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Disturbance intensity and above- and belowground herbivory effects on long-term (14 y) recovery of a semiarid grassland

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Abstract

The importance of disturbance intensity and herbivory by cattle and white grubs, or the larvae of June beetles (including *Phyllophaga fimbripes*), to recovery of shortgrass steppe ecosystems in Colorado, U.S.A. were evaluated over a fourteen year time period. Disturbance intensity was defined by survival of the dominant grass species (*Bouteloua gracilis*) after an outbreak of root feeding activity by white grubs. Sixteen patches of vegetation consisting of four pairs of adjacent ungrazed-grazed by cattle locations with two replicates that were recently affected by white grubs were selected in 1977. Disturbance intensity was determined in 1977 by the area in each patch that contained live tillers of *B. gracilis*. Permanent plots were located both within and outside of each patch. Plant basal cover and density by species were estimated at time of peak aboveground biomass in six different years on each plot.

Successional dynamics on patches was similar to areas affected by other types of disturbances, however, rate of recovery was faster for patches affected by grubs. Grazing by cattle was infrequently important to plant recovery, a result similar to effects of grazing on other aspects of shortgrass steppe ecosystems. Disturbance intensity was important to recovery of *B. gracilis* since tiller survival in 1977 was linearly related to cover in each year of sampling. For ungrazed patches, initial conditions were important to recovery of *B. gracilis* for as many as 14 years. For grazed patches, initial conditions decreased and grazing increased in importance through time. Changes in resource quality and a more uniform distribution of roots due to grazing likely resulted in more complete mortality of plants by grubs under grazed compared to ungrazed conditions.

Persistence of shortgrass ecosystems in spite of disturbances with different intensities are determined at least in part by characteristics of disturbances interacting with the ability of plants to respond, and in part by the evolutionary history of the system. Although white grubs affect shortgrass communities infrequently, they have large and important effects on plant community structure through time, and represent an important class of disturbance defined by intensity.

Introduction

Characteristics of a disturbance (e.g., intensity or severity, size, frequency of occurrence) are important features that determine its effects on ecosystems as well as the potential for recovery of the vegetation (Sousa 1984; Pickett & White 1985; Coffin & Lauenroth 1988). Disturbance intensity may be one of the least-studied, yet most important characteristics. Disturbances with different intensities result in differential survival of plants with important effects on species diversity (Collins & Barber 1985) and recovery patterns through time (Malanson 1984; Milchunas et al. 1989). A direct evaluation of disturbance intensity is needed to test the hypothesis that differential plant survival is an important factor determining rate and pattern of vegetative recovery. The objective of this study was to evaluate effects of intensity associated with one disturbance type on successional dynamics for a semiarid grassland.

Larvae of June beetles (including *Phyllophaga fimbripes* LeConte) feed on roots of perennial grasses and create disturbances in perennial grasslands that are patchily distributed across the landscape with different intensities as indicated by plant mortality and survival. Disturbed areas are of variable size with a mixture of complete and incomplete mortality of plants (Fluke et al. 1932; Ueckert 1979; Weiner & Capinera 1980). Although observations indicate the importance of white grubs, little information is available about the ecological relationships between these larvae and other aspects of grasslands, including plant recovery patterns, climate, and grazing by cattle.

In shortgrass steppe communities of North America, perennial grasses and in particular *Bouteloua gracilis* (H.B.K.) Lag. ex Griffiths, dominate plant cover and biomass (Lauenroth & Milchunas 1991). *B. gracilis* accounts for 75 to 90% of aboveground net primary production and 80 to 90% of plant basal cover in most communities (Hanson 1955; Milchunas et al. 1989). Therefore, most reduction in plant cover and density as a result of feeding activity of white grubs in shortgrass ecosystems is due to mortality of *B. gracilis* tillers and plants. Because recovery of *B.gracilis* after disturbance is reported to be very slow as a result of slow tillering rates (Hyder et al. 1971; Samuel 1985) and infrequent seedling establishment events (Riegel 1941; Briske & Wilson 1977; Lauenroth et al. 1994), the mortality of this species can have important effects on shortgrass ecosystems.

The specific objectives of this study were to address the following questions: (1) What are characteristics of patches of vegetation disturbed by white grubs? (2) What are recovery patterns of shortgrass plants through time on areas affected by white grubs? (3) How does disturbance intensity or survival of *B. gracilis* tillers affect vegetation recovery? (4) What are effects of grazing by cattle, an important component of shortgrass ecosystems, on characteristics of patches and on plant recovery?

Methods

Site description

All data were collected at the Central Plains Experimental Range (CPER) located 60 km northeast of Fort Collins, Colorado, U.S.A. (40 °49′ N, 107 °47′ W). Climate of the CPER is semiarid: long-term (52y) mean annual precipitation is 321 mm (sd = 98 mm) of which 70% occurs during the growing season from 1 April to September 30. Mean monthly temperatures range from −5 °C in January to 22 °C in July with an annual average of 8.8 °C. During the study (1977 to 1990), annual precipitation was below-average the first two years (avg = 270 mm yr^{-1}), followed by six years of above-average amounts (avg = 427 mm yr^{-1}) and then six years of average and below-average amounts (avg = 318 mm/y) (Lauenroth & Sala 1992). Average annual temperatures were above-average throughout the fourteen years (avg = 9.8 °C). In addition, the three years prior to the study (1974 to 1976) were average or below-average in precipitation (avg = 284 mm yr^{-1}), and above-average in temperature (avg = 9.2 °C). Observations suggest that it is these previous years that may be most important to dynamics of larvae and adult beetle populations, similar to other species of soil-dwelling insects (Havelock Fidler 1936; Stanton 1988).

Moderate grazing by cattle occurs throughout the area. Lightly (1.4), moderately (1.1) and heavily (0.7 ha $yearling^{-1}$ mo^{-1}) grazed pastures and a cattle exclosure within each pasture have been maintained since 1939. These stocking rates represent approximately an average of 20%, 40%, and 60% removal, respectively, of annual aboveground production over a 6-mo period during the growing season (Klipple & Costello 1960).

Undisturbed vegetation at the CPER is typical of shortgrass communities. Basal cover of all plants ranges from 25–40%, of which 85–90% is perennial grasses, and in particular *B. gracilis* (Hanson 1955; Milchunas et al. 1989). Other important perennial graminoids include the C_3 grass, *Agropyron smithii* Rydb., the C_4 grass *Buchloe dactyloides* (Nutt.) Engelm., and the sedges *Carex eleocharis* Bailey and *Carex heliophila* Mack (nomenclature follows The Great Plains Flora Association 1986). A number of succulents, including *Opuntia polyacantha* Haw., half-shrubs (e.g., *Gutierrezia sarothrae* [Pursh] Britt & Rusby and *Chrysothamnus nauseosus* [Pall.] Britt.), forbs including *Sphaeralcea coccinea* (Pursh) Rydb., and annual grasses (e.g., *Vulpia octoflora* [Walt.] Rydb.) account for the remainder.

Patch characteristics

High densities of white grubs and large numbers of patches of vegetation presumably affected by grubs were observed in fall, 1977 (Wiener & Capinera 1980). High grub densities in dead patches and near margins of undisturbed vegetation (Wiener & Capinera 1980) as well as low densities of nematodes (Stanton et al. 1984) indicated that grubs were the most likely factor affecting the vegetation. Grub densities decreased markedly from fall, 1977 to fall, 1978, likely as a result of drought during the 1978 growing season (Wiener & Capinera 1980). No new patches were observed and no additional damage occurred after 1977. Subsequent outbreaks by grubs have been observed at the site that did not affect the patches under study.

Sixteen patches were selected in fall, 1977 that consisted of four pairs of adjacent ungrazed-grazed locations on sandy loam soils (avg= 70% sand, 19% silt, and 11% clay) with two replicate patches in each location. The eight ungrazed patches were in 0.4 ha (1 acre) cattle exclosures that have not been grazed since 1939. Of the eight grazed patches, three locations (6 patches) have been summer grazed at a moderate level and one location (2 patches) has been grazed at a heavy level during the summer since 1939.

Four permanent transects were established in cardinal directions in each patch to define its extent and shape. Each transect began at the center of the patch and extended four to ten meters into undisturbed vegetation. This sampling scheme allowed a comparison of patches with undisturbed vegetation and a determination of changes in patch size through time. Because earlier simulation model analyses indicated the importance of disturbance size to successional dynamics (Coffin & Lauenroth 1989a; 1994, Coffin et al. 1993) and patches were unequal in size, patch size was expected to be important to plant recovery. Because of the irregular shape of each patch, size (m) was estimated as the average length of the transects from the center of the dead area to the start of the transition area containing a mixture of live and dead *B. gracilis* plants. Analysis of variance was used to determine if grazing treatment had a significant ($P<0.05$) effect on average patch size at the start of the study in 1977.

Vegetation sampling

Vegetation was sampled six times from 1977 to 1990 using permanently marked plots located on the four transects within each patch and the surrounding undisturbed area. Near time of peak aboveground biomass (July 15 to August 15) in each year (1977, 1978, 1979, 1980, 1982, and 1990), plant basal cover and density by species were estimated using 30×30 cm quadrats located on each transect. A similar number of quadrats was used to sample within the patch (avg=20 quadrats/patch) compared to the undisturbed vegetation (avg=24 quadrats/area).

Basal cover of live perennial plants by species, dead *B. gracilis* crowns, litter, bare ground, and lichens were visually estimated in each quadrat. Density of annuals was determined by counting individual stems. Tillers of *B. gracilis* were counted in a 10 cm × 10 cm quadrat placed in a standard location within each large quadrat.

Statistical analyses of vegetation

In 1977, each quadrat was designated as either within: (1) the patch where dead *B. gracilis* plants dominated cover, (2) the transition zone containing a mixture of live and dead plants, or (3) the undisturbed vegetation consisting mostly of live plants. This initial designation was maintained for all sampling dates. Because transition zones were variable in the degree and severity of plant mortality, the analyses focused on plant recovery within patches and on vegetation of undisturbed areas. Variability in patch size resulted in variability in number of quadrats sampled per patch (9 to 22) and undisturbed area (11 to 25). Because of the expected importance of variability in survival of *B. gracilis* tillers to recovery, an index of disturbance intensity was defined as the area (m^2) in each patch containing live *B. gracilis* tillers in 1977, calculated by the total number of plots with live *B. gracilis* tillers. Therefore, the patches with the highest intensity of disturbance and lowest survival of tillers had the smallest value of this index. The index was used as a covariate in all AOV statistical analyses. In addition, regression analysis was used to evaluate the relationship between disturbance intensity and cover of *B. gracilis* through time. A separate regression analysis was conducted for each year of sampling using the area containing live *B. gracilis* tillers (m^2) within each patch in 1977 as the independent variable and percentage cover of *B. gracilis* in each year for each patch as the dependent variable.

Table 1. Basal cover (%) and density (no./m^2) of live and dead *B. gracilis*, five species groups, total live cover and litter for undisturbed vegetation and patches killed by white grubs for two grazing treatments and six sample dates from 1977 to 1990[1].

		1977	1978	1979	1980	1982	1990	Slope
Cover								
Live *B. gracilis*								
ungrazed	undisturbed	$37.4_{\#}$	$17.6_{\#}$	$18.7_{\#}$	$40.2_{\#}$	$57.5_{\#}$	$22.9_{\#}$	
	patch	3.9^{p}	3.3^{p}	6.1^{p}	16.4^{p}	31.1^{p}	10.2^{p}	
grazed	undisturbed	35.4_{a}	16.8_{b}	18.6_{b}	38.4_{a}	57.8_{c}	32.2_{a}	
	patch	1.5_{a}	1.6_{a}	2.4_{b}	8.5_{b}	20.7_{d}	16.2_{e}	
Perennial C_4 grasses								
ungrazed	undisturbed	0.9	0.2	0.2	$0.5_{\#}^{*}$	$1.1_{\#}$	$1.1_{\#}$	Linear (Grazing)
	patch	0.8	0.4	0.7*	2.2	4.8	5.5*	
grazed	undisturbed	0.2_{a}	0.3_{a}	1.1_{b}	0.1_{c}	0.2_{d}	1.0_{d}	
	patch	0.1_{a}	0.4_{a}	0.3_{b}	2.2_{c}	13.7_{d}	9.4_{d}	
Perennial C_3 graminoids								
ungrazed	undisturbed	1.1	0.3	0.6	$1.3_{\#}$	$2.1_{\#}$	$5.9_{\#}$	
	patch	0.2	0.2	0.7	5.2*	8.7	9.5	
grazed	undisturbed	1.6_{a}	0.8_{b}	0.8_{b}	1.1_{a}	3.1_{c}	2.0_{c}	
	patch	0.1_{a}	0.2_{a}	0.3_{b}	1.9_{c}	6.4_{d}	3.0_{e}	
Perennial forbs, shrubs, and cactus								
ungrazed	undisturbed	$2.1_{\#}$	$3.9_{\#}$	$3.7_{\#}$	$4.9_{\#}$	7.5	$10.6_{\#}^{*}$	
	patch	7.6*	5.9	8.4	11.6	12.1	11.3	
grazed	undisturbed	1.1_{a}	3.1_{b}	2.8_{b}	4.2_{c}	4.6_{d}	6.6_{e}	
	patch	3.4_{a}	6.0_{a}	7.6_{b}	13.1_{c}	12.4_{c}	8.4_{c}	
Total live cover								
ungrazed	undisturbed	$41.5_{\#}$	$22.1_{\#}$	$23.2_{\#}$	$46.9_{\#}$	$68.3_{\#}$	$40.6_{\#}$	Linear
	patch	12.5	9.7	15.9	35.3	56.6	36.4	
grazed	undisturbed	38.2_{a}	21.0_{b}	22.4_{b}	43.7_{a}	65.6_{c}	41.8_{a}	
	patch	5.1_{a}	8.2_{a}	10.5_{b}	5.6_{c}	53.2_{d}	37.0_{c}	
Dead B. gracilis								
ungrazed	undisturbed	$10.4_{\#}$	30.4	15.5	7.3	0.8	$13.6_{\#}$	
	patch	31.6	31.7	13.9	5.7	0.5	6.8	
grazed	undisturbed	12.0_{a}	28.6_{b}	15.1_{a}	6.2_{c}	0.6_{d}	14.7_{a}	
	patch	31.0_{a}	28.2_{a}	12.9_{b}	5.1_{c}	0.5_{d}	7.6_{c}	
Litter								
ungrazed	undisturbed	$12.4_{\#}$	$15.4_{\#}$	$17.0_{\#}^{*}$	$6.7_{\#}$	$9.6_{\#}^{*}$	$23.8_{\#}$	Linear
	patch	15.5	20.3	20.4	12.9	11.2	31.1	
grazed	undisturbed	9.5_{a}	13.1_{b}	12.7_{b}	6.5_{c}	7.9_{a}	16.5_{d}	
	patch	15.4_{a}	15.0_{a}	14.1_{a}	13.0_{b}	11.0_{b}	19.3_{c}	
Density								
B. gracilis tillers								
ungrazed	undisturbed	$19.1_{\#}$	$13.8_{\#}$	$28.8_{\#}$	$23.6_{\#}$	$18.8_{\#}$	$17.3_{\#}$	Linear (Grazing)
	patch	1.9^{p}	2.0^{p}	9.0	9.9^{p}	8.0^{p}		6.5
grazed	undisturbed	22.5	13.5	31.1	25.7	20.7	25.5	
	patch	0.7_{a}	0.7_{a}	2.8_{b}	2.8_{b}	4.5_{b}	13.2_{c}	

Table 1. Continued

		1977	1978	1979	1980	1982	1990	Slope
Annuals								
ungrazed	undisturbed	32.6#	62.9#	99.3#	8.2#	3.6#	8.8#	
	patch	239.0	131.1	109.0	15.7	10.0*	6.4	
grazed	undisturbed	40.7	95.6	60.8	35.3	4.7	14.3	
	patch	329.6_a	192.8_b	89.9_c	83.3_d	2.8_e	8.9_f	

[1]* indicates significance of grazing on cover or density on patches or undisturbed areas within each date and within species group. [P] indicates significance of patchiness in *B. gracilis* in 1977 to differences in grazing treatments within each date and species group. Subscripts indicate significance of time within each species group for both grazing treatments combined. Values not sharing common letters are significantly different ($P < 0.05$). #indicates significance between patch and undisturbed cover or density within each date and within species group for both grazing treatments combined.

Analyses were conducted for basal cover (%) and tiller density (no. m^2) of *B. gracilis* and four groups of species: (1) cover of other C_4 perennial grasses; (2) cover of C_3 perennial graminoids; (3) cover of perennial forbs, shrubs, and cactus; and (4) density of annuals. Cover (%) of litter and dead crowns of *B. gracilis* were also analyzed. Average plant cover or tiller density on a patch, expressed as a proportion of average cover or density of the surrounding undisturbed area, was analyzed as an additional measure of recovery by *B. gracilis*. A repeated measures analysis of variance was used to evaluate cover and density of each species or group through time within patches and for the undisturbed vegetation, as well as effects of grazing and location on cover and density. The repeated measures design included location and grazing as the between subject factors and quadrat type (patch or undisturbed) and time as the within subject factors. A preliminary analysis with a similar statistical design yet using grazing intensity as a covariate indicated that grazing intensity differences were not important to the results; therefore two grazing treatments (ungrazed, grazed) were used in subsequent analyses. A significance level of $P<0.05$ was used for all analyses.

Three separate means comparisons tests were conducted for each repeated measures AOV. Effects of grazing on plant recovery in each sample year were determined by comparing cover or density of each species or group on ungrazed versus grazed patches. A similar analysis was conducted for grazed and ungrazed undisturbed areas. Trends through time for each grazing treatment were evaluated separately by comparing slopes of the regression lines from 1978 to 1982 for vegetation within patches with vegetation of undisturbed areas. The first sample date (1977) was excluded from the slope analysis because of large decreases in cover or density from 1977 to 1978 that preceded plant recovery, and subsequent increases in cover or density after 1978 made a regression difficult to fit. The last sample date (1990) was not included in the slope analysis because of the large effects a single endpoint distant from previous points can have on a regression. Vegetation measures were also compared among subsequent years by combining grazing treatments to evaluate significant changes in plant recovery through time within patches as well as significant fluctuations in vegetation of undisturbed areas.

Results

Patch characteristics

At the start of plant recovery in 1977, patches located in ungrazed exclosures were significantly smaller (avg=3.9 m) and had higher survival by *B. gracilis* tillers (65%) than patches in adjacent grazed pastures (avg=4.5 m; 41%) (Figure 1). The trend of ungrazed patches having a higher proportion of live tillers than grazed patches was found only for the first three years. The initial decrease from 1977 to 1978 in proportion of a patch containing live *B. gracilis* tillers under both grazing treatments indicates a delayed mortality response. These patch sizes represent the largest sizes attained during the study since patch size did not increase through time, and plant recovery began immediately.

Plant recovery: species composition

Grazing did not have important effects on patterns in relative cover through time on undisturbed areas

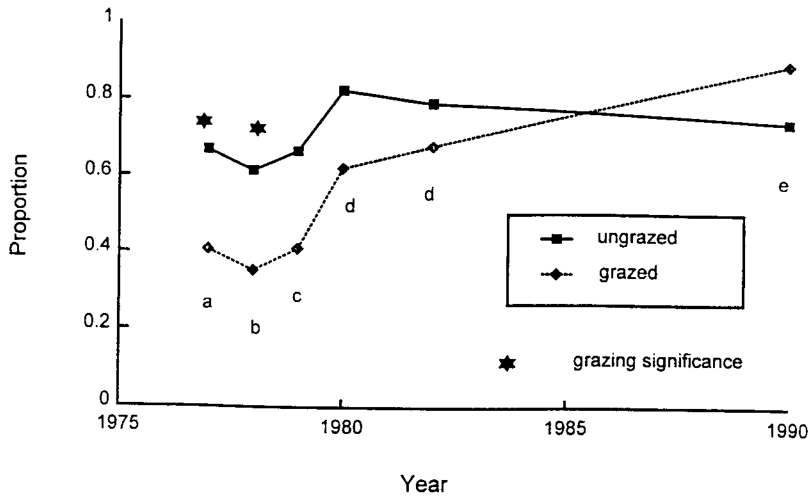

Figure 1. Proportion of each patch containing live *B. gracilis* tillers through time for grazed and ungrazed patches. Different letters indicate significant differences in subsequent proportions averaged for grazed and ungrazed patches in each year.

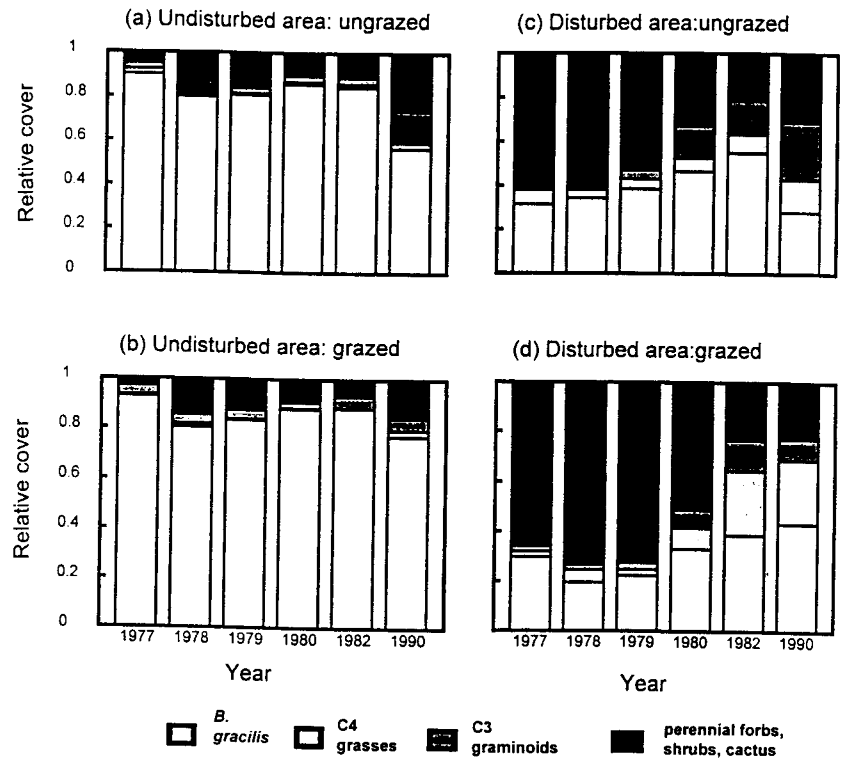

Figure 2. Basal cover of *B. gracilis* and three species groups relative to the total for undisturbed vegetation that was either (a) ungrazed or (b) grazed, and for patches affected by white grubs that were either (c) ungrazed or (d) grazed for six sample years.

surrounding patches or on patches killed by grubs (Figure 2). However, species composition was different on undisturbed areas compared to patches. Plant cover on undisturbed areas was dominated by *B. gracilis* with other perennial graminoids having small contributions ($<15\%$) (Figures 2a, b). Large variability in cover of perennial forbs, shrubs, and cactus was observed.

By contrast, plant cover on grazed and ungrazed patches was dominated by perennial forbs, shrubs, and cactus for the first three years after recovery began (Figures 2c, d); relative cover of this group varied from 21 to 73%. Perennial graminoids were important components of cover in 1980, 1982, and 1990 with C_3 graminoids having higher cover on ungrazed patches and C_4 grasses having higher cover on grazed patches. Relative *B. gracilis* cover varied from 20 to 55%, and this species dominated plant cover starting in 1980 on ungrazed patches and in 1982 on grazed patches.

Plant recovery: cover and density

Cover or density of *B. gracilis* and other groups on undisturbed areas and on patches killed by white grubs was infrequently related to grazing by cattle (Table 1). In general, cover and density were similar to or higher for ungrazed compared to grazed conditions. For undisturbed areas, grazing resulted in lower cover than ungrazed areas for perennial C_4 grasses and perennial forbs, shrubs, and cactus in only one year for each group, and for litter in two years. For patches, cover of perennial C_4 grasses was higher under grazing for one year (1990), and lower under grazing for another year (1979). Ungrazed patches had higher cover than grazed patches in only one year for the two other groups (perennial C_3 graminoids and perennial forbs, shrubs, and cactus). Density of annuals was higher under grazing than for ungrazed patches in only one year (1982). In addition, grazing explained differences in slopes of lines between patches and undisturbed vegetation for cover of only one group (perennial C_4 grasses) and for density of *B. gracilis* tillers.

Undisturbed vegetation Large variability in cover on undisturbed areas was observed through time for *B. gracilis* and all species groups of live plants and dead plant material whereas density of *B. gracilis* tillers and annual plants were similar through time (Table 1). For *B. gracilis*, a similar magnitude of response was observed for decreases ($0.5\times$; 1977 to 1978) and increases in cover ($2\times$; 1979 to 1980). A doubling in tiller density was also observed in the time period between decreases and increases in cover of this species (1978 to 1979). Increases and decreases in cover of *B. gracilis* between years tended to be associated with decreases and increases, respectively, in cover of litter and dead crowns of *B. gracilis*. Cover of perennial C_4 grasses and perennial forbs, shrubs, and cactus increased through time whereas cover of perennial C_3 graminoids did not show trends through time.

Vegetation on patches Significant differences in cover and density of *B. gracilis* were found on grazed and ungrazed patches for most sample years (Table 1) as a result of differences in disturbance intensity and survival of *B. gracilis* tillers, the covariate in the analysis (Figure 1). Survival of *B. gracilis* was not important to cover or density of other groups. Cover and density of *B. gracilis* on patches was similar or increased through time until 1982 (cover) or 1990 (density) (Table 1). By contrast, density of *B. gracilis* tillers on patches was highest on the last sample year (1990). Corresponding to increases or decreases in *B. gracilis* cover through time were increases or decreases in total cover and decreases or increases in cover of dead *B. gracilis* crowns. Cover of perennial forbs, shrubs, and cactus was the highest of all groups in 1977, and increased or remained similar until 1990. Cover of perennial C_4 grasses and C_3 graminoids was the lowest of all groups in 1977 and 1978; cover of these two groups increased through time until 1982 (C_4 grasses) or 1990 (C_3 graminoids). The combined cover of these two perennial graminoid groups was less than *B. gracilis* cover throughout the sample period. Density of annuals was very high in 1977, and decreased through time until 1990. No clear trends were observed in cover of litter. Total cover followed a recovery phase from 1977 to 1982 in that cover was similar or increased though time.

Vegetation on patches compared to undisturbed vegetation. Total cover, and cover and density of *B. gracilis* tillers were significantly less on patches compared to undisturbed areas for all sample years regardless of grazing treatment (Table 1). High mortality of *B. gracilis* in 1976 and 1977 is indicated by the significantly larger cover of dead *B. gracilis* crowns on patches compared to undisturbed areas in 1977. The corresponding increase in bare ground (not shown) on patches compared to undisturbed areas in 1978 indicates a lag between the time that *B. gracilis* plants die, and when crowns become dislodged and blow away.

This difference in cover of dead crowns was not found for the subsequent four sample years. In 1990, cover of dead crowns was higher on undisturbed areas compared to patches, likely as a result of natural mortality of older plants and tillers compared to patches where plants were recently established. Cover of perennial forbs, shrubs, and cactus, and litter were higher on patches throughout the sampling period, and density of annuals was higher on patches than on undisturbed areas for all except the last sample date (1990). Cover of perennial graminoids other than *B. gracilis* was higher on undisturbed areas initially after the disturbance (1977, 1978), and higher on patches starting in 1980.

Recovery of B. gracilis. Another measure of recovery of *B. gracilis* is the cover or density on patches expressed as the proportion of cover or density of this species on undisturbed areas. Proportions were small, yet > 0 in 1977 (< 0.1) and increased to an average for the last two sample years of 0.43 (cover) and 0.38 (density); grazing was infrequently important to this proportion (Figure 3). Grazed and ungrazed patches were significantly different in proportion of undisturbed cover or density for only two years; the years were not the same for cover and density, and no patterns were observed between grazing treatments. Cover on patches as a proportion of undisturbed cover increased through time until 1982; density of tillers as a proportion of undisturbed density continued to increase until 1980 for ungrazed patches and until 1990 for grazed patches.

Significant linear relationships were found between disturbance intensity or survival of *B. gracilis* on patches in 1977 and the cover of this species in each year of sampling. Grazed and ungrazed patches differed in the variability around each line as indicated by the r^2 values (Figure 4). In addition, high r^2 values were found for all years for ungrazed patches whereas r^2 were low (< 0.41) after 1979 for grazed patches.

Discussion

Recovery dynamics

Successional dynamics of species groups on patches affected by white grubs were similar to dynamics reported both in shortgrass ecosystems as well as other grasslands in the central grassland region of North America (Shantz 1917; Judd & Jackson 1940; Tolstead 1941; Costello 1944; Tomanek et al. 1955; Collins & Adams 1983). The general pattern of dominance by annuals followed by dominance by short-lived perennial forbs and grasses, and finally dominance by long-lived perennial shortgrasses observed on other disturbance types for shortgrass systems (Shantz 1917; Costello 1944) was also found in this study.

However, rate of recovery, based upon the length of time the vegetation remained within each stage, was faster for areas disturbed by white grubs than for more intense disturbance types, such as cultivation and subsequent abandonment where all plants are killed. Results using chronosequences of abandoned fields and roads in the shortgrass region have indicated a period of 1 to 5 years in the annual-dominated stage, 5 to 15 years in the short-lived perennial forb stage, and 5 to 15 years in a short-lived perennial grass stage. This old field model of succession predicts 25 to >50 years being required for return to dominance by long-lived shortgrasses (Shantz 1917; Judd & Jackson 1940; Costello 1944). These time intervals were estimated by comparing disturbed areas of differing ages, and not by long-term monitoring of individual disturbances. Faster recovery rates on old fields than those indicated by chronosequences have been predicted by simulation analyses (Coffin et al. 1993) and observed using replicate fields of known age (Coffin et al. 1996). In the current study, annuals had highest densities on patches affected by white grubs in the first three years of recovery. Perennial forbs, shrubs, and cactus were also important during this time period by contributing the most to total plant cover of any group. By 1980, four years after recovery began, plant cover on patches was not clearly dominated by any species group. This trend of similar cover among groups continued for the next two sample years and was still observed in 1990.

Because total cover and cover of *B. gracilis* were still less, and density of short-lived species (annuals and perennial forbs) was greater on patches than undisturbed areas after 14 years, the patches had not fully recovered to their predisturbed state. However, recovery on these patches where *B. gracilis* mortality, as well as mortality of other perennial graminoids, was incomplete is expected to be much faster than predicted by the old field successional model (Judd & Jackson 1940; Costello 1944). Small disturbances (< 2.4 m^2) where complete plant mortality occurred have been observed over a similar time period (1984 to 1994; Coffin & Lauenroth unpublished data), and found to also have higher cover of short- and long-lived perennial graminoids than predicted from the

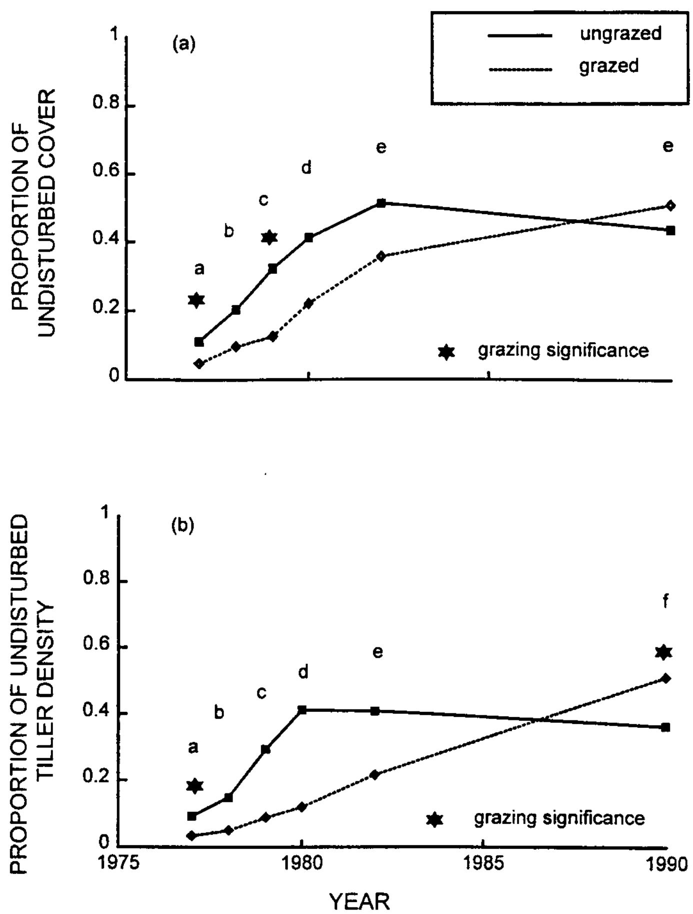

Figure 3. Recovery of *B. gracilis* on patches through time measured by (a) cover as a proportion of average undisturbed cover and (b) density of tillers as a proportion of average undisturbed tiller density. Different letters indicate significant differences in subsequent proportions averaged for grazed and ungrazed patches in each year.

old field model, and comparable total cover as areas affected by white grubs. Cover of *B. gracilis* is low on these small, high intensity disturbances, yet higher than predicted for old fields after 10 years of recovery indicating the importance of disturbance size as well as intensity to recovery. In addition, recovery on large areas, such as old fields, is not spatially homogeneous. Spatially-explicit sampling and simulation of old fields indicate that recovery is faster near the edge of fields with undisturbed vegetation, and slower as distance increases (Coffin et al. 1993, 1996). Similar recovery rates near field edges and on small patches may be expected since both are close to undisturbed areas containing propagules at the start of plant recovery. Simulation analyses have also indicated the importance of disturbance size, environmental factors such as soil texture, and climatic factors such as precipitation to plant recovery of shortgrass systems (Coffin & Lauenroth 1989a, 1990, 1994; Coffin et al. 1993). Previous studies have found intensity as well as other characteristics to be important to plant recovery (Collins & Barber 1985; Milchunas et al. 1989; Coffin & Lauenroth 1989b; Umbanhowar 1992)

In this study, precipitation and temperature may have had important effects on plant survival and recovery after disturbance. Both the year preceding (1976) and the year when large numbers of severely damaged patches of vegetation were observed (1977) were dry and warm. Plants under drought stress are likely to be more negatively affected by other sources of stress and mortality, such as loss of roots by grubs, than plants that are not stressed; therefore the severity of the damage may have been increased due to harsh climatic conditions. Root feeders may also exacerbate effects of drought by further depriving plants of water (Brown & Gange 1990; Masters et al. 1993; Mas-

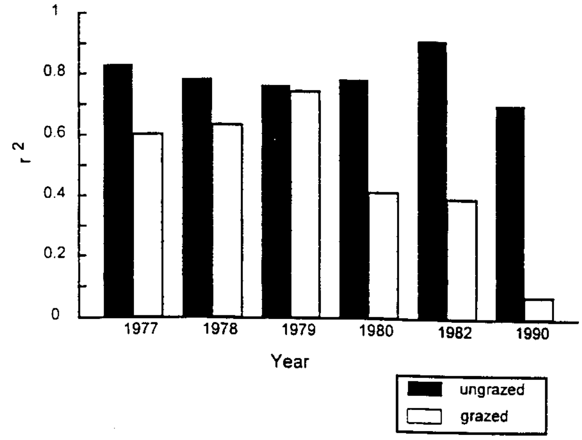

Figure 4. R^2 values from separate regression analyses for grazed and ungrazed patches. Regressions were conducted using tiller survival of *B. gracilis* in 1977 (ie., disturbance intensity) from Figure 1 as the independent variable and cover of this species in each year of sampling as the dependent variable.

ters 1995). Although the biology of white grubs is poorly understood and controls on population dynamics are unknown, these climatic conditions coincided with high densities of grubs in the soil in 1977 (Wiener & Capinera 1980). This combination of high densities of grubs and drought-stressed plants likely resulted in the widespread, severe damage to vegetation; the likes of which have not been observed since that time at the CPER or in northeastern Colorado. Subsequent outbreaks have been followed by favorable climatic conditions that promoted plant survival and recovery.

Importance of above- and belowground herbivory

Variability in disturbance intensity based upon the degree of plant mortality between grazed and ungrazed patches affected by grubs likely resulted from indirect effects of cattle on grubs rather than direct effects of cattle on grubs or on plant survival. Because aboveground production and belowground root biomass are similar in ungrazed exclosures and moderately grazed pastures (Sims et al. 1978; Leetham & Milchunas 1985; Milchunas & Lauenroth 1989), the observed responses were not due to differential responses of plants to grazing by cattle. It is also unlikely that aboveground grazing by cattle would have direct effects on belowground feeding by white grubs, although trampling by cattle can compact the soil with detrimental effects on belowground insect herbivores.

An alternative explanation for more complete mortality of *B. gracilis* plants on grazed compared to ungrazed patches is a more effective consumption of roots by white grubs as an indirect effect of cattle grazing. Certain groups of root-feeding fauna (ie., nematodes, arthropods, detritivores, and herbivores) have been found to increase in density when foliage was grazed by vertebrate herbivores (Waters 1955; Hutchinson & King 1980; Stanton 1983; Roberts & Morton 1985; Seastedt 1985). Although belowground herbivores may respond to amount, quality, and temporal and spatial distribution of resources (Andersen 1987), the positive response to grazing is likely not due to increases in resource availability since root productivity and biomass either decline or are not related to foliage removal in a number of grassland types (Seastedt 1985; Milchunas & Lauenroth 1993), including the shortgrass steppe (Leetham & Milchunas 1985; Milchunas & Lauenroth 1989). Changes in resource quality of roots as a result of foliage removal has been suggested as an explanation for the increase in density of belowground feeders with foliage removal (Seastedt et al. 1988). Another possibility is differences in small-scale heterogeneity of belowground resources. More uniform spatial distribution of root biomass has been found on heavily grazed pastures compared to adjacent ungrazed exclosures (Milchunas & Lauenroth 1989). These positive responses of root feeders to herbivory by cattle are in contrast to previous studies indicating a negative effect of aboveground herbivory on belowground herbivores if root growth is reduced, in particular for annual-dominated communities (Masters & Brown 1992; Masters et al. 1993; Masters 1995). Differential importance of belowground consumers has also been reported for early successional communities dominated by annuals compared to mature grasslands dominated by perennials (Brown & Gange 1989a, 1989b; Gibson et al. 1990; Mueller-Scharer & Brown 1995).

Recovery dynamics of B. gracilis

Although cover and density of *B. gracilis* were similar through time on grazed and ungrazed patches after disturbance intensity was considered, grazing was important to the relationship between survival of *B. gracilis* at the start of recovery and cover of this species on patches in each subsequent sample year. Degree of survival explained >70% of the variability in *B. gracilis* cover on ungrazed patches for all years indicating the importance of initial conditions in determining recovery of this species for as many as 14 years after recovery began. By contrast, tiller survival explained >60% of variability in cover on grazed patches for the first three years, and <41% of variability for remaining years. The increasing importance of direct and indirect effects of grazing, and decreasing importance of initial conditions on recovery of *B. gracilis* may account for the decrease in variability explained through time by initial survival of this species on grazed patches. Grazing has also been found to decrease the production of viable *B. gracilis* seed (Coffin & Lauenroth 1992) and to increase the vegetative spread of *B. gracilis* (Milchunas et al. 1989); two characteristics expected to be important to plant recovery.

Increase in variability in plant response through time on grazed patches likely reflects differential utilization by cattle both among pastures and among locations within pastures as a result of cattle grazing behavior patterns (Senft et al. 1985). Cattle typically spend more time in lowlands than uplands (Senft et al. 1985). The length of time varies both intra- and inter-annually with changes in plant growth and stocking rate, and likely results in a gradient in utilization within a pasture that decreases with increasing elevation. Although utilization studies have not been conducted, this gradient is supported by decreasing frequency of fecal pat deposition with increasing elevation (Coffin & Lauenroth 1988). As a result, each pasture has a large variability in utilization rates through time and space, and lightly, moderately, and heavily grazed uplands are typically more similar in utilization or actual grazing intensity than topographic positions within a single pasture (Coffin & Lauenroth 1988; Milchunas et al. 1989). In the current study of moderately and heavily grazed level uplands, even though utilization rates were expected to be similar, complex interactions among direct and indirect effects of grazing, soil and topographic factors, and cattle grazing behavior may have resulted in differential responses of plants to grazing through time. These differences became evident four years after recovery began, and may reflect the positive effects of grazing on reproductive effort and rate of spread of *B. gracilis* (Milchunas et al. 1989; Coffin & Lauenroth 1992) as well as other species rather than the negative effects of grazing on seed production (Coffin & Lauenroth 1992).

Summary and conclusions

Successional patterns on patches killed by larvae of June beetles were similar to patterns in species groups found on other types of disturbances, in that annuals initially dominated vegetation, followed by short-lived perennials, and finally long-lived perennial grasses. However, rate of recovery was faster on grub-killed patches compared to higher intensity disturbances where all plants are killed. The importance of disturbance intensity, as measured by tiller survival of the dominant grass species, to plant recovery has not been well-studied in grasslands, but was found to be more important than other factors (ie., grazing by cattle) to plant recovery through time for shortgrass communities.

Disturbance intensity was important to variability in cover of *Bouteloua gracilis* on ungrazed patches throughout the study period. However, grazing became more important through time compared to initial intensity for grazed patches. Therefore, grazing by cattle had important initial affects on plant survival due to interactions with grubs, and also had continuing effects through time on variability in *B. gracilis* cover. The lack of direct effects of grazing by cattle on other measures of plant recovery is similar to other grazing responses of shortgrass steppe ecosystems, and indicates the importance of the long evolutionary history of these systems in the presence of large ungulate herbivores (Stebbins 1981; Milchunas et al. 1988). Other rangelands with a short evolutionary history of grazing, such as the Intermountain zone of the U.S., can have large shifts in species composition with grazing (reviewed in Milchunas & Lauenroth 1993), and are expected to have much larger effects of grazing on plant recovery after grub damage than observed in the current study.

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