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THE IMPORTANCE OF SOIL WATER IN THE RECRUITMENT OF *BOUTELOUA GRACILIS* IN THE SHORTGRASS STEPPE[1]

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Abstract. In the shortgrass steppe region of North America there is a controversy about the ability of the dominant species to recruit from seedlings. The prevailing view is that *Bouteloua gracilis* is incapable of recruitment from seedlings in areas receiving <380 mm of annual precipitation. A common explanation for this situation is that environmental conditions permitting seedling establishment are infrequent. To assess the frequency of environmental conditions appropriate for the recruitment of *B. gracilis* we used a soil water simulation model and long-term climatic data in conjunction with detailed information about the ecophysiological requirements for seed germination and growth of seminal and adventitious roots.

We found that recruitment events occur as frequently as every 30–50 yr on silty clay, silty clay loam, and silty loam soils, but less than once in 5000 yr on sandy soils. Simulated frequencies of recruitment were sufficient to account for the observed abundance of *B. gracilis* in 7 of 11 soil textures evaluated. The differences in silt content and available water holding capacity accounted for the difference among soil textures in the probability of occurrence of recruitment events. Therefore, soil texture variability may explain the spatial pattern of recruitment and of population recovery after disturbance that occur at the soil type and microsite scales.

Annual precipitation explained a large fraction of the temporal variability in recruitment. On average, recruitment occurred in years when precipitation was above the mean. The occurrence of recruitment events in some dry years (precipitation < mean), and their absence during some wet years (precipitation > mean), emphasizes the importance of the intraseasonal distribution of precipitation.

The sensitivity of recruitment to soil water availability suggests that climate change, particularly changes that increase or decrease the amount or the effectiveness of soil water, could have important effects on the future of populations of *B. gracilis.*

Key words: Bouteloua gracilis; *disturbance; germination; recruitment; shortgrass steppe; simulation; soil texture effect; soil water; spatial variability; temporal variability.*

INTRODUCTION

Grasslands in the temperate semiarid region of North America are dominated by clonal grasses, most of which are characterized by infrequent recruitment from seeds (Weaver and Albertson 1956, Neilson 1986). The continued dominance by these grasses has led to the view that current populations are maintained by vegetative propagation. While this explanation is acceptable for rhizomatous and stoloniferous growth forms, it does not necessarily account for the persistence of caespitose or bunch growth forms, especially when disturbance rates are high relative to the rate of vegetative propagation (Samuel 1985, Coffin and Lauenroth 1988).

In the shortgrass steppe region of North America there is a controversy about the ability of the dominant species to recruit from seedlings. The prevailing view is that *Bouteloua gracilis* H.B.K. Lag ex Griffiths is incapable of recruitment from seedlings in areas receiving <380 mm of annual precipitation (Laycock 1989, 1991), although there is some recent evidence to the contrary (D. P. Coffin et al., *unpublished manu-*

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script). *B. gracilis* is a C_4 bunchgrass that has specific microenvironmental requirements for seedling emergence and recruitment (Hyder et al. 1971, Van Der Sluijs and Hyder 1974, Briske and Wilson 1977). According to Hyder et al. (1971), working at the Central Plains Experimental Range (CPER) (320 mm of annual precipitation), seeds planted in warm moist soil emerge quickly and abundantly, but seedlings typically die at 6–10 wk of age. Seedling mortality has been associated with the developmental stage during which seedlings must make a transition from a seminal root system to an adventitious root system that constitutes the permanent root system of grasses (Hyder et al. 1971, Wilson et al. 1976). Individuals that fail to develop a functional adventitious root system die from desiccation because of the limited ability of the seminal root system to supply water to the growing seedling.

A large amount of the work on problems associated with the recruitment of *B. gracilis* has been conducted at the Central Plains Experimental Range (CPER) in north-central Colorado, where Hyder et al. (1975) reported that workers failed to find natural reproduction of this species in the previous 40 yr. The prevailing view is that *B. gracilis* became established at a time when weather was more favorable than it is at the present time (Briske and Wilson 1977). This has led to the conclusion that *B. gracilis* is no longer capable of sexual reproduction in the region, and that population dynamics are the result of fluctuations in vegetative propagation. However, vegetative propagation requires that successive tillers each develop their own adventitious roots (Hyder et al. 1975), and is also subject to soil water limitations. The important difference between seedling recruitment and vegetative propagation is that a new tiller is supported by the parent plant, therefore substantially increasing its probability of success (Williams and Briske 1991, Welker and Briske 1992). Additionally, the absence of rhizomes or stolons, and therefore the very short internode distances characteristic of *B. gracilis,* result in vegetative spread being sufficiently slow that it is essentially ineffective for colonization except on the smallest disturbances (Samuel 1985).

Is *B. gracilis* a relict species at the CPER and in other portions of the shortgrass steppe receiving annual precipitation <380 mm/yr? A large part of the evidence for this view is based upon observations of slow recovery by this species on abandoned agricultural fields (Klipple and Costello 1960, Hyder and Bement 1972). If *B. gracilis* is incapable of recruiting new individuals from seedlings, and its rates of vegetative spread are slow, how does it maintain itself as the dominant species in the presence of a variety of natural disturbance events that result in death of individual *B. gracilis* plants (Coffin and Lauenroth 1988)?

While most of the work on the recruitment of *B. gracilis* has focused on the importance of microenvironmental control on emergence, establishment, and survival, this is by no means the only constraint. Coffin and Lauenroth (1990) used a simulation model to explore controls on recovery of *B. gracilis* following a disturbance and identified seed availability as an important potential limitation. Subsequent investigations of seed banks (Coffin and Lauenroth 1989) and seed production (Coffin and Lauenroth 1992) confirmed the importance of seed availability. Aguilera and Lauenroth (1993) investigated the effects of established individuals on the survival of seedlings of *B. gracilis.* They found that competition from adult plants was also an important constraint on seedling survival.

The objective of the work reported here was to assess the frequency of occurrence of the specific microenvironmental conditions required for the recruitment of *B. gracilis* at the CPER, assuming that viable seeds and safe sites are always present. The dependence of both seedling emergence and seedling establishment on soil water conditions raises the issue of an interaction of soil texture with any particular sequence of weather conditions. A precipitation event that deposits a sufficient amount of water to wet a sandy loam soil to field capacity to a depth of 10 cm may wet a clay loam soil to a depth of only 5 cm, with important implications for seedling recruitment (Sala and Lauenroth 1985). Therefore, our second objective was to evaluate the effect of soil texture on the frequency of seedling recruitment. Our approach was to use a daily time step, multilayer simulation model of soil water dynamics (Parton 1978), daily weather data collected at the CPER, and ecophysiological information about the requirements for seedling recruitment (Briske and Wilson 1977, 1978, Wilson and Briske 1978) to predict the frequency of recruitment from seedlings for a range of soil textures.

METHODS

Model and input data

The soil water model simulates the movement of water through the canopy and into 11 soil layers on a daily basis (Parton 1978, Sala et al. 1992). Interception of precipitation, infiltration, rapid and slow soil water drainage, evaporation from the canopy and surface soil layers, and transpiration are represented. The model is described in detail by Parton (1978). Results of a validation analysis of soil water content by layer at the CPER reported by Parton (1978) indicated good correspondence between model predictions and observed soil water for 14 sample dates in one year. We conducted an additional test of the model to specifically investigate its performance for the soil layers that were most important in controlling conclusions about recruitment of *Bouteloua gracilis.* Data were available from the CPER for a single year from five locations, each with a sandy loam soil. The model output for the same year was compared to the average soil water content for the five locations (Fig. 1). The results dem-

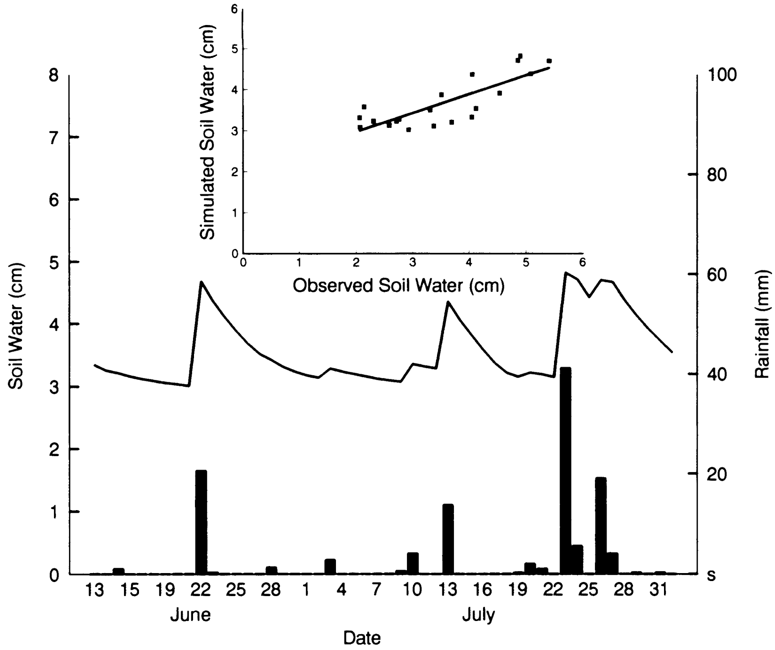

FIG. 1. Results of a validation test of the 0–30 cm layer of the soil water model. Bars are rainfall events in 1991, and the solid line is the simulated soil water content. The inset shows the relationship between simulated and observed soil water content ($F = 40.76$; df $= 1, 21$; $P < 0.001$; $r^2 = 0.66$).

onstrate that the model is responding correctly to precipitation inputs and that simulated results explain 66% of the variability in the field data. An important reason for the discrepancy between the model and the data is that while the soil textures at all of the sites are classified as sandy loams, each site has different percentages of sand, silt, and clay. Based upon the USDA texture triangle (U.S. Department of Agriculture 1951; see also Fig. 5), a soil termed a sandy loam can have 50–70% sand, 18–22% clay, and 0–50% silt. Since our objective was to characterize the responses for the "typical" sandy loam, we chose parameters for the model that corresponded to the midpoint of the sandy loam polygon in the texture triangle (Cosby et al. 1984).

Input data for the model were available from the CPER and the literature. Estimates of aboveground biomass and belowground biomass by depth were available on a monthly basis from work at the CPER (Sims and Singh 1978). Monthly cloud cover and relative humidity were estimated from maps published by the National Oceanic and Atmospheric Administration (U.S. Department of Commerce 1968); daily temperature and precipitation have been collected at the CPER over the past 40 yr. The temperature and precipitation data were used in a first-order Markov analysis to construct a random weather generator for the site. Markov techniques have been widely used to generate precipitation for hydrologic models (Osborn et al. 1982). The performance of the weather generator was tested against the data to insure that it was producing appropriate means and standard deviations.

Conditions for recruitment of B. gracilis

Definition of the microenvironmental conditions required for the emergence and establishment of seedlings of *B. gracilis* has been the topic of a large number of studies (Hyder et al. 1971, Van Der Sluijs and Hyder 1974, Briske and Wilson 1977, 1978, 1980, Wilson and Briske 1978, 1979). *B. gracilis* generally emerges rapidly from seed planted in moist soil (Hyder et al. 1971). Following emergence, the growth of the seminal root and the development of adventitious roots are quite sensitive to soil water availability. The seminal primary root begins to elongate at the time of emergence of the seedling from the soil (Wilson and Briske 1979). At that time, moist soil to a depth of 30–40 cm is necessary for seminal root growth. Wilson and Briske (1979) observed growth of seminal roots in soil with water potentials ranging from −0.03 to −0.8 MPa. The most rapid elongation rates occurred with the greatest soil water availability. Adventitious roots cannot develop prior to 10 d of age, based upon anatomical or substrate limitations (Van Der Sluijs and Hyder 1974). They must develop before the end of the growing season or the seedling will die over the winter (Wilson and Briske 1979). Furthermore, few seedlings survive the very dry conditions of late summer if they have not developed adventitious roots because of the limited capacity of the seminal root system to supply water to the expanding shoot system. Briske and Wilson (1977, 1978, 1980) and Wilson and Briske (1978, 1979) concluded, based upon a series of related laboratory and

TABLE 1. Percentages of clay, sand, and silt, and available water-holding capacity (AWHC) for 11 soil texture classes used in the simulation of the probability of recruitment of *Bouteloua gracilis* (p).*

Texture	Clay (%)	Sand (%)	Silt (%)	AWHC (%)	p (1/yr)	RT (yr)	Sens
Sand	3	92	5	11.5	.0000	>5000	.0000
Sandy clay	42	52	6	13.6	.0006	1667	.0004
Loamy sand	6	82	12	13.8	.0004	2500	.0006
Sandy clay loam	27	58	15	15.4	.0090	111	.0100
Clay	58	22	20	13.6	.0016	625	.0000
Sandy loam	10	58	32	18.4	.0140	71	.0614
Clay loam	34	32	34	17.2	.0184	54	.0184
Loam	18	43	39	19.4	.0178	56	.0586
Silt clay	47	6	47	17.2	.0238	42	.0092
Silt clay loam	34	10	56	20.1	.0344	29	.0340
Silt loam	13	17	70	27.0	.0270	37	.1918

* The probabilities of recruitment were calculated from results using the −0.1-MPa criterion for the 0–30 cm layer. Return time for a recruitment event (RT) was calculated as $1/p$. The sensitivity results (Sens) are ranges of probabilities of recruitment (results for −0.7 MPa minus results for −0.1 MPa). The probability of recruitment for a soil water criterion of −0.7 MPa in the 0–30 cm layer can be obtained by adding the sensitivity values to the probabilities of recruitment calculated for −0.1 MPa.

field experiments, that *B. gracilis* recruitment requires the following set of conditions.

Emergence phase.

1) Soil temperature ≥15°C in the top 4 cm.

2) Sufficient water in the top 4 cm of the soil to allow for germination and emergence.

Establishment phase.

3) Sufficient water in the 0–30 cm layer to allow for growth of the seminal root to a depth of 30 cm into the soil.

4) Sufficient water in the near surface soil and throughout the profile to promote development of adventitious roots.

Although there is abundant work on the issue of emergence and establishment, there are still uncertainties associated with these conditions, in particular the definition of "sufficient water." For emergence, we used conditions in the simulation model that required the top soil layer (0–4 cm) to be >15°C and to have a soil water potential ≥ −0.15 MPa for three consecutive days. This is a very conservative condition since Wilson and Briske (1979) reported emergence in the field at −1.5 MPa. Sensitivity analysis (results not shown) indicated that the results were not sensitive to the value chosen for this parameter. For growth of the seminal root, we evaluated a range of conditions from −0.1 to −0.7 MPa, because of the range of soil water conditions reported by Wilson and Briske (1979) for root development. Sensitivity analysis (Table 1) indicated that the results were very sensitive to the value chosen for this parameter. These soil water conditions had to occur for the 0–30 cm layer within 4 d of emergence. For development of adventitious roots, the top soil layer, in the simulation model, had to remain at or above −0.15 MPa for a period of three consecutive days beginning at least 10 d following emergence. To account for the high probability of seedling mortality by desiccation in August if adventitious roots do not develop, the model also required that seedlings develop adventitious roots at least 70 d after emergence; otherwise they died. For growth of newly initiated adventitious roots into the lower layers, soil water potential in the 0–30 cm layer must have been ≥ −0.10 MPa within 4 d of the three consecutive days of −0.15 MPa conditions. A recruitment event was assumed to have occurred when the appropriate sequence of environmental conditions for emergence and seedling establishment were met during a particular growing season.

Experimental simulations

Because recruitment conditions are dependent upon soil water dynamics, soil texture should influence the recruitment success of *B. gracilis* in a particular growing season. To account for the effects of soil texture in our simulations, we ran the model for 11 of the 12 different soil textures in the USDA soil texture triangle (Cosby et al. 1984). Silt soils were omitted because of lack of data to estimate physical parameters (Cosby et al. 1984). Regression equations from Cosby et al. (1984) were used in the simulation model to estimate the physical parameters required to run a simulation for a particular soil texture. To account for the uncertainty in the soil water criterion in the 0–30 cm layer for the growth of seminal roots, we used six alternative criteria: −0.1, −0.15, −0.2, −0.3, −0.5, and −0.7 MPa. Simulations were run for the same 5000-yr random weather sequence for each of the 11 soil textures and six soil water criteria. Annual recruitment probabilities were calculated from the number of years out of the total of 5000 simulated years in which all of the conditions for emergence and establishment were satisfied.

RESULTS

The probability of recruitment for *Bouteloua gracilis* varied with both soil texture and the severity of the soil water potential criterion for the 0–30 cm soil layer. Sandy soils had the smallest probability of recruitment, and soils with high silt contents had the largest (Table 1). Return times for recruitment events, calculated as

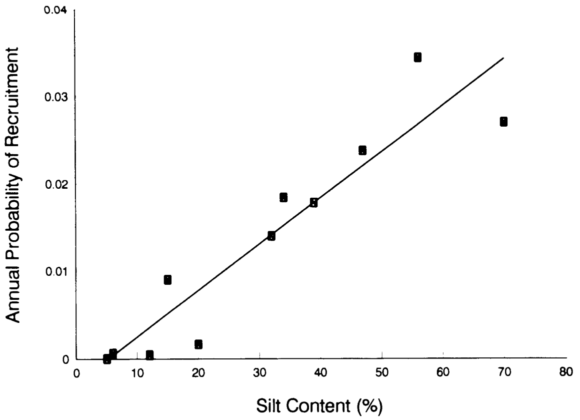

FIG. 2. Relationship between the probabilty of recruitment of *Bouteloua gracilis* at the Central Plains Experimental Range and the silt content of the soil.

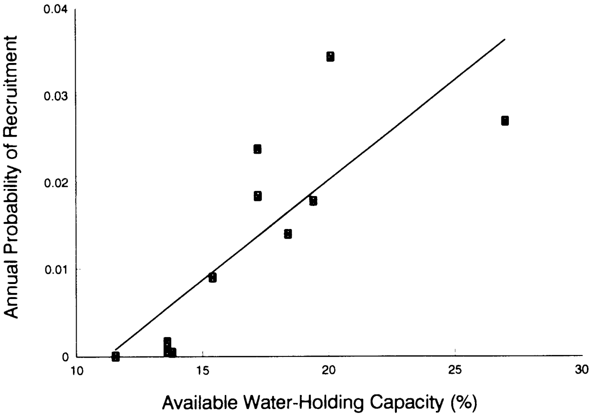

FIG. 3. Relationship between the probability of recruitment of *Bouteloua gracilis* at the Central Plains Experimental Range and the available water-holding capacity of the soil.

the inverse of the probability, ranged from >5000 yr for sandy soils to <50 yr for silty clay, silty clay loam, and silty loam soils. The probability of recruitment decreased as the severity of the soil water criterion increased. Results for silt loam soils showed the greatest sensitivity as the severity of the soil water criterion increased from −0.7 to −0.1 MPa. By contrast, sandy, sandy clay, and loamy sand soils showed the least sensitivity (Table 1). In general, there was a positive relationship between the probability of recruitment and sensitivity. To simplify presentation and to be conservative, we chose the most restrictive case (−0.1 MPa) as the standard for the remaining results.

Probability of recruitment was positively and significantly ($F = 61.09$; df = 1, 9; $P < 0.001$; $r^2 = 0.87$) related to the silt content of the soil (Fig. 2) by the equation

$$p = 0.000529 \cdot (\%\text{silt}) - 0.0028. \qquad (1)$$

Soils with either high sand contents or high clay contents had low probabilities of recruitment compared to soils with high silt contents. An equation with both sand and clay contents resulted in the same percentage of the variability explained as the silt equation, but the coefficients for both sand and clay were negative. This reflects the negative effects of both sand and clay contents on the probability of recruitment of *B. gracilis* and explains some of the variability in the relationship between recruitment and silt content. Single variable relationships for both sand and clay indicated that sand content was a more important explanatory variable than clay. The negative y intercept in Eq. 1 suggests that there is a threshold silt content (x intercept) for a greater than zero probability of recruitment. The x intercept is ≈5%, which is nearly equal to the average silt contents of sandy and sandy clay soils (Table 1) (Cosby et al. 1984). Predictions for recruitment probability were very low for both of these soils.

Part of the explanation for the good relationship between recruitment and silt content is provided by Eq. 2, which relates the probability of recruitment to available water-holding capacity ($F = 18.08$; df = 1, 9; $P < 0.01$; $r^2 = 0.68$) (Fig. 3):

$$p = 0.002299 \cdot \%\text{AWHC} - 0.02577. \qquad (2)$$

Available water-holding capacity (AWHC) was estimated by calculating the amount of water held by the soil between −0.03 and −1.5 MPa. Soils with a large amount of available water per unit of depth had a high probability of supporting emergence and establishment by *B. gracilis.* The classification of soil textures according to their storage of available water is essentially the same as a classification by silt content (Table 1); the exception to this is the silty clay texture. It has a high silt content (47%), but it also has a very high clay content (47%).

Evaluation of annual precipitation data for years with and without recruitment events on silt loam soils suggested some climatic differences between the two categories of years (Fig. 4). Mean annual precipitation for years with a recruitment event was 371 mm compared to 319 mm for years without an event (CPER mean = 320 mm/yr). The driest year with a recruitment event had an annual precipitation of 300 mm, and the wettest year without a recruitment event had an annual precipitation of 500 mm. The degree of overlap between the two distributions suggests that the distribution of precipitation among and within seasons has an important effect on recruitment of *B. gracilis.* A similar evaluation for temperature indicated no differences between years with and without recruitment events. Mean temperature for the two types of years was the same and the breadth of the distributions was essentially the same.

DISCUSSION

Our results suggest that *Bouteloua gracilis* is not a relict species in the shortgrass steppe. The prevailing view that *B. gracilis* is no longer able to establish from seeds in areas receiving precipitation inputs of <380 mm/yr (Briske and Wilson 1977, Laycock 1989) was not supported by the results of our analysis using a simulation model and input data from the CPER. Using a conservative approach to the definition of conditions for recruitment, we found that recruitment could be expected to occur as often as once every 29 yr on silty clay loam soils, but less than once in 5000 yr on sandy soils for a site with 320 mm of average annual precipitation (Table 1).

Our analysis indicated that soil texture and precipitation both had important influences on recruitment. Soil texture, and specifically silt content, was important because of its role in determining available water-holding capacity (Figs. 2 and 3). Silt content of soils at the CPER may explain the spatial pattern of *B. gracilis* recruitment. Information about the spatial distribution of soil textures should be useful in making predictions about the distribution of recruitment probabilities and therefore the ability of a particular location or microsite to recover following a disturbance that removes *B. gracilis* as the dominant species. Annual precipitation accounted for a large fraction of the temporal variability in recruitment. We found that recruitment occurred, on average, in years with higher precipitation than the mean for the site (Fig. 4). The occurrence of recruitment events during years with annual precipitation as low as 300 mm and the absence of recruitment events during years with an annual precipitation as high as 500 mm demonstrated the additional importance of the intraseasonal distribution of precipitation on recruitment.

Five of the 11 soil textures had recruitment probabilities that would result in two to three recruitment events each century. Two more textures had probabilities that would result in one event each century. How often must recruitment occur to maintain current populations? *B. gracilis* is a long-lived clonal plant with no known maximum age. Best estimates based upon data from Coffin and Lauenroth (1988) suggest a maximum age, under heavy grazing conditions, of 450 yr. Maximum age would be longer under lightly or moderately grazed conditions. This suggests that during the life-span of an individual of *B. gracilis,* and for 7 of 11 soil textures, several recruitment events occur which apparently are sufficient to account for the observed dominance of *B. gracilis* at the CPER.

Our analysis focused on differences among spatial units at the scale of an individual soil type. However, there are two reasons why it is also important to consider microsite scale variability. First, the most frequent known source of mortality for *B. gracilis* is small disturbances at the scale of an individual plant (Coffin and Lauenroth 1988). Second, microscale variability in soil properties resulting from patterns of plant cover is of a magnitude similar to variability resulting from geomorphic or pedogenic processes (Hook et al. 1991).

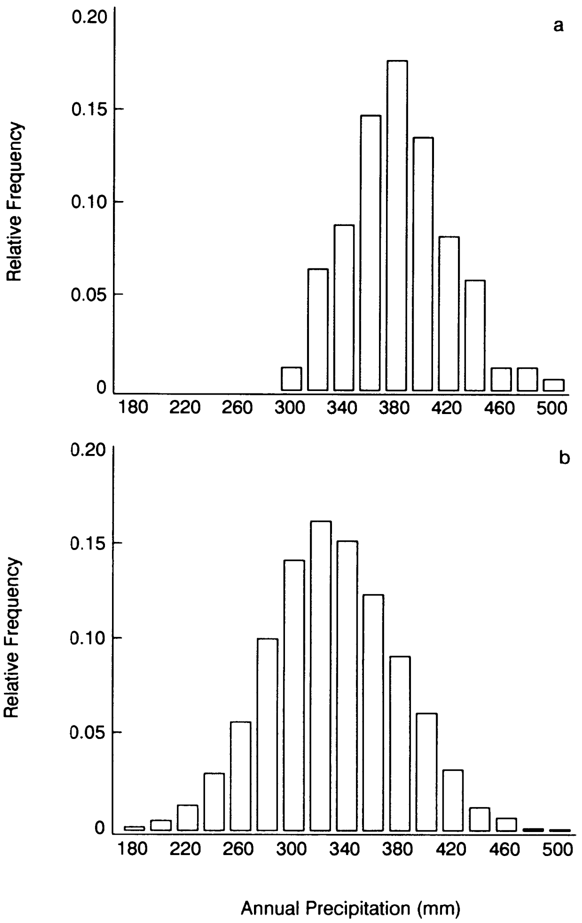

FIG. 4. Frequency distributions of annual precipitation during years with (a) and without (b) recruitment events for *Bouteloua gracilis* at the Central Plains Experimental Range.

Therefore, we might expect similar differences in probability of recruitment between openings and plant-covered patches as between locations with different soil types. Since patches with existing or recently dead plants have higher silt content than openings (Hook et al. 1991), and perhaps a higher seed density, recruitment in these patches may also be higher, which will tend to reinforce the present microscale pattern. This pattern will be influenced by the negative effect of established plants on the survival of seedlings (Aguilera and Lauenroth 1993). The spatial outcome in terms of established plants will be determined by the balance of facilitation and competition in different microsites (Aguiar et al. 1992).

We have assumed that conditions for the midpoint of a texture class would represent that class, and that recruitment would be uniform within a soil texture class when conditions were favorable. Neither of these assumptions is absolutely correct. There is substantial variability in particle size distributions within soil textural classes. Based upon our results, the most significant variability for the recruitment of *B. gracilis* is

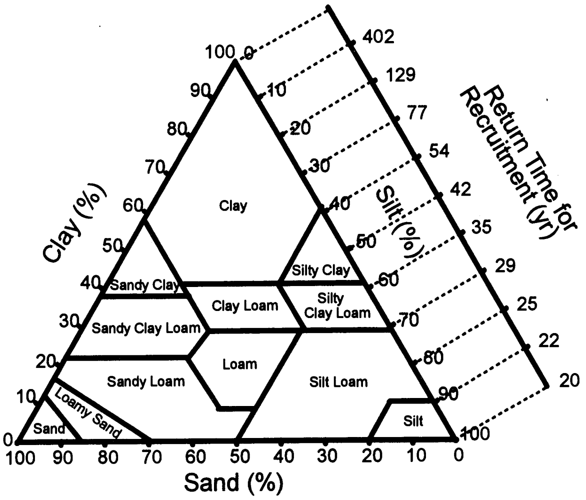

FIG. 5. Illustration using the USDA soil texture triangle of the relationship between the return time for a recruitment event and soil textural classes.

that which occurs in silt content. Using Eq. 1 and the USDA texture triangle (USDA 1951), we can assess the potential importance of this variability (Fig. 5). As an example, sandy loam soils can have silt contents that range from 0 to 50%, corresponding to return times for recruitment events ranging from >400 yr to <50 yr. This representation in terms of the triangle allows us to see some broad patterns of recruitment with soil texture. All of the silty soils have return times <50 yr and all have within class ranges of 10–20 yr. The sandy and clay soils mostly have return times >50 yr.

A broad interpretation of our results must recognize that spatial variability in soil texture, even within a texture class, will result in quantitative differences in recruitment among locations. As an example, a favorable year for recruitment on a silt loam soil may be an unfavorable year on a sandy loam soil. During favorable years, conditions for recruitment may occur on all the microsites of locations with silty soils, but only on a few of the locations; those with the highest silt contents, on sandy soils. During unfavorable years, recruitment may occur only on the most favorable microsites of silt soils. This results, at the soil-type scale, in a gradient in the proportion of seeds that become established. This pattern may be partially offset by the pattern of seed production. Coffin and Lauenroth (1992) reported that seed production was related to soil texture such that seed production decreased from sandy to silty soils.

Primary production in the shortgrass steppe is most frequently constrained by the interaction of water and nitrogen availabilities (Lauenroth et al. 1978). Additionally, structural factors such as plant density may limit primary production under certain conditions. The constrained ability of the system to recruit large numbers of individuals partially explains the limited response in production observed during wet years that follow a sequence of dry years (Lauenroth and Sala 1992). A better understanding of the occurrence of recruitment events will improve our ability to assess structural limitations to primary production and to predict primary production and carrying capacity.

Our results indicated that conditions for the recruitment of *B. gracilis* occur even in one of the driest portions of the shortgrass steppe, and that their occurrence is heavily influenced by soil texture. The rate of natural disturbance characteristic of the steppe (Coffin and Lauenroth 1988), and the relatively slow rate of vegetative spread (Samuel 1985), suggest that recruitment plays an important role in maintaining the dominance of *B. gracilis*.

MANAGEMENT IMPLICATIONS

Bouteloua gracilis is the most drought resistant and the most grazing resistant grass species in the shortgrass steppe. To a very large extent, successful management of shortgrass steppe ecosystems is synonymous with management of populations of *B. gracilis*. Replenishment of populations following disturbance is a critical step in the maintenance of *Bouteloua gracilis* as the dominant species in the steppe. Our results emphasize the importance of using different management schemes for different years, and pastures with different soil textures (Westoby et al. 1989).

The CPER is located in the northern portion of Weld County, Colorado. Most of the soils at the CPER and in northern Weld County are sandy loams (United States Department of Agriculture 1982). At the CPER >95% of the area has a sand content of >35%; ≈70% of the area has a sand content >50% (Burke and Lauenroth 1993). Approximately 60% of the soils in Weld County have sand contents >50%. Furthermore, land use in Weld County is a mixture of cropland and rangeland and it is very likely that most of the locations with loam or silt loam soils (sand contents <50%) are currently in crop production. This means that the rangelands are on the sandiest soils with the lowest probabilities of recruitment. If we assume that most of the rangelands are on sandy loam soils, which make up 58% of the area in Weld County and 68% of the area at the CPER, they have a predicted average recruitment probability of ≈0.014/yr. Conditions for emergence and recruitment may occur only once in 70 yr. This makes the rangelands of the region very vulnerable to disturbances that cause mortality of *B. gracilis*.

These results also have implications for land put into the Conservation Reserve Program (Skold 1989). One of the objectives of this program is to return marginal cropland to perennial grassland. If we assume that marginal cropland is located on sites with soils of low productive potential, in northeastern Colorado that means that the textures of these soils are relatively sandy. Recruitment of *B. gracilis* on such sites will be difficult because of the low frequency of occurrence of appropriate environmental conditions (Table 1). This will mean that even with careful planning, the vegetation on most of these areas will be composed of species other than *B. gracilis.*

Predictions of climatic change as a result of humankind's modification of the chemistry of the atmosphere represent an important threat to populations of *B. gracilis,* and therefore to shortgrass steppe ecosystems. The shortgrass steppe is predicted to experience increases in air temperature and decreases or no change in precipitation over the next 40 yr (Mitchell et al. 1992). Depending upon the seasonal distribution of the changes, recruitment of *B. gracilis* could be substantially influenced. Our results indicate that a reduction in water availability will reduce the probability of recruitment of *B. gracilis.* However, more detailed predictions than currently available on the seasonal distribution of precipitation will be necessary to predict the impact of climate change on *B. gracilis* recruitment and on the fate of shortgrass ecosystems.

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