

Response of Individual *Bouteloua gracilis* (Gramineae) Plants and Tillers to Small Disturbances

JULIE L. FAIR, DEBRA P. C. PETERS^{1,2} AND WILLIAM K. LAUENROTH

Department of Rangeland Ecosystem Sciences, Natural Resources Ecology Laboratory and Graduate Degree Program in Ecology, Colorado State University, Fort Collins 80523

ABSTRACT.—We evaluated effects of small disturbances that kill parts of individual plants on plant survival by measuring tiller survival for the perennial bunchgrass, *Bouteloua gracilis* (H.B.K.) Lag ex Griffiths (blue grama). The importance of soil texture, grazing by cattle, disturbance type and severity were evaluated. Two disturbance types (covering or removing tillers) and three disturbance severities (50, 75 and 90% tiller mortality) were used to represent effects of natural disturbances in shortgrass communities (cattle fecal pats, nest sites of Western harvester ants, burrows of small animals).

Tiller survival was not affected by soil texture or grazing intensity, but was affected by disturbance type and severity. Plants that were covered showed a 33% increase in tiller survival for all levels of disturbance severity from August (1991) to June (1992). No net change in tiller number was observed for removed or reference plants. Different responses between disturbance types were likely due to increases in root:shoot ratios of covered plants that increased tiller production as a result of increased soil water acquisition. The number of tillers produced was small, but statistically significant (average = 20 tillers/plant), which shows that *B. gracilis* plants do not produce independent tillers, but consist of integrated physiological units (IPUs). The lack of plant mortality, even with 90% tiller mortality, indicates that small disturbances must kill entire plants before gaps in resource space are produced to initiate gap dynamics that result in the recovery of an individual *B. gracilis* plant. Because recovery through seedling establishment by *B. gracilis* occurs infrequently, the ability of this species to survive after partial plant mortality is important to its continued dominance of shortgrass steppe communities in the presence of these small but frequent disturbances.

INTRODUCTION

Grassland communities have recently been conceptualized as dynamic mosaics of patches, each undergoing its own successional dynamics through time (Loucks *et al.*, 1985; Coffin and Lauenroth, 1988, 1990a). Gaps created by the death of an individual plant of the dominant species are one type of patch that initiate successional processes called gap dynamics (Watt, 1947; Shugart, 1984). Growth, senescence, death and regeneration of individual plants govern succession on gaps and, consequently, determine community composition through time on larger spatial scales (Watt, 1947; Bormann and Likens, 1979). The basic premise of the gap dynamics concept is that an individual of a dominant species must die before a gap is produced and successional dynamics are initiated (Watt, 1947; Shugart, 1984; Coffin and Lauenroth, 1990a). In grasslands dominated by long-lived perennials, natural mortality of dominant grasses occurs infrequently (Wright and Van Dyne, 1976; Loucks *et al.*, 1985). Other factors, such as disturbances, that cause mortality of individual plants or parts of plants may be essential to gap formation.

Small-scale disturbances are important in maintaining spatial heterogeneity and species richness in grasslands (*i.e.*, Baxter and Hole, 1967; Platt, 1975; Hobbs and Mooney, 1985;

¹ Present address: USDA-ARS, Jornada Experimental Range, Box 30003, MSC 3JER, NMSU, Las Cruces, NM 88003-0003

² Corresponding author: e-mail: debpeter@nmsu.edu

Rabinowitz and Rapp, 1985; Collins, 1989; Gibson, 1989). Studies have focused on plant recolonization of patches (*i.e.*, Rabinowitz and Rapp, 1985; McConnaughay and Bazazz, 1987; Coffin and Lauenroth, 1989a, 1990b; Coffin *et al.*, 1998), attributes of disturbances such as size and frequency (Miller, 1982; Coffin and Lauenroth, 1988) and activities of insects that cause small disturbances (Rottman and Capinera, 1983). Little is known about how the type and severity of small disturbances affect mortality of dominant individual plants to create gaps in different environments within grasslands. Furthermore, disturbances similar in size to individual plants may kill all or part of a plant, and, thus may, or may not, produce a resource gap that allows replacement or recovery of an individual of the dominant species. Although small disturbances occur frequently in grasslands, affecting large amounts of cover through time and space (Coffin and Lauenroth, 1988), the ability of perennial clonal plants to respond after tiller mortality has not been studied, yet may be important especially for species that reproduce infrequently through seedling establishment.

Naturally occurring small disturbances are an integral part of shortgrass steppe communities in North America (Coffin and Lauenroth, 1988; Hook *et al.*, 1994). These plant communities are dominated by the C₄ perennial bunchgrass *Bouteloua gracilis* (H.B.K.) Lag. ex Griffiths (blue grama) (nomenclature follows Great Plains Flora Association, 1986). This species accounts for 80 to 90% of plant basal cover in undisturbed shortgrass steppe communities (Milchunas *et al.*, 1989). Because of the inverse relationship between disturbance size and frequency of occurrence, small disturbances cause the highest percentage of *B. gracilis* plant and tiller mortality and result in the largest effects on community structure through time and space (Coffin and Lauenroth, 1988). Other types of disturbances, such as prolonged drought and cultivation, may cause large-scale mortality of *B. gracilis* plants, but occur infrequently (Albertson and Tomanek, 1965; Coffin *et al.*, 1996). *Bouteloua gracilis* recovers slowly after disturbances that kill plants because of low and variable seed production (Coffin and Lauenroth, 1992), low seed storage in the soil (Coffin and Lauenroth, 1989b) and infrequent seedling establishment (Hyder *et al.*, 1971; Lauenroth *et al.*, 1994). The ability of *B. gracilis* to recover after partial plant mortality is unknown, but may provide an important mechanism for its continued dominance and persistence in shortgrass steppe communities.

Cattle fecal pats are the smallest, most frequent faunal disturbance capable of killing *Bouteloua gracilis* plants in grazed shortgrass steppe ecosystems (Coffin and Lauenroth, 1988). Fecal pats are similar in size to individual *B. gracilis* plants (10 to 25 cm diam) (Coffin and Lauenroth, 1988). Therefore, when a fecal pat is deposited, it may cover all or part of a plant. In most cases the portion of a *B. gracilis* plant directly covered by a fecal pat will not survive because of the low stature of tillers compared to thickness of pats. Because of their high frequency of occurrence and ability to kill individual plants, cattle fecal pats may contribute substantially to the shifting mosaic of patches on landscapes (Lieth, 1959; Coffin and Lauenroth, 1988, 1990a).

Activities of Western harvester ants [*Pogonomyrex occidentalis* (Cresson)] and burrowing animals, such as skunks and badgers, also result in small disturbances to shortgrass steppe vegetation (Coffin and Lauenroth, 1989a, 1990b). Mature ant mounds average 1.4 m diam and animal burrows range in size from 1 to 2 m diam (Coffin and Lauenroth, 1988). Ants kill plants by removing meristematic tissue below the soil surface on and around the nest and disk (Coffin and Lauenroth, 1990b). Small animals kill plants by covering them with soil and removing them through digging. Both activities affect larger areas but occur less frequently than fecal pats, and may kill all or parts of plants (Coffin and Lauenroth, 1988, 1989a).

TABLE 1.—Percentage clay, silt and sand (0–10 cm depth) and soil texture classification for six locations

	Location and texture class					
	Sandy clay		Silty clay loam		Sandy loam	
	Clay loam	loam				
	1	2	3	4	5	6
Clay (%)	30	21	36	34	12	10
Silt (%)	16	15	30	28	13	6
Sand (%)	54	64	34	38	75	84

Although a number of studies have examined recovery of shortgrass steppe communities after disturbances that kill one or more *Bouteloua gracilis* plants (Coffin and Lauenroth, 1989a, 1990b; Coffin *et al.*, 1998), it is not known if small disturbances which kill a portion of a *B. gracilis* plant will kill the entire plant to produce a gap in these communities. We hypothesized that covering or removing part of a *B. gracilis* plant would have negative effects on the remaining tillers and would result in mortality of the plant. Soil texture and grazing by cattle can have important effects on plant population and community dynamics in these communities (Sala *et al.*, 1988; Liang *et al.*, 1989; Milchunas *et al.*, 1989; Lane *et al.*, 1998). Our objectives were to address the following questions: Do soil texture and grazing by cattle affect the number of surviving tillers of *B. gracilis* plants that have been disturbed? What are the effects of type (*i.e.*, covering versus removal of tillers) and severity of disturbance (*i.e.*, the degree to which plants are covered or removed) on tiller and plant survival?

METHODS

Site description.—This study was conducted at the Central Plains Experimental Range (CPER; 40°49'N, 107°47'W) located 60 km northeast of Fort Collins, Colorado. Long-term (52 y) average annual precipitation is 321 mm (SD = 98 mm), 75% of which occurs between April and September (Lauenroth and Sala, 1992). Mean monthly temperatures range from -3 C in January to 22 C in July and mean annual air temperature is 8.6 C.

The CPER has a complex geomorphic history which has resulted in high spatial heterogeneity of soil textures and landform (Yonker *et al.*, 1988). Soil surface horizons range from clay loam to loamy sand with sandy loam the most common. The CPER has a long history of grazing by large herbivores over the past 8000 to 10,000 y and has been grazed by domestic cattle since at least 1939 (Klippel and Costello, 1960; Milchunas *et al.*, 1988). Topography consists of level lowlands and uplands connected by gentle slopes. Total basal cover of vegetation for undisturbed communities is 25 to 40% of which 80 to 90% is *Bouteloua gracilis* (Milchunas *et al.*, 1989). Other species include a number of grasses, subshrubs, forbs and succulents.

Experimental design.—Six locations were selected to represent three soil textures at the CPER with two locations per texture. Level uplands or lowlands moderately grazed by cattle during the growing season since at least 1970 were selected. To verify soil textures 10 soil cores to a depth of 10 cm were collected at each location, combined and analyzed for composition of particle sizes using the hydrometer method (Bouyoucos, 1962). Locations 3 and 4 (paired for high silt content) were classified as silty clay loam and locations 5 and 6 (paired for high sand content) were classified as sandy loam (Table 1). Locations 1 and

2 (paired for high clay content) had similar particle size distributions and were classified into two closely-related groups (clay loam, sandy clay loam).

Seventy individual *Bouteloua gracilis* plants were randomly selected within a 10 m × 10 m area at each location in August 1991. An individual was defined as a group of tillers currently connected by a crown (*sensu* Coffin and Lauenroth, 1988). Initial basal diameter was estimated for each plant by averaging the longest diameter and the diameter perpendicular to it. Plants in each location were divided into 5 blocks with 14 plants per block. Half of each block was protected from grazing by cattle using temporary exclosures. Each grazed or ungrazed plant within a block was randomly assigned to one of four disturbance severity treatments: 0 (undisturbed), 50, 75 or 90% of the basal area of the plant disturbed; and to one of two disturbance types: removed or covered (described below). Because of the large number of live tillers possible for individual *B. gracilis* plants (>100) and the large number of plants to be manipulated (420), the proportion of each plant to disturb was determined using basal diameter. A significant linear relationship between basal diameter and number of tillers for 10 undisturbed plants in each location confirmed that basal diameter is a good predictor of tiller number ($TILLERS = -59.5 + 20.6 \times DIAMETER$; $r^2 = 0.63$; $n = 60$; $P < 0.0001$).

Two disturbance types were selected to represent effects of naturally occurring disturbances in shortgrass communities. Removal of portions of plants by digging from small animals and clipping by harvester ants was simulated by severing and removing all above- and belowground plant tissue to a depth of 10 cm below the soil surface. Covering of plants by cattle fecal pats and small animal soil mounds was simulated by placing rubber inner-tubing over a portion of each plant. The rubber was painted white to reflect radiation and represent heat loads similar to brown pats, then pinned to ground level. Actual fecal pats were not used in the experiment due to their nonuniform basal area, thickness and age or stage of decomposition. Because some tillers could not be contained under the innertubing as a result of their height, tillers were clipped before covering to ensure that they would be covered completely. To determine if clipping affected the results, effects of fecal pats deposited by cattle onto *Bouteloua gracilis* plants in 1991 were evaluated by counting surviving tillers in June and August (1992). Plants were selected that had 50, 75 or 90% of their basal area covered by a pat in 1991; half the plants in each category were clipped similar to the experimental plants. Results using fecal pats were consistent with results from the covering experiment: no differences were found in surviving number of tillers for clipped or unclipped plants.

Live tillers per plant were counted in August (1991), June and August (1992). These data are the number of surviving tillers either immediately following, one winter after or one growing season after disturbance treatments, respectively. Disturbed tillers were not counted during the study since they all died.

Statistical analysis.— A repeated measures analysis of variance (ANOVA) was used to evaluate effects of four main factors and their interactions: (1) soil texture, (2) grazing by cattle, (3) type of disturbance (covering versus removal), (4) severity of disturbance (0, 50, 75, 90%), and interactions among these factors on number of surviving tillers per plant for three sample dates. The experimental design was a split-split-plot with nested subsampling and repeated measures. The four main effects and their interactions were tested as an interaction with time, which became a fifth factor.

The whole-plot analysis included three textures (two locations per texture) with five blocks per location. The split-plot analysis included two grazing treatments and the split-split-plot analysis included two levels of type of disturbance at three levels of severity plus an undisturbed plant for a total of seven plants per grazing treatment. Locations and blocks

were treated as random effects. Texture, grazing, type and severity of disturbance and time were treated as fixed effects. Two preliminary tests were conducted to determine if errors for: (1) locations (nested within textures) and (2) grazing by locations (nested within textures) could be pooled. Because paired locations within textures were significantly different, they were not pooled. Grazing by locations within textures was not significantly different, and was pooled in the main analysis.

An examination of residuals vs. predicted values showed that the assumption of homogeneous variances was violated. Therefore, number of tillers was log-transformed and the analysis was repeated. Because results were similar for both transformed and untransformed data with one major exception and a few minor ones, the untransformed data are presented for ease of interpretation, although statistical analyses are reported from transformed variables. Type-III sums of squares were used to estimate F-statistics and a significance level of 0.05 was used.

Mean numbers of tillers for the four main factors and their interactions were analyzed for significant differences within treatments between August (1991) and June (1992) and between June (1992) and August (1992) using least significant difference (LSD) tests (Sokal and Rohlf, 1998). Mean number of tillers was not compared between treatments for each main factor because initial basal diameters of *Bouteloua gracilis* plants and number of tillers per plant differed by soil texture. All means within each main factor were pooled across all other main factors for the analyses. For example, numbers of surviving tillers in disturbed plants for different soil textures were analyzed for treatment differences by comparing them within soil texture type and between sample dates after pooling across grazing and disturbance treatments.

RESULTS

When portions of *Bouteloua gracilis* plants were killed, survival of remaining tillers and plants among dates was not affected within each soil texture class or grazing treatment (Fig. 1a, b) but was affected by disturbance type (Fig. 1c). Average number of surviving tillers increased with increasing sand content and decreasing silt content although the statistical significance of this trend could not be evaluated due to different initial plant sizes among locations (Fig. 1a). Tiller survival was related to plant size since locations with the largest plants (sandy loam) had the largest numbers of live tillers and locations with the smallest plants (clay loam/sandy clay loam) had the smallest numbers of live tillers. Average basal diameter of *B. gracilis* plants decreased with increasing clay content ($\text{DIAMETER} = 21.4 - 0.34 \times \text{CLAY}$; $r^2 = 0.72$; $n = 420$, $P < 0.0001$). Number of surviving tillers was similar through time within each grazing treatment (Fig. 1b). Disturbance type had significant positive effects on number of surviving tillers through time (Fig. 1c). Plants that were covered showed a 33% increase in tiller survival between August (1991) and the beginning of the next growing season (June 1992). Number of surviving tillers did not change during the 1992 growing season. By contrast, tiller survival for plants in which tillers were removed and for undisturbed plants were similar throughout the study indicating no significant change in tiller recruitment or death through time.

Severity of disturbance had significant effects on tiller survival through time for covered plants, but not for plants where tillers were removed (Fig. 2). Plants with 50, 75 and 90% of basal area covered showed significant increases in number of surviving tillers (average = 29%) between August (1991) and June (1992) with no subsequent changes (Fig. 2a). Plants that had tillers removed and undisturbed plants showed no significant changes in tiller survival throughout the time of the study (Fig. 2b).

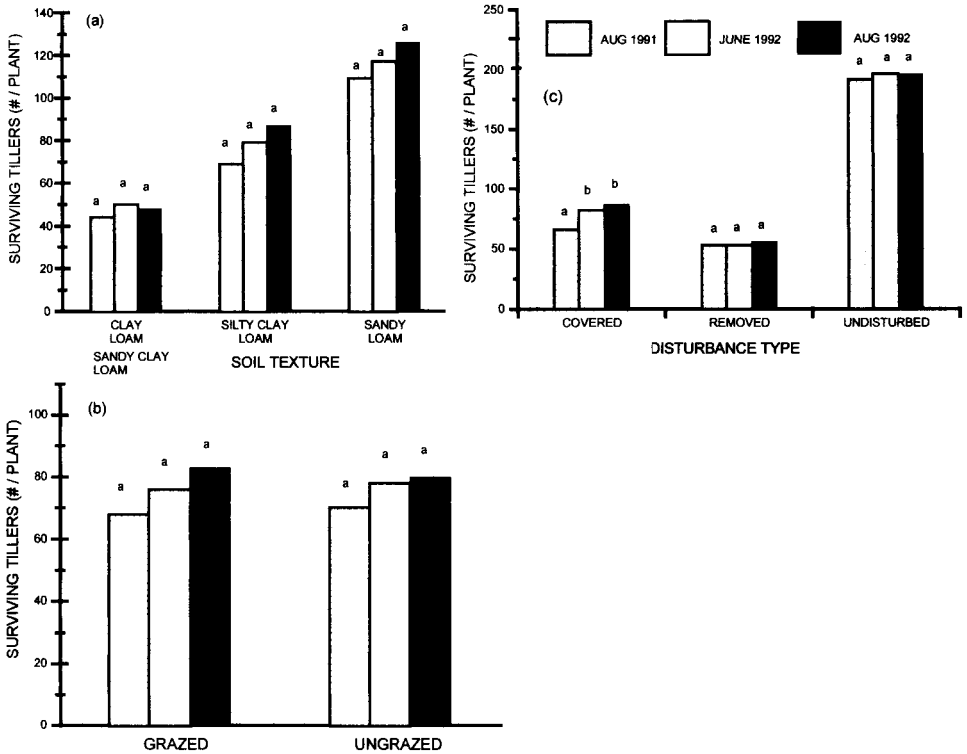


FIG. 1.—Average tiller survival per *Bouteloua gracilis* plant for: (a) three dates and three soil texture groups ($n = 140$); (b) three dates and two grazing treatments ($n = 210$); (c) two types of disturbance ($n = 180$) and undisturbed plants ($n = 60$) for three dates. Means were pooled across all other factors; bars not sharing common letters within each soil texture class, grazing treatment or disturbance type are significantly different between dates

DISCUSSION

Contrary to our hypothesis, simulated small disturbances which killed 50 to 90% of the basal area (and a similar percentage of tillers) of individual *Bouteloua gracilis* plants did not produce negative effects on short-term plant and remaining tiller survival. Number of surviving tillers was either similar through time or increased initially after tiller mortality. Because only short-term (1 y) tiller survival was evaluated, it is impossible to determine long-term responses to disturbance type, soil texture and grazing. However, we expect that the most important negative responses to tiller mortality would occur the first year following the reduction in aboveground plant material. Short-term negative responses following tiller mortality were found previously for another bunchgrass, *Schizachyrium scoparium* (Briske and Butler, 1989). Favorable weather conditions during the time of the study contributed to the observed response although the pattern through time shows a lag in tiller response. Monthly precipitation was higher than long-term averages during most of the study, except for April to June (1992), when number of surviving tillers increased for covered plants (Fig. 3a). Average monthly temperatures were also higher than long-term averages during this study (Fig. 3b). Periods of peak rainfall during the growing season (June to August 1992) occurred with

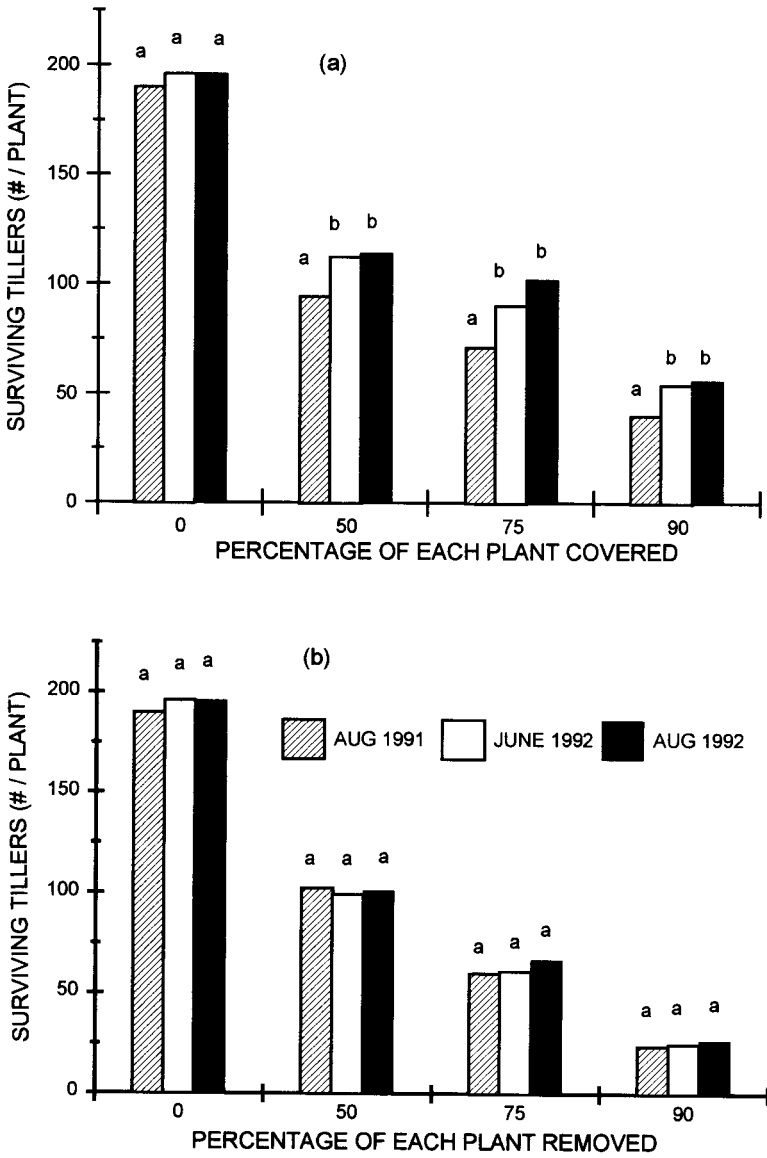


FIG. 2.—Average tiller survival per *Bouteloua gracilis* plant for three dates, three severity treatments and two disturbance types: (a) covering treatments (n = 60) and (b) removal treatments (n = 60). 0% represents undisturbed plants (n = 60). Means were pooled across all other factors; bars not sharing common letters within each disturbance severity class are significantly different

no increase in tillering of disturbed or undisturbed plants. Time lags of 1 y or more in response of production of *B. gracilis*—dominated communities to above-average growing season precipitation have been found previously which suggests that additional positive responses may have occurred following the cessation of this study (Hyder *et al.*, 1975; Lauenroth and Sala, 1992).

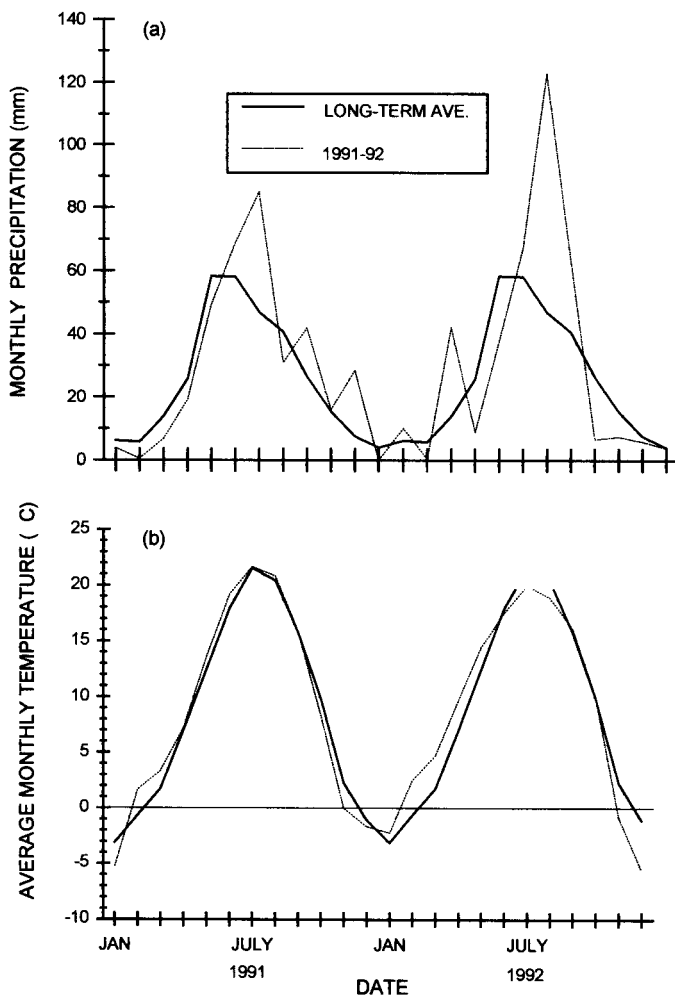


FIG. 3.—Monthly long-term (52 y) averages and 1991–1992 (a) precipitation (mm) (b) temperatures (C)

These results show that small disturbances similar in size to *Bouteloua gracilis* plants must cover or remove all tillers to kill plants and initiate gap dynamics in shortgrass communities. In this way, shortgrass systems are similar to forests where entire trees must be killed before these dynamics occur (Shugart and West, 1977). A gap dynamics approach has been used extensively in temperate and tropical forests, both experimentally (Denslow, 1980; Brokaw, 1987; White *et al.*, 1985) and using simulation models (Shugart and West, 1977; Doyle, 1981; Shugart, 1984). An important difference between gap dynamics in shortgrass systems compared to forests is in the resource space associated with gaps. In forests death of an individual tree creates a gap in above- and belowground resources, whereas in shortgrass systems death of an individual *B. gracilis* plant results in a gap primarily in belowground resources, since light is infrequently limiting (Coffin and Lauenroth, 1990a). Belowground

resources, specifically soil water, are the most frequent controls on plant growth and community structure in semiarid grasslands since precipitation is low and variable (Noy-Meir, 1973; Lauenroth *et al.*, 1978). Because disturbances that kill only portions of *B. gracilis* plants do not kill plants, it is unlikely that these small disturbances are important to gap dynamics of shortgrass communities. These results are supported by a study showing that bare areas >30 cm diam are required for *B. gracilis* seedling establishment (Aguilera and Lauenroth, 1995). Furthermore, most naturally occurring openings in shortgrass communities are smaller than this size and do not show evidence of disturbance or recovery (Hook *et al.*, 1994).

Lack of response of *Bouteloua gracilis* plants to soil texture and grazing treatments, and differences in response to covering vs. removal of tillers can be explained by the effect these treatments had on root:shoot ratios of individual plants following disturbance. Covering of plants resulted in death of aboveground plant material and some or all roots may have survived. If so, covering of plants would have increased root:shoot ratios. Removal of tillers resulted in death of both above- and belowground plant material; therefore, root:shoot ratios among removal classes would have remained similar to those of undisturbed plants. Covered plants with higher root:shoot ratios would have acquired more belowground resources during the overwinter period (August to June) to increase tiller number. This ability was apparently lost during the following growing season (June to August) when the added carbon-producing capacity from new tillers was transferred to production of new roots instead of tillers (Lauenroth *et al.*, 1987). Alternatively, since tillering in *B. gracilis* tends to be directional from the center of a plant to its periphery (Hook and Lauenroth, 1994), additional tillering during the growing season would have been constrained by neighboring plants located at the leading edge of disturbed plants (Aguilera and Lauenroth, 1993) or by tillers of the inappropriate orientation being located at the plant edge.

Although soil texture, and its effects on soil water and nitrogen availability, has important influences on recovery of shortgrass vegetation after disturbance (Coffin and Lauenroth, 1989a, 1994; Coffin *et al.*, 1993b) and on *Bouteloua gracilis* seed production and storage of seeds in the soil (Coffin and Lauenroth, 1989b, 1992), soil texture was not important relative to effects of disturbances that cover plants. Greater aboveground production of *B. gracilis* on coarse- than fine-textured soils (Sala *et al.*, 1988) would account for differences in tiller survival observed between locations for each date, yet this process was not important to patterns in survival of tillers through time.

Grazing was also less important than disturbance to tiller survival. Because the shortgrass steppe has a long evolutionary history of grazing by large herbivores, these systems are well-adapted to withstand grazing by cattle (Stebbins, 1981; Milchunas *et al.*, 1988). Lack of an effect of grazing on tiller survival is similar to responses of other characteristics of shortgrass communities including species composition (Milchunas *et al.*, 1989), aboveground net primary production (Sims *et al.*, 1978), root biomass (Leetham and Milchunas, 1985) and recovery of vegetation after low intensity, patchy disturbances (Coffin *et al.*, 1998).

Plants that were covered increased an average of 20 tillers per plant; this statistically significant, but modest, response can be explained by the hypothesis that *Bouteloua gracilis* crowns are not completely integrated, but instead consist of many integrated physiological units (IPU). A physiological unit consists of a group of tillers that actively share resources and function as autonomous units within a clone (Watson and Casper, 1984; Williams and Briske, 1991). Increasing evidence suggests that entire crowns of caespitose grasses are not integrated and that physiological individuals may be quite small, mainly because tillers of bunchgrasses are short-lived (Welker and Briske, 1992). In the bunchgrass *Schizachyrium*

scoparium physiological integration is limited to units consisting of three tillers with their associated crowns and roots (Williams and Briske, 1991).

If *Bouteloua gracilis* plants consist of IPUs, or small groups of integrated tillers, then the increase in tillering after a plant was covered would be the response by the physiological units along the disturbance edge and not by individual tillers or the entire plant. The response would then be limited by the average condition of the physiological units, and a modest response would occur as shown by the similar responses of different-sized plants growing on different soil textures. If *B. gracilis* tillers were completely integrated, the response to covering would be much larger since tillers would respond favorably to an overall higher root:shoot ratio. The response of integrated plants to removal of tillers would be negative. Alternatively, plants with independent tillers would show no response to covering that results in increases in the root:shoot ratio of plants or to tiller removal with no change in root:shoot ratio. Neither plant integration nor independent tillers was supported by the results of this study suggesting that *B. gracilis* plants consist of IPUs.

The lack of plant mortality, even with 90% tiller mortality, shows that small disturbances must kill entire plants before gap dynamics are initiated. Because *Bouteloua gracilis* recovery is very slow after disturbances that kill plants (Coffin *et al.*, 1996), the ability of this species to survive after tiller mortality is important to its continued dominance of shortgrass steppe communities in the presence of small frequent disturbances.

Acknowledgments.—This study was supported by National Science Foundation Grants BSR-9013888 and BSR-9011659 to Colorado State University, INT-9896168 to New Mexico State University and the Colorado State University Experiment Station Project, Long-Term Grassland Ecosystem Research. The CPER is administered by the Great Plains Systems Research Unit of the United States Department of Agriculture—Agricultural Research Service. We thank Dave Steingraeber, Tamera Minnick and several reviewers for helpful comments on the manuscript. Gary Richardson assisted with the statistical analyses.

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