

Disturbances and gap dynamics in a semiarid grassland: A landscape-level approach

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Abstract

We developed a spatially-explicit gap dynamics simulation model to evaluate the effects of disturbances at the scale of a landscape for a semiarid grassland in northcentral Colorado, USA. The model simulates the establishment, growth, and death of individual plants on a small plot through time at an annual time step. Long-term successional dynamics on individual plots (single gaps) and on a landscape composed of a grid of plots were evaluated. Landscapes were simulated as either a collection of independent plots or as a collection of interacting plots where processes on one plot were influenced by processes on adjacent plots. Because we were interested in the recovery of the dominant plant species, the perennial grass blue grama (*Bouteloua gracilis* (H.B.K.) Lag. ex Griffiths) after disturbances, we focused on scale-dependent processes, such as seed dispersal, that are important to the recruitment of individuals of *B. gracilis*.

The type of simulated landscape was important to the recovery time of *B. gracilis* after a disturbance. Landscapes composed of independent plots recovered more rapidly following a disturbance than landscapes composed of interacting plots in which the recovery time was dependent on the spatial scale of the disturbance.

Introduction

Disturbances operate over a wide range of spatial scales (Pickett and White 1985). The recolonization of disturbed areas may be dependent on the size of the disturbance since different physical and biological processes may be important at different spatial scales (Delcourt *et al.* 1983). Disturbances, viewed in the context of a landscape, produce a patch in the background matrix (Forman and Godron 1981, 1986). Understanding the relationship among disturbance size, degree of interaction among disturbed and undisturbed patches, and pattern of recolonization is one of the most important issues to be addressed in the development of landscape ecology.

Successional studies in the shortgrass steppe region of North America have focused on large-scale disturbances, such as abandoned agricultural fields (Savage and Runyon 1937; Judd and Jackson 1939; Costello 1944; Judd 1974; Reichhardt 1982). An important conclusion from these studies is that the dominant plant species, blue grama (*Bouteloua gracilis* (H.B.K.) Lag. ex Griffiths (Nomenclature follows McGregor (1986))) recovers very slowly after a disturbance or not at all because of climatic constraints on seed germination and seedling establishment (Riegel 1941; Hyder *et al.* 1971; Briske and Wilson 1977).

A recent study of small-scale disturbances indicated that conclusions reached about the inability of *Bouteloua gracilis* to recolonize large disturb-

ances may not hold for all disturbances, and in particular, small disturbances that occur frequently (Coffin and Lauenroth 1988). Results from a simulation model based on a gap dynamics conceptualization of succession in shortgrass communities suggested that the availability of seeds may be a more limiting factor in the recovery of *B. gracilis* than climatic constraints on seed germination and seedling establishment, and furthermore that the availability of seeds may be a function of the spatial scale of the disturbance (Coffin and Lauenroth unpublished).

The availability of seeds of *Bouteloua gracilis* at a particular point on a landscape depends on several factors, including the production, dispersal, and storage of seeds in the soil. The production and dispersal of seeds of *B. gracilis* each year may be particularly important since a field study found relatively few seeds of *B. gracilis* stored in the soil (54 seeds/m² averaged over a two-year sampling period) with a large variability in the number of seeds stored through time (Coffin and Lauenroth 1989). Seeds of *B. gracilis* are primarily wind dispersed; therefore the recovery of *B. gracilis* may depend on the spatial scale of the disturbance relative to the dispersal distance of the seeds.

Our objective in this analysis was to evaluate the effects of disturbance size and the spatially-explicit process of seed dispersal on the recovery of *Bouteloua gracilis* after disturbances. Our approach was to incorporate spatial structure into the gap dynamics simulation model for a semiarid grassland (Coffin and Lauenroth unpublished) by conceptualizing the landscape as a grid of plots in which either processes on one plot may affect processes on other plots (Fig. 1a) or processes on one plot are independent of processes on other plots (Fig. 1b).

Site description

All data were collected at the Central Plains Experimental Range (CPER) in northcentral Colorado approximately 60 km northeast of Fort Collins (40° 49' N latitude, 107° 47' W longitude). The CPER is administered by the USDA Agricultural Service. Mean annual precipitation is 311 mm (sd = 79 mm) and mean monthly temperatures range

from -5° C in January to 22° C in July. The topography consists of relatively flat uplands and lowlands connected by gentle slopes. The vegetation is typical of the shortgrass steppe in that most sites are dominated by the perennial grass *Bouteloua gracilis*. Moderate grazing by cattle occurs throughout the area.

Model description

The effects of spatially-explicit processes on the recovery of *Bouteloua gracilis* after disturbances was evaluated using a modification of a gap dynamics simulation model developed for a semiarid grassland (Coffin and Lauenroth unpublished). The gap model is similar to models developed for forests (Botkin *et al.* 1972; Shugart 1984), and simulates the establishment, growth, and death of individual plants on a small plot (0.12 m²) through time at an annual time step. The establishment and mortality of plants are modeled as stochastic processes: there is a probability associated with each species that establishment of plants will occur each year either as seedlings or vegetative propagules, while the probability of mortality for an individual each year is based on the disturbance rate, the longevity of the species, and the greater risk of death associated with slow-growing individuals than with plants of average growth rates (Shugart 1984). Plant growth is based on the importance of belowground processes associated with the acquisition of soil water resources, since soil water is the most frequent control on plant growth and community structure in semiarid grasslands (Noy-Meir 1973; Lauenroth *et al.* 1978) and belowground net primary production contributes approximately 85% to total net primary production (Sims and Singh 1978). Details of the model can be found in Coffin (1988) and Coffin and Lauenroth (unpublished).

Spatial structure was incorporated into the model by considering the landscape to consist of a grid of plots in which processes on one plot could affect processes on other plots. Because we were interested in the recovery of *Bouteloua gracilis* after disturbances, we were concerned with processes important to the recruitment of individuals of *B. gracilis*

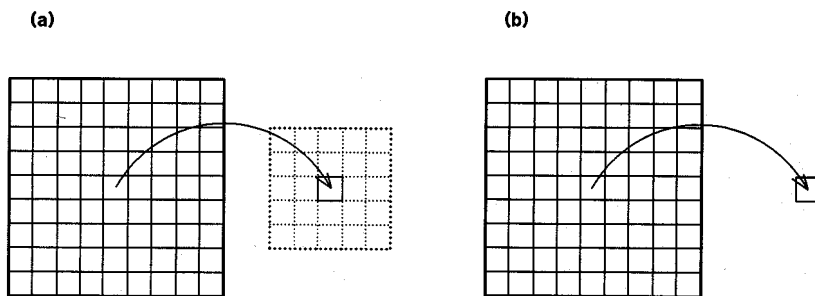


Fig. 1. Two conceptualizations of a landscape (a) a grid of plots in which processes on one plot may affect processes on other plots (b) a grid of plots in which processes on one plot are independent of processes on other plots.

onto each plot. Three general processes were included with at least one probability associated with each process:

1. The probability (0.125) that the **microenvironmental** conditions required for the germination and establishment of *B. gracilis* seedlings would occur each year was based on the timing of precipitation and temperature, and the effects of soil texture from Briske and Wilson (1977) and Laurenroth *et al.* (1987).

2. The availability of seeds of *B. gracilis* to each plot was based on probabilities associated with the production and dispersal of seeds of *B. gracilis*. The probability of seeds being produced was a function of the amount of aboveground biomass of *B. gracilis* and the amount of precipitation received in the previous year, since seeds of *B. gracilis* produced in the fall of one year are available to germinate in the spring of the following year (Dickinson and Dodd 1976; Coffin and Lauenroth 1989). We assumed that 49 g/m², or 50% of the maximum biomass of *B. gracilis*, was necessary for seeds to be produced. Therefore, the probability was calculated as:

$$P_b = 1.0 \quad \text{if BIOMASS} \geq 49 \text{ g/m}^2 \quad (1)$$

$$P_b = 0.0 \quad \text{if BIOMASS} < 49 \text{ g/m}^2 \quad (2)$$

where P_b is the probability that seeds of *B. gracilis* were produced and BIOMASS is the biomass of *B. gracilis* on the plot.

If the biomass of *B. gracilis* was sufficient for seed production, then the probability associated with annual precipitation was calculated by the function:

$$P_s = 1.0 - 0.99 \cdot \exp(-0.0018953 \cdot (\text{LYPPT} - 105)) \quad (3)$$

where P_s is the probability of seeds of *B. gracilis* being present on the plot and LYPPT is the amount of precipitation in the previous year. The values of P_s range from 0.01 in the driest year (LYPPT = 105 mm) to 0.55 in the wettest year (LYPPT = 520 mm). We assumed that even in the wettest year the probability of seeds being present is **small** since few seeds of *B. gracilis* persist in the soil through time (Coffin and Lauenroth 1989); thus the production of seeds in one year does not necessarily result in seeds being available the following year.

3. The probability of seeds dispersing to a plot was a function of the distance from the source of seeds, the height of the inflorescence, the average wind speed, and the aerodynamics of the seeds. We assumed the distribution of seeds dispersing from a parent plant was described by a negative exponential function (Werner 1975):

$$P_d = \exp(-\text{RATE} \cdot \text{DIST}) \quad (4)$$

where P_d is the probability that at least one seed will disperse to a distance of DIST from the parent plant, and RATE is a measure of the dispersability of the seeds. The value of RATE (3.78) was calculated by assuming $P_d = 0.005$ at the maximum distance (MAXD) that seeds of *B. gracilis* can travel under field conditions. MAXD was estimated using an equation for winddispersed seeds (Greene and Johnson 1986):

$$\text{MAXD} = (H \cdot V_w) / V_t \quad (5)$$

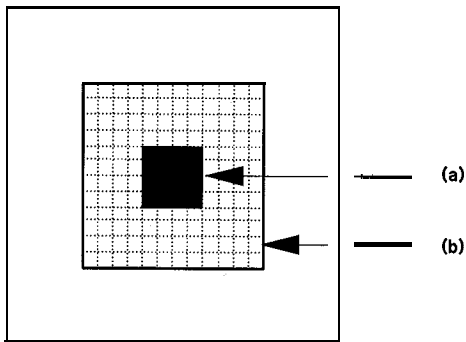


Fig. 2. A simulated landscape consists of a grid of plots that contains (a) the disturbed plots (b) the plots surrounding the disturbance within the maximum dispersal distance of *Bouteloua gracilis* seeds (MAXD).

where H is the average release height of the inflorescences (30 cm), V_w is the mean horizontal wind speed (500 cm/sec), and V_t is the average sinking velocity of the seeds (100 cm/sec). H and V_w were estimated from field data from the CPER, and V_t was estimated using data from wind-dispersed grassland species with similar seed aerodynamics as seeds of *B. gracilis* from Rabinowitz & Rapp (1981). The value of MAXD used in the model (14 m) was based on an even number (4) of 35 cm x 35 cm square plots.

Experimental simulations

The effects of five disturbance sizes (2, 8, 18, 31, and 49 m²) on the recovery of *Bouteloua gracilis* were evaluated for landscapes consisting of a grid of plots. The corresponding number of 0.12 m² plots in each square disturbance was: 16, 64, 144, 256, and 400. Each 300-year simulation began by initializing each plot in the grid with plants. The species composition on each plot was based on the proportion of plots in a steady-state landscape with a given species composition from Coffin & Lauenroth (unpublished). A disturbance was then positioned within the grid of plots with the restriction that the entire disturbance and the surrounding plots within the maximum dispersal distance of seeds of *B. gracilis* (MAXD) were included inside the grid (Fig. 2). We assumed all plants on the plots

in the disturbance were killed. The simulations were conducted in two ways: (1) the landscape was considered a collection of interacting plots in which the recovery of *B. gracilis* on a single plot was a function of the dynamics of *B. gracilis* on that plot as well as on surrounding plots within the dispersal distance of seeds of *B. gracilis* (dependent landscapes) (Fig. 1a); (2) the landscape was considered a collection of independent plots in which the recovery of *B. gracilis* on a single plot was only a function of the dynamics of *B. gracilis* on that plot (independent landscapes) (Fig. 1b).

In the case of the dependent landscapes, each disturbance was considered a separate unit; therefore 25 replicate landscapes, or disturbance events, were simulated for each disturbance size. For each disturbance event, there was a probability of the microenvironmental conditions occurring for seed germination and seedling establishment, and a probability that annual precipitation was sufficient to allow the production of seeds. The probability of seeds of *Bouteloua gracilis* being available to each plot in the disturbed area was then a function of the distance from the plot to the nearest plot with sufficient biomass for seeds to be produced. For the independent landscapes, each plot represented a separate unit; therefore one disturbance event was simulated for each disturbance size. Each plot was simulated independently of the other plots in the grid and the probabilities associated with seedling establishment were calculated for each plot separately. We assumed the only constraint on seed availability to these plots was the effect of precipitation on the production of seeds.

The average aboveground biomass of *Bouteloua gracilis* for the dependent landscapes for each time step was found by averaging the biomass on all plots contained within each disturbed area. Those values were then averaged for the 25 replicates for each disturbance size. The 95% confidence intervals for the average biomass values were calculated based on the standard deviations among the 25 replicates. The average aboveground biomass of *B. gracilis* for the independent landscapes was based on the biomass for all plots within the disturbed area for each size. The 95% confidence intervals for the average biomass values were calculated based

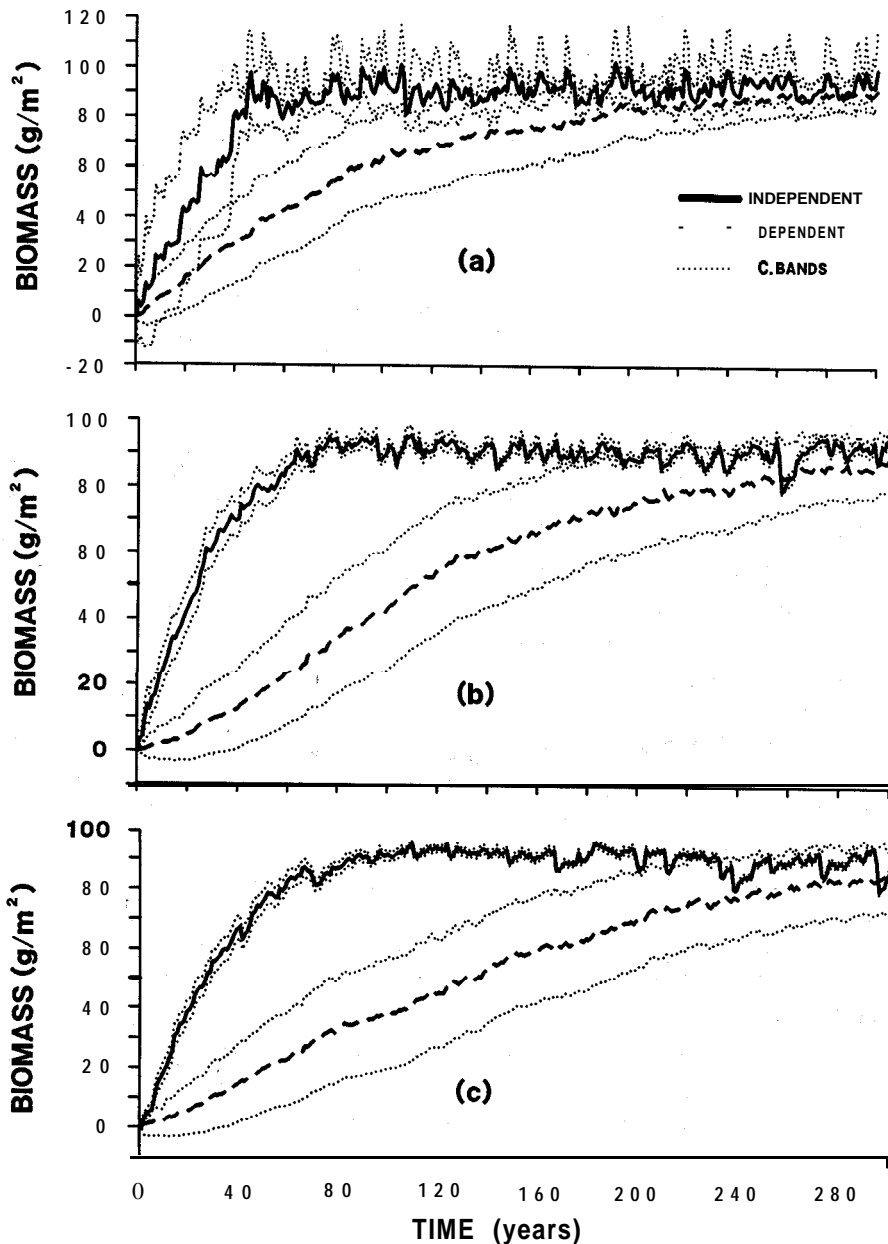


Fig. 3. Average aboveground biomass of *Bouteloua gracilis* and 95% confidence bands for 300 years for two types of landscapes and three disturbance sizes (a) 2 m² (b) 18 m² (c) 49 m².

on the standard deviations among the plots.

For both types of landscapes and each disturbance size, the recovery time of *Bouteloua gracilis* was defined as the time at which the five year running average of the upper 95% confidence interval of biomass of *B. gracilis* reached steady-state (89 g/m²). The recovery times were calculated as an

average for all plots in each disturbance and as an average for different types of plots. Plot type was based on the distance from a plot in the disturbance to the first row of plots bordering the disturbance. Each plot in the disturbance was identified based on the number of maximum seed dispersal distances of *B. gracilis* between the plot and the border plots

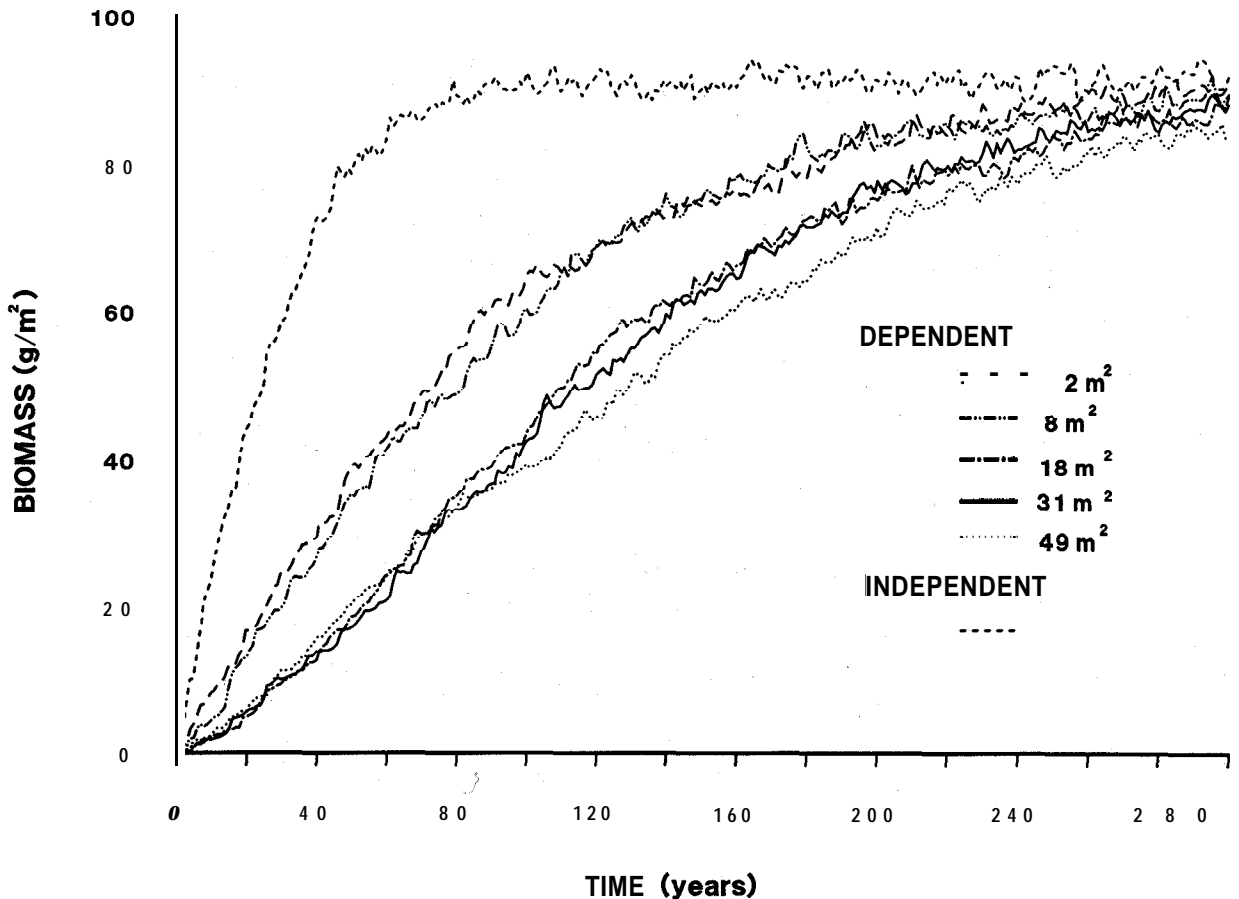


Fig. 4 Average aboveground biomass of *Bouteloua gracilis* for 300 years for two landscape types and five disturbance sizes. The average of the five sizes is shown for the landscapes consisting of independent plots.

(plot type 1 = 1*MAXD, plot type 2 = 2*MAXD, and plot type 3 = 3*MAXD).

Results and discussion

The recovery of *Bouteloua gracilis* after a disturbance was affected by the degree of interaction between plots making up the landscape, and the size of the disturbance. Landscapes consisting of a collection of interacting, dependent plots had smaller average aboveground biomass of *B. gracilis* through time and longer recovery times for all disturbance sizes than landscapes consisting of independent plots (Fig. 3). Although the results are only shown for the smallest-, intermediate-, and largest-sized disturbances, the results for the re-

maintaining two disturbance sizes (8 and 31 m²) were similar. The variability in biomass, as indicated by the width of the confidence bands, was less for the independent than for the dependent landscapes for all five disturbance sizes. The decrease in the variability of biomass of *B. gracilis* as the disturbance size increased for the independent landscapes was a result of the increase in the number of plots averaged to obtain the mean (from 16 for the 2 m² to 400 for the 49 m² disturbance size). The similar variability for all disturbance sizes for the dependent landscapes was a result of averaging across the 25 disturbance events for each size.

The average aboveground biomass of *Bouteloua gracilis* on the five disturbance sizes for the dependent landscapes were smaller through time than for the overall average of the five sizes for the indepen-

dent landscapes (Fig. 4). The overall average biomass for each time step is shown for the independent landscapes since the values were not significantly different. Two classes of curves are distinguishable for the dependent landscapes based on the size of the disturbance relative to the maximum dispersal distance of seeds of *B. gracilis*. Biomass on the two smallest disturbance sizes were similar and larger through time until steady-state was reached than biomass values on the three largest disturbance sizes. All plots within the two smallest sizes were within the maximum dispersal distance of seeds of *B. gracilis* from plots surrounding the disturbance; therefore all plots were accessible to seeds of *B. gracilis* at the start of each simulation. In contrast, plots in the center of the three largest disturbance sizes were beyond the maximum dispersal distance of seeds of *B. gracilis* from the surrounding undisturbed plots; therefore plots within the disturbed area that were accessible to seeds of *B. gracilis* from the undisturbed plots had to be recolonized by *B. gracilis* before seeds were available to the center plots and recolonization could begin.

The average time required for *Bouteloua gracilis* to reach steady-state and dominate the biomass on a disturbance was less for the landscapes consisting of independent plots for each disturbance size than for the landscapes of dependent plots (Fig. 5a). Recovery time increased as disturbance size increased for the dependent plots while similar values were found for all disturbance sizes for the independent plots.

The average recovery times of *Bouteloua gracilis* (136-206 years) associated with the landscapes that incorporated the spatially-explicit process of seed dispersal (dependent plots) were more similar to recovery times reported from experimental studies than the average recovery times for the independent plots (34-65 years). Most successional studies in the shortgrass steppe of North America have been conducted on abandoned agricultural fields where a shortgrass community dominated by *B. gracilis* has been suggested to occur after greater than 50 years of plant recovery (Hyder *et al.* 1971; Reichardt 1982), although the recovery of *B. gracilis* has not actually been monitored for this length of time.

Most fields were abandoned in the 1930's and currently *B. gracilis* is a minor component of the plant communities (Hyder *et al.* 1971); *B. gracilis* frequency values of 2% were recently recorded (Reichardt 1982).

The model results indicate that *Bouteloua gracilis* achieved 20–50% of its average biomass on the dependent plots 50-60 years after a disturbance (Fig. 4). Because of the important effects of disturbance size on the recovery of *B. gracilis* for the dependent plots, the simulation of sizes comparable to abandoned fields (> 1 ha) is expected to result in longer recovery times than for the largest size evaluated in this study (49 m²). Therefore, the recovery times that include the dispersal of *B. gracilis* seeds as a spatially-explicit process are still faster than those observed experimentally. It is possible that other processes important to the recovery of *B. gracilis* are scale-dependent, such as the occurrence of the microenvironmental conditions required for the germination and establishment of seedlings of *B. gracilis*, or that seeds of *B. gracilis* are present on disturbed areas less frequently than used in the simulations. Long-term experimental studies on a range of disturbance sizes are necessary to evaluate the recovery of *B. gracilis* after disturbances. Recently a study was initiated to evaluate successional dynamics on disturbances, such as western harvester ant mounds (*Pogonomyrex occidentalis* (Cresson)), that are comparable in size to the smallest size simulated (2 m²) (Coffin 1988).

The distance from a disturbed plot to the plots bordering the disturbance, as distinguished by plot type, had a more important effect on the recovery time of *Bouteloua gracilis* than the size of the disturbance (Fig. 5b). Plots closest to the edge of the disturbance (type 1) had the fastest recovery times with an average for the five disturbance sizes of 162 years. Plots located at two dispersal distances of seeds of *B. gracilis* (type 2) had an intermediate average recovery time (243 years) while plots at three dispersal distances (type 3) had the longest average recovery time (289 years).

The similar recovery times of *Bouteloua gracilis* for each disturbance size for plots at comparable seed dispersal distances from the edge of the disturbance indicate that recovery time will increase as

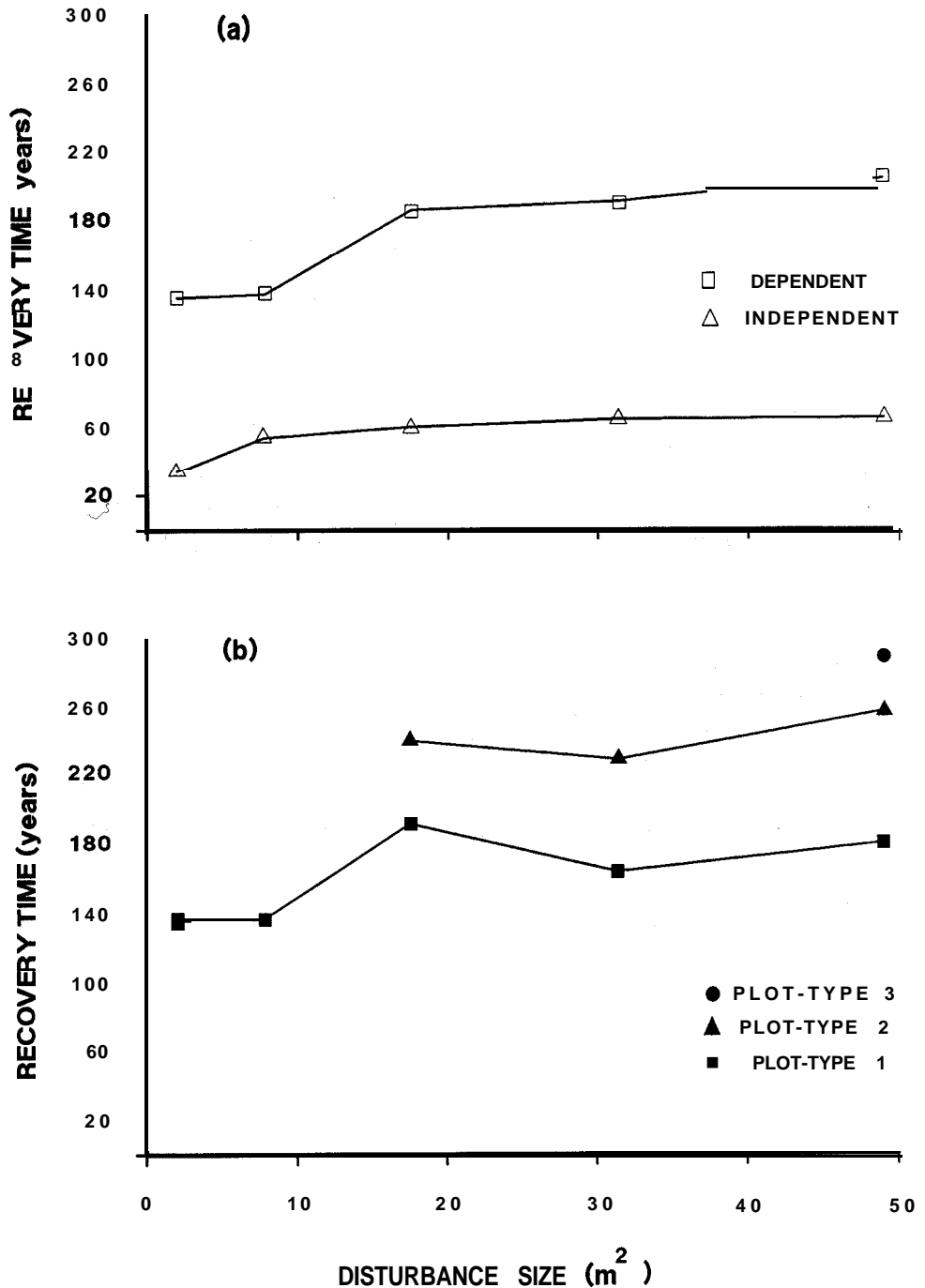


Fig. 5. Average time required for *Bouteloua gracilis* to dominate the biomass on a disturbance for two landscape types and five disturbance sizes (a) average of three plot types (b) average for each plot type.

the number of different types of plots contained in a disturbed area increases rather than as disturbance size increases; disturbances of different sizes yet with the same number of plot types will have

similar recovery times. The incorporation of other factors into the model, such as spatial heterogeneity in soil texture, may result in different recovery times for plots of the same type, and different

recovery times for disturbances with the same number of plot types yet of different sizes.

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