.8 mm	5.0 mm	
Total number of sequences over 53-yr period	16	7	4	27
Probability of sequence per year	0.30	0.13	0.08	0.51

cipitation minimum and thus were counted, and another seven 5-day sequences that did not meet this minimum and were not counted. Only one 7-day sequence was recorded over the 53-yr period; however, it did not meet the 4-day precipitation minimum.

It is widely recognized that only a small proportion of introduced plant species are able to persist and spread following introduction (Mack et al. 2000). Limited soil water availability defines desert ecosystems and has been recognized as the likely reason for a smaller proportion of nonnative plant species present in desert wildlands relative to more mesic environments (Rejmánek 1989). Collectively, our data suggest that summer precipitation patterns in the northern Sonoran Desert are conducive to regular buffelgrass seedling emergence events. Given the average lifespan (> 10 yr) and seed production potential of buffelgrass plants that survive at least 3 mo (Cox et al. 1988), our results indicate that insufficient soil moisture to elicit seedling emergence is not likely to impede buffelgrass invasion in areas of this region with precipitation similar to that of Tucson. Linking our biological results with models using physical environmental data from areas considered subject to invasion (e.g., Arriaga et al. 2003) could greatly improve the identification of areas at greatest risk for invasion.

Understanding and identifying the conditions that favor success during the critical life stage can also be used to focus the timing of weed management actions. This may be especially critical in natural areas where actions to prevent or limit seedling emergence are relatively difficult to execute. For example, following manual removal of mature buffelgrass plants at Saguaro National Park near Tucson (T. E. Bean, personal communication), treatment areas are typically revisited to evaluate the effectiveness of control and to treat seedlings with herbicides. Based on our findings, we suggest that resource managers plan evaluation and seedling-removal visits at least 4 days following periods when precipitation exceeds about 17 mm over a 2 to 4 day period.

Sources of Materials

[1] Ray Leach Cone-tainers™, Stuewe and Sons, Inc., 2290 SE Kiger Island Drive, Corvallis, OR 97333–9425.

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