

DISSERTATION

GAP-PHASE DYNAMICS AND
SUCCESSION IN THE SHORTGRASS STEPPE

Submitted by

Debra P. Coffin

Department of Range Science

In partial fulfillment of the requirements

for the Degree of Doctor of Philosophy

Colorado State University

Fort Collins, Colorado

Spring 1988

COLORADO STATE UNIVERSITY

November 20, 1987

WE HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER OUR
SUPERVISION BY Debra P. Coffin
ENTITLED Gap-Phase Dynamics and Succession in the
Shortgrass Steppe
BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE
DEGREE OF Doctor of Philosophy.

Committee on Graduate Work

[Redacted]

[Redacted]

[Redacted]

[Redacted]

Adviser

[Redacted]

Department Head

J

ABSTRACT OF DISSERTATION
GAP-PHASE DYNAMICS AND SUCCESSION
IN THE SHORTGRASS STEPPE

Previous conceptualizations of succession in shortgrass plant communities have focused on the effects of large-scale disturbances with the conclusion that the dominant plant species, blue grama [Bouteloua gracilis (H.B.K.) Lag. ex Griffiths] fails to recover after a disturbance. My overall objective was to apply a gap dynamics approach based on small, frequently-occurring disturbances to shortgrass plant communities with the hypothesis that the death of a full-size B. gracilis plant results in a gap in the belowground resource space and initiates the successional processes of gap dynamics. I concluded that a gap dynamics conceptualization of shortgrass communities provides a promising alternative to a conceptual model that emphasizes the effects of large disturbances.

My first objective was to evaluate the effects of three small, patch-producing disturbances (cattle fecal pats, western harvester ant mounds, and small animal burrows) on B. gracilis-dominated plant communities by developing a spatially-explicit simulation model. Propagating the effects

of these disturbances through time suggested that B. gracilis is able to recover after small disturbances.

My second objective was to evaluate the short-term successional dynamics on small disturbances. I conducted a field study to evaluate the effects of three types of disturbances and their associated characteristics of size, seasonality, and location by soil texture on the recovery of plants. The density and cover of plants on the two naturally-occurring disturbances (western harvester ant mounds and small animal burrows) were dominated by perennials one year after the disturbances occurred while the majority of the cover on the artificially-produced disturbances was attributed to annuals.

My third objective was to evaluate the long-term successional dynamics on small disturbances and the time required for B. gracilis to recover after a disturbance. I developed a gap dynamics simulation model based on the belowground gap in the resource space that results when an individual B. gracilis plant dies. The faster recovery time of B. gracilis in the model than observed experimentally on large disturbances suggests that processes associated with the recovery of B. gracilis may be scale-dependent.

Debra P. Coffin
Department of Range Science
Colorado State University
Fort Collins, Colorado 80523
Spring, 1988

ACKNOWLEDGEMENTS

I would especially like to thank Dr. William K. Lauenroth for his help and guidance during the course of this project. My educational experience and professional development are in large part a result of my interactions with him.

I would also like to thank the members of my graduate committee for their assistance, and for their faith in my abilities. Drs. Robert Woodmansee, Thomas Kirchner and Edward Redente provided encouragement and support that I greatly appreciated.

A number of people helped to make this project successful, including Barbara Berg, Don Hazlett, Cathy Lee, Dan Milchunas, Gary Richardson, Ray Souther, Liang Yimin, and Greg Zimmerman. I thank them for their generous help in the field and on campus. A special thank you is due Bob Dougherty for his willingness to help me at all times and with all facets of my work, and Osvaldo Sala for our many stimulating discussions.

My deepest appreciation goes to my husband, Paul, for his patience and understanding throughout my time at CSU.

This research was supported by the National Science Foundation, Shortgrass Steppe Long-Term Ecological Research Project (grant number BSR-8114822).

TABLE OF CONTENTS

<u>Chapter</u>	<u>Page</u>
I. INTRODUCTION	1
Literature Cited	6
II. THE EFFECTS OF DISTURBANCE SIZE AND FREQUENCY ON A SHORTGRASS PLANT COMMUNITY	
Introduction	9
Site Description	11
Methods	12
<u>B. gracilis</u> size distributions and cover ..	12
Determination of disturbance sizes and frequency	13
Construction of simulations	15
Results	17
Size distributions and occurrence	17
Effects of disturbances	18
Relative importance of disturbance types ..	20
Discussion	22
Literature Cited	26
III. SMALL-SCALE DISTURBANCES AND SUCCESSIONAL DYNAMICS IN A SHORTGRASS COMMUNITY: INTERACTIONS OF DISTURBANCE CHARACTERISTICS	
Introduction	35
Methods	38
Western harvester ant mounds	38
Small animal burrows	39
Artificial plots	40
Data collection and analysis	40
Results	42
Species composition and disturbance type ..	43
Disturbance type and date	45
Disturbance location, date and size	47
Discussion	50
Literature Cited	57
IV. A GAP DYNAMICS SIMULATION MODEL OF SUCCESSION IN A SEMIARID GRASSLAND	
Introduction	74
Conceptual Model of Gap Dynamics in a Semiarid Grassland	77

Site Description	80
Model Description	80
Establishment of plants	81
Growth of plants	83
Mortality of plants	89
Experimental Simulations	92
Results and Discussion	93
50-year simulations	93
250-year simulations	97
Successional dynamics and <u>B. gracilis</u> seed availability	101
Spatial variability of a simulated landscape	103
Model Analysis	105
Conclusions	106
Literature Cited	108
 V. SUMMARY AND CONCLUSIONS	 135
Literature Cited	141

Appendix

Page

I. SPATIAL DISTRIBUTION OF <u>Bouteloua gracilis</u> ROOTS AND THE EFFECTS OF COMPETITION	
Introduction	143
Methods	144
Results and Discussion	147
Literature Cited	151
 II. SPATIAL AND TEMPORAL VARIATION IN THE SEED BANK OF A SEMIARID GRASSLAND	
Introduction	158
Methods	159
Results	161
Discussion	165
Literature Cited	168
 III. GAP MODEL SENSITIVITY ANALYSIS	
Introduction	176
Sampling Design	177
Statistical Design	177
Results and Discussion	179
Conclusions	181
Literature Cited	182
 IV. GAP MODEL DOCUMENTATION	
Introduction	187
Conceptual Model of Gap Dynamics in a Semiarid Grassland	187
Simulation Model Structure	190
FORTRAN Code Documentation	192
Literature Cited	223

I. INTRODUCTION

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] recovers very slowly after a disturbance or not at all (Riegel 1941, Hyder et al 1971, Briske and Wilson 1977).

The disturbance regime of shortgrass communities includes a number of disturbances operating over a range of spatial and temporal scales. Physical and biological processes may be scale dependent (Delcourt et al 1983), and conclusions reached about the inability of B. gracilis to recolonize large disturbances may not hold for all disturbances, and in particular, small disturbances that occur frequently.

An alternative, scale-oriented conceptualization of shortgrass communities, such as the theory of gap-phase dynamics, may provide information about the apparent contradiction between the results of the large-scale disturbance studies and the continued dominance of B. gracilis in the presence of frequently-occurring

disturbances that reduce populations of B. gracilis. A gap dynamics approach focuses on small, patch-producing disturbances that affect a single individual of the dominant species (Watt 1947). The long-term result of gap dynamics processes is a landscape composed of a 'shifting mosaic' of patches, each undergoing its own successional dynamics through time (Bormann and Likens 1979). This approach has been used extensively in temperate and tropical forests and focuses on the canopy gap produced by the death of an individual tree in the canopy. Experimental studies have been used to evaluate the importance of gap characteristics to successional dynamics and community structure (Denslow 1980, Runkle 1981, Brokaw 1982;1985;1987, White et al 1985), while simulation models have been used to study long-term successional dynamics on gaps (Botkin et al 1972, Shugart and West 1977, Doyle 1981, Shugart 1984).

My general objective was to apply a gap dynamics approach to shortgrass plant communities. An important consideration in applying this approach is the resource space associated with plants, and in particular with individual B. gracilis plants. Belowground resources are of greater relative importance than aboveground resources in semiarid grasslands since the low and variable pattern of precipitation results in soil water being the most frequent control on plant growth and community structure (Noy-Meir 1973, Lauenroth et al 1978). It has been estimated for a shortgrass plant community that belowground net primary

production contributes approximately 85% to total net primary production (Sims and Singh 1978), and basal cover of all plants ranges from 25-40% of which 85-90% is attributed to B. gracilis. Therefore, I hypothesized that the death of a full-size B. gracilis plant results in a gap in the belowground resource space and initiates the successional processes of gap dynamics.

A number of small, patch-producing disturbances affect shortgrass communities, including cattle fecal pats, Western harvester ant mounds [Pogonomyrex occidentalis (Cresson)], and burrows from small animals, such as skunks and badgers. There is typically an inverse relationship between the size and frequency of occurrence of a disturbance (Pickett and White 1985); therefore, small disturbances that occur frequently may have a large effect on plant communities through time.

Objective 1. My first objective was to evaluate the effects of small, patch-producing disturbances on B. gracilis-dominated plant communities. I developed a spatially-explicit simulation model that considered the effects on the cover and abundance of B. gracilis populations of three types of disturbances (cattle fecal pats, western harvester ant mounds, and small animal burrows) based on their size and frequency of occurrence. This objective is addressed in Chapter 2.

A number of studies have been conducted to evaluate the successional dynamics on large disturbances (Savage and

Runyon 1937, Judd and Jackson 1939, Costello 1944, Judd 1974, Reichhardt 1982). Because physical and biological processes may be scale-dependent (Delcourt et al 1983), successional dynamics may be different on small disturbed areas than on large disturbances. The characteristics of the disturbance have also been found to influence the recovery of plants (Sousa 1984, Pickett and White 1985).

Objective 2. My second objective was to evaluate the short-term successional dynamics on small disturbances. I used a field study that considered the effects of different types of small-scale disturbances and their associated characteristics on the recovery of plants. Three types of disturbances were studied (western harvester ant mounds, small animal burrows and plots that were produced artificially), on two sites by soil texture (coarse- and fine-textured), of three sizes (50, 100 and 150 cm-diameter), and on four dates (September, 1984; and March, May and July, 1985). This objective is addressed in Chapter 3.

Objective 3. My third objective was to evaluate the long-term successional dynamics on small disturbances and the time required for B. gracilis to recover after a disturbance. I developed a gap dynamics simulation model based on the belowground gap in the resource space that results when an individual B. gracilis plant dies. The same three types of small disturbances discussed in Chapter 2. were incorporated into the model based on their frequencies

of occurrence. This objective is addressed in Chapter 4.

Test of Assumptions

(1) My third objective required an evaluation of the spatial distribution of roots of individual B. gracilis plants, and the differences in the distribution as a result of neighboring plants. This is a test of the assumption in the simulation model that the size of the gaps produced in the belowground resource space upon the death of full-size individual B. gracilis plants is a constant. I tested this assumption with a field study using a radioactive tracer. This is addressed in Appendix I.

(2) Most gap dynamics models developed for forests assume the establishment of plants is a stochastic event. Seeds are available for all species every year and filters are used to determine the species that are eligible to have seedlings become established each year depending on the environmental conditions (Shugart 1984). Few studies have been conducted on the storage of seeds in shortgrass communities (Weaver and Mueller 1942, Lippert and Hopkins 1950), and the spatial and temporal variability in the seed bank has not been evaluated. Therefore, I tested the assumption that an abundance of seeds are stored in the soil and available to recolonize disturbances that vary in time and space. The greenhouse study that I used to test this assumption is addressed in Appendix II.

LITERATURE CITED

- Bormann, F. H., and G. E. Likens. 1979. Pattern and process in a forested ecosystem. Springer-Verlag. New York.
- Botkin, D. B., J. F. Janak, and J. R. Wallis. 1972. Some ecological consequences of a computer model of forest growth. *Journal of Ecology* 60:849-873.
- Briske, D. D., and A. M. Wilson. 1977. Temperature effects on adventitious root development in blue grama seedlings. *Journal of Range Management* 30:276-280.
- Brokaw, N. V. L. 1982. The definition of treefall gap and its effect on measures of forest dynamics. *Biotropica* 14:158-160.
- Brokaw, N. V. L. 1985. Gap-phase regeneration in a tropical forest. *Ecology* 66:682-687.
- Brokaw, N. V. L. 1987. Gap-phase regeneration of three pioneer tree species in a tropical forest. *Journal of Ecology* 75:9-19.
- Costello, D. F. 1944. Natural revegetation of abandoned plowed land in the mixed prairie association of northeastern Colorado. *Ecology* 25:312-326.
- Delcourt, H. R., P. A. Delcourt, and T. Webb III. 1983. Dynamic plant ecology: The spectrum of vegetational change in space and time. *Quaternary Science Reviews* 1:153-175.
- Denslow, J. S. 1980. Gap partitioning among tropical rainforest trees. *Biotropica* 12 (Supplement):47-55.
- Doyle, T. W. 1981. The role of disturbance in the gap dynamics of a montane rain forest: An application of a tropical forest succession model. Pages 56-76 in D. C. West, H. H. Shugart, and D.B. Botkin, editors. *Forest succession: Concepts and applications*. Springer-Verlag. New York.

- Hyder, D. N., A. C. Everson, and R. E. Bement. 1971. Seedling morphology and seeding failures with blue grama. *Journal of Range Management* 24:287-292.
- Judd, I. B. 1974. Plant succession of old fields in the Dust Bowl. *Southwestern Naturalist* 19:227-239.
- Judd, I. B., and M. L. Jackson. 1939. Natural succession of vegetation on abandoned farmland in the Rosebud soil area of western Nebraska. *American Society of Agronomy Journal* 39:541-547.
- Lauenroth, W. K., J. L. Dodd, and P. L. Sims. 1978. The effects of water- and nitrogen-induced stresses on plant community structure in a semiarid grassland. *Oecologia (Berlin)* 36:211-222.
- Lippert, R. D., and H. H. Hopkins. 1950. Study of viable seeds in various habitats in Mixed Prairie. *Transactions of the Kansas Academy of Sciences* 53:355-364.
- McGregor, R. L. 1986. *Flora of the Great Plains*. University Press of Kansas, Lawrence, Kansas.
- Noy-Meir, I. 1973. Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics* 4:25-51.
- Pickett, S. T. A., and P. S. White. 1985. *The ecology of natural disturbances and patch dynamics*. Academic Press, Orlando, Florida.
- Reichhardt, K. L. 1982. Succession of abandoned fields on the shortgrass prairie, northeastern Colorado. *Southwestern Naturalist* 27:299-304.
- Riegel, A. 1941. Life history habits of blue grama. *Kansas Academy of Sciences Transactions* 44:76-83.
- Runkle, J. R. 1981. Gap regeneration in some old-growth forests of the eastern United States. *Ecology* 62:1041-1051.
- Savage, D. A., and H. E. Runyon. 1937. Natural revegetation of abandoned farmland in the central and southern Great Plains. *Fourth International Grassland Congress*. Aberystwyth, Great Britain, Section 1. *Grassland Ecology* 178-182.

- Shugart, H. H., and D. C. West. 1977. Development of an Appalachian deciduous forest succession model and its applications to assessment of the impact of the chestnut blight. *Journal of Environmental Management* 5:161-179.
- Shugart, H. H. 1984. *A theory of forest dynamics*. Springer-Verlag. New York.
- Sims, P. L., and J. S. Singh. 1978. The structure and function of ten western North American grasslands. III. Net primary production, turnover and efficiencies of energy capture and water use. *Journal of Ecology* 66:573-597.
- Sousa, W. P. 1984. The role of disturbances in natural communities. *Annual Review of Ecology and Systematics* 15:353-391.
- Watt, A. S. 1947. Pattern and process in the plant community. *Journal of Ecology* 35:1-22.
- Weaver, J. E., and I. M. Mueller. 1942. Role of seedlings in recovery of Midwestern ranges from drought. *Ecology* 23:275-294.
- White, P. S., M. D. MacKenzie, and R. T. Busing. 1985. Natural disturbance and gap phase dynamics in southern Appalachian spruce-fir forests. *Canadian Journal of Forest Research* 15:233-240.

II. THE EFFECTS OF DISTURBANCE SIZE AND FREQUENCY ON A SHORTGRASS PLANT COMMUNITY

Introduction

The disturbance regime of most plant communities includes a number of kinds of disturbances that collectively operate over a wide range of spatial and temporal scales. The importance of the characteristics of a disturbance to its effects on community structure has been recognized for many different plant communities (Sousa 1984; Pickett and White 1985). Two characteristics of particular importance are size and frequency of occurrence (Denslow 1980; Miller 1982). The relationship between size and frequency is typically inverse. Recent studies in grasslands have suggested the importance of within-community patch-producing disturbances on spatial pattern, and on the persistence of species able to utilize small, relatively short-lived patches (Platt 1975; King 1977; Hobbs and Mooney 1985; Loucks et al, 1985). The objective of this study was to evaluate the role of patch-producing processes on the dynamics of a semiarid grassland in Colorado.

The shortgrass steppe in northcentral Colorado is dominated by the perennial grass, blue grama (Bouteloua gracilis (H.B.K.) Lag. ex Griffiths. (Nomenclature follows

McGregor (1986)). Bouteloua gracilis accounts for 75-90% of net primary production on most sites, and it is the processes that reduce B. gracilis cover or abundance that have the largest effects on community structure. Therefore, I chose to focus on disturbances that reduce either the number of tillers of B. gracilis (basal cover) or the density of B. gracilis plants (number). Recolonization by B. gracilis is a relatively slow process that differs depending on the spatial extent of the patch. Disturbances smaller than an individual plant reduce B. gracilis cover by killing tillers. Recolonization is primarily by tiller replacement from the damaged plant. As patch size increases, and entire B. gracilis plants are killed, recolonization is through seedling establishment.

Disturbance types operating over a wide range of spatial scales influence the biomass of this community. In this study, I examined three types of disturbances: cattle fecal pats, western harvester ant mounds [Pogonomyrex occidentalis (Cresson)], and burrows from small animals (including skunks, badgers and pocket gophers). Each disturbance type has an associated size distribution and frequency of occurrence that can be used to evaluate its effects on a B. gracilis population; both size and frequency may vary as a result of different topographic positions and grazing regimes. Field estimates were combined with information available in the literature to determine the size and frequency distributions of these three disturbance

types, and the size distributions and cover of B. gracilis plants. I then used simulation modeling to calculate a set of summary variables (plant cover killed, number of plants killed, and turnover rates) to compare the impact of these disturbances on B. gracilis.

Site Description

All data were collected at the Central Plains Experimental Range (CPER) located in northcentral Colorado approximately 60 km northeast of Fort Collins (40° 49' N latitude, 107° 47' W longitude). 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 flat uplands and lowlands connected by gentle slopes. The vegetation is typical of the shortgrass steppe. Basal cover of all plants ranges from 25-40% of which 85-90% is B. gracilis. A number of grasses, succulents, half-shrubs, and forbs account for the remainder. Moderate grazing by cattle occurs throughout the site. Light (1.4 ha/yearling-month), moderate (1.1 ha/yearling-month), and heavy (0.7 ha/yearling-month) grazed pastures have been maintained since 1939. These average stocking rates represent an average of 20, 40, and 60% removal, respectively, of the standing crop over a 6-month period during the growing season (Klippel and Costello 1960).

Methods

The effects of disturbance size and frequency on B. gracilis-dominated plots were evaluated using a spatially-explicit simulation model. Plots were simulated for each combination of three topographic positions (uplands, slopes and lowlands) and three grazing intensities (light, moderate and heavy). Although the specific disturbance agents associated with the three disturbance types differ, each produce a patch in which B. gracilis tillers are killed. The low stature of B. gracilis plants guarantees that the portion of the plant beneath a fecal pat is unlikely to survive. Western harvester ants remove all of the vegetation from their mound while small burrowing animals produce a mound of soil at the surface that covers and kills the vegetation.

B. gracilis size distributions and cover

The sizes of individual B. gracilis plants were measured in five 4 m² quadrats randomly located in each of the three topographic positions in a heavily grazed pasture. An individual B. gracilis plant was defined as all tillers currently connected by a crown. Topographic position was expected to have a greater effect on plant size than grazing regime since cattle behavior patterns within a grazing treatment, and hence the potential effects of grazing on plant size, have been found to be strongly related to topographic position (Senft et al 1985). Therefore, I assumed that the size distributions of B. gracilis in each

topographic position were similar in the lightly and moderately grazed pastures to those in the same topographic position in the heavily grazed pasture. The average B. gracilis cover for each topographic position in the heavily grazed pasture was calculated by averaging the cover values of the field quadrats. Cover values were calculated for the lightly and moderately grazed pastures from comparable data from Gill (1985) for similar sites in the same three pastures.

Determination of disturbance sizes and frequencies

Fecal pats were measured in randomly located quadrats in the heavily grazed pasture from the same sites in which plant size was measured. I assumed that approximately 300 pats would be necessary to adequately describe each size distribution; therefore, the number of 400 m² quadrats required depended on the density of pats in each topographic position. I assumed size distributions were similar in a particular topographic position in all three grazing treatments because of the effect of topographic position on cattle behavior (Senft et al 1985). The frequencies of fecal pat deposition were estimated in each topographic position under each grazing regime using average stocking rates (Klippel and Costello 1960) and data on excretion rates, behavior patterns and time spent in each topographic position from Schwartz (1977) and Senft (1983). I assumed cattle behavior patterns and excretion rates were comparable across grazing treatments.

The size distribution of western harvester ant mounds was obtained by measuring all full-size mounds in a 2.5 ha lightly grazed upland. Size distributions were assumed to be similar for all topographic positions and grazing treatments since a previous study found average mound sizes to be similar for the three grazing intensities and pooled across topographic positions (Rogers and Lavigne, 1974). The total number of mounds at different stages of development in the lightly grazed upland pasture was used to estimate the frequency of occurrence. Mound construction involves three stages in which the size of the mound increases through time until the full-size stage is reached (Cole 1932). An analysis based on the number of mounds in each stage and the approximate length of time a mound will remain in each stage was used to estimate the number of new mounds, initiated each year, that would become full-size mounds. Relative frequencies of occurrence for the moderately and heavily grazed pastures were estimated using density data for these pastures from Rogers and Lavigne (1974) by assuming stable mound densities through time. The frequencies of occurrence of ant mounds were assumed to be similar for each topographic position within each grazing treatment because the density data from Rogers and Lavigne (1974) was obtained by pooling across topographic positions.

Due to the relatively infrequent occurrence of small animal burrows, the size distribution was obtained by

measuring burrows in the three grazing treatment pastures and pooling across treatments and topographic positions. The number of burrows produced over a two year period on a 2.5 ha moderately grazed upland was used to estimate the frequency of occurrence of burrows. Field observations indicated that soil texture, not grazing treatment or topographic position, may be the most important factor determining the location of a burrow.

Construction of simulations

Fifteen replicate plots were simulated for each of the nine grazing regime-topographic position combinations. Each 9 m² plot was simulated by a 101 x 101 point grid (a distance of 3 cm between points). Bouteloua gracilis plants were randomly selected from one of the field-estimated size-class distributions. Seven size classes of rectangular plants from 18-648 cm² were used in the simulation. The use of size classes of plants resulted in the model being relatively insensitive to the assumption of similar plant size distributions within a given topographic position. Each plant was assigned to a set of contiguous points. For example, a 648 cm² plant consisted of a set of 7 x 13 points, or an 18 x 36 cm rectangle. Plants were randomly positioned in the simulated plot with two restrictions: the entire plant must be contained within the plot, and the plant must not overlap other plants. Plants were added to each plot until a critical cover value was reached. Critical cover values were drawn from normal distributions with the

means and standard deviations estimated as described above.

Each disturbance was represented by a square of contiguous points whose size was randomly selected from the sizes of disturbances of that type measured in the field. Although only one ant mound or animal burrow constituted an event, more than one fecal pat was possible for each excretion event. Each disturbance event was positioned randomly within the plot, with the restriction that overlap was not allowed between disturbance types or events except for the potential overlap of pats within one event.

The amount of each B. gracilis plant covered by each disturbance event was determined. The number of plants killed was estimated by assuming that 100% of the plant must be hit for the plant to be killed; an indirect hit merely reduced its size. This assumption is supported by field observations of fecal pats of a variety of ages. The cover was reduced by the portion of the plant under the disturbance. The total amount of cover lost and number of plants killed in the plot were calculated. The average amount of disturbed area and the average number of plants killed were calculated after 100 events for each disturbance type on each plot. The 100 events represent simulations ranging from 400-6700 years (fecal pats), 69000-716800 years (ant mounds), and 222200 years (burrows). The values were then averaged over the fifteen plots for each of the nine locations.

Relative turnover rates (in %/year) were calculated as:

the percentage basal cover affected per year, and the percentage of the number of plants killed per year. Turnover rate is therefore very closely related to the relative area affected by disturbances (i.e., the relative amount of disturbed area). These two variables will not take identical values due to the variation introduced by the simulation model. The relative area affected by disturbances will also differ from the turnover rate of plants (but not the turnover rate of cover) for another reason. For a given area affected by disturbances, the smaller the size of each disturbance event, the fewer plants that will be killed: as disturbance size decreases, the perimeter length to surface area ratio increases resulting in more plants that are only partially covered, and therefore will survive. At one extreme, some fecal pats may cover no plants completely, and result in no deaths.

Results

Size distributions and occurrence

Size distributions of B. gracilis plants were similar for the three topographic positions (Fig. 2.1). Average plant sizes were 134 cm² (uplands, n=360), 118 cm² (slopes, n=288) and 142 cm² (lowlands, n=344). The highest cover value for each grazing treatment was found in the lowlands, with no differences between treatments, while the lowest value occurred in the uplands under the heavy grazing regime (Table 2.1).

Average sizes of fecal pats were 134 cm² (uplands, n=329), 167 cm² (slopes, n=295) and 190 cm² (lowlands, n=432), overlapping the size range of B. gracilis plants (Fig. 2.1). Within each grazing treatment, cattle tend to spend more time in lowlands than in slopes or uplands (Schwartz 1977; Senft 1983) which is reflected in the estimated numbers of fecal pats at each topographic position within a grazing treatment, as well as in differences among grazing treatments (Table 2.1).

Ant mounds and animal burrows were always larger than B. gracilis plants. The sizes of mature ant mounds were approximately normally distributed (mean=1.4 m², sd=0.28 m², n=62). The frequency of mound occurrence varies with grazing treatment (Rogers and Lavigne 1974): 0.16 (heavy), 1.5 (light), and 1.6 mounds·ha⁻¹·y⁻¹ (moderate). The sizes of animal burrows were approximately uniformly distributed between 1.0 and 2.0 m² (n=10) with a frequency of 0.5 burrows·ha⁻¹·y⁻¹.

Effects of disturbances

The relative importance of disturbance type to turnover rates was related to disturbance size and topographic position. The smallest disturbance type (fecal pats) affected the largest area each year in most sites because fecal pats were so abundant. However, the plant turnover rates for a given amount of area affected were always less for fecal pats than mounds or burrows because fecal pats

were smaller and so were less likely to cover plants entirely (see Methods).

The effects of fecal pats and ant mounds on the turnover rate of B. gracilis populations was primarily a function of their frequency of occurrence, since the measured size distributions of fecal pats were similar across topographic positions and were assumed to be similar across grazing treatments, and ant mounds were assumed to have a constant size distribution (Figs. 2.2 and 2.3). Estimated reductions in plant cover ranged from a low of $0.0245 \text{ m}^2 \cdot \text{ha}^{-1} \cdot \text{y}^{-1}$ by ant mounds under heavy grazing to a high of $7.2 \text{ m}^2 \cdot \text{ha}^{-1} \cdot \text{y}^{-1}$ by fecal pats in heavily grazed lowlands. The corresponding turnover rates were 0.00002 to 0.00205%/y. The estimated average number of plants killed per year ranged from 1.6 (ant mounds) to 119.4 (fecal pats), resulting in turnover rates for plants of 0.00002 to 0.00047%/y. Animal burrows were assumed to have a constant frequency of occurrence and a constant size; their effect therefore varied only with plant cover. On the average, animal burrows reduced plant cover by $0.20 \text{ m}^2 \cdot \text{ha}^{-1} \cdot \text{y}^{-1}$ and killed $13.5 \text{ plants} \cdot \text{ha}^{-1} \cdot \text{y}^{-1}$. Average turnover rates due to animal burrows were 0.00008%/y (cover) and 0.00006%/y (number).

The number of plants killed by each disturbance type is a conservative estimate based on the assumption that the entire plant must be hit for the plant to be killed. The level of coverage required to kill a B. gracilis plant most

likely depends on the environmental conditions following the disturbance since a given reduction in size probably causes a larger increase in the probability of death when conditions are adverse. Incorporating the death of partially disturbed plants would increase the estimated turnover rates, especially for fecal pats. Most of the time, pats only partially covered B. gracilis plants while ant mounds and animal burrows completely covered most of the plants they hit.

The turnover rates for the three disturbances were combined to estimate the total turnover rate for the plot (Fig. 2.4). The average estimated turnover rates for plant cover ranged from 0.00028 to 0.00213%/y; turnover rates for number of plants were 0.00011 to 0.00051%/y. Turnover rates would decrease if disturbances were allowed to overlap within a simulated plot, although the effect of overlap is not expected to change the results significantly.

Relative importance of disturbance types

As described above, the three types of disturbances differed in size distributions and in frequency, and in some cases differences in these characteristics were found or estimated among topographic positions and among grazing treatments for a particular type of disturbance. The effects of these differences are summarized by the estimated turnover rates (Fig. 2.5). In all but upland sites, fecal pats were responsible for the largest part of the total

turnover of cover, and a substantial part of the turnover of individual plants.

Topographic position was more important than grazing intensity in determining the effects of these three types of disturbances (Fig. 2.5). The rates of plant cover turnover were higher on lowlands and slopes than on uplands. The heavily grazed pasture had the lowest plant turnover rates in the uplands; grazing regime did not have a large effect elsewhere. The relatively small turnover rates of the heavily grazed uplands is the result of the low occurrences of ant mounds in the heavily grazed pasture and of fecal pats in upland positions.

The importance of topographic position rather than grazing treatment on the contribution of fecal pats to the total turnover rates was a result of the different frequencies of occurrence of pats among topographic positions within a grazing treatment rather than the effects of pat size; the measured size distributions were similar across topographic positions and were assumed to be similar across grazing treatments. The greater contribution by ant mounds and animal burrows in uplands relative to other locations is an indirect result of the relatively infrequent occurrence of fecal pats in upland sites; the size distributions of mounds and burrows were assumed to be constant while the frequencies of occurrence of mounds and burrows were assumed to be similar for all topographic positions within a grazing treatment.

Discussion

An important characteristic for a disturbance in the shortgrass steppe is its size in relation to the average size of a B. gracilis plant. Disturbances equal to or larger than the average size of a B. gracilis plant will have a larger impact per disturbance than smaller disturbances because they will kill plants as well as reduce cover. Furthermore, bigger disturbances have relatively less perimeter length compared to surface area, and will kill more plants for the same total area affected (see Methods). Therefore, the effects of a given set of disturbances on cover and on plant numbers are not equivalent (Fig. 2.5).

The total impact of a disturbance depends upon its frequency as well as its size, and frequency tends to be inversely related to size. The effect of these small-scale disturbances on the cover and abundance of B. gracilis plants was primarily a function of their frequency of occurrence. Size and frequency together determine the total area affected by disturbances.

Disturbance size relative to the size of B. gracilis plants distinguished two classes of disturbances: fecal pats were similar in size to B. gracilis plants; ant mounds and animal burrows were always larger than B. gracilis plants. Neither class of disturbance was consistently more important than the other (Fig. 2.5). Topographic position was more important than grazing intensity in determining relative

turnover rates and the relative effects of the different disturbances on B. gracilis cover and abundance.

Factors not included in this study may be important in determining the frequency and effects of ant mounds and animal burrows. Localized concentrations of mounds and burrows are known to occur, most likely as a result of local environmental conditions related to soil texture. A field study conducted at the CPER in several locations of high pocket gopher densities reported a much larger area was affected by the mounds (6%/y from Grant et al. 1980) than was determined from this study (0.0084%/y). The effects on the vegetation would be more pronounced in these areas resulting in larger turnover rates than those determined from my conservative estimates of numbers of burrows.

Most of the information about responses to and recovery from disturbances in the shortgrass steppe region of North America is based on large disturbances, such as abandoned agricultural fields (Savage and Runyon 1937, Judd and Jackson 1939, Costello 1944, Judd 1974, Reichhardt 1982). These studies suggest that reestablishment of B. gracilis occurs very slowly after a disturbance or not at all (Riegel 1941, Hyder et al 1971, Briske and Wilson 1977), and that a large-scale B. gracilis establishment event has not occurred in the past 50 years (Reichhardt 1982).

It has therefore been suggested that B. gracilis may have become established under a previous climatic regime in which environmental conditions frequently favored the

germination and establishment of seedlings. Alternatively, it has been hypothesized that infrequent, large-scale B. gracilis establishment events occur with a sufficiently high frequency to enable the population to maintain its dominance through time. Studies have indicated that a restrictive set of environmental conditions based on soil water and temperature must be present for B. gracilis seedling germination and establishment (Wilson and Briske 1979; Briske and Wilson 1977; 1978). Under these hypotheses, B. gracilis dominance must be maintained by frequencies of disturbance that are very low.

If either of the above hypotheses were accurate, B. gracilis cover should decrease each year as the effects of disturbances accumulate. In the first case the decrease in B. gracilis cover would be uninterrupted and in the latter case B. gracilis cover would increase only after a rare establishment event. In addition, the effects of disturbances on the B. gracilis population should be dependent on disturbance rate. For example, in lowland sites the loss of cover should be faster where stocking rates are higher, since disturbance rates are higher there (Fig. 2.5). Calculations of the area disturbed by the three small disturbances included in this study (fecal pats, ant mounds, and animal burrows) indicate that the basal cover of B. gracilis should have declined by 3% during the past 48 years in lowlands under heavy grazing. However, recent data suggest that basal cover is significantly ($p < 0.05$) higher in

grazed swales than on adjacent ungrazed swales, although ungrazed swales receive no fecal pats (the major form of disturbance in grazed swales). The average difference between grazed and ungrazed swales was 10% (Milchunas et al 1988). It is unlikely that tillering alone could account for the observed difference in cover. Therefore, these results suggest that the recolonization potential of B. gracilis may differ for different sizes of disturbances. Although large-scale establishment events may be necessary for the return of B. gracilis after large, infrequent disturbances, B. gracilis survival and continued dominance is related to its ability to revegetate small, frequently occurring disturbances.

Watt (1947) suggested that the removal of a mature individual of the dominant species from a plant community initiated successional processes that he collectively called gap-phase dynamics. If these processes operate in shortgrass plant communities, the removal of an entire B. gracilis plant will result in a gap in the resource space and initiate gap-phase dynamics. Patch-producing disturbances that are always larger than B. gracilis plants tend to occur less frequently than disturbances comparable in size to B. gracilis plants, although they may have a longer lasting effect because they always require the establishment of new B. gracilis individuals.

LITERATURE CITED

- Briske, D. D., and A. M. Wilson. 1977. Temperature effects on adventitious root development in blue grama seedlings. *Journal of Range Management* 30:276-280.
- Briske, D. D., and A. M. Wilson. 1978. Moisture and temperature requirements for adventitious root development in blue grama seedlings. *Journal of Range Management* 31:174-178.
- Cole, A. C., Jr. 1932. The rebuilding of mounds of the ant, *Pogonomyrex occidentalis* Cress. *Ohio Journal of Science* 32:245-246.
- Costello, D. F. 1944. Natural revegetation of abandoned plowed land in the mixed prairie association of northeastern Colorado. *Ecology* 25:312-326.
- Denslow, J. S. 1980. Patterns of plant species diversity during succession under different disturbance regimes. *Oecologia (Berlin)* 46:18-21.
- Gill, J. L. 1985. The effect of grazing intensity on plant cover and diversity on a shortgrass steppe. M. S. Thesis. Colorado State University, Fort Collins, Colorado, USA.
- Grant, W. E., N. R. French, and L. J. Folse, Jr. 1980. Effects of pocket gopher mounds on plant production in shortgrass prairie ecosystems. *Southwestern Naturalist* 25:215-224.
- Hobbs, R. J., and H. A. Mooney. 1985. Community and population dynamics of serpentine grassland annuals in relation to gopher disturbance. *Oecologia (Berlin)* 67:342-351.
- Hyder, D. N., A. C. Everson, and R. E. Bement. 1971. Seedling morphology and seeding failures with blue grama. *Journal of Range Management* 24:287-292.
- Judd, I. B. 1974. Plant succession of old fields in the Dust Bowl. *Southwestern Naturalist* 19:227-239.

- Judd, I. B. and M. L. Jackson. 1939. Natural succession of vegetation on abandoned farmland in the Rosebud soil area of western Nebraska. *American Society of Agronomy Journal* 39:541-547.
- King, T. J. 1977. The plant ecology of ant-hills in calcareous grasslands. I. Patterns of species in relation to ant-hills in southern England. *Journal of Ecology* 65:235-256.
- Klipple, G. E., and D. F. Costello. 1960. Vegetation and cattle responses to different intensities of grazing on short-grass ranges on the Central Great Plains. United States Department of Agriculture-Agricultural Research Service Technical Bulletin 1216.
- Loucks, O. L., M. L. Plumb-Mentjes, and D. Rogers. 1985. Gap processes and large-scale disturbances in sand prairies. Pages 71-83 in S. T. A. Pickett and P. S. White, editors. *The ecology of natural disturbance and patch dynamics*. Academic Press, Orlando, Florida, USA.
- McGregor, R. L. 1986. *Flora of the Great Plains*. University Press of Kansas, Lawrence, Kansas.
- Milchunas, D. G., W. K. Lauenroth, P. L. Chapman, and M. K. Kazempour. 1988. Plant communities in relation to grazing, topography, and precipitation in a semiarid grassland. *Ecology* (submitted).
- Miller, T. E. 1982. Community diversity and interactions between the size and frequency of disturbance. *American Naturalist* 120:533-536.
- Pickett, S. T. A., and P. S. White. 1985. *The ecology of natural disturbance and patch dynamics*. Academic Press, Orlando, Florida, USA.
- Platt, W. J. 1975. The colonization and formation of equilibrium plant species associations on badger disturbances in a tall-grass prairie. *Ecological Monographs* 45:285-305.
- Reichhardt, K. L. 1982. Succession of abandoned fields on the shortgrass prairie, northeastern Colorado. *Southwestern Naturalist* 27:299-304.
- Riegel, A. 1941. Life history habits of blue grama. *Kansas Academy of Sciences Transactions* 44:76-83.

- Rogers, L. E., and R. J. Lavigne. 1974. Environmental effects of western harvester ants on the shortgrass plains ecosystem. *Environmental Entomology* 3:994-997.
- Savage, D. A., and H. E. Runyon. 1937. Natural revegetation of abandoned farmland in the central and southern Great Plains. Fourth International Grassland Congress. Aberystwyth, Great Britain, Section 1. *Grassland Ecology* 178-182.
- Schwartz, C. C. 1977. Pronghorn grazing strategies on the shortgrass prairie, Colorado. Dissertation. Colorado State University, Fort Collins, Colorado, USA.
- Senft, R.L. 1983. The redistribution of nitrogen by cattle. Dissertation. Colorado State University, Fort Collins, Colorado, USA.
- Senft, R. L., L. R. Rittenhouse, and R. G. Woodmansee. 1985. Factors influencing patterns of cattle grazing behavior on shortgrass steppe. *Journal of Range Management* 38:82-87.
- Sousa, W. P. 1984. The role of disturbance in natural communities. *Annual Review of Ecology and Systematics* 15:353-391.
- Watt, A. S. 1947. Pattern and process in the plant community. *Journal of Ecology* 35:1-22.
- Wilson, A. M., and D. D. Briske. 1979. Seminal and adventitious root growth of blue grama seedlings on the Central Plains. *Journal of Range Management* 32:205-213.

Table 2.1. Average percent cover of B. gracilis and estimated frequencies of occurrence of fecal pats for three topographic positions and three grazing intensities.

GRAZING INTENSITY	TOPOGRAPHIC POSITION		
	Uplands	Slopes	Lowlands
---Average <u>B. gracilis</u> basal cover---			
(percent)			
light	27	23	30
moderate	27	23	34
heavy	19	23	31
---Estimated fecal pat deposition rate---			
(pats·ha·y ⁻¹)			
light	67	284	569
moderate	84	360	724
heavy	133	567	1138

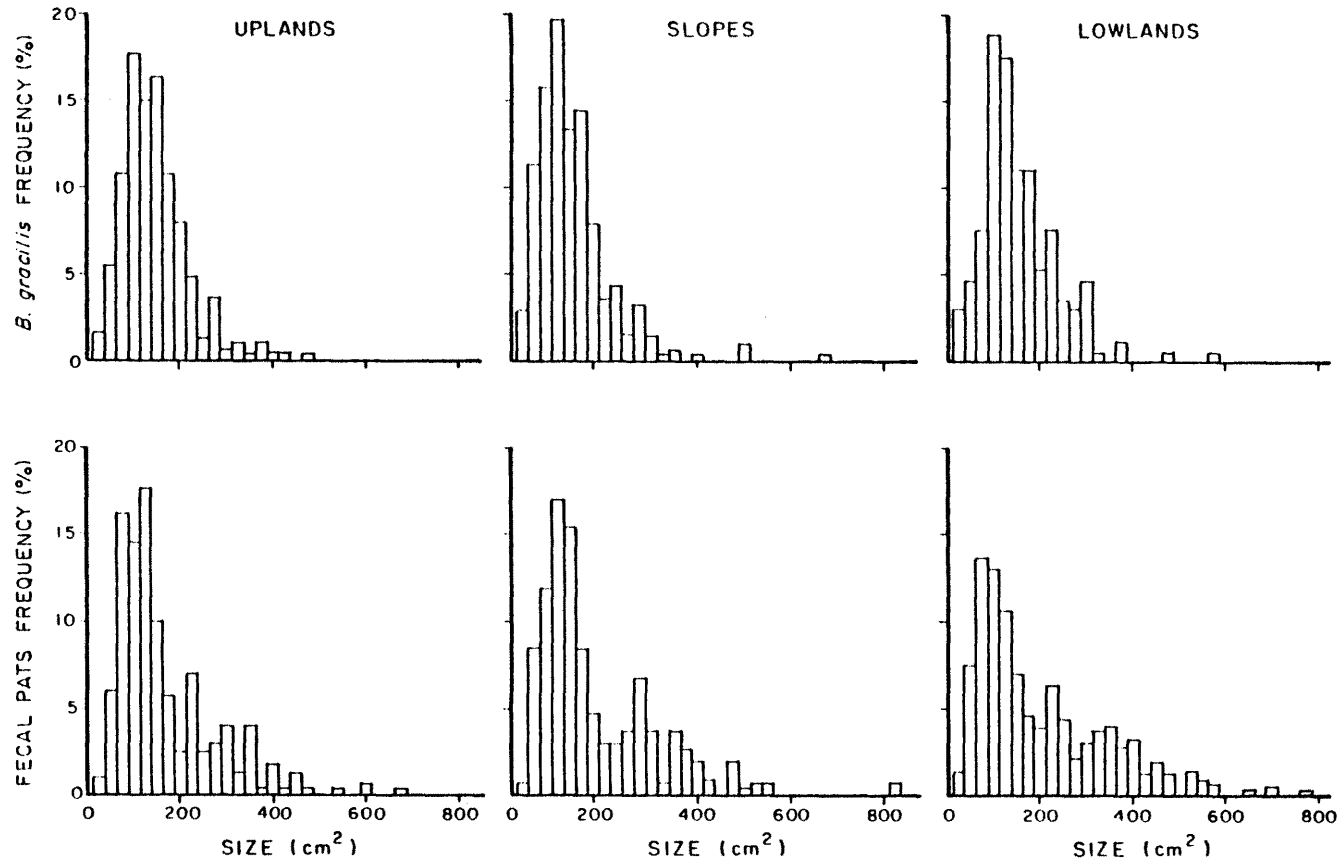


Fig. 2.1. Size distributions for *B. gracilis* and fecal pats for uplands, slopes and lowlands in a heavily grazed pasture.

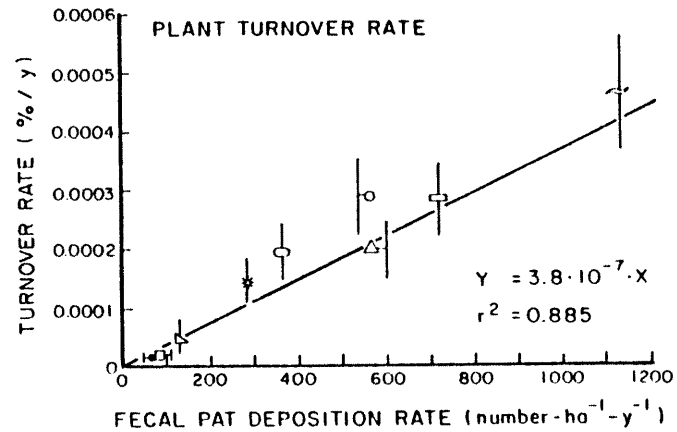
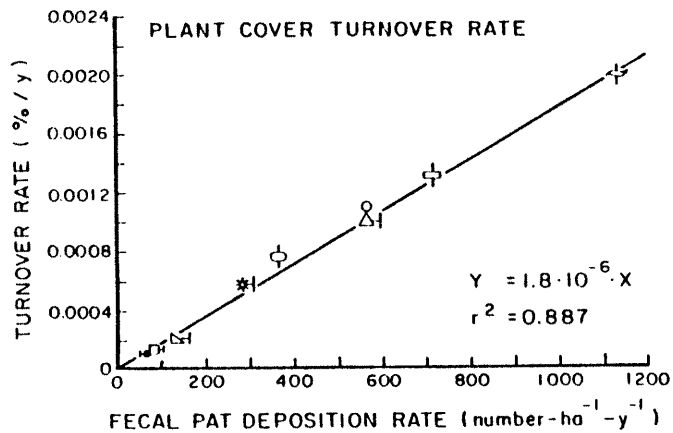
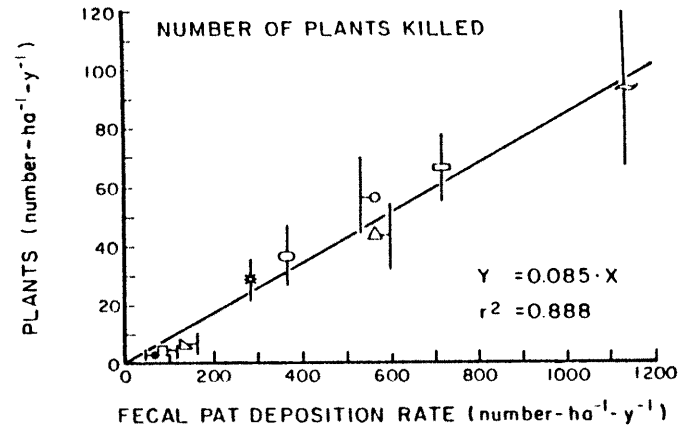
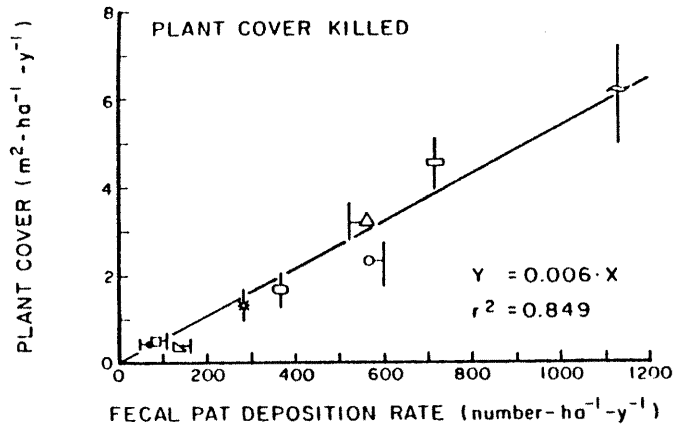


Fig. 2.2. Amount of basal cover and number of *B. gracilis* killed per year as a function of fecal pat deposition rate with corresponding turnover rates. Symbols represent the average value of the fifteen replicate plots and the associated line represents the range in values. (Location by grazing intensity and topographic position: heavy- \sim lowlands, \circ slopes, \square uplands; moderate- \square lowlands, \circ slopes, \square uplands; light- Δ lowlands, \ast slopes, \bullet uplands). Regressions are based on 135 points (15 replicates for each of the 9 grazing intensity-topographic positions combinations).

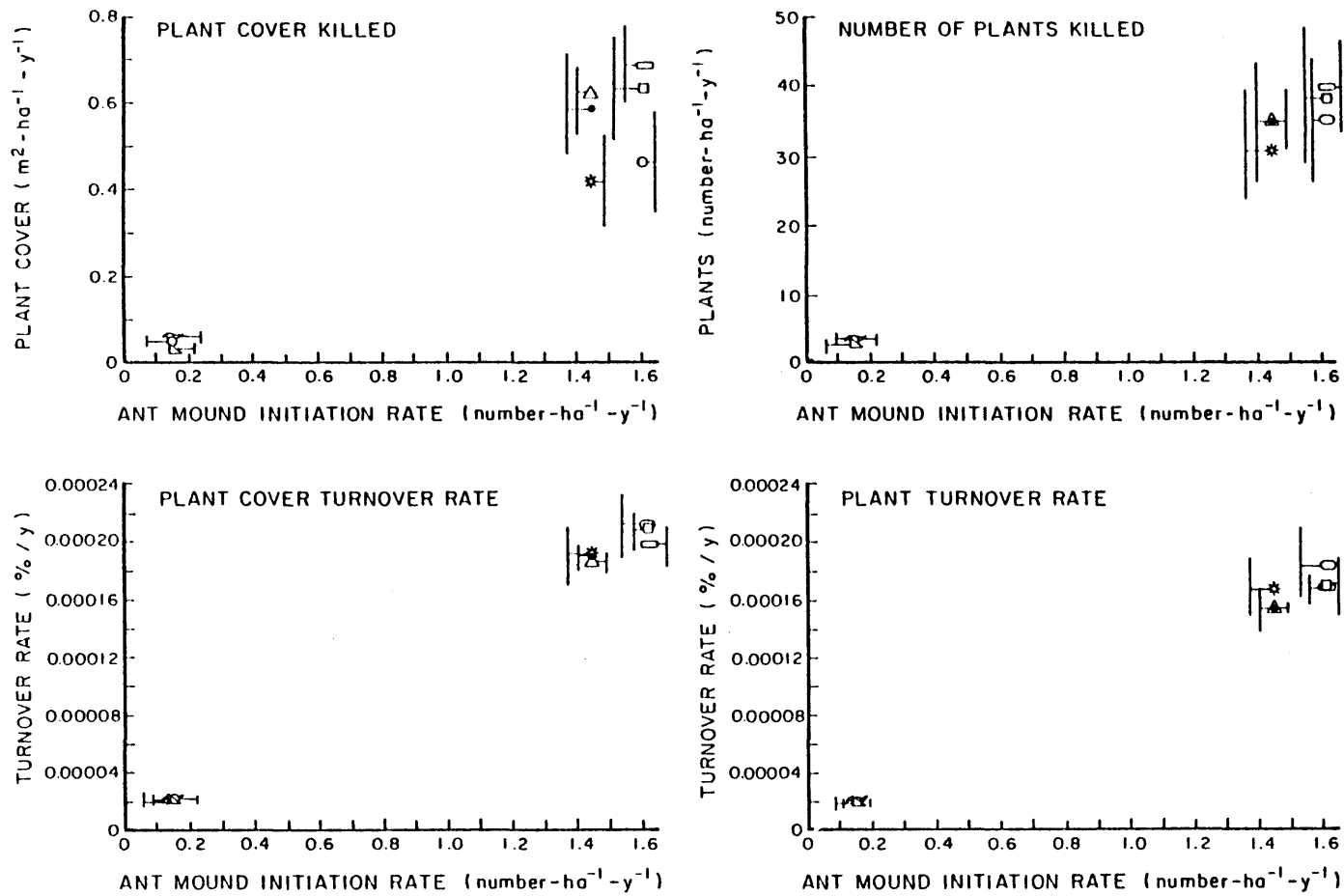


Fig. 2.3. Amount of basal cover and number of *B. gracilis* plants killed per year as a function of the rate of initiation of western harvester ant mounds with corresponding turnover rates. Symbols as in Fig. 2.2.

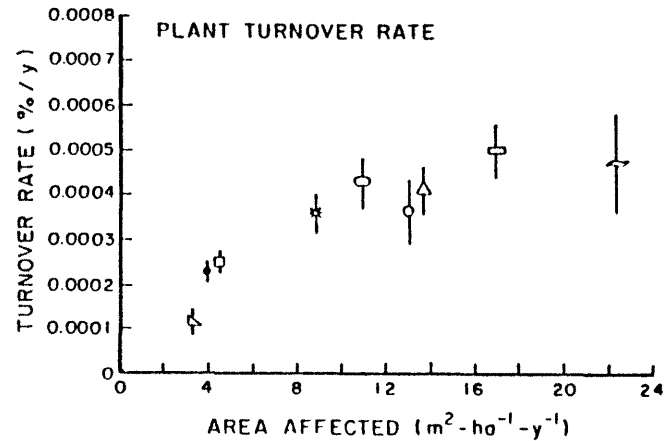
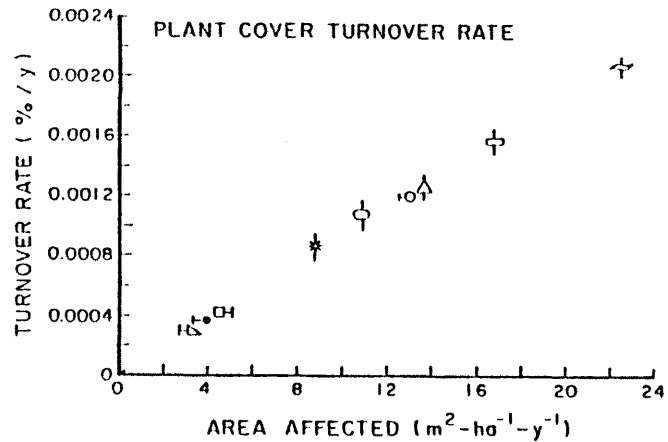
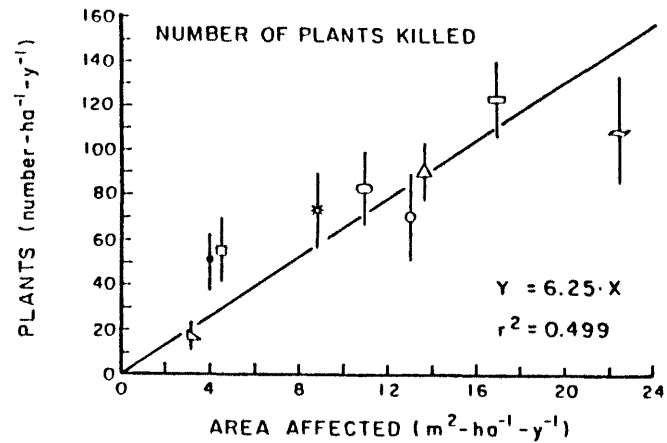
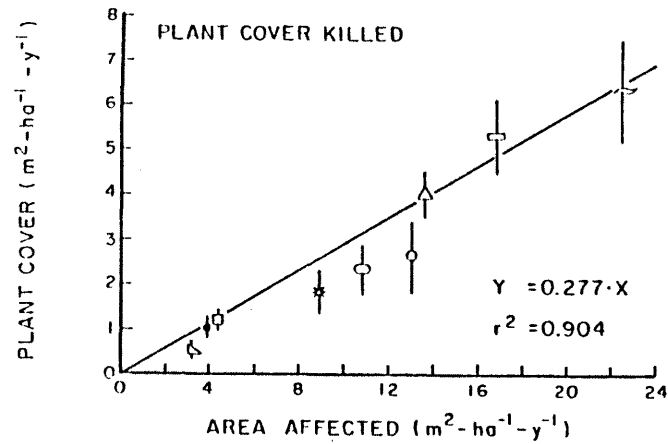


Fig. 2.4. Amount of basal cover and number of *B. gracilis* plants killed per year by fecal pats, ant mounds and animal burrows combined as a function of the total area affected per year with corresponding turnover rates. Symbols and regressions as in Fig. 2.2.

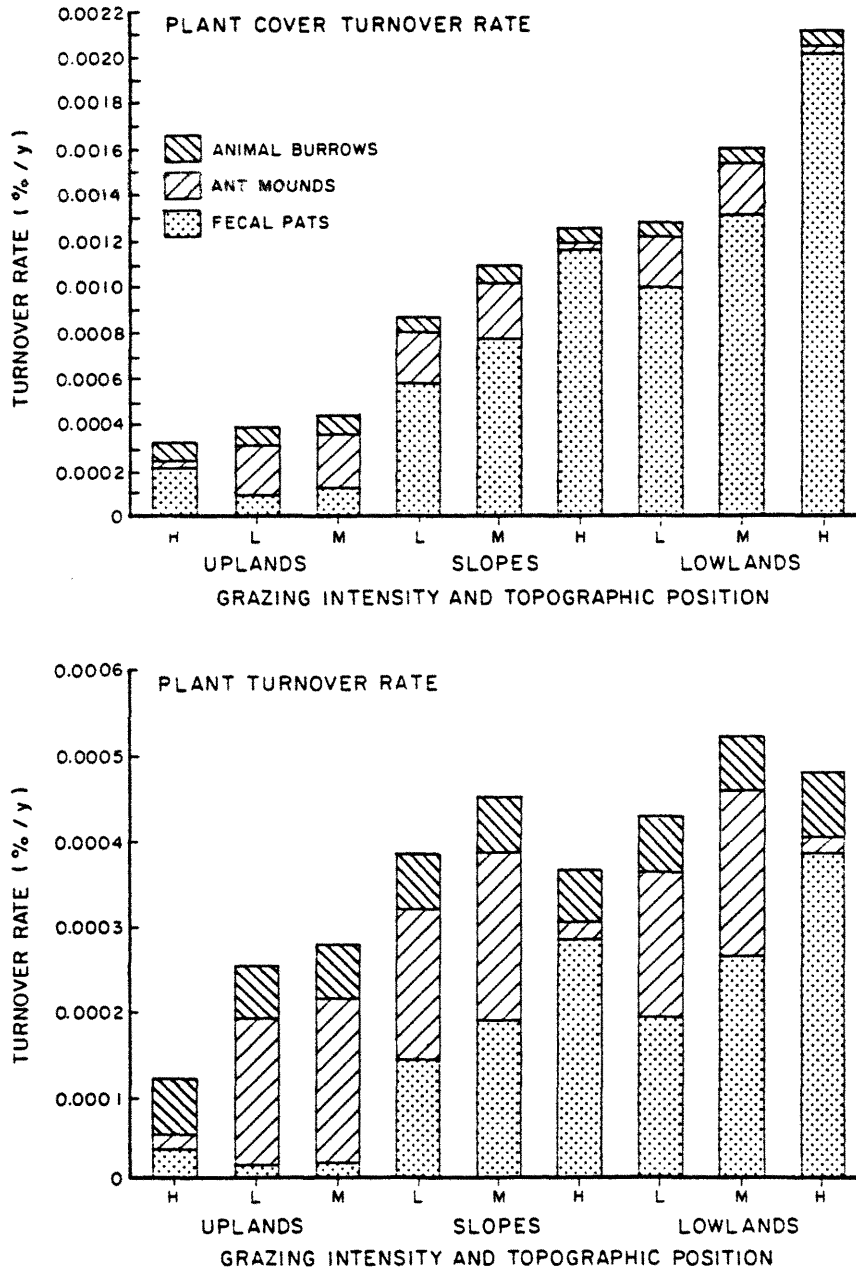


Fig. 2.5. Average contribution to turnover rates of basal cover and number of *B. gracilis* plants by each disturbance type for nine locations by grazing intensity and topographic position. (Grazing intensity: L=light, M=moderate, H=heavy)

III. SMALL-SCALE DISTURBANCES AND SUCCESSIONAL DYNAMICS
IN A SHORTGRASS PLANT COMMUNITY: INTERACTIONS OF
DISTURBANCE CHARACTERISTICS

Introduction

The disturbance regime of a plant community is composed of a number of disturbance types each with its associated characteristics (Pickett and White 1985). The rate and pattern of reestablishment of plants following a disturbance is dependent on the life history characteristics of plants available to enter the disturbed site and the characteristics of the site (Sousa 1984). Most studies in grasslands have focused on the independent effects of different disturbance characteristics, including size (Davis and Cantlon 1969), seasonality (Perozzi and Bazzaz 1978), and type, such as ant mounds (King 1977), small burrowing animals (Platt 1975; Hobbs and Mooney 1985), drought (Albertson and Weaver 1944), and comparisons of several types (Collins and Barber 1985; Belsky 1987; Milchunas et al 1988).

Interactions among disturbance characteristics are also important (Collins and Uno 1983; Collins 1987). However, the nonuniformity of natural disturbances in characteristics such as size and seasonality causes difficulties in

evaluating the separate effects of interacting disturbance characteristics. Several researchers have used manually produced plots to control for the heterogeneous characteristics commonly found associated with natural disturbances (Rapp and Rabinowitz 1985; Belsky 1986), but the simulated disturbances may not be representative of all conditions found on natural disturbances. An example is the resource gradient associated with western harvester ant mounds as a result of the activities of the ants (Rogers and Lavigne 1974). A comparison of natural disturbances with artificial disturbances of comparable, yet uniform characteristics, is necessary to evaluate the effects of different disturbance characteristics on successional dynamics.

In shortgrass steppe plant communities of the Central and Southern Great Plains, most successional studies have focused on the independent effects of large-scale disturbances, such as abandoned agricultural fields (Savage and Runyon 1937; Judd and Jackson 1939; Costello 1944; Judd 1974; Reichhardt 1982). Small patch-producing disturbances are also important, but they have been largely ignored (Chapter 2). In shortgrass communities dominated by the perennial grass, blue grama [Bouteloua gracilis (H.B.K.) Lag. ex Griffiths], disturbances that kill at least one individual B. gracilis have the largest potential effect on community structure (Chapter 2).

Two examples of small-scale disturbances of sufficient intensity and spatial scale to always kill at least one B. gracilis plant are western harvester ant mounds [Pogonomyrex occidentalis (Cresson)] and burrows from small animals (skunks and badgers). The effects of these two disturbance types on the plant community are different. Western harvester ants remove the vegetation from around their mounds by clipping the plants below the soil surface while small animals produce a mound of soil at the surface that covers and kills the vegetation.

Disturbance characteristics, such as size and seasonality, are also associated with different disturbance types and may affect the successional dynamics on disturbed areas. The texture of the soil on the disturbed site is also important to plant recovery in shortgrass communities because of the effects of soil texture on plant community composition (Anderson 1983).

My objective was to evaluate the effects of interactions among disturbance characteristics on the successional dynamics of small-scale disturbances in shortgrass steppe plant communities by comparing naturally-occurring and artificially produced disturbances of different type, seasonality, size and location by soil texture.

Methods

This study was conducted 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). Mean annual precipitation over the past 45 years is 311 mm (sd=79 mm) and mean monthly temperatures range from -5° C in January to 22° C in July. Moderate grazing by cattle occurs throughout the area.

Two disturbance locations based on soil texture and with similar climate were chosen: coarse-textured sites on sandy loam soils and fine-textured sites on clay to clay loam soils. Seasonality of the disturbance was studied using four dates during the growing season: September 1 (1984), March 1, May 1 and July 1 (1985). Disturbance size was studied by producing artificial plots comparable in size and shape to the range of sizes observed for ant mounds and animal burrows (0.20-1.77 m²).

Western harvester ant mounds

Previous studies in Wyoming (Kirkham and Fisser 1972), and observations at the CPER indicated that harvester ant mounds rarely occur on fine-textured sites; therefore, the location chosen to study plant recolonization on ant mounds was a site on a sandy loam soil. The surface area of all full-size mounds in a 1.5 ha area was estimated by measuring the longest diameter of each mound and the diameter perpendicular to the first diameter. Eight mounds were randomly assigned to each of the four disturbance dates.

During the time that western harvester ants inhabit a nest site, the ants inhibit plant growth on the mound by clipping the plants below the soil surface. Therefore, it was necessary to remove the ants in order to study the recolonization of plants on the mounds. Environmental conditions in the nest were altered by placing a plywood box over each of the eight mounds, two weeks prior to the September, May and July disturbance dates. This resulted in the ants relocating their nests. The plywood boxes were ineffective for the March disturbance date since harvester ants overwinter below the soil surface and do not become fully active until late-March or mid-April (Lavigne 1969). A biocide (Diazinon) was used to kill the ants of the eight mounds for the March disturbance date.

Small animal burrows

Observations at the CPER indicated that small animal burrows occur primarily on coarse-textured sites with a relatively low frequency of occurrence ($0.5 \text{ burrows} \cdot \text{ha}^{-1} \cdot \text{y}^{-1}$ from Chapter 2). Therefore, a relatively large area (5-10 ha) on sandy loam soils was examined during the time of the study (September 1, 1984-July 1, 1985) for the occurrence of newly formed burrows. Seven burrows were found for one disturbance date, July (1985). Newly formed burrows were not found for the other three dates. The surface area of the pile of soil produced by small burrowing animals was estimated by measuring the longest diameter and the diameter perpendicular to the first diameter.

Artificial plots

Artificial plots were produced on two locations differing in soil texture: a coarse- and a fine-textured site. Circular plots of three sizes (50, 100 and 150 cm-diameter) were produced by removing all above- and belowground plant material to a depth of 10 cm. The soil was sieved using a 1 cm-mesh screen to remove all perennial organs, then replaced. Eight plots were produced for each site, date and size. A randomized block design was used where plots were located within eight 16x20 m² blocks of homogeneous soil and vegetation separated by 10 m borders of undisturbed vegetation within a 0.75 ha area at each site. For each disturbance date, one plot of each of the three sizes was randomly assigned to one of the 20-16 m² cell positions within each block. The result was that the blocks and plots were separated by undisturbed vegetation to allow each plot to be near a potential source of propagules from the undisturbed plant community.

Data collection and analysis

The number of plants were counted and the percent canopy cover was estimated by species in early June and late July (1985,1986) on each of the ant mounds, animal burrows, and artificial plots. The sampling dates were chosen to correspond to the maximum development of cool and warm season species. Density and cover values were obtained within concentric circles of 25, 50 and 100 cm in diameter to determine the relative location of all plants within the

disturbed areas. The short-term effects of the disturbance characteristics on plant recovery were analyzed for the data collected one year after the disturbances occurred.

Therefore, the data collected for the two sampling dates in 1985 were pooled and used for the disturbances that occurred in September (1984), while the data collected in 1986 were pooled and used for the disturbances of the three dates in 1985. Analysis of variance was used to evaluate the effects of disturbance type, location by soil texture, date and size on the density and cover of four groups: 1) all plants, 2) perennial grasses, 3) perennial forbs, shrubs and succulents, and 4) annual grasses and forbs. Tukey's Q values were used to compute least significant ranges (LSR) and to evaluate the significantly different means at the $p < 0.05$ level (Sokol and Rolff 1981).

The compositions of the undisturbed plant communities (controls) were determined using fifty 0.25 m^2 quadrats randomly positioned on transects in the vicinity of the disturbances at each of the three sites (artificial plots: coarse- and fine-textured sites; ant mound site). Because the animal burrows were located in an area that included the ant mound site, the control for ant mounds also represented the control for animal burrows. The number of individuals were counted and canopy cover by species was estimated for each quadrat. The data were collected at the same time as for the disturbances (early June and late July, 1985 and 1986). The values for the four sampling dates were pooled in

an analysis of variance to evaluate the effect of soil type on the density and cover of the four groups of species for the undisturbed plant communities.

Results

The undisturbed plant communities of the ant mound site and the coarse- and fine-textured sites of the artificial plots were typical of shortgrass communities (Sims et al 1978) by having greater than 60% of their total density and 80% of their total cover attributed to perennial grasses (Table 3.1). The plant communities were dominated by the perennial grass, B. gracilis which contributed greater than 70% to the total cover. Other important perennial grasses and sedges were Carex heliophila Mack. (sunsedge) and Buchloe dactyloides (Nutt.) Engelm. (buffalograss). [Nomenclature follows McGregor (1986)].

The plant communities at the coarse-textured site and the ant mound site were similar and significantly different from the plant community at the fine-textured site for all groups except perennial grasses. Density and cover of annuals [primarily Vulpia octoflora = Festuca octoflora (Walt.) Rydb. (sixweeksgrass)] were significantly higher on the fine-textured site, while the density and cover of perennial forbs, shrubs and succulents were significantly higher on the other two sites. The succulent, Opuntia polyacantha Haw. (plains pricklypear) and the perennial

forb, Sphaeralcea coccinea (Pursh) Rydb. (scarlet globemallow) were important contributors to density and cover on all three sites while the shrubs, Chrysothamnus nauseosus (Pall.) Britt. (rabbitbrush), Gutierrezia sarothrae (Pursh) Britt & Rusby (broom snakeweed), and Atriplex canescens (Pursh) Nutt. (four-wing saltbush) occurred primarily on the coarse-textured and ant mound sites.

Because plant recovery on western harvester ant mounds and animal burrows was only monitored on coarse-textured sites and the average surface area of ant mounds (0.916 m^2) and burrows from small animals (0.977 m^2) were most similar in size to the 100 cm diameter artificial plots (0.785 m^2), the density and canopy cover of plants on ant mounds and animal burrows were compared with the 100 cm-diameter artificial plots on the coarse-textured site. The density and cover values for the plant communities on the coarse-textured site and the ant mound site were pooled and used as the control for the effects of disturbance type and seasonality. The effects of the location of the disturbance by soil type, disturbance date and size were evaluated using the data from the artificial plots.

Species composition and disturbance type

The density and cover of the four groups of species were different on the three disturbance types, although the species found on the disturbances were similar. The first year after western harvester ant mounds were vacated, most of the total density (>70%) and total canopy cover (>80%) of

plants on the mounds were perennials (Figs. 3.1 and 3.2), including forbs (S. coccinea, Oenothera caespitosa Nutt. (evening primrose), and Picrodeniopsis oppositifolia (Nutt.) Rydb. (plains bahia), the succulent (O. polyacantha), the half-shrub (Artemisia frigida Willd. (fringed sagewort)), the grasses [Sporobolus cryptandrus (Torr.) A. Gray (sand dropseed) and Sitanion hystrix Nutt. (squirreltail)], and the sedge C. heliophila. Important annual species were V. octoflora, Plantago patagonica Jacq. (Patagonian plantain), and Lepidium densiflorum Schrad. (prairie pepperweed). For most dates, the density and cover of perennial forbs, shrubs and succulents on ant mounds were greater than perennial grasses while the reverse was true for the surrounding undisturbed vegetation.

Most of the density (71%) and cover (53%) of plants on small animal burrows were from perennial grasses (Figs. 3.1 and 3.2). Large contributions to density (23%) and cover (44%) were also made by perennial forbs, shrubs and succulents. The same species of perennial plants were found on animal burrows as for ant mounds with the addition of a large contribution to cover by B. gracilis (20%). Relatively few annuals were found on the burrows and were primarily the forb species, Chenopodium album L. (lamb's quarters). Although the density of perennial grasses was significantly higher on the burrows than the control vegetation found on coarse-textured sites, the cover of perennial grasses was significantly lower.

In contrast to ant mounds and animal burrows, the densities of plants for annuals, perennial grasses and perennial forbs, shrubs and succulents were comparable within and among dates on the 100 cm-diameter artificial plots on the coarse-textured site, while the total densities of plants were comparable among dates (Fig. 3.1). Greater than 43% of the total cover on the plots was due to annuals and more than 33% was due to perennial forbs, shrubs and succulents (Fig. 3.2). Important species on artificial plots were the perennials: S. coccinea, O. caespitosa, P. oppositifolia, C. heliophila, S. cryptandrus, S. hystrix, and B. dactyloides, and the annuals: V. octoflora, L. densiflorum, P. patagonica, and C. album. Significantly lower density and cover values of perennial grasses occurred on the artificial plots than for the surrounding undisturbed vegetation, and for most dates the cover of annuals was significantly higher on the plots than for the controls.

Disturbance type and date

The highest total density (228 plants/m²) and canopy cover values (30%) of the three disturbance types were found on animal burrows (Fig. 3.3). For most dates, ant mounds had intermediate density (66-227 plants/m²) and cover values (14-25%) while artificial plots had the lowest density (29-70 plants/m²) and cover values (8-20%). Significant effects of disturbance date were indicated by the low density and cover values on ant mounds vacated in May, and the low cover values on artificial plots produced in September.

The density (162 plants/m²) and cover (16%) of perennial grasses on animal burrows were significantly higher than on ant mounds or artificial plots (Fig. 3.4). Most of the perennial grasses and sedges on the three disturbance types were from the rhizomatous species, C. heliophila. For most dates, the lowest density and cover values were found on the artificial plots. The high density values for the July ant mounds (87 plants/m²) and the low cover values for the September artificial plots (0.2%) were the significant date effects for perennial grasses.

Ant mounds and animal burrows had higher density (30-116 plants/m²) and cover values (9-17%) of perennial forbs, shrubs and succulents for all disturbance dates than the artificial plots (Fig. 3.5). Sphaeralcea coccinea was the most important species in this group for the three disturbance types. Significant date effects were indicated by the high densities on the March plots, low cover values on the September plots, and the low density and cover values on ant mounds vacated in May. The density of annual plants was comparable on the three disturbance types, except for the high densities of annuals found on ant mounds vacated in September and July (Fig. 3.6a). The percentage cover of annuals was significantly higher on artificial plots than on mounds or burrows for all dates except September (Fig. 3.6b). Most of the cover on the artificial plots was attributed to two species, L. densiflorum and V. octoflora.

Disturbance location, date and size

Similar species were found on the artificial plots at the fine- and coarse-textured sites, although the density and cover values of the four groupings of species were significantly different. The total density of plants on artificial plots at the fine-textured site (33-211 plants/m²) was higher for all sizes and all dates than the density of plants on plots at the coarse-textured site (34-81/m²) (Fig. 3.7). Density values on the plots were less than for the controls and were comparable for most dates and sizes within each site. Although the percentage canopy cover for the control on the fine-textured site was significantly less than the control on the coarse-textured site, the reverse was true for the percentage cover of plants on the plots for all dates except September (Fig. 3.7c).

Similar density and cover values of perennial grasses were found for both sites, although the values on the plots were less than on the controls (Fig. 3.8). The 50 cm-diameter plots had significantly higher density values, due to C. heliophila on the fine-textured site and B. dactyloides on the coarse-textured site, than the 100 or 150 cm-diameter plots for both sites and most dates. The September plots for both sites and all three sizes had significantly lower cover values than found on the other plots.

The density of perennial forbs, shrubs and succulents on the artificial plots for both sites were comparable to or significantly higher than for the controls (Fig. 3.9a and b). The March plots on the fine-textured site had significantly higher density values for all three plot sizes than the plots for the other dates primarily because of differences in the densities of S. coccinea (Fig. 3.9b). In most cases, the 50 cm-diameter plots had the lowest density values of the three sizes within a date and site. Although the percentage cover of perennial forbs, shrubs and succulents was significantly different for the two controls, significant site differences were not found for the cover of plants on the plots (Fig. 3.9c). The plots produced in September had significantly lower cover values for all three sizes than plots for the other three dates.

The density and cover of annuals was higher for the three plot sizes on the fine-textured site and for the control vegetation than for plots on the coarse-textured site (Fig. 3.10a,b). Significantly higher density and cover values of annuals (primarily L. densiflorum and C. album) were found on the 150 cm-diameter plots than on the 50 cm-diameter plots for the fine-textured site. The September plots had significantly lower cover values of annuals than plots for the other three dates (Fig. 3.10c).

An analysis based on the density and cover of plants located in the 50 cm-diameter center circle of each artificial plot was conducted to further evaluate the

effects of disturbance size on plant recovery. Other factors besides perimeter length and surface area, such as microenvironmental gradients and the ability of plants to disperse over the entire plot, may change as plot size changes, and would be indicated by a difference in the density and cover of plants in the center of the different sizes of plots.

The total density of plants located in the center circle of each plot was higher on the 50 cm-diameter plots than the 100 or 150 cm-diameter plots for both sites and most dates (Fig. 3.11a and b). Although total density was higher on the 50 cm-diameter plots, percentage canopy cover was significantly higher on the 100 (18%) and 150 (19%) than on the 50 cm-diameter plots (11%). Significantly higher density and cover values were found for perennial grasses and sedges (primarily C. heliophila and B. dactyloides) for the 50 cm-diameter plots (than for the 100 or 150 cm-diameter plots on both sites (Fig. 3.12). Size was not a significant factor for the density or cover of perennial forbs, shrubs and succulents except for the high density and cover values on the March 150 cm-diameter plots, due to S. coccinea (Fig. 3.13). Although the densities of annuals were not affected by disturbance size, the cover values were significantly higher on the 100 (10%) and 150 cm-diameter plots (11%) than on the 50 cm-diameter plots for all dates (3%).

Discussion

The species composition on the two naturally-occurring disturbances (western harvester ant mounds and small animal burrows) were similar one year after the disturbances occurred, and were different from the composition on the artificially produced disturbances. This distinction between natural and human-caused disturbances was also found for grasslands and savannas of the Serengeti National Park (Belsky 1987). The high density and cover of perennials on ant mounds and animal burrows indicates that perennial organs, such as rhizomes of C. heliophila and tap roots of S. coccinea, were not killed by the clipping activity of harvester ants or the pile of soil from burrowing animals. Similar growth of perennial grasses and forbs on badger mounds was observed in the first growing season in a tallgrass prairie (Platt 1975).

The recolonization of western harvester ant mounds was primarily by perennials, and the density of annuals on the mounds was significantly larger than on animal burrows and most artificial plots. The activities of western harvester ants may affect the recovery of plants on abandoned mounds in several ways due to the interactions of ants with their environment (Weins 1976) during the 20-40 years that a colony may inhabit a nest site (Chapter 4). The foraging and clipping activities of the ants affect the microenvironmental conditions on the nest as well as the availability of reproductive and vegetative propagules.

Nutrients and seeds are concentrated in a nest as a result of the foraging and storage of seeds and other organic materials in underground chambers by harvester ants, and soil water is significantly higher ($p < 0.05$) in a nest than at points away from the nest due the clipping of all plants from the mound (Rogers 1974, Rogers and Lavigne 1974). The significantly larger ($p < 0.05$) standing crop of plants surrounding a nest compared to points located away from the nest (Rogers and Lavigne 1974) may also result in an increased availability of seeds and vegetative propagules to an abandoned nest compared to disturbances that are recolonized immediately after being produced (artificial plots and animal burrows). The number of germinable seeds found near the soil surface of nests in September, 1984 (6755 seeds/m² from Coffin and Lauenroth unpubl.) was significantly larger ($p < 0.05$) than the number of seeds in the soil at the coarse-textured site for the same date (2748 seeds/m² from Appendix II). The length of time these conditions persist on an abandoned nest is unknown, however, the largest effects on plant recovery most likely occur in the short-term. For example, the effects of seasonality on the recolonization of ant mounds may not continue in the long-term as other factors become increasingly important through time. The 6% cover by the dominant plant species, B. gracilis, on animal burrows was primarily due to the vegetative growth of B. gracilis plants partially covered by soil. Bouteloua gracilis was not found in significant

amounts on ant mounds or artificial plots. These results suggest that the time required for B. gracilis to dominate the plant community on animal burrows will be less than for ant mounds or artificial plots, and less than the estimated recovery time of greater than 50 years for B. gracilis to dominate abandoned agricultural fields (Reichhardt 1982). The recovery time for abandoned fields was based on the observation that it took 33 years for B. gracilis to occur on the fields and another decade to reach 2% in frequency of occurrence (Reichhardt 1982).

In contrast to ant mounds and animal burrows, the majority of the cover on the artificially produced disturbances for the coarse- and fine-textured sites, and most dates and sizes, was attributed to annuals. This is similar to plant communities found on old roads and abandoned agricultural fields in the shortgrass steppe region within five years after the beginning of plant recovery (Shantz 1917; Costello 1944; Judd 1974; Reichhardt 1982). Perennials colonized the plots in the first year as indicated by the comparable densities of annuals, perennial grasses, and perennial forbs, shrubs and succulents.

The seasonality and size of the disturbance had important effects on the density and cover of plants on artificial plots. The effects of seasonality on short-term successional dynamics are due to interactions between the availability of propagules to the site and the microenvironmental conditions on the site relative to the

requirements for germination, establishment and growth of the propagules (Sousa 1984). The low cover of annuals and perennials on artificial plots produced in September may be a combination of: (1) the seasonal dynamics in the relatively few germinable seeds stored in the soil at the two sites (964 seeds/m² averaged over two years from Appendix II), (2) the low and variable patterns of precipitation found in the shortgrass region (Sala and Lauenroth 1982), and (3) the timing of the precipitation events relative to factors such as temperature. Similar effects of seasonality may have been important to the low density and cover of perennials on ant mounds vacated in May, along with effects associated with the activities of harvester ants or the ant removal procedures. Because of the variability in precipitation within and among years, conducting the study in another year would most likely indicate the timing of the disturbance to have important effects on plant recovery, however, the specific effect observed in this study (low values for September plots) may not occur.

Although annuals and perennials responded similarly to the effects of seasonality, they responded differently to disturbance size. The size of the disturbance may be important to the availability of propagules to the disturbed site and the resources available to the propagules. As disturbance size increases, propagules must disperse over larger distances to colonize the entire disturbed area,

while competition from plants around the edge increases as the size of the disturbance decreases (Sousa 1984).

The source of propagules for annuals included seeds stored in the soil and the dispersal of seeds onto the plot. The density of annuals was not affected by disturbance size while the effects of competition by plants surrounding the plots on the growth of annuals was indicated by the significantly smaller cover values on the smallest compared to the largest plots.

Perennials may recover either from seedling establishment or vegetative growth. Relatively few perennial grass (187 seeds/m²) or perennial forb, shrub and succulent seeds were found stored in the soil (30 seeds/m²) compared to annual seeds (721 seeds/m²) (Appendix II). Most of the perennials on the plots were the result of vegetative growth by C. heliophila, B. dactyloides, and S. coccinea. The recovery of C. heliophila by rhizomes and B. dactyloides by stolons occurred as ingrowth from the edge of the plots. The greater perimeter-to-area ratio of small compared to large plots (Miller 1982, Sousa 1984) resulted in significantly larger cover and density values of perennial grasses on the smallest plots for most dates and both sites.

The cover of the perennial forb, S. coccinea, responded similarly to disturbance size as annuals by having the highest values in the center circle of the largest plots, or the farthest distance from potential competitive interactions with plants in the surrounding undisturbed

community. Although the density of annuals was not affected by disturbance size, the density of S. coccinea responded similarly to the cover values. The recovery of this important forage species (Hyder et al 1975) was primarily from deep tap roots either from plants at the edge of the plot or by regrowth of plants on the plot.

The interaction between disturbance size, seasonality and location by soil texture was also important to the cover and density of S. coccinea. The period of growth of this species (April and early May from Dickinson and Dodd 1976) corresponds to the significantly higher density and cover values on the largest plots cleared in March on the fine-textured site for perennial forbs, shrubs and succulents than for plots of the other dates. Similar results on the importance of the timing of the availability and growth of propagules relative to the seasonality of the disturbance were found for the recovery of an annual grassland following small disturbances (Hobbs and Mooney 1985).

Although the long-term monitoring of the disturbed sites for the three disturbance types and their associated characteristics is necessary to evaluate the time required for each disturbed area to be dominated by a shortgrass plant community, the results after one year of recovery suggest that animal burrows will have the most rapid recovery time of the disturbance types studied because of the presence of B. gracilis and other perennials on the burrows. Artificial plots, and in particular the largest

plots, will have the slowest recovery time since relatively few perennials were found on the plots compared to ant mounds or animal burrows.

LITERATURE CITED

- Albertson, F. A., and J. E. Weaver. 1944. Nature and degree of recovery of grassland from the Great Drought of 1933 to 1940. *Ecological Monographs* 14:394-479.
- Anderson, M. D. 1983. Soil and vegetation pattern on shortgrass catenas. MS Thesis. Colorado State University, Fort Collins, Colorado, USA.
- Belsky, A. J. 1986. Revegetation of artificial disturbances in grasslands of the Serengeti National Park, Tanzania. I. Colonization of grazed and ungrazed plots. *Journal of Ecology* 74:419-437.
- Belsky, A. J. 1987. Revegetation of natural and human-caused disturbances in the Serengeti National Park, Tanzania. *Vegetatio* 70:51-60.
- Collins, S. L., and G. E. Uno. 1983. The effects of early spring burning on vegetation in buffalo wallows. *Bulletin of the Torrey Botanical Club* 110:474-481.
- Collins, S. L., and S. C. Barber. 1985. Effects of disturbance on diversity in mixed-grass prairie. *Vegetatio* 64:87-94.
- Collins, S. L. 1987. Interaction of disturbances in tallgrass prairie: A field experiment. *Ecology* 68:1243-1250.
- Costello, D. F. 1944. Natural revegetation of abandoned plowed land in the mixed prairie association of northwestern Colorado. *Ecology* 25:312-326.
- Davis, R. M., and J. E. Cantlon. 1969. Effects of size area open to colonization on species composition in early old-field succession. *Bulletin of the Torrey Botanical Club* 96:660-673.
- Dickinson, C. E., and J. L. Dodd. 1976. Phenological pattern in the shortgrass prairie. *American Midland Naturalist* 96:367-378.

- Hobbs, R. J., and H. A. Mooney. 1985. Community and population dynamics of serpentine grassland annuals in relation to gopher disturbance. *Oecologia*(Berlin)67:342-351.
- Hyder, D. N., R. E. Bement, E. E. Remenga, and D. F. Hervey. 1975. Ecological responses of native plants and guidelines for management of shortgrass range. United States Department of Agriculture Agricultural Research Service Technical Buletin 1503.
- Judd, I. B. 1974. Plant succession of old fields in the Dust Bowl. *Southwestern Naturalist* 19:227-239.
- Judd, I. B., and M. L. Jackson. 1939. Natural succession of vegetation on abandoned farmland in the Rosebud soil area of western Nebraska. *American Society of Agronomy Journal* 39:541-547.
- King, T. J. 1977. The plant ecology of ant-hills in calcareous grasslands. I. Patterns of species in relation to ant-hills in southern England. *Journal of Ecology* 65:235-256.
- Kirkham, D. R., and H. G. Fisser. 1972. Rangeland relations and harvester ants in northcentral Wyoming. *Journal of Range Management* 25:55-60.
- McGregor, R. L. 1986. *Flora of the Great Plains*. University Press of Kansas, Lawrence, Kansas.
- Milchunas, D. G., W. K. Lauenroth, P. L. Chapman, and M. K. Kazempour. 1988. Community structure relationships along a multi-disturbance-type gradient. *American Naturalist* (submitted).
- Miller, T. E. 1982. Community diversity and interactions between the size and frequency of disturbance. *American Naturalist* 120:533-536.
- Perozzi, R. E., and F. A. Bazzaz. 1978. The response of an early successional community to shortened growing season. *Oikos* 31:89-93.
- Pickett, S. T. A., and P. S. White. 1985. *Natural disturbance: The patch dynamics perspective*. Academic Press, New York.

- Platt, W. J. 1975. The colonization and formation of equilibrium plant species associations on badger disturbances in a tall-grass prairie. *Ecological Monographs* 45:285-305.
- Rapp, J. K., and D. Rabinowitz. 1985. Colonization and establishment of Missouri prairie plants on artificial soil disturbances. I. Dynamics of forb and graminoid seedlings and shoots. *American Journal of Botany* 72(10):1618-1628.
- Reichhardt, K. L. 1982. Succession of abandoned fields on the shortgrass prairie, northeastern Colorado. *Southwestern Naturalist* 27(3):299-304.
- Rogers, L. E. 1974. Foraging activity of the western harvester ant in the shortgrass plains ecosystem. *Environmental Entomology* 3:420-424.
- Rogers, L. E., and R. J. Lavigne. 1974. Environmental effects of western harvester ants on the shortgrass plains ecosystem. *Environmental Entomology* 3:994-997.
- Sala, O. E., and W. K. Lauenroth. 1982. Small rainfall events: An ecological role in semiarid regions. *Oecologia (Berlin)* 53:301-304.
- Shantz, H. L. 1917. Plant succession on abandoned roads in eastern Colorado. *Journal of Ecology* 5:19-42.
- Sims, P. L., J. S. Singh, and W. K. Lauenroth. 1978. The structure and function of ten western North American grasslands. I. Abiotic and vegetational characteristics. *Journal of Ecology* 66:251-285.
- Sokal, R. R., and F. J. Rohlf. 1981. *Biometry*. Second Edition. Freeman, New York.
- Sousa, W. P. 1984. The role of disturbance in natural communities. *Annual Review of Ecology and Systematics* 15:353-391.
- Weins, J. A. 1976. Population responses to patchy environments. *Annual Review of Ecology and Systematics* 7:81-120.

Table 3.1. Average density and canopy cover of four groupings of species for three undisturbed plant communities.

	Fine- Textured Site	Coarse- Textured Site	Ant Mound Site
<hr/>			
Density (number/m ²) -----			
Perennial grasses	85.6	81.3	72.0
Perennial forbs, shrubs and succulents	7.9*	16.4	18.6
Annual grasses and forbs	40.5*	14.1	9.7
Total	134.0*	111.8	100.3
Canopy Cover (percent) -----			
Perennial grasses	37.6	38.1	40.5
Perennial forbs, shrubs and succulents	4.3*	6.9	7.9
Annual grasses and forbs	2.0*	1.0	0.7
Total	43.8*	46.0	49.1
<hr/>			

* indicates significance at $p < 0.05$ among sites for each species group

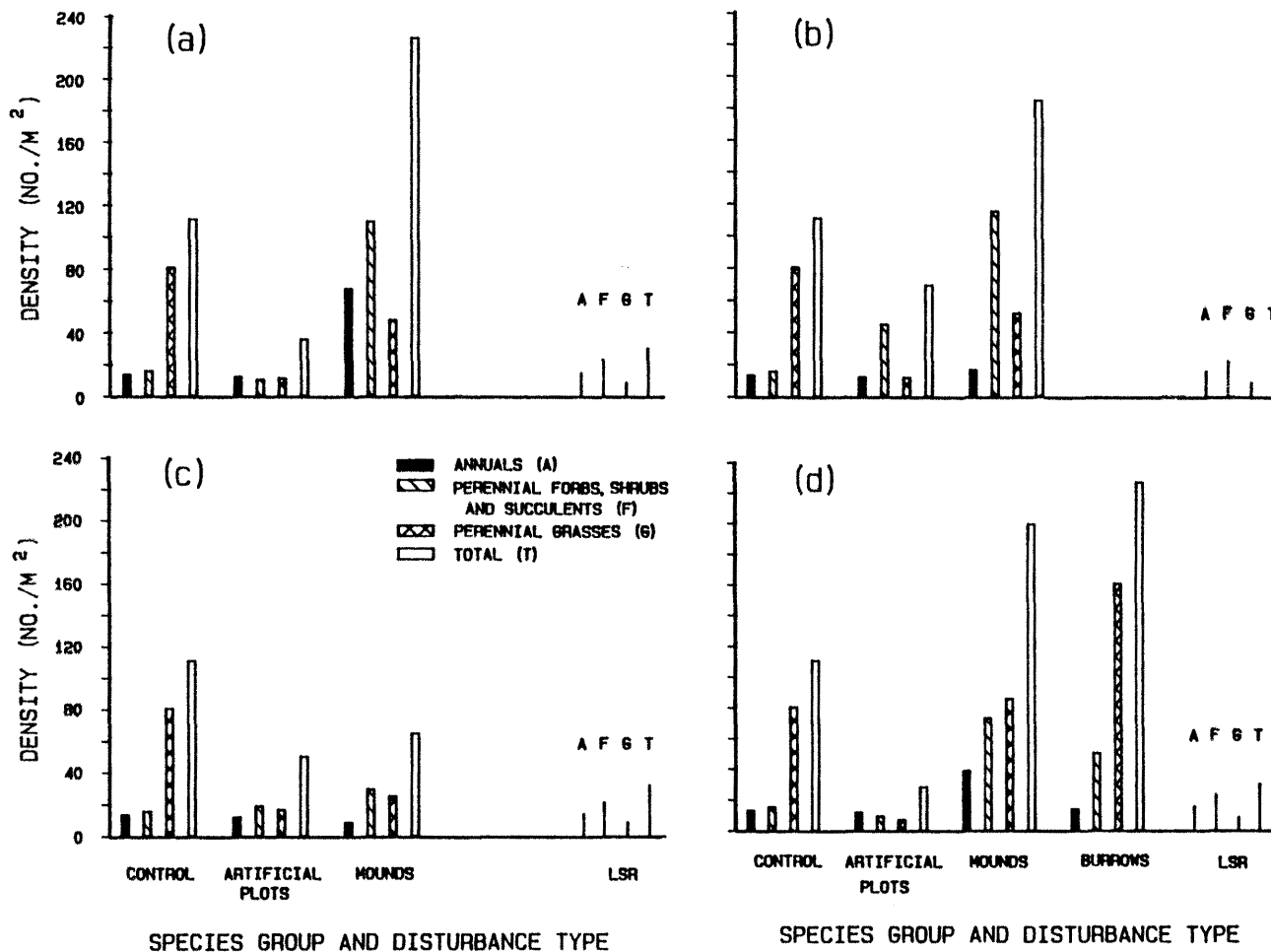


Fig. 3.1. Density of plants of four groups of species for three disturbance types and the control for four disturbance dates (a) September, 1984 (b) March, 1985 (c) May, 1985 (d) July, 1985. Use LSR_A for significance of annuals between disturbance types and the control and within dates, LSR_F for perennial forbs, shrubs and succulents, LSR_G for perennial grasses, LSR_T for total density.

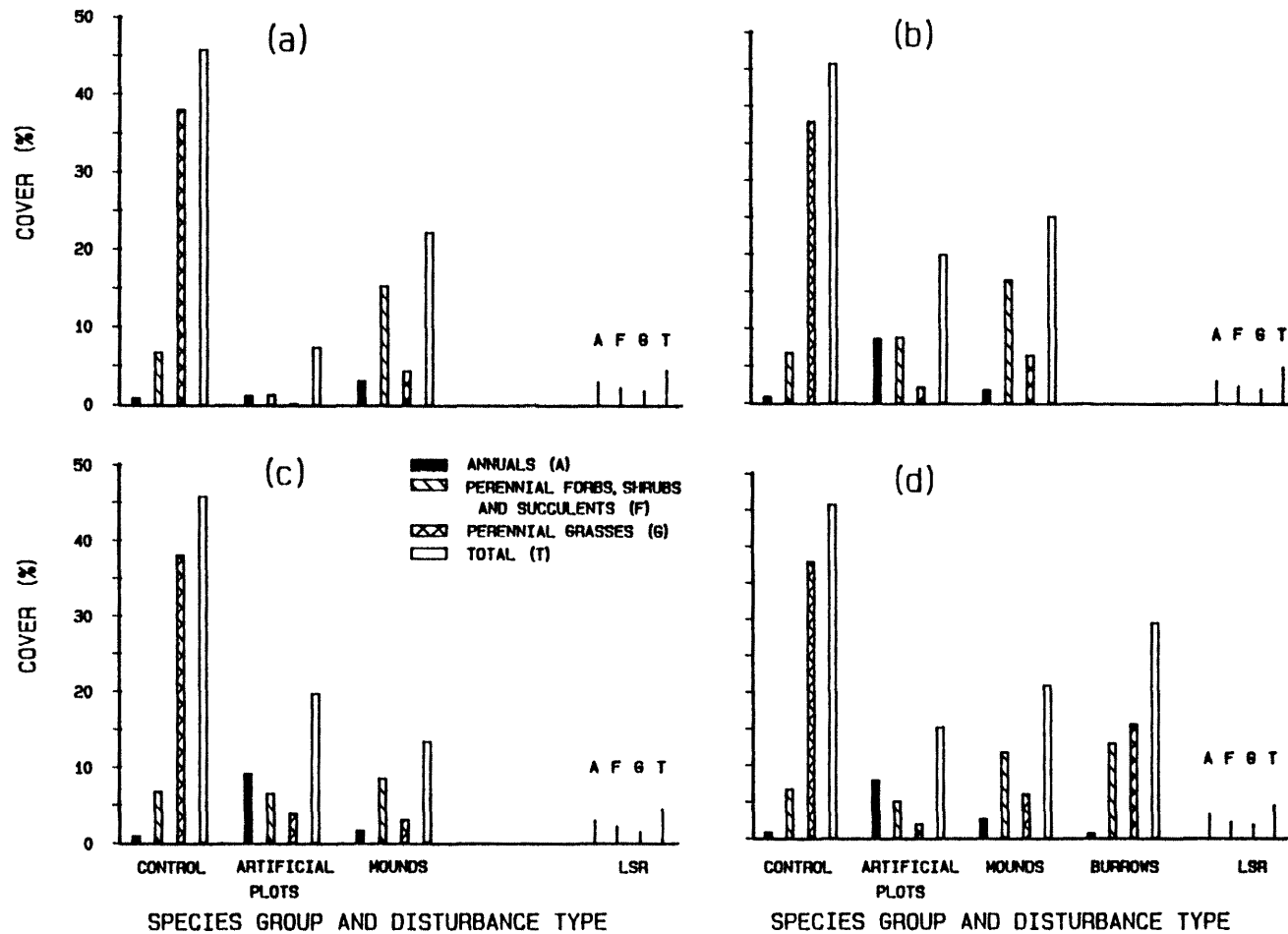


Fig. 3.2. Cover of plants for four groups of species for three disturbance types and the control for four disturbance dates (a) September, 1984 (b) March, 1985 (c) May, 1985 (d) July, 1985. For explanation on use of significance ranges (LSR) see Fig. 3.1.

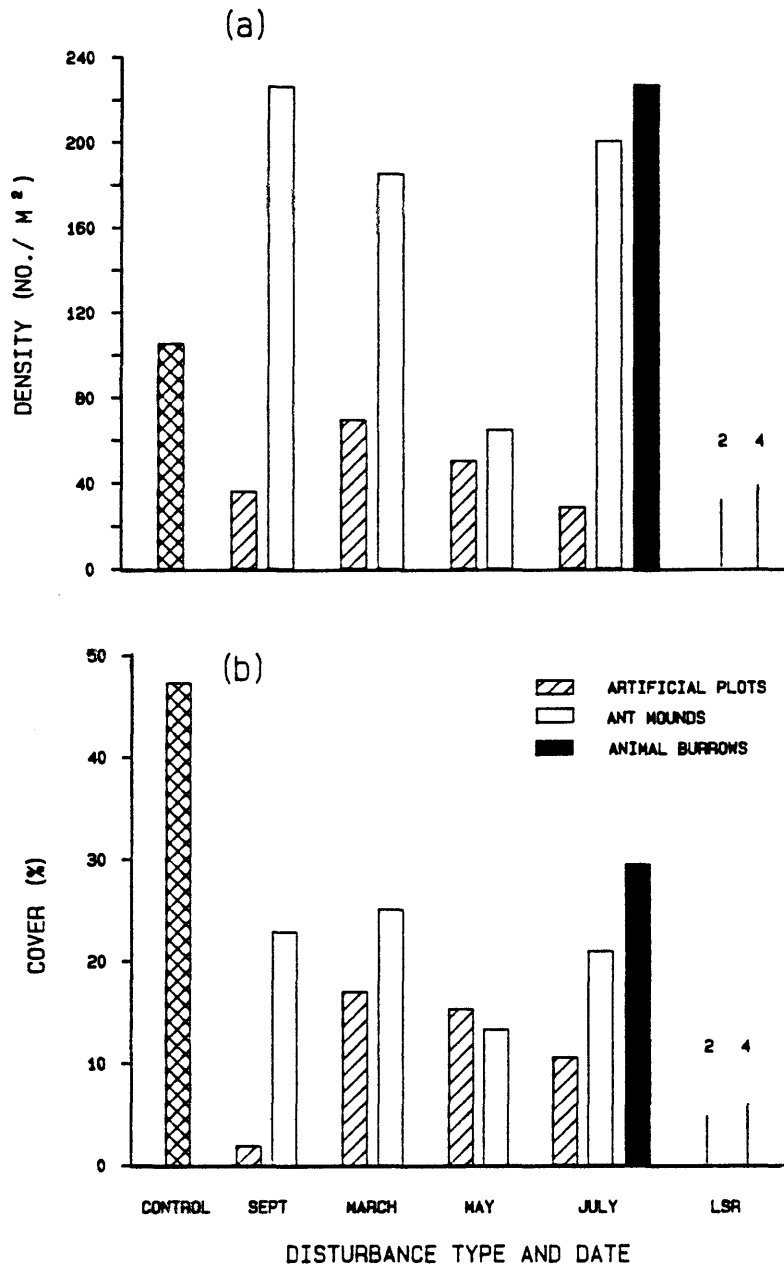


Fig. 3.3. Density and cover of plants for three disturbance types and the control for four disturbance dates. Use LSR_2 for significance of type within dates and LSR_4 for significance of date within types.

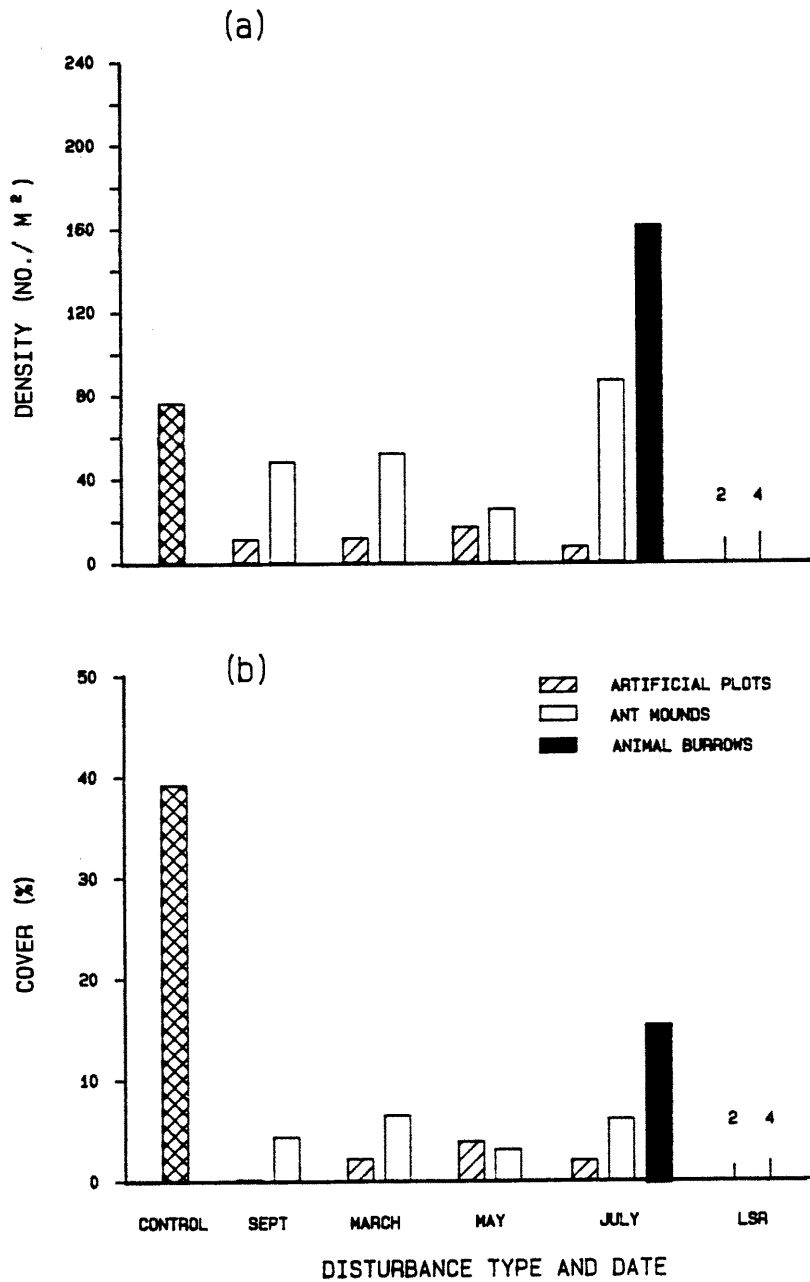


Fig. 3.4. Density and cover of perennial grasses for three disturbance types and the control for four disturbance dates. For explanation on use of significance ranges (LSR) see Fig. 3.3.

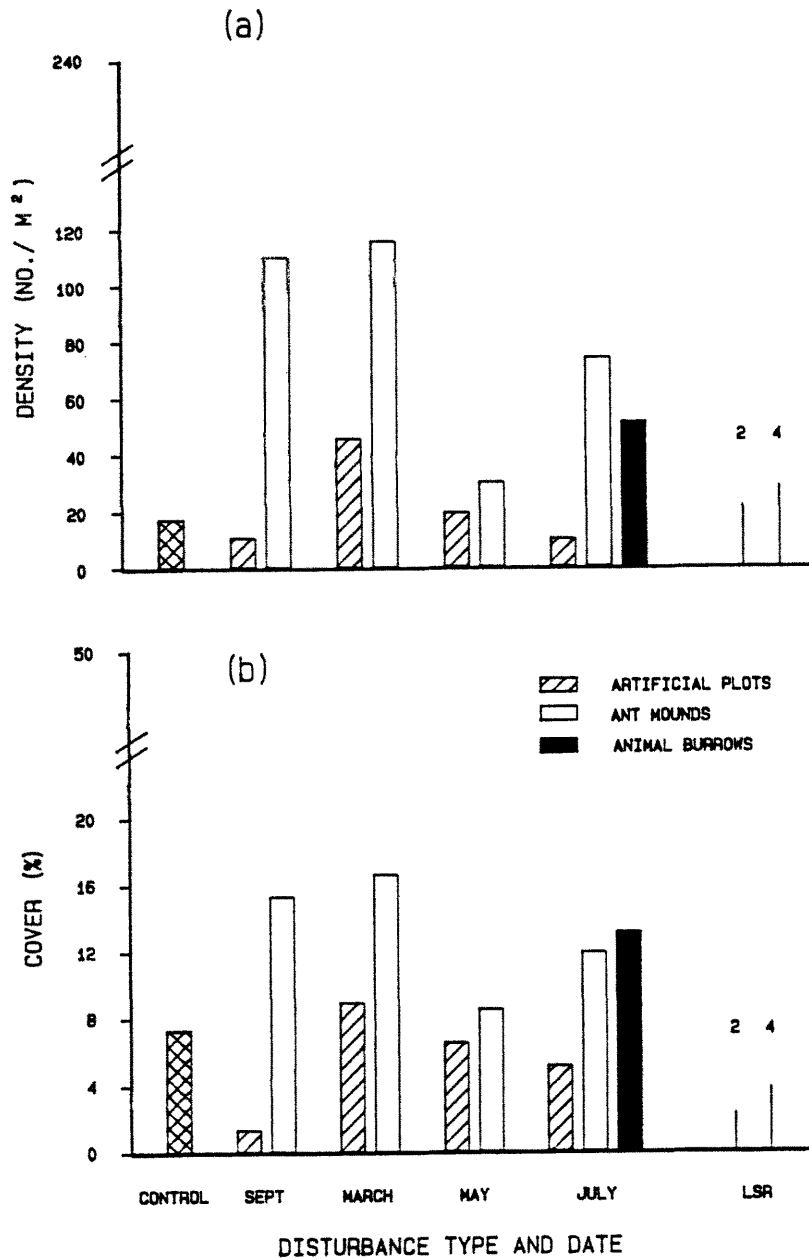


Fig. 3.5. Density and cover of perennial forbs, shrubs and succulents for three disturbance types and the control for four disturbance dates. For explanation on use of significance ranges (LSR) see Fig. 3.3.

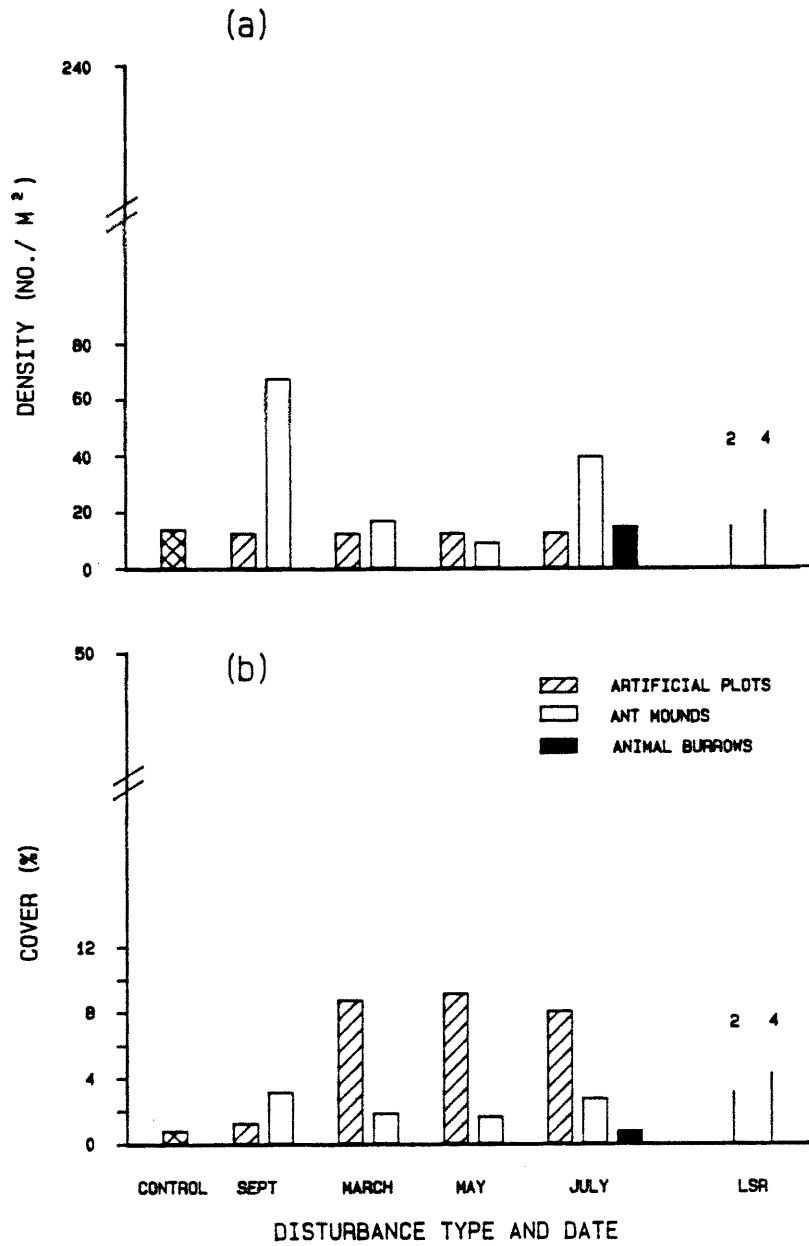


Fig. 3.6. Density and cover of annuals for three disturbance types and the control for four disturbance dates. For explanation on use of significance ranges (LSR) see Fig. 3.3.

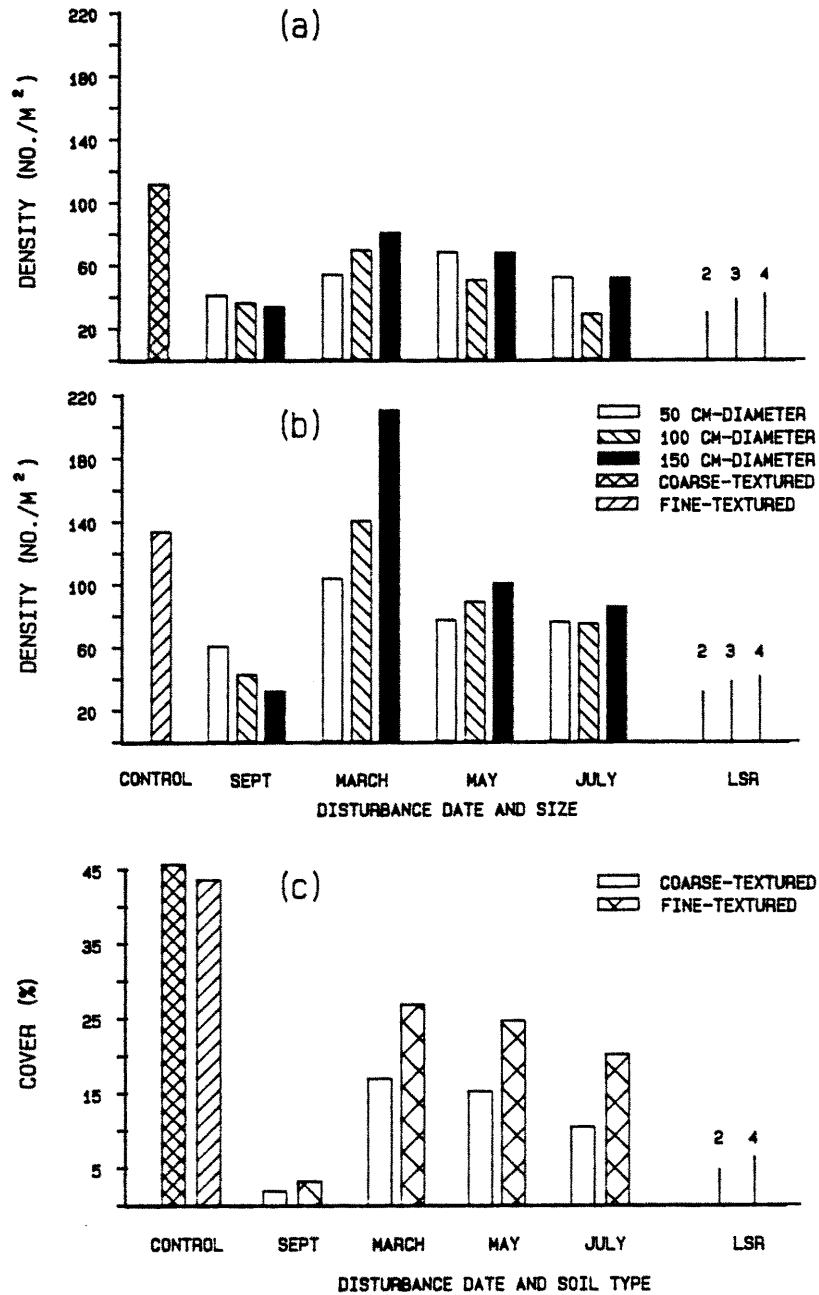


Fig. 3.7. Density of plants on artificial plots of three sizes for four dates, and the control for two sites (a) coarse- (b) fine-textured. (c) Cover of plants on artificial plots of three sizes for four dates. Use LSR_2 for significance of site within size and date, LSR_3 for size within site and date, and LSR_4 for date within site and size.

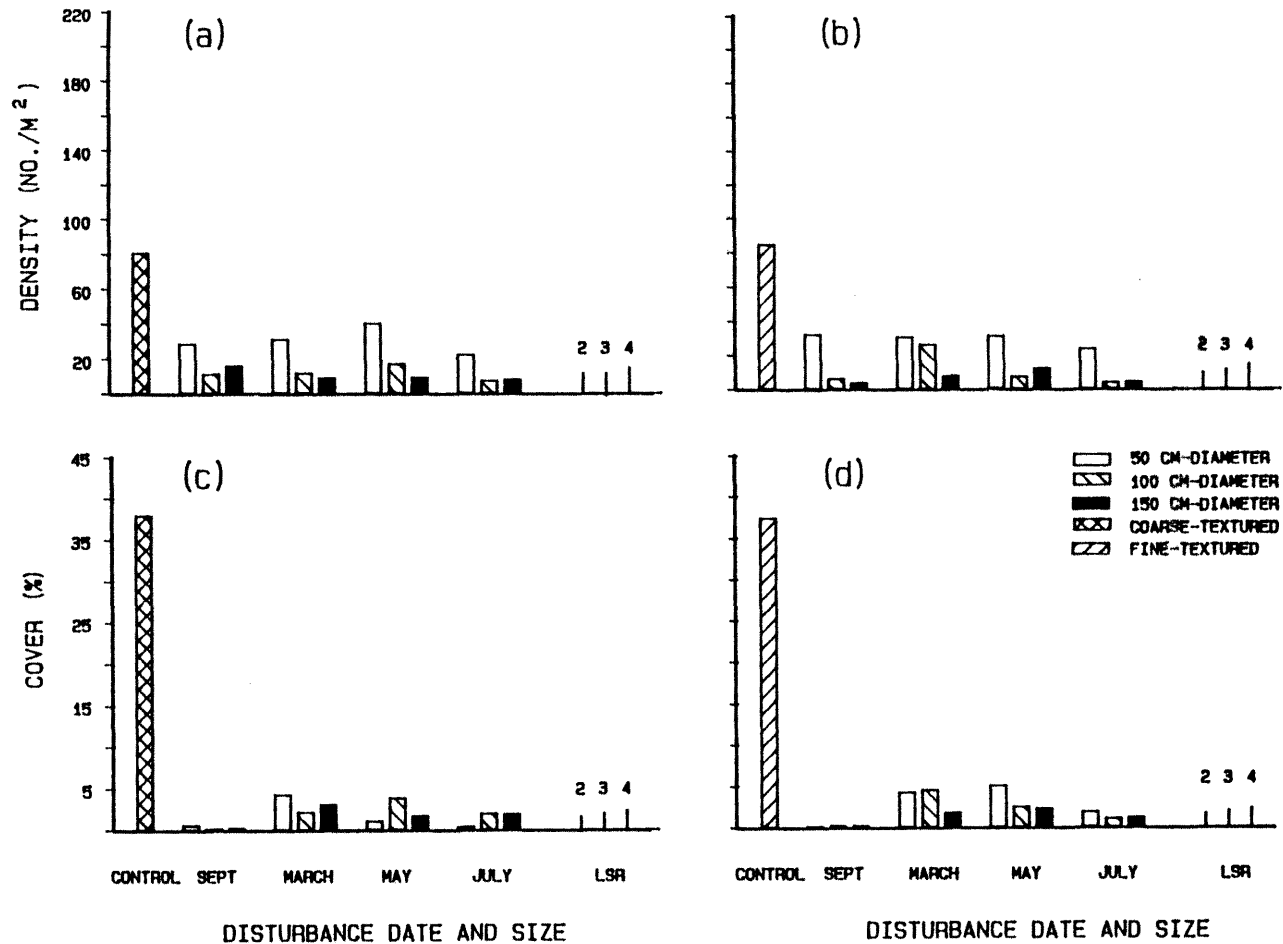


Fig. 3.8. Density of perennial grasses on artificial plots of three sizes for four dates, and the control for two sites (a) coarse- (b) fine-textured. Cover of perennial grasses on artificial plots of three sizes for four dates, and the control for two sites (a) coarse- (b) fine-textured. For explanation on use of significance ranges (LSR) see Fig. 3.7.

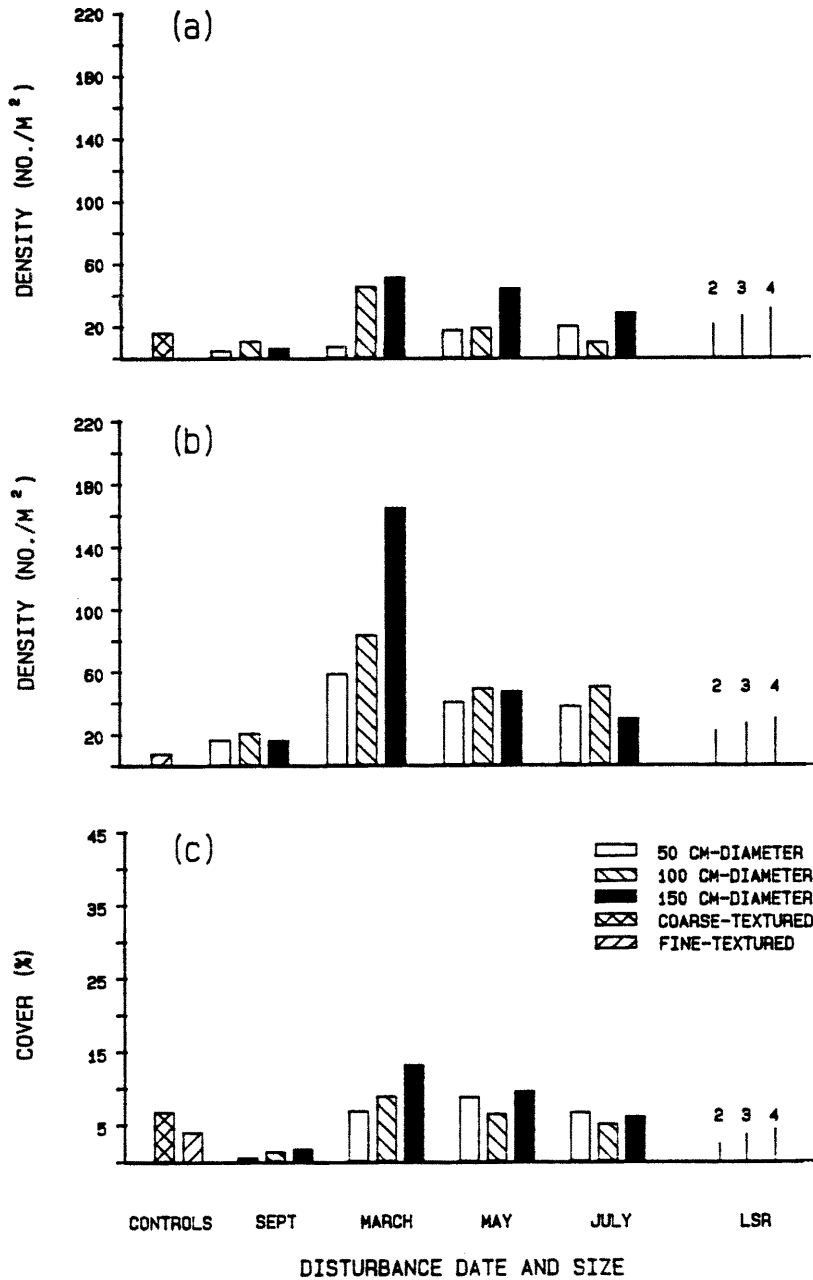


Fig. 3.9. Density of perennial forbs, shrubs and succulents on artificial plots of three sizes for four dates, and the control for two sites (a) coarse- (b) fine-textured. (c) Cover of perennial forbs, shrubs and succulents on artificial plots of three sizes for four dates, and the controls. For explanation on use of significance ranges (LSR) see Fig. 3.7.

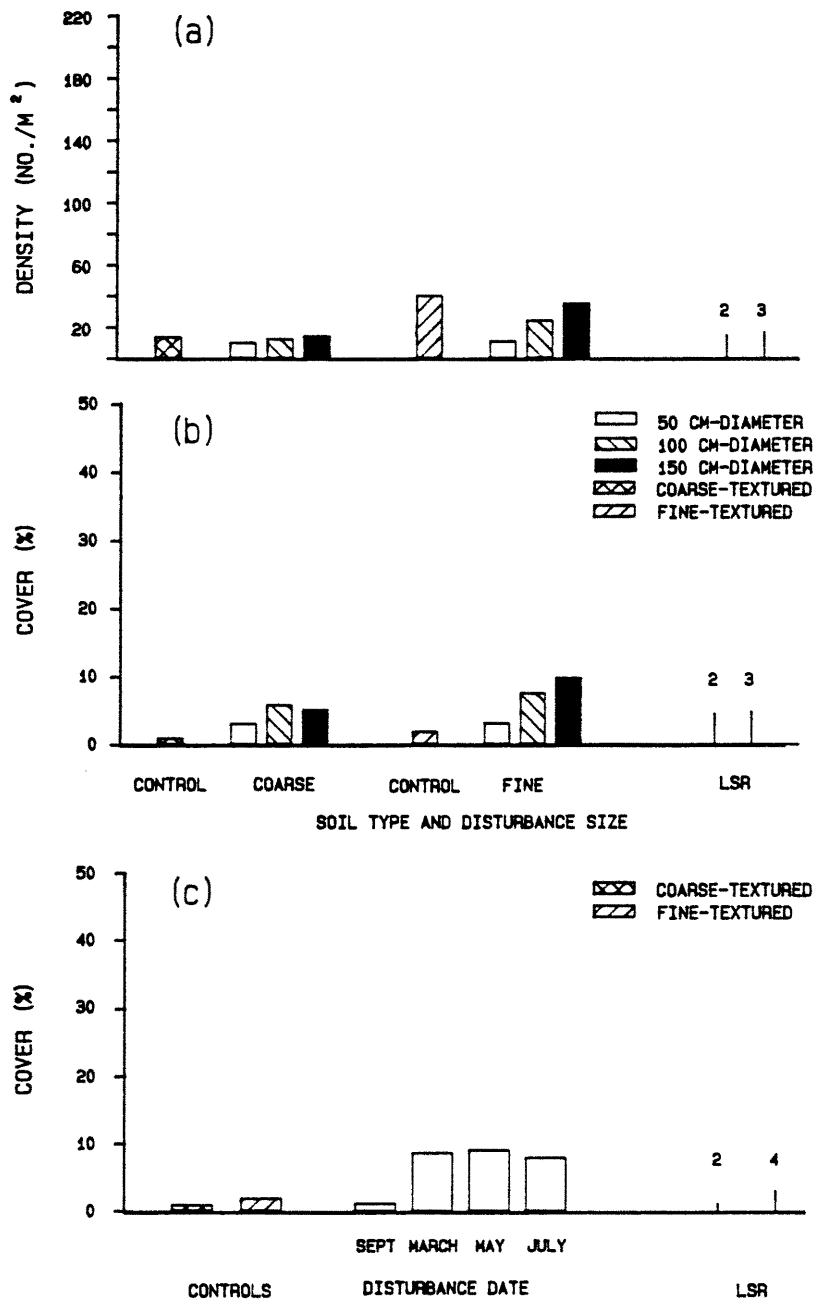


Fig. 3.10. (a) Density of annuals on artificial plots of three sizes for four dates, and the control for two sites. Cover of annuals on artificial plots of three sizes for four dates, and the control for two sites.

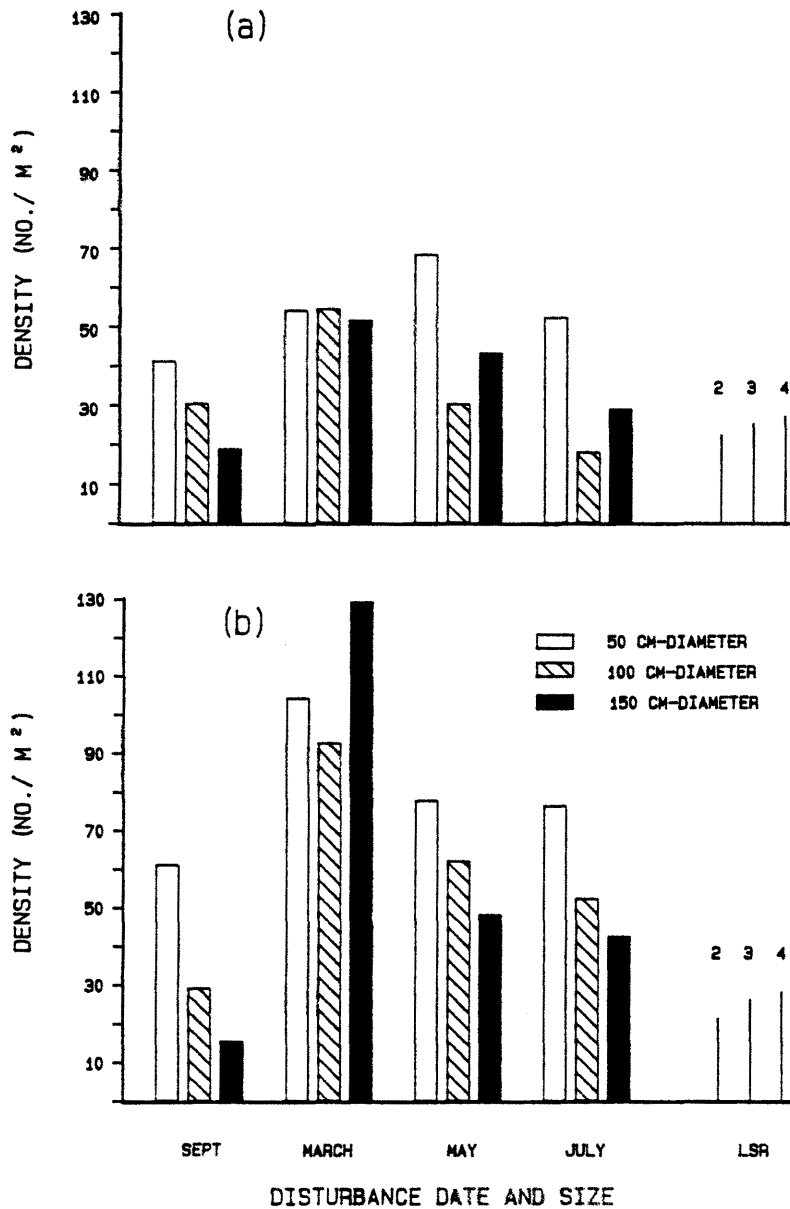


Fig. 3.11. Density of plants in the center 50 cm-diameter circle of artificial plots of three sizes for four dates and two sites (a) coarse- (b) fine-textured. For explanation on use of significance ranges (LSR) see Fig. 3.7.

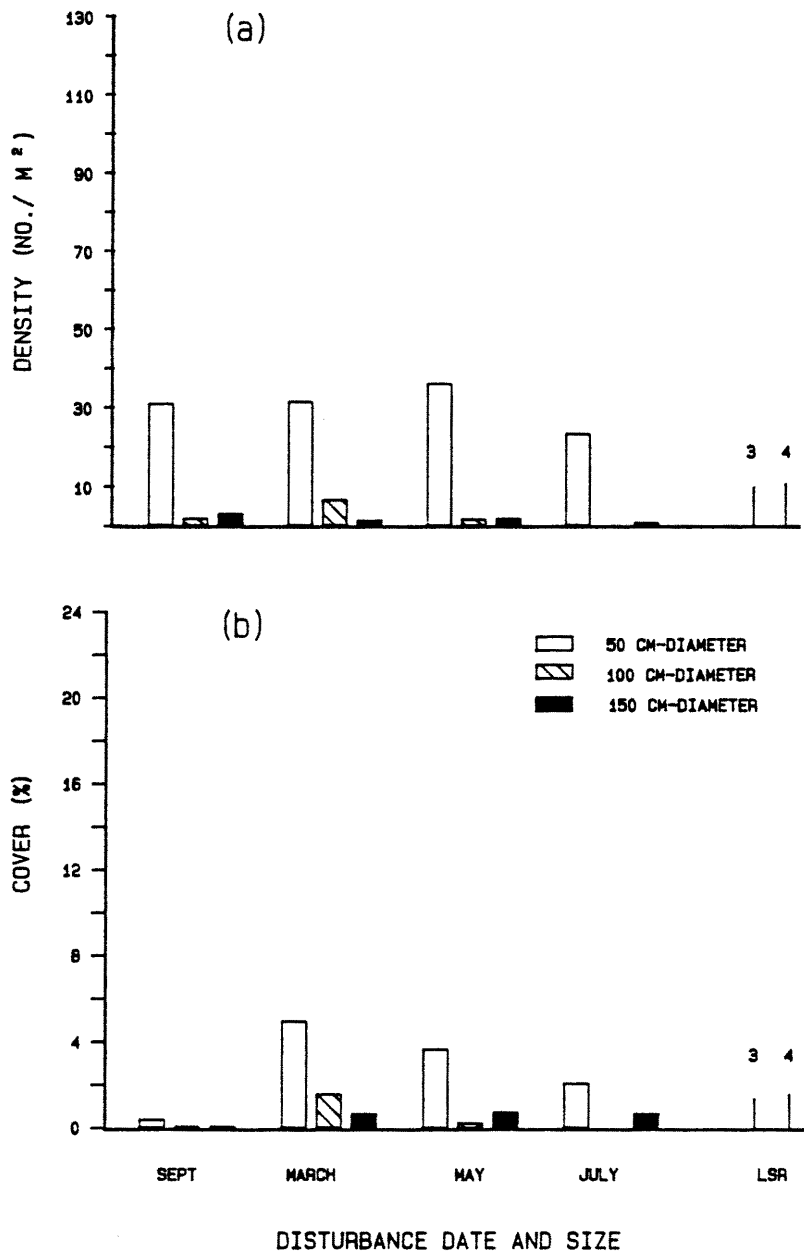


Fig. 3.12. Density and cover of perennial grasses in the center 50 cm-diameter circle of artificial plots of three sizes for four dates. Use LSR_3 for significance of size within date and LSR_4 for date within size.

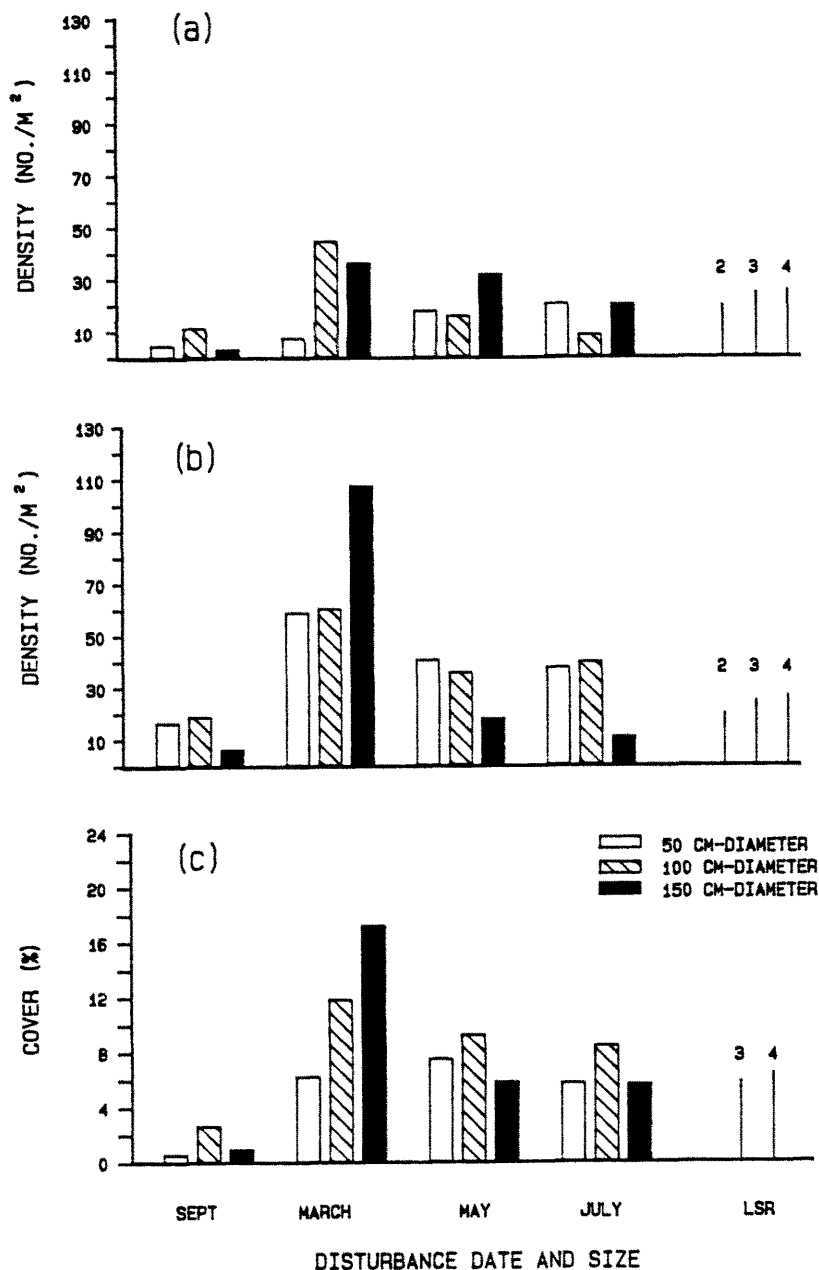


Fig. 3.13. Density of perennial forbs, shrubs and succulents in the center 50 cm-diameter circle of artificial plots of three sizes for four dates and two sites (a) coarse- (b) fine-textured. For use of significance ranges (LSR) see Fig. 3.7. (c) Cover of perennial forbs, shrubs and succulents in the center 50 cm-diameter circle of artificial plots of three sizes for four dates. For use of significance ranges (LSR) see Fig. 3.12.

IV. A GAP DYNAMICS SIMULATION MODEL OF SUCCESSION IN A SEMIARID GRASSLAND

Introduction

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] recovers very slowly after a disturbance or not at all (Riegel 1941, Hyder et al 1971, Briske and Wilson 1977).

The disturbance regime of shortgrass communities includes a number of disturbances operating over a range of spatial and temporal scales (Chapter 2). Physical and biological processes may be scale dependent (Delcourt et al 1983), and conclusions reached about the inability of B. gracilis to recolonize large disturbances may not hold for all disturbances, and in particular, small disturbances that occur frequently (Chapter 2).

An alternative, scale-oriented conceptualization of shortgrass communities, such as the theory of gap-phase dynamics, may provide information about the apparent contradiction between the results of the large-scale

disturbance studies and the continued dominance of B. gracilis in the presence of frequently-occurring disturbances that reduce populations of B. gracilis (Chapter 2). A gap dynamics approach focuses on small, patch-producing disturbances that affect a single individual of the dominant species (Watt 1947). The long-term result of gap dynamics processes is a landscape composed of a 'shifting mosaic' of patches, each undergoing its own successional dynamics through time (Bormann and Likens 1979). This approach has been used extensively in temperate and tropical forests and focuses on the canopy gap produced by the death of an individual tree in the canopy. Experimental studies have been used to evaluate the importance of gap characteristics to successional dynamics and community structure (Denslow 1980, Runkle 1981, Brokaw 1982;1985;1987, White et al 1985), while simulation models have been used to study long-term successional dynamics on gaps (Botkin et al 1972, Shugart and West 1977, Doyle 1981, Shugart 1984).

An important consideration in applying the gap dynamics approach to shortgrass communities is the resource space associated with plants, and in particular with individual B. gracilis plants. Belowground resources are of greater relative importance than aboveground resources in semiarid grasslands since the low and variable pattern of precipitation results in soil water being the most frequent control on plant growth and community structure (Noy-Meir

1973, Lauenroth et al 1978). It has been estimated for a shortgrass plant community that belowground net primary production contributes approximately 85% to total net primary production (Sims and Singh 1978), and basal cover of all plants ranges from 25-40% of which 85-90% is attributed to B. gracilis. Therefore, I hypothesized that the death of a full-size B. gracilis plant results in a gap in the belowground resource space and initiates the successional processes of gap dynamics.

A number of small, patch-producing disturbances affect shortgrass plant communities, including cattle fecal pats, western harvester ant mounds [Pogonomyrex occidentalis (Cresson)], and burrows from small animals, such as skunks and badgers. These small, frequently-occurring disturbances affect relatively large amounts of shortgrass communities through time (Chapter 2). The temporal variability in successional dynamics and the recovery time of B. gracilis on these small disturbed areas may be different than on large disturbed areas.

My objectives were to evaluate: (1) the long-term successional dynamics on gaps in shortgrass plant communities, (2) the time required for B. gracilis to recolonize gaps, and (3) the spatial variability of gap dynamics at the scale of the landscape. My approach was to develop a gap dynamics simulation model similar to the models used in forests (Shugart 1984), but based on the belowground resource use and life history characteristics of

plants in shortgrass communities. The model incorporates the effects of small-scale disturbances and stochastic environmental factors.

Conceptual Model of Gap Dynamics in a Semiarid Grassland

The gap dynamics conceptualization of plant communities focuses on the resource space associated with individual plants in the community. The conceptual model of gap dynamics for shortgrass communities is based on belowground resource space with a focus on the gaps produced in the resource space by the death of individual B. gracilis plants. The model associates a particular proportion of resource space with individual species or groups of species. The proportion associated with a species or group is a function of its root distribution with depth, the distribution of resources with depth, and the temporal variability of both distributions.

The distribution of resources is based on the average distribution of soil water availability with depth in the soil profile (Fig. 4.1a) since soil water is the most frequent control on plant growth and community structure in semiarid grasslands (Noy-Meir 1973, Lauenroth et al 1978). The initial increase in resources with depth is the result of high evaporation rates at the soil surface. This initial increase is followed by a gradual decrease in resources with depth as the penetration of soil water declines (Sala and Lauenroth 1985).

The root distributions with depth (Fig. 4.1b) were approximated by grouping the more than 300 plant species that may occur in shortgrass communities into five resource-groups based on similar life histories and spatial distributions of root biomass: B. gracilis, other perennial grasses besides B. gracilis, perennial forbs and shrubs, annual grasses and forbs, and succulents (Weaver 1919; 1958, Turner and Costello 1942, Coupland and Johnson 1965, Dougherty 1986, Lee 1988, Appendix I). The distribution of roots for each group, or the distribution of potential resource use, is shown as a proportion of the total root biomass, or total resource use, with depth (Fig. 4.1b).

The product of the resource abundance (Fig. 4.1a) and potential resource use distributions (Fig. 4.1b) represents the partitioning of the available resources by the groups (Fig. 4.2). The area between the curves represents the proportion of the resources that are associated with each group, or the resource space for that group.

I assumed the shape of the potential resource use curves are constant through time, although the proportion of the resources available to each group varies with plant growth, death and establishment. Resources that are not used by one group are available to the other groups depending on the similarity in the distribution of roots and the morphology of the root systems. I hypothesized that B. gracilis plants were not able to use resources associated with other groups. This hypothesis is supported by the lack

of response of the spatial distribution of B. gracilis roots to the removal of neighboring plants (Appendix I). Resources not used by B. gracilis plants are available to other groups except succulents. Perennial grasses, perennial forbs and shrubs, and annuals have roots at similar depths in the soil profile as B. gracilis while the roots of succulents are concentrated near the soil surface where few B. gracilis roots are found. Because of the spatial overlap in the location of perennial grass, perennial forb and shrub, and annual roots, I assumed that resources not used by one of these groups are available to the other two groups. Resources associated with succulents are not available to other groups and succulents can not use resources of the other groups.

I assumed the resource abundance curve (Fig. 4.1a) varies with the amount of annual precipitation. Most of the precipitation events at the CPER are small events (<5 mm), while most of the precipitation is contributed by a few large events (Sala and Lauenroth 1982). The important difference between average precipitation years and wet or dry years is the number of large events (≥ 20 mm). In above-average precipitation years there are typically more large events and in below-average precipitation years there are fewer large events than in average years (Bourgeron et al 1987). The result is that the difference in the resource abundance curves for these three general conditions is in the deep soil layers rather than at the soil surface (Fig.

4.3). Therefore, in years of above-average precipitation the resource-group with a large proportion of its roots in the deep soil layers (perennial forbs and shrubs) is affected more by the increase in resources than the other groups. In years of below-average precipitation, shallow-rooted groups (*B. gracilis* and succulents) are affected less by the decrease in resources than the other groups.

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 Research 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, and includes a number of grasses, succulents, half-shrubs and forbs. Moderate grazing by cattle occurs throughout the area.

Model Description

The gap model simulates the establishment, growth, and death of individual plants on a small plot through time on an annual time step. The plot size (0.12 m²) was calculated from the relationship between the surface area and rooting

volume of B. gracilis plants determined from a study using a radioactive tracer (Appendix I).

The five resource-groups were divided into fifteen species-groups based on similar life history characteristics and responses to environmental factors (Table 4.2). A representative species is used for each of the groups. The size and age of each plant on the plot are kept track of through time (Fig. 4.4a). The effects of the three driving variables (precipitation, temperature and disturbances) and interactions within and among species-groups on the establishment, growth or mortality of plants are specific to each group. A generalized Forrester diagram is shown for two representative species in Figure 4.4b.

Establishment of Plants

The establishment of plants occurs either by seedlings or vegetative propagation (Table 4.2).

Seedling establishment

I assumed that seeds of all species-groups are present on the plot and resources are available for establishment every year. The probability that a seedling from a particular group will become established is based either on suitable microenvironmental conditions occurring or the relative abundance of seeds on the plot. The establishment of B. gracilis seedlings is based on the probability (0.125) that a restrictive set of microenvironmental conditions required for germination and establishment will occur each

year (Briske and Wilson 1977, Lauenroth et al 1987). In years in which B. gracilis seedlings do become established, 1-3 seedlings are added to the plot at the estimated size of a one-year-old plant (approximately 23 tillers).

I assumed for the other species-groups that favorable conditions for establishment occur sometime during every year. The probability of seedling establishment for each species-group is based on the relative abundance of seeds produced by each group from seed production data for a moderately grazed upland site in 1985 (Coffin et al 1987). I assumed 1-5 species-groups have seedlings established each year with 1-3 seedlings being added to the plot for each group. Seedling size is based on the estimated size of a one-year-old plant and ranges from 0.022g to 2.25g (Table 4.2).

Vegetative propagation

Vegetative propagation is possible for two species-groups. The majority of grasses and sedges in the C. heliophila group recover from rhizomes while S. coccinea, the most important forb in that group, recovers from deep tap roots. I assumed there is a 90% chance of regrowth if a plant from these groups is killed either by a disturbance, the effects of a slow growth rate, or due to an intrinsic likelihood of mortality, and a 75% chance of regrowth if a plant died due to insufficient resources. If vegetative propagation occurs for a group, then 1-3 one-year-old plants are added to the plot.

Growth of Plants

The annual increase in size of each plant on the plot is a function of its optimum growth rate, the effects of precipitation and temperature, and interactions with other plants for belowground resources. The optimum growth rate is used to calculate the amount of resources required by each individual in each resource group. Precipitation and the effects of other plants are used to calculate the amount of resources available to each group. The actual growth rate for each individual is a function of the relationship between the resources required to sustain the optimum growth rate and the resources available to the plant. This relationship is mediated by the effects of temperature.

The optimum growth rate for each plant is calculated by:

$$dR/dt = r * (1.0 - \text{size}(t)) \quad (1)$$

where dR/dt is the optimum growth rate, r is the intrinsic rate of growth, and $\text{size}(t)$ is the relative size of the plant at time t . Intrinsic growth rates for each species-group were estimated from information about the number of years required for an individual to reach its full-size while growing under optimum conditions (Table 4.2).

The resources available to each resource-group were estimated using a function to account for the effects of precipitation on the distribution of soil water, and the different spatial distributions of roots for plants in the five groups (Fig. 4.5). The proportional change in the space

for each resource-group in a not extreme precipitation year (205-420 mm) is calculated by :

$$P_a = 0.00093 * PPT + 0.70935 \quad (2)$$

where $P_a = 1.0$ in an average precipitation year (311 mm).

The annual precipitation (PPT) is obtained from a distribution based on more than 30 years of data from the CPER. I assumed the distribution to be truncated normal with a mean of 311 mm (sd=79.4 mm, maximum=520 mm, minimum=105 mm). In dry years (<205 mm), equation (2) is used for groups that obtain most of their resources in relatively shallow layers of the soil profile (B. gracilis and succulents). The proportional change in the space for all other resource-groups is determined by:

$$P_d = 0.004 * PPT + 0.08 \quad (3)$$

resulting in fewer resources for a given precipitation amount for species that obtain most of their resources deeper in the soil profile than B. gracilis and succulents. A similar equation is used in wet years (>420 mm) to distinguish species (shrubs and perennial forbs) that obtain a large proportion of their resources from deep soil layers:

$$P_w = 0.004 * PPT - 0.58 \quad (4)$$

The total resources available to a group is the proportion associated with the group from eqs. (2-4) and the proportion of the resources not used by other groups that obtain their resources at similar depths in the soil profile.

To compare requirements of resource-groups with resource availability, the amounts required are converted to the requirements of an equivalent number of full-size individuals, and the amounts available are converted to an equivalent number of full-size individuals. The density of individuals from field data (Chapter 3) and the proportion of the resources available to each group in an average precipitation year (Table 4.1) are used to calculate the proportional requirement for a full-size individual of each group to use as the conversion factor (Table 4.1). A further conversion is required to obtain aboveground biomass at the end of each year for plants on the plot. This conversion is based on the size of each plant in relation to a full-size plant of each species-group (Tables 4.1, 4.2). Basal cover and density values are computed in a similar manner.

The common situations encountered in allocating resources for plant growth are:

1. resources required by plants in a group are less than those available
2. resources required are greater than those available.

Case 1

If sufficient resources are available for all individuals in a resource-group to grow at their optimum rate, then a logistic function is used to determine the response. Because of the spatial and temporal heterogeneity

of resources, I assumed resources became limiting as the amount required approached the amount available:

$$R_L = 1.0 - 0.95/(1+99\exp(-10.5*PR)) \quad (5)$$

where R_L is the proportional reduction in the optimum growth rate and PR is the ratio of the amount required and the amount available.

Case 2

The first year in which resources are insufficient for the optimum growth of all plants in a resource-group, the effect on growth rates is based on the proportion of the amount of resources required to the amount available (PR):

$$R_g = PR^{-1} \quad (6)$$

I assumed the plant community could adjust to short-term stresses due to insufficient resources since it is not unusual for soil water to be limiting in semiarid grasslands (Noy-Meir 1973).

If the availability of resources is less than those required by a group for two consecutive years, then plants are killed and the growth rates of the remaining plants in each of the resource-group are reduced. The degree of the reduction depends on the difference between the availability and requirement for resources.

The effect of resource reduction on plant growth is determined using equation 6. The number of plants killed in a resource-group is also based on this proportion:

$$N_k = N_p*(1-R_g) \quad (7)$$

where N_k is the number of plants killed and N_p is the number

of plants in the resource-group. I assumed the probability of mortality is inversely related to plant size; therefore the smallest plants are killed first until the total number of plants to be killed is reached.

Clonal plants

I assumed that clonal plants, B. gracilis and O. polyacantha, have additional constraints on their growth. A probability of mortality is calculated based on the number of years that resources are limiting if plants are not killed in (7):

$$P_m = 0.04*(Y)^2 \quad (8)$$

where P_m is the probability that plants will be killed, and Y is the number of consecutive years that resources are limiting. If mortality occurs:

$$N_k = N_p*0.9 \quad (9)$$

This source of mortality occurs most frequently when two B. gracilis plants of comparable size occur on a plot with a combined resource requirement small enough that both plants survive indefinitely if the only source of mortality is based on equation (7).

If B. gracilis or O. polyacantha plants are not killed, then individual clumps are reduced in size by decreasing tillers of B. gracilis and cladodes of O. polyacantha. The sizes of the clumps are reduced until resource requirements are approximately equal to availability. Small plants suffer a greater proportional reduction than large plants.

Opuntia polyacantha clumps are reduced in size further in years of above-average precipitation based on the negative response of this species to relatively high amounts of precipitation during the growing season (Dougherty 1986):

$$PR_O = \text{absolute value}[-0.0025 * GSPPT + 0.776] \quad (10)$$

where PR_O is the proportion of the clump killed and GSPPT is the amount of the annual precipitation that occurs during the growing season (April 1-Sept. 30). On the average, 86% of the annual precipitation at the CPER occurs during the growing season.

Temperature Response

The average daily maximum temperature during the growing season for each year is obtained from a distribution based on more than 20 years of data from the CPER. I assumed the distribution was truncated normal with a mean of 24.54° C (sds=1.0° C, maximum=35° C, minimum=15° C). Parabolic curves are used to determine the effect of temperature on growth rates. Separate curves are used for cool and warm season plants and succulents (Williams and Markley 1973, Salisbury and Ross 1978, Monson et al 1983):

$$T_C = 0.1014 * (TEMP + 2) - 0.00257 * (TEMP + 2)^2 \quad (12)$$

$$T_W = 0.1014 * (TEMP - 11) - 0.00257 * (TEMP - 11)^2 \quad (13)$$

where T_C is the temperature response for cool season plants, T_W is the temperature response for warm season plants and succulents, and TEMP is the current year's temperature. The curve for T_C has a maximum of 1.0 when TEMP equals 20°C, and T_W has a maximum of 1.0 when TEMP equals 32°C.

Mortality of Plants

The three sources of plant mortality used in the model are based on information from Shugart(1984), and are specific to each species-group (Table 4.2).

1. I assumed that each species-group has an age-independent intrinsic likelihood of mortality since a certain percentage of a cohort growing under optimum conditions will not reach the maximum age (AGEMAX). This mortality is represented by the probability that a plant will be dead by the nth year:

$$P_n = 1 - (1 - E)^n \quad (14)$$

where P_n is the probability of mortality by year n and E is the annual mortality probability. I assumed that 1% of a cohort will reach the maximum age; thus when n is equal to AGEMAX:

$$E = 4.605 / \text{AGEMAX} \quad (15)$$

The maximum age of each species-group was approximated using longevity data for similar species from other plant communities since the maximum age of shortgrass plants is unknown (Nelson 1934, Canfield 1957, Kerster 1968, Ragsdale 1969, Wright 1972).

2. I assumed that slow-growing plants have a greater risk of death because of a greater vulnerability to disease, insects and severe environmental conditions than plants with average growth rates. A slow growing individual was defined as a plant having a growth rate less than 5% of its maximum rate for two consecutive

years. Maximum growth rates were approximated as 90% of the intrinsic rate of growth. The probability of mortality (0.368) resulted in a slow-growing plant having a 1% chance of surviving ten years.

Bouteloua gracilis and O. polyacantha were excluded from the first two sources of mortality because I assumed that the clonal growth exhibited by plants of these species would more likely result in parts of the plants dying (tillers of B. gracilis and cladodes of O. polyacantha) due to slow growth or an intrinsic likelihood of mortality rather than the entire plant. The mortality of B. gracilis clumps occurs only as a result of insufficient resources (eq. 7) or disturbances (in the following section), while the mortality of O. polyacantha also includes a probability based on growing season precipitation (Dougherty 1986):

$$PD_O = (-0.0217 * GSPPT + 6.73568) / 100 \quad (16)$$

3. The third source of mortality is due to disturbances. The effects of cattle fecal pats, Western harvester ant mounds, and burrows from small animals are incorporated into the model using their frequencies of occurrence from Chapter 2:

- a) The probability of a fecal pat event occurring on the plot is 0.002/y. Once a fecal pat is deposited on a plot, there is a probability (0.025) that it will either

decompose or be physically removed from the plot due to cattle activity shortly after deposition. If the pat is removed, B. gracilis plants and species-groups composed primarily of low-growing plants are not killed, however, pats that remain on the plot result in the death of these plants. In the case of B. gracilis, I assumed a fecal pat that remains on a plot always kills the entire plant (Chapter 2), and that even when pats are on the plot for a short time it is always sufficient to kill annual plants and the seedlings of shrubs, forbs and some grasses. I also assumed that Opuntia polyacantha clumps, and shrubs, forbs and some grasses larger than seedlings are not affected by fecal pats. Because of the relatively slow average rate of decomposition of fecal pats in shortgrass communities (Lussenhop et al 1982), I assumed that the time when recolonization begins on the plot is described by a probability distribution in which the probability of colonization increases with time after the event:

$$P(t) = 0.0975 * T(f) + 0.025 \quad (17)$$

where $P(t)$ is the probability that recolonization begins in year t , and $T(f)$ is the

time (in years) after the fecal pat event occurred on the plot.

b) The probability of a western harvester ant mound occurring on a plot is 0.00002/y. I assumed that the presence of an ant mound on a plot results in the death of all plants, except shrubs and some perennial grasses larger than a seedling, and O. polyacantha clumps. I based this assumption on the physical stature of the plants and field observations of the nest selection process by harvester ants. The recovery of plants begins 20-40 years after the ant mound was initiated. The time for recovery to begin is based on the estimated time that harvester ants occupy a particular nest site calculated from an analysis of mound turnover times (Chapter 2).

c) The probability of a small animal burrow occurring on a plot is 0.000006/y. I assumed that the pile of soil produced by small burrowing animals always kills all plants on the plot, and recolonization is possible immediately based on field data from Chapter 2.

Experimental Simulations

The successional dynamics of plants on gaps was evaluated using simulations of 50- and 250-years for plants

on a single plot and for the average of 50 plots. All simulations started at a bare plot stage and were parameterized for a moderately grazed swale at the CPER. For clarity of presentation, the dynamics of the aboveground biomass of plants through time are shown by resource-groups (Table 4.1). The recovery time of B. gracilis was calculated as the time required for B. gracilis to reach 90% of its average aboveground biomass.

The spatial variability in gap dynamics across a landscape was evaluated using 250 plots for simulations of 1000 years each. The aboveground biomass for each resource- and species-group at the end of the simulation was used to generate a statistical distribution of the composition of the landscape.

Results and Discussion

50-year simulations

The recovery of plants on a single plot in the first fifty years after a disturbance indicates a large variability in the aboveground biomass both within and among the five resource-groups (Fig. 4.6a). Biomass values ranged from 4 g/m² in the first year to >200 g/m² in year 15 due to the presence of a large shrub, C. nauseosus. The shrub was on the plot for 5-10 years and died as a result of insufficient resources. Bouteloua gracilis entered the plot in year 13 and achieved its average aboveground biomass (92 g/m²) after five years (Fig. 4.6a). During the initial

sixteen years of recovery, perennial grasses and perennial forbs and shrubs had the highest biomass values. After B. gracilis dominated the plot, perennial grass biomass ranged from 0-25 g/m² and perennial forb and shrub biomass ranged from 2-15 g/m². Succulents entered the plot in year 10 after which time their biomass values ranged from 8-29 g/m², while annuals entered the plot the first year and had biomass values ranging from 0-13 g/m² (Fig. 4.6b). The variability in the biomass of succulents was a function of the effects of precipitation, and indicates a change of <1 to 7 cladodes/m² between two years.

A large variability was also found in the basal cover of Bouteloua gracilis. Cover values ranged from 28-51% with an average of 35% after the initial recovery period (Fig. 4.7a). Perennial grasses, forbs and shrubs had the highest proportion of the aboveground biomass for the 16 years immediately following the disturbance, and a much lower proportion thereafter (Fig. 4.7b). Bouteloua gracilis contributed 54-84% of the biomass for the remainder of the simulation. After entering the plot, succulents were an important component of the biomass by contributing 7-13% to the total biomass. A relatively small percentage (<5%) of the biomass throughout the 50 years was attributed to annuals.

The aboveground biomass for each resource-group was less variable for the average of 50 plots over 50 years than for a single plot (Fig. 4.8a,b). In the first six years,

perennial grasses had the highest biomass values of the five groups, with a peak of 44 g/m² in year 4, while annuals also had high biomass values in the first year. Starting in year 7, B. gracilis had the highest biomass values and reached its average of 89 g/m² in year 20. Perennial grasses averaged 24 g/m² and perennial forb and shrub biomass averaged 6 g/m² over the 50 year time period. The biomass of succulents increased for the first 25 years with an average over the 50 years of 12 g/m², while the biomass of annuals peaked in the first year (6 g/m²) and averaged 3 g/m² (Fig. 4.8b).

The basal cover of B. gracilis averaged 34% after the first 20 years of recovery (Fig. 4.9a). The relatively large range in cover values found on a single plot (Fig. 4.7a) was reduced by averaging over 50 plots (31-38%). In the first year after a disturbance, 45% of the aboveground biomass was attributed to perennial grasses, 23% to annuals, 17% to B. gracilis, 12% to succulents, and 3% to perennial forbs and shrubs.

These results are comparable to the results from an experimental study of short-term dynamics on three small disturbances (plots produced artificially, western harvester ant mounds, and animal burrows), with several exceptions related to the effects of the characteristics of the disturbance on the source of propagules (Chapter 3). Perennial grasses were important on all three types of disturbances, while annuals were only important on

artificially-produced plots and ant mounds. The relatively few annuals found on small animal burrows may be a result of the soil being removed by the animals from deeper depths in the profile (> 5cm) than where seeds are stored in grasslands (Roberts 1981). In contrast to the model results, perennial forbs were also important on ant mounds and animal burrows in the field, primarily as a result of vegetative growth by S. coccinea.

The most important effects of different disturbance characteristics may be on the recovery time of B. gracilis. Of the three disturbance types studied in the field, B. gracilis was only found on animal burrows. The average time required for B. gracilis to occur (7 years) on the simulated plots is slower than on animal burrows; therefore the time required for B. gracilis to dominate the simulated plots may also be slower than for animal burrows. The long-term monitoring of small disturbances in the field is necessary to evaluate the effects of different disturbances on the recovery time of B. gracilis.

An average of 68% of the aboveground biomass on the simulated plots was attributed to B. gracilis after the initial 20 year recovery period, with 14-17% attributed to perennial grasses, 3-8% to perennial forbs and shrubs, 1-3% annuals, and 9-13% succulents (Fig. 4.9b). The relative proportion of the aboveground biomass and the average biomass values for each group are comparable to the composition of shortgrass plant communities (Sims et al

1978), although a formal validation analysis has not been conducted.

250-year simulations

The variability in aboveground biomass of plants on a single plot over a long time period (250 years) indicates the dominance of B. gracilis through time until the occurrence of a disturbance (Fig. 4.10a). A cattle fecal pat occurred on the plot in year 165 and B. gracilis did not reestablish until favorable environmental conditions developed eight years later. Succulents were found on the plot throughout the 250 years, while there were years when perennial grasses, forbs, shrubs, and annuals were not found on the plot (Fig. 4.10a,b).

The average basal cover of B. gracilis on the plot was 32% for the 250-year period (Fig. 4.11). The 250-year simulation revealed a second scale of variability not evident in the 50-year data. The peaks and subsequent decreases in cover were the result of the establishment of seedlings on the plot followed by the death of plants due to insufficient resources. Bouteloua gracilis seedling establishment events occurred on the average once every 12.5 years. The relatively small changes in cover were due to changes in number of tillers as affected by annual precipitation and available resources.

A large amount of variability was found in the proportion of aboveground biomass on the plot attributed to each resource-group through time with average values of 63%

(B. gracilis), 15% (perennial grasses), 5% (perennial forbs and shrubs), 3% (annuals), and 15% (succulents).

The average aboveground biomass of B. gracilis for 50 plots over 250 years was 88 g/m², with values ranging from 5-103 g/m² (Fig. 4.12a). In most years, perennial grasses had the second highest biomass values with an average of 18 g/m², followed by succulents (16 g/m²), perennial forbs and shrubs (9 g/m²), and annuals (3 g/m²) (Fig. 4.12a,b). The relatively large increases in the average biomass of perennial forbs and shrubs on the plot were a result of C. nauseosus. Although this species occurred infrequently, it had a large effect on the average biomass since the plants are much larger (19.7 g/plant) than plants of other species in this resource-group (average=1.1 g/plant).

Although the basal cover of B. gracilis averaged over 50 plots for 250 years (32%) was the same as the average for a single plot over the same time period, the variability in the cover values was less due to the nonsynchronization for the 50 plots of the three sources of variability in cover through time: B. gracilis seedling establishment events, changes in number of tillers, and disturbance events (Fig. 4.13a). Most of the biomass on the plots through time was attributed to B. gracilis with an average of 66% (Fig. 4.13b). Average percentages of the total biomass for the other resource-groups were 14% (perennial grasses), 6% (perennial forbs and shrubs), 3% (annuals), and 12% (succulents).

The model results indicate that the average time for B. gracilis to dominate the biomass on a plot (20 years) is a more rapid recovery time than has been reported from long-term experimental studies. Most successional studies have been conducted on abandoned agricultural fields where four general vegetation-types were distinguished through time (Costello 1944, Judd 1974, Reichhardt 1982). Annuals typically dominated the plant communities for the first 4-5 years after the fields were abandoned. Short-lived perennials were the dominants for the next 5-10 years followed by long-lived perennials for 10-30 years. The final stage, a shortgrass community dominated by B. gracilis, has been suggested to occur after greater than 50 years of plant recovery (Hyder et al 1971, Reichhardt 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 (Reichhardt 1982).

The recovery of B. gracilis after a disturbance may occur either through tillering or seed germination and establishment. Tillering is a relatively slow process (Hyder et al 1975), and the establishment of seedlings is dependent on two conditions: a restrictive set of microenvironmental conditions must occur (Wilson and Briske 1974, Briske and Wilson 1977; 1978), and germinable seeds

must be present. My initial set of simulations assumed B. gracilis seeds were always present and the control on the establishment of B. gracilis seedlings was solely the occurrence of the microenvironmental conditions. Little information is known about the availability of B. gracilis seeds to disturbed areas, although a field study indicated relatively few B. gracilis seeds were stored in the soil (60 seeds/m² averaged over a two-year sampling period), and a large variability was found in the number of seeds stored through time (Appendix II). These results suggest that seeds may be a limiting factor in the recovery of B. gracilis after disturbances.

Therefore, I conducted a second 250-year simulation to evaluate the effects of seed availability on the average recovery time of B. gracilis after a disturbance, and on the successional dynamics through time averaging over 50 plots. I assumed the microenvironmental conditions had the same probability of occurrence as in the first set of simulations (Figs. 4.6-4.13), and I included an independent probability that B. gracilis seeds were present on the plot based on the annual precipitation. The probability was a function of the amount of precipitation received in the previous year since B. gracilis seeds produced in the fall of one year are available for germination in the spring of the following year (Dickinson and Dodd 1976, Appendix II). I assumed that even in the wettest year the probability of seeds being present is small since few B. gracilis seeds persist in the

soil through time (Appendix II); thus the production of seeds in one year does not necessarily result in seeds being available the following year. Therefore, the probability function was:

$$P_s = 1.0 - 0.99 \cdot \exp(-0.0018953 \cdot (\text{LYPPT} - 105)) \quad (18)$$

where P_s is the probability of B. gracilis seeds 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 (precipitation=105 mm) to 0.55 in the wettest year (precipitation=520 mm).

Successional dynamics and B. gracilis seed availability

The average recovery time (65 years) for B. gracilis to achieve its average biomass (87 g/m²) was significantly higher ($p=0.0$) when seed availability was a function of annual precipitation (Fig. 4.14b) than when seeds were always present (Fig. 4.14a). The greatest effect on successional dynamics was during the initial recovery period of B. gracilis (the first 65 years) when the biomass of perennial grasses (30 g/m²), and perennial forbs and shrubs (10 g/m²) were higher when B. gracilis seeds were based on a probability distribution than when seeds were always present (23 and 7 g/m² respectively). The average biomass values for each resource-group and B. gracilis basal cover, after the initial recovery of B. gracilis, were not significantly different for the two conditions of seed availability. The proportions of the aboveground biomass attributed to each resource-group were also similar for the 250-year period,

except for the larger proportion of biomass for a longer time period attributed to perennial grasses and associated with the longer recovery time of B. gracilis when seeds were not always present on the plot (Fig. 4.15).

The recovery time of 65 years is comparable to estimates from field data. However, the model results indicate that B. gracilis achieved 50% of its average biomass 30 years after the disturbance occurred in order for it to dominate the biomass on the plot in 65 years. Therefore, this is still a faster recovery time than was observed experimentally. It is possible that B. gracilis seeds are present on disturbed areas less frequently than was used in the simulation, or their presence may be a function of the spatial scale of the disturbance. Experimental work on the relationship between disturbance size and the production, dispersal and storage of germinable B. gracilis seeds is necessary to distinguish between the two possibilities associated with the availability of seeds. Another possibility for the difference between the results from the model and the field studies is the scale-dependence of other successional processes, such as the occurrence of the microenvironmental conditions required for the establishment of B. gracilis seedlings.

Bouteloua gracilis may also recolonize disturbed areas by tillering, which may be an effective process over relatively short distances. Tillering by surrounding plants was not included in the simulation model and has apparently

not occurred on abandoned fields. Although tillering by the B. gracilis plants surrounding ant mounds or animal burrows did not occur in the first year after plant recovery began (Chapter 3), it is possible that this process will be important in the recolonization of small disturbances through time. The result would be a faster recovery time by B. gracilis on small disturbances than indicated by the simulation model or the large-scale disturbance studies.

Spatial variability of a simulated landscape

Most of the plots in the simulated landscape (>76%) had 60-80% of their aboveground biomass attributed to B. gracilis while >96% of the plots had greater than 40% of their biomass attributed to B. gracilis (Fig. 4.16a). A relatively small percentage of the plots (<2%) were composed entirely of species other than B. gracilis.

The plots were grouped into five biomass classes based on the percentage contribution of B. gracilis to the total biomass (Fig. 4.16b). Plots without B. gracilis (0-20% class) were dominated by perennial grasses with a biomass of 6 g/plot. Most of the grasses on these plots were A. purpurea var. longiseta (3 g/plot), S. hystrix (2 g/plot), and C. heliophila (1 g/plot) (Table 4.3). Two species-groups of annuals were also important (V. octoflora and L. densiflorum). Plots in the 20-40% B. gracilis biomass class had large amounts of perennial forbs and shrubs (19 g/plot), primarily due to the C. nauseosus species-group (18

g/plot). Biomass values of perennial grasses, succulents, and annuals on these plots were less than 3 g/plot each.

The species composition on plots in the 40-60% and 60-80% biomass classes were similar; B. gracilis, perennial grasses, and succulents had the highest biomass values followed by perennial forbs and shrubs, and annuals. Important species-groups on these plots besides B. gracilis were A. purpurea var. longiseta, C. heliophila, S. hystrix, S. coccinea, and O. polyacantha. Plots with greater than 80% of their biomass attributed to B. gracilis had relatively small biomass values of the four other resource-groups (≤ 1 g/plot). Sphaeralcea coccinea, S. hystrix, and O. polyacantha were important species-groups on these plots.

Although the gap dynamics conceptualization of plant communities is based on population dynamics occurring on small patches, a landscape composed of patches, each undergoing its own successional dynamics through time, was representative of the species composition of shortgrass communities. The species composition averaged over the simulated landscape was obtained by weighting the biomass of each species-group within each B. gracilis biomass class by the frequency of the class. The result was a B. gracilis-dominated landscape with an average biomass of 134 g/m^2 of which 90 g/m^2 was due to B. gracilis and 17 g/m^2 was due to O. polyacantha, the species-group with the second highest average biomass value (Fig. 4.17). The perennial grasses, A. purpurea var. longiseta, C. heliophila, and S. hystrix,

the perennial forb S. coccinea, and the perennial shrub C. nauseosus were also important components of the simulated landscape with biomass values ranging from 3-7 g/m². The remaining species-groups had biomass values less than 1.1 g/m². These results support Whittaker's (1975) hypothesis of the connection among population ecology and community ecology that results from considering landscapes to be composed of a mosaic of microsites where interactions among individual plants produces the structure of the community.

Model Analysis

A sensitivity analysis was conducted to evaluate the relative response of the recovery time of B. gracilis and the average biomass of the five resource-groups to variability in the parameter values. Details of the analysis can be found in Appendix III. Due to the large number of parameters in the model (109), a subset (30) was chosen for the analysis based on the structure of the model and the expected effect of the parameters on the output variables.

The output variables were generally insensitive to variability in the parameter values as indicated by the relatively small partial correlation coefficients (0.0-0.474). The recovery time of B. gracilis was most sensitive to the growth rate of B. gracilis, while the biomass values of each resource-group was most sensitive to parameters directly associated with each group (for example, the

biomass of annuals and the proportion of the resource space associated with annuals). Parameters associated with B. gracilis or the size of the resource space in years of average precipitation were also important. The biomass values of perennial forbs and annuals were also sensitive to the probabilities associated with the availability of seeds. The average biomass of B. gracilis, perennial grasses and annuals were the output variables found to be the most sensitive to these parameters based on the large F-values associated with their parameters. The recovery time of B. gracilis and the biomass of succulents were of intermediate sensitivity and the biomass of perennial forbs was relatively insensitive to variability in the parameters.

Conclusions

The aboveground biomass on the simulated plots from the gap dynamics model was dominated by B. gracilis through time and space. The relative proportion of the aboveground biomass and the average biomass values for each species are comparable to the composition of shortgrass plant communities (Sims et al 1978). Therefore, I can tentatively accept my hypothesis that a gap dynamics conceptualization of shortgrass plant communities based on the importance of small, frequently-occurring disturbances and belowground resources provides a promising alternative to a conceptual model that emphasizes the effects of large-scale disturbances. Although further experimental work on gap

processes in semiarid grasslands is required to provide support for my hypothesis, initial indications suggest that gap processes are important to this community. The gap dynamics conceptualization has been used extensively in temperate and tropical forests (Botkin et al 1972, Denslow 1980, Doyle 1981, Runkle 1981, Brokaw 1982;1985;1987, Shugart 1984, White et al 1985), and the successful extension of the approach to a semiarid grassland may indicate that similar processes are occurring across different types of plant communities.

LITERATURE CITED

- Bormann, F. H., and G. E. Likens. 1979. Pattern and process in a forested ecosystem. Springer-Verlag. New York.
- Botkin, D. B., J. F. Janak, and J. R. Wallis. 1972. Some ecological consequences of a computer model of forest growth. *Journal of Ecology* 60:849-873.
- Bourgeron, P. S., W. K. Lauenroth, W. J. Parton, and G. Zimmerman. 1987. Analysis of precipitation in the shortgrass region of North America: Implications for the soil-plant system. *Journal of Ecology* (submitted).
- Briske, D. D., and A. M. Wilson. 1977. Temperature effects on adventitious root development in blue grama seedlings. *Journal of Range Management* 30:276-280.
- Briske, D. D., and A. M. Wilson. 1978. Moisture and temperature requirements for adventitious root development in blue grama seedlings. *Journal of Range Management* 31:174-178.
- Brokaw, N. V. L. 1982. The definition of treefall gap and its effect on measures of forest dynamics. *Biotropica* 14:158-160.
- Brokaw, N. V. L. 1985. Gap-phase regeneration in a tropical forest. *Ecology* 66:682-687.
- Brokaw, N. V. L. 1987. Gap-phase regeneration of three pioneer tree species in a tropical forest. *Journal of Ecology* 75:9-19.
- Canfield, R. H. 1957. Reproduction and life span of some perennial grasses of southern Arizona. *Journal of Range Management* 10:199-203.
- Coffin, D. P., and R. D. Dougherty, and W. K. Lauenroth. 1987. Influences of soil texture and vegetation structure on seed dynamics of a shortgrass site. Abstracts of the 40th Annual Meeting, The Society for Range Management, Boise, Idaho.

- Costello, D. F. 1944. Natural revegetation of abandoned plowed land in the mixed prairie association of northeastern Colorado. *Ecology* 25:312-326.
- Coupland, R. T., and R. E. Johnson. 1965. Rooting characteristics of native grassland species in Saskatchewan. *Journal of Ecology* 53:475-507.
- Delcourt, H. R., P. A. Delcourt, and T. Webb III. 1983. Dynamic plant ecology: The spectrum of vegetational change in space and time. *Quaternary Science Reviews* 1:153-175.
- Denslow, J. S. 1980. Gap partitioning among tropical rainforest trees. *Biotropica* 12 (Supplement):47-55.
- Dickinson, C. E., and J. L. Dodd. 1976. Phenological pattern in the shortgrass prairie. *American Midland Naturalist* 96(2):367-378.
- Dougherty, R. L. 1986. The soil water resource of Opuntia polyacantha in semiarid grasslands. Ph. D. Dissertation. Colorado State University, Fort Collins, CO.
- Doyle, T. W. 1981. The role of disturbance in the gap dynamics of a montane rain forest: An application of a tropical forest succession model. Pages 56-76 in D. C. West, H. H. Shugart, and D.B. Botkin, editors. *Forest succession: Concepts and applications*. Springer-Verlag. New York.
- Hyder, D. N., A. C. Everson, and R. E. Bement. 1971. Seedling morphology and seeding failures with blue grama. *Journal of Range Management* 24:287-292.
- Hyder, D. N., R. E. Bement, E. E. Remenga, and D. F. Hervey. 1975. Ecological responses of native plants and guidelines for management of shortgrass range. United States Department of Agriculture-Agricultural Research Service Technical Report No. 1503.
- Judd, I. B. 1974. Plant succession of old fields in the Dust Bowl. *Southwestern Naturalist* 19:227-239.

- Judd, I. B., and M. L. Jackson. 1939. Natural succession of vegetation on abandoned farmland in the Rosebud soil area of western Nebraska. *American Society of Agronomy Journal* 39:541-547.
- Kerster, H. W. 1968. Population age structure of the prairie forb, *Liatris aspera*. *Bioscience* 18(5):430-432.
- Lauenroth, W. K., O. E. Sala, and T. B. Kirchner. 1987. Soil water dynamics and the establishment of seedlings of *Bouteloua gracilis* in the shortgrass steppe: A simulation analysis. Abstracts of the 40th Annual Meeting, The Society for Range Management. Boise, Idaho.
- Lauenroth, W. K., J. L. Dodd, and P. L. Sims. 1978. The effects of water- and nitrogen-induced stresses on plant community structure in a semiarid grassland. *Oecologia (Berlin)* 36:211-222.
- Lee, C. A. 1988. The spatial distribution of roots for three plant life-forms in the shortgrass steppe. M.S. Thesis. Colorado State University, Fort Collins, Colorado. (in prep.).
- Lussenhop, J., D. T. Wisklow, R. Kumar, and J. E. Lloyd. 1982. Increasing the rate of cattle dung decomposition by nitrogen fertilization. *Journal of Range Management* 35:249-250.
- McGregor, R. L. 1986. *Flora of the Great Plains*. University Press of Kansas, Lawrence, Kansas.
- Monson, R. K., R. O. Littlejohn, Jr., and G. J. Williams. III. 1983. Photosynthetic adaptation to temperature in four species from the Colorado shortgrass steppe: a physiological model for coexistence. *Oecologia(Berlin)* 58:43-51.
- Nelson, E. 1934. The influence of precipitation and grazing upon black grama grass range. United States Department of Agriculture Technical Bulletin 409.
- Noy-Meir, I. 1973. Desert ecosystems:environment and producers. *Annual Review of Ecology and Systematics* 4:25-51.
- Reichhardt, K. L. 1982. Succession of abandoned fields on the shortgrass prairie, northeastern Colorado. *Southwestern Naturalist* 27:299-304.

- Riegel, A. 1941. Life history habits of blue grama. *Kansas Academy of Sciences Transactions* 44:76-83.
- Roberts, H. A. 1981. Seed banks in soils. *Advances in Applied Biology* 7:1-55.
- Runkle, J. R. 1981. Gap regeneration in some old-growth forests of the eastern United States. *Ecology* 62:1041-1051.
- Sala, O. E., and W. K. Lauenroth. 1982. Small rainfall events: An ecological role in semiarid regions. *Oecologia (Berlin)* 53:301-304.
- Sala, O. E., and W. K. Lauenroth. 1985. Root profiles and the ecological effect of light rainshowers in arid and semiarid regions. *The American Midland Naturalist* 114:406-408.
- Salisbury, F. B., and C. W. Ross. 1978. *Plant physiology*. Wadsworth Publishing Co., Inc. Belmont, CA.
- Savage, D. A., and H. E. Runyon. 1937. Natural revegetation of abandoned farmland in the central and southern Great Plains. Fourth International Grassland Congress. Aberystwyth, Great Britain, Section 1. *Grassland Ecology* 178-182.
- Shugart, H. H., and D. C. West. 1977. Development of an Appalachian deciduous forest succession model and its applications to assessment of the impact of the chestnut blight. *Journal of Environmental Management* 5:161-179.
- Shugart, H. H. 1984. *A theory of forest dynamics*. Springer-Verlag. New York.
- Sims, P. L., and J. S. Singh. 1978. The structure and function of ten western North American grasslands. III. Net primary production, turnover and efficiencies of energy capture and water use. *Journal of Ecology* 66:573-597.
- Sims, P. L., J. S. Singh, W. K. Lauenroth. 1978. The structure and function of ten western North American grasslands. I. Abiotic and vegetational characteristics. *Journal of Ecology* 66:251-285
- Turner, G. T., and D. F. Costello. 1942. Ecological aspects of the prickly pear problem in Eastern Colorado. *Ecology* 23:419-426.

- Watt, A. S. 1947. Pattern and process in the plant community. *Journal of Ecology* 35:1-22.
- Weaver, J. E. 1919. The ecological relations of roots. Carnegie Institute of Washington Publications.
- Weaver, J. E. 1958. Classification of root systems of forbs of grassland and a consideration of their significance. *Ecology* 39:393-401.
- White, P. S., M. D. MacKenzie, and R. T. Busing. 1985. Natural disturbance and gap phase dynamics in southern Appalachian spruce-fir forests. *Canadian Journal of Forest Research* 15:233-240.
- Whittaker, R. H. 1975. The design and stability of plant communities. Pages 169-181 in W. H. van Dobben and R. H. Lowe-McConnell, editors. *Unifying concepts in ecology*. Dr. W. Junk, The Hague, Pudoc, Wageningen.
- Williams, G. J. III., and J. L. Markley. 1973. The photosynthetic pathway type of North American shortgrass prairie species and some ecological implications. *Photosynthetica* 7:262-270.
- Wilson, A. M., and D. D. Briske. 1979. Seminal and adventitious root growth of blue grama seedlings on the Central Plains. *Journal of Range Management* 32:205-213.
- Wright, R. G. 1972. A demographic study of a semi-desert grassland. Ph.D. Dissertation. Colorado State University, Fort Collins, Colorado.

Table 4.1. Model parameters for resource-groups

RESOURCE-GROUP	PROPORTION OF THE RESOURCE SPACE	DENSITY ¹ (NO/PLOT)	RESOURCE REQUIREMENT PER PLANT
<u>B. gracilis</u>	0.51	1.00	0.510
PERENNIAL GRASSES	0.07	0.33	0.209
PERENNIAL FORBS AND SHRUBS	0.28	1.56	0.180
ANNUAL GRASSES AND FORBS	0.07	1.67	0.042
SUCCULENTS	0.07	0.31	0.226

1 from Chapter 3

Table 4.2. Model Parameters for the fifteen species-groups

RESOURCE- AND SPECIES-GROUPS ¹	AGEMAX (years)	MAXIMUM GROWTH RATE	DISTURBANCE ² CLASS	SEED ESTABL. PROB.	SEEDLING SIZE (g)	VEG. OR CLONAL GROWTH	GROWTH RATE	TEMP. ³ CLASS	BIOMASS ⁴ (g/plant)
<u>Bouteloua gracilis</u> (H.B.K.)Lag. ex Griffiths	NA	NA	1	0.125	0.605	Y	0.474	1	12.096
PERENNIAL GRASSES									
<u>Aristida purpurea</u> Nutt. var. <u>longiseta</u>	25	0.426	3	0.170	0.153	N	0.474	1	3.055
<u>Carex heliophila</u> Mack.	25	0.426	1	0.120	0.070	Y	0.474	2	1.399
<u>Sitanion hystrix</u> (Nutt.)J.G. Sm.	10	0.426	3	0.190	0.153	N	0.474	2	3.055
<u>Schedonnardus</u>									
<u>paniculatus</u> (Nutt.)Trel.	10	0.426	1	0.010	0.153	N	0.474	1	3.055
PERENNIAL FORBS AND SHRUBS									
FORBS									
<u>Sphaeralcea coccinea</u> (Pursh)Rydb.	35	0.426	2	0.015	0.035	Y	0.474	2	0.707
<u>Picrodeniopsis</u>									
<u>oppositifolia</u> (Nutt.)Rydb.	35	0.426	2	0.001	0.106	N	0.474	1	0.707
<u>Machaeranthera</u>									
<u>tanacetifolia</u> (H.B.K.)Nees	10	0.663	2	0.060	0.022	N	0.737	1	0.429
<u>Gaura coccinea</u> Pursh	10	0.663	2	0.011	0.022	N	0.737	2	0.429
SHRUBS									
<u>Chrysothamnus</u>									
<u>nauseosus</u> (Pall.)Britt.	35	0.426	3	0.002	0.986	N	0.474	2	19.726
<u>Gutierrezia sarothrae</u> (Pursh)Britt. and Rusby	10	0.663	3	0.001	0.106	N	0.737	2	2.126

1 Nomenclature follows McGregor (1986)

2 Disturbance Class
 1 = low-statured perennial grasses
 2 = perennial forbs and annuals
 3 = shrubs and bunchgrasses
 4 = succulents

NA = Not Applicable

3 Temperature Class
 1 Warm season and succulents
 2 Cool season

4 from Lauenroth and Milchunas (unpubl.),
 Dougherty (1986), Chapter 3

Table 4.2. (continued)

RESOURCE- AND SPECIES-GROUPS ¹	AGEMAX (years)	MAXIMUM GROWTH RATE	DISTURBANCE ² CLASS	SEED ESTABL. PROB.	SEEDLING SIZE (g)	VEG. OR CLONAL GROWTH	GROWTH RATE	TEMP. ³ CLASS	BIOMASS ⁴ (g/plant)
ANNUAL GRASSES AND FORBS									
GRASSES									
<u>Vulpia octoflora</u> (Walt.) Rydb.	1	0.852	2	0.170	0.022	N	0.947	2	0.429
FORBS									
<u>Chenopodium album</u> L.	1	0.852	2	0.170	0.022	N	0.947	1	0.429
<u>Lepidium densiflorum</u> Schrad.	1	0.852	2	0.170	0.022	N	0.947	2	0.429
SUCCULENTS									
<u>Opuntia polyacantha</u> Haw.	NA	NA	4	0.020	2.250	Y	0.289	1	15.000

1 Nomenclature follows McGregor (1986)

2 Disturbance Class 1 = low-statured perennial grasses

2 = perennial forbs and annuals

3 = shrubs and bunchgrasses

NA = Not Applicable 4 = succulents

3 Temperature Class

1 Warm season and succulents

2 Cool season

4 from Lauenroth and Milchunas (unpubl.), Dougherty (1986), Chapter 3

Table 4.3. Aboveground biomass (g/plot) by species-group for five biomass classes of plots based on the percentage of the total biomass attributed to B. gracilis

SPECIES-GROUP	<u>B. gracilis</u> Biomass Class				
	0-20%	20-40%	40-60%	60-80%	80-100%
<u>B. gracilis</u>	0.0	10.0	10.3	11.4	12.9
<u>A. purpurea</u> var <u>longiseta</u>	2.9	0.8	2.2	0.8	0.1
<u>C. heliophila</u>	1.2	0.6	0.6	0.7	0.5
<u>S. hystrix</u>	1.5	0.0	0.9	0.3	0.1
<u>S. paniculatus</u>	0.3	0.0	0.0	0.1	0.0
<u>S. coccinea</u>	0.0	0.1	0.2	0.4	0.5
<u>C. nauseosus</u>	0.0	18.4	2.0	0.0	0.0
<u>P. oppositifolia</u>	0.0	0.0	0.0	T	0.0
<u>M. tanacetifolia</u>	0.0	0.2	0.1	0.1	0.1
<u>G. coccinea</u>	0.0	0.0	0.0	T	T
<u>G. sarothrae</u>	0.0	0.0	0.0	T	T
<u>V. octoflora</u>	0.1	T	0.2	0.1	0.1
<u>C. album</u>	T	0.0	0.2	0.1	0.1
<u>L. densiflorum</u>	0.1	0.2	0.1	0.1	0.1
<u>O. polyacantha</u>	2.5	2.6	2.7	2.2	1.0
TOTAL	8.6	32.9	19.5	16.3	15.5

T = TRACE (< 0.1 g/plot)

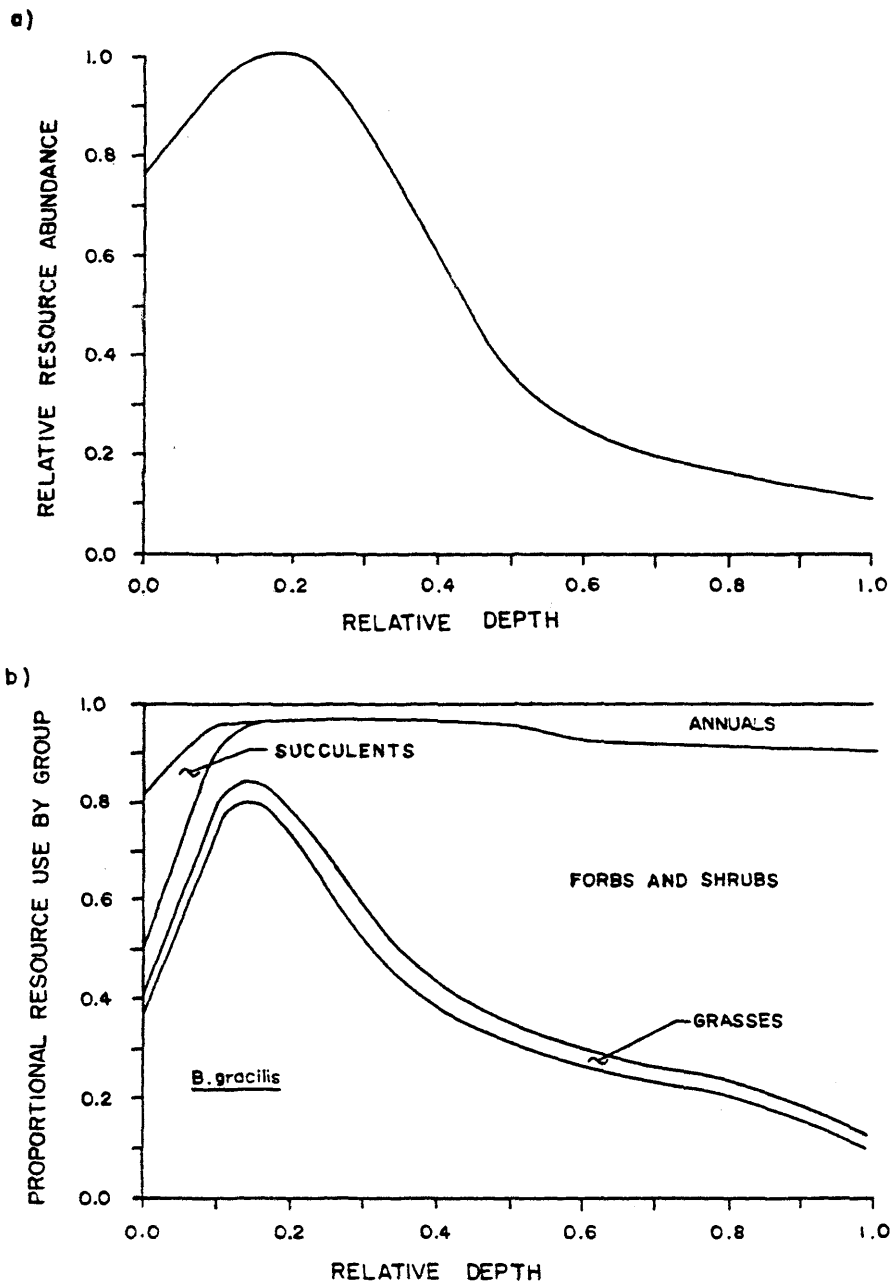


Fig. 4.1. (a) Distribution of soil water resources with depth in the soil profile. (b) Distribution of resource use as a proportion of the total for five resource-groups with depth in the soil profile.

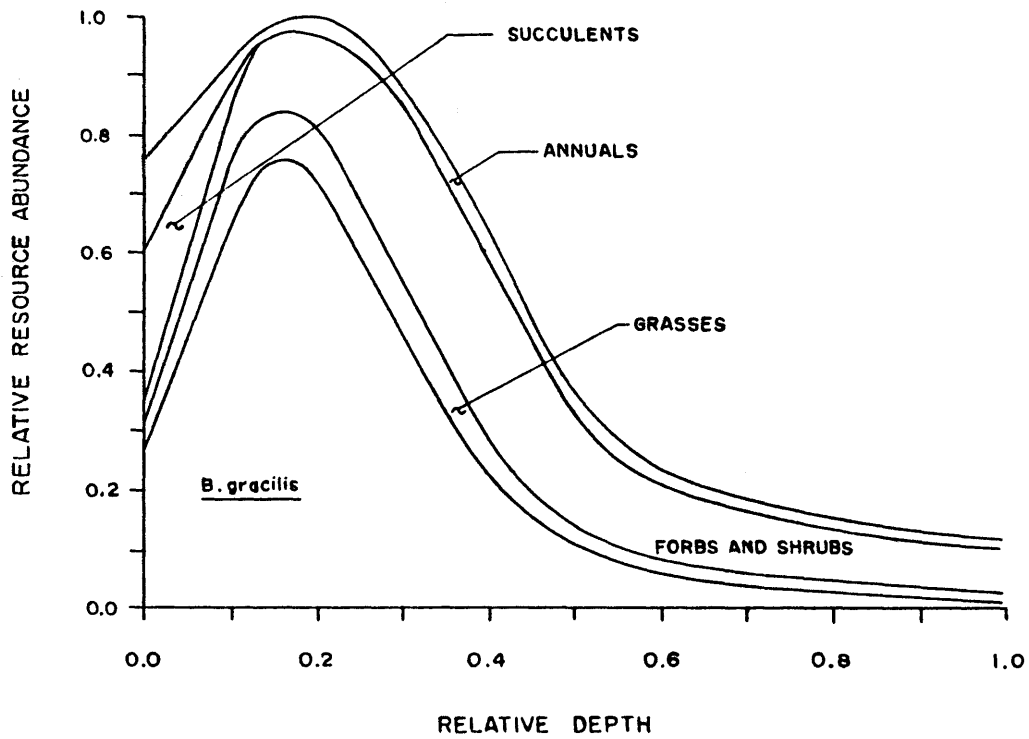


Fig. 4.2. Distribution of resource use with depth in the soil profile as a proportion of the total resources available for five resource-groups.

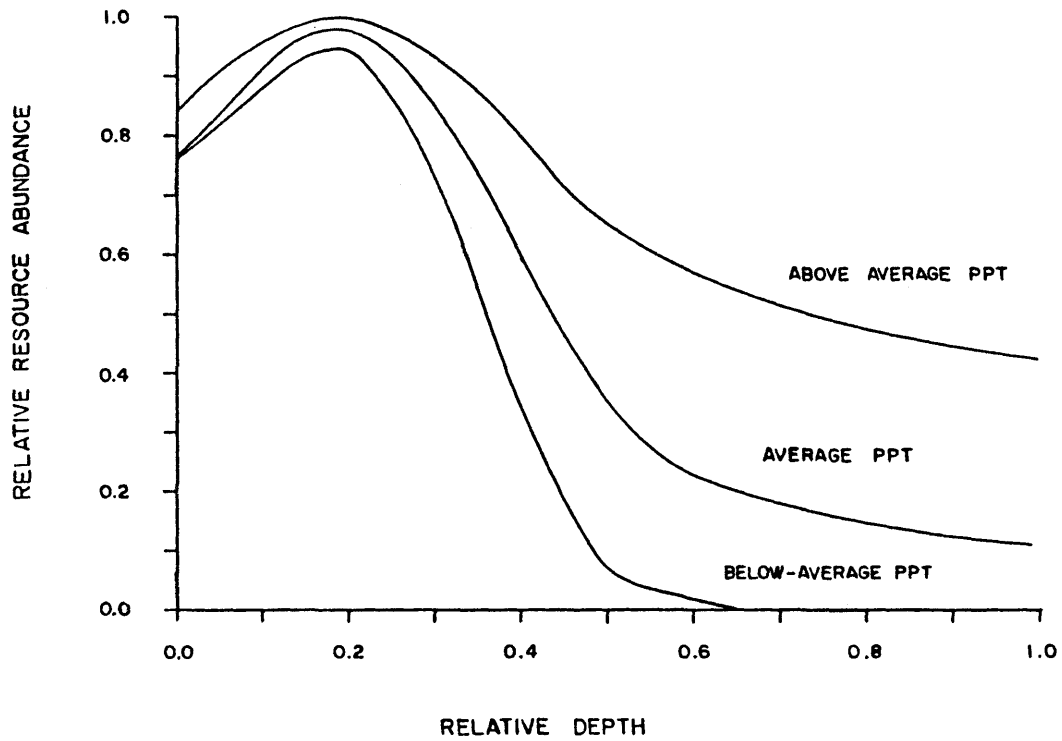


Fig. 4.3. Distribution of soil water resources with depth for three conditions of annual precipitation.

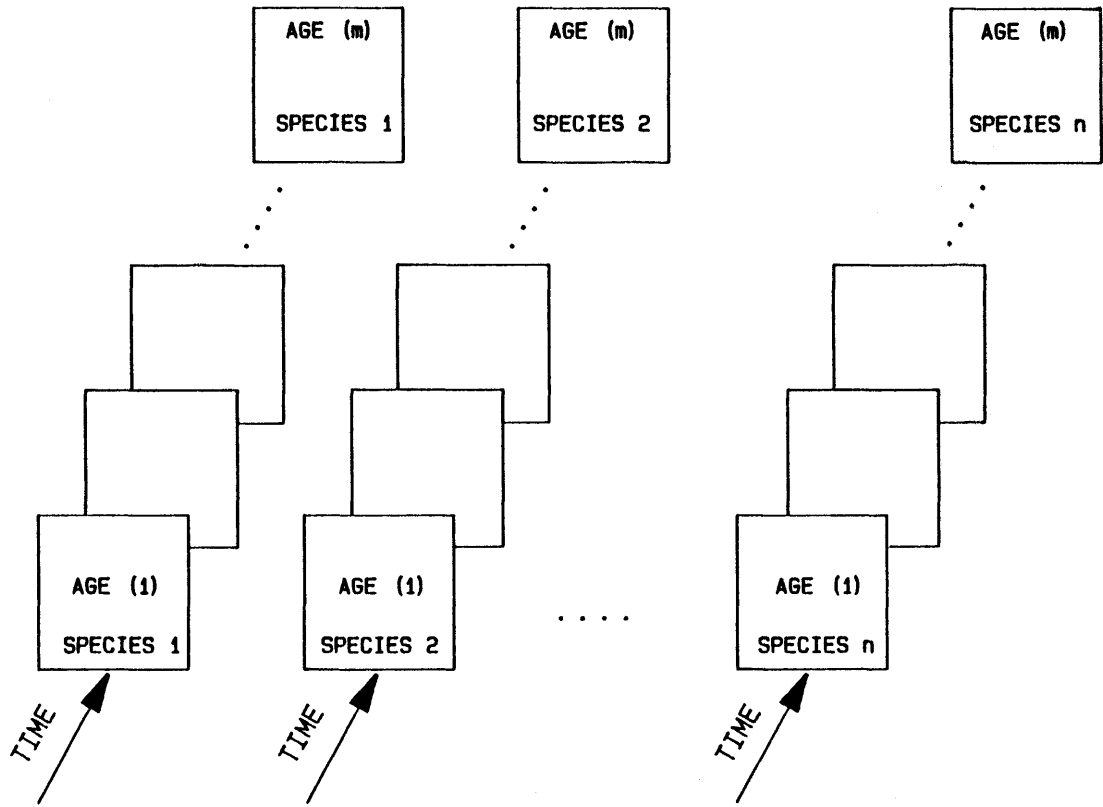
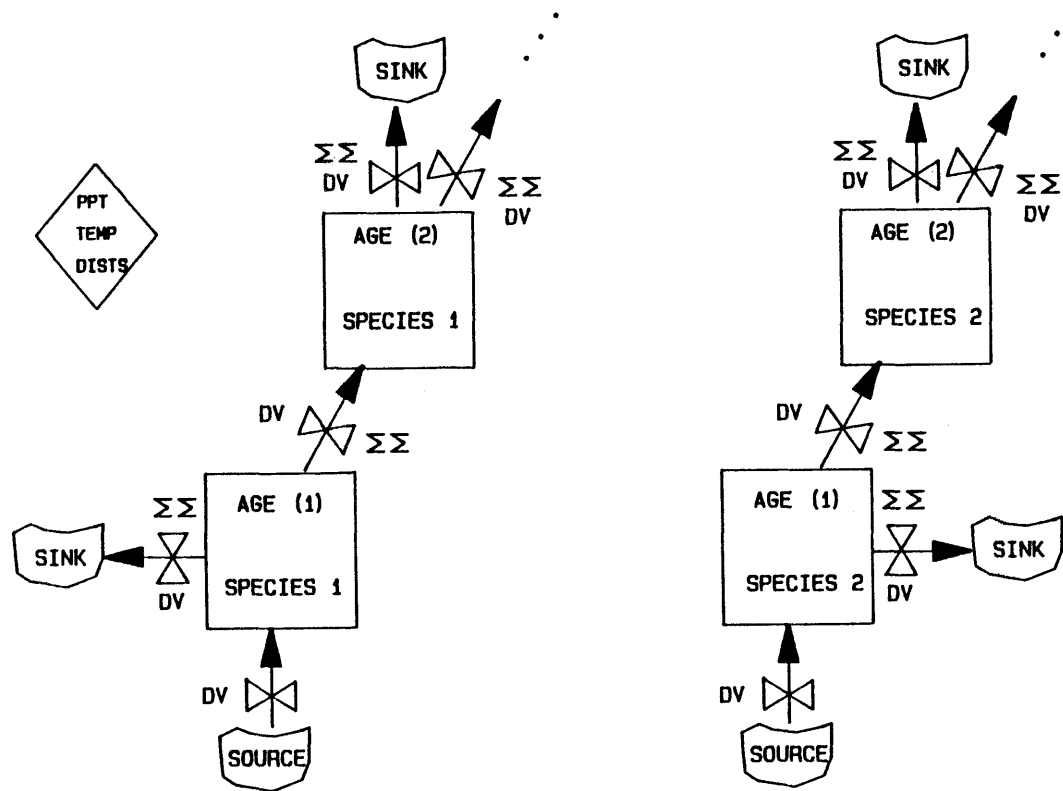


Fig. 4.4a. Diagram for $n=15$ species-groups through time for plants in 1 to m age classes.



PPT = PRECIPITATION
 TEMP = TEMPERATURE
 DISTS = DISTURBANCES

DV INFORMATION FLOW FROM DRIVING VARIABLES
 $\sum_{i=1}^n \sum_{j=1}^m$ INFORMATION FLOW FROM 1-1 TO n SPECIES
 AND j=1 TO m AGE CLASSES

Fig. 4.4b. Generalized Forrester diagram for two representative species-groups.

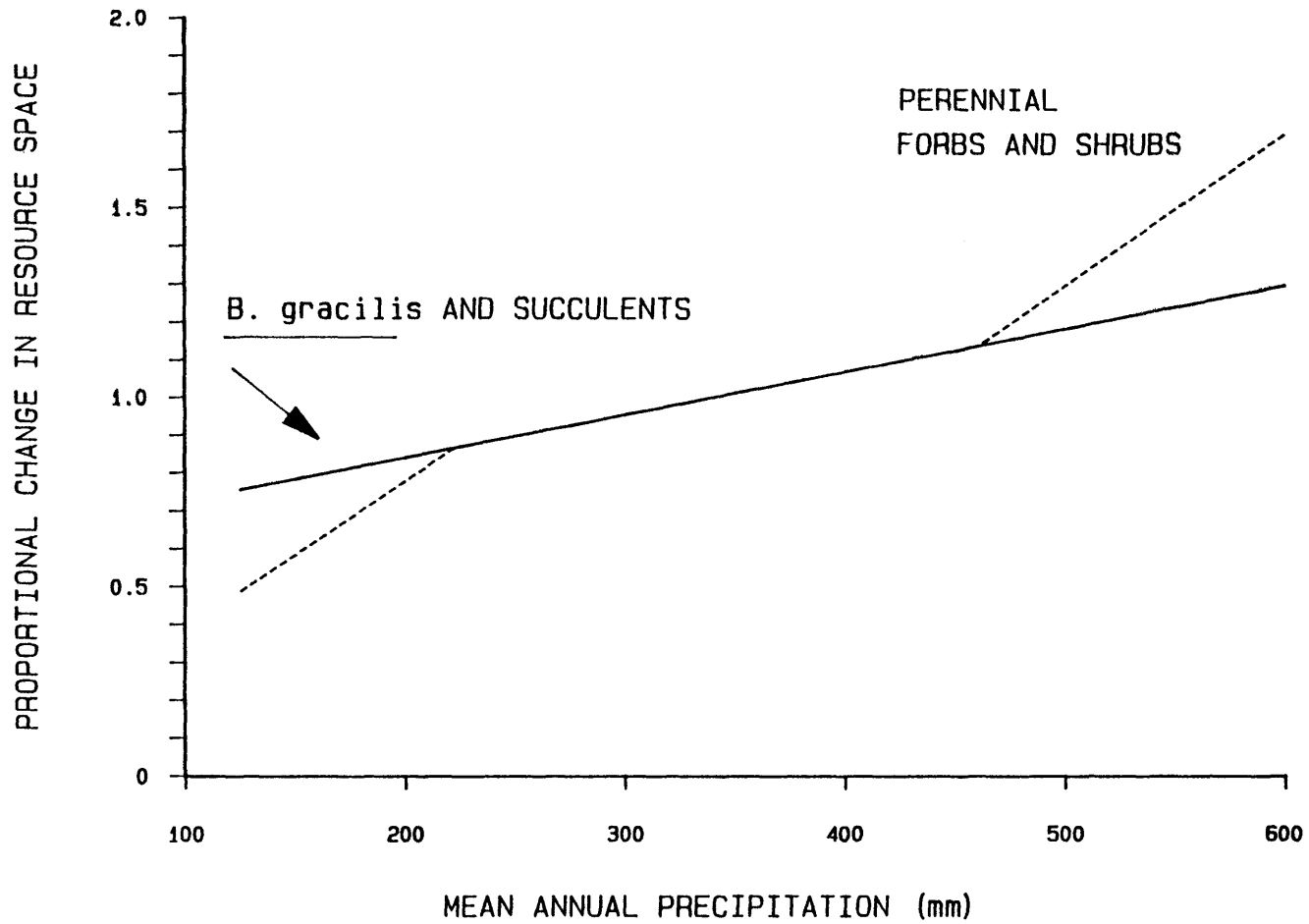


Fig. 4.5. Proportional change in the total resource space as a function of annual precipitation.

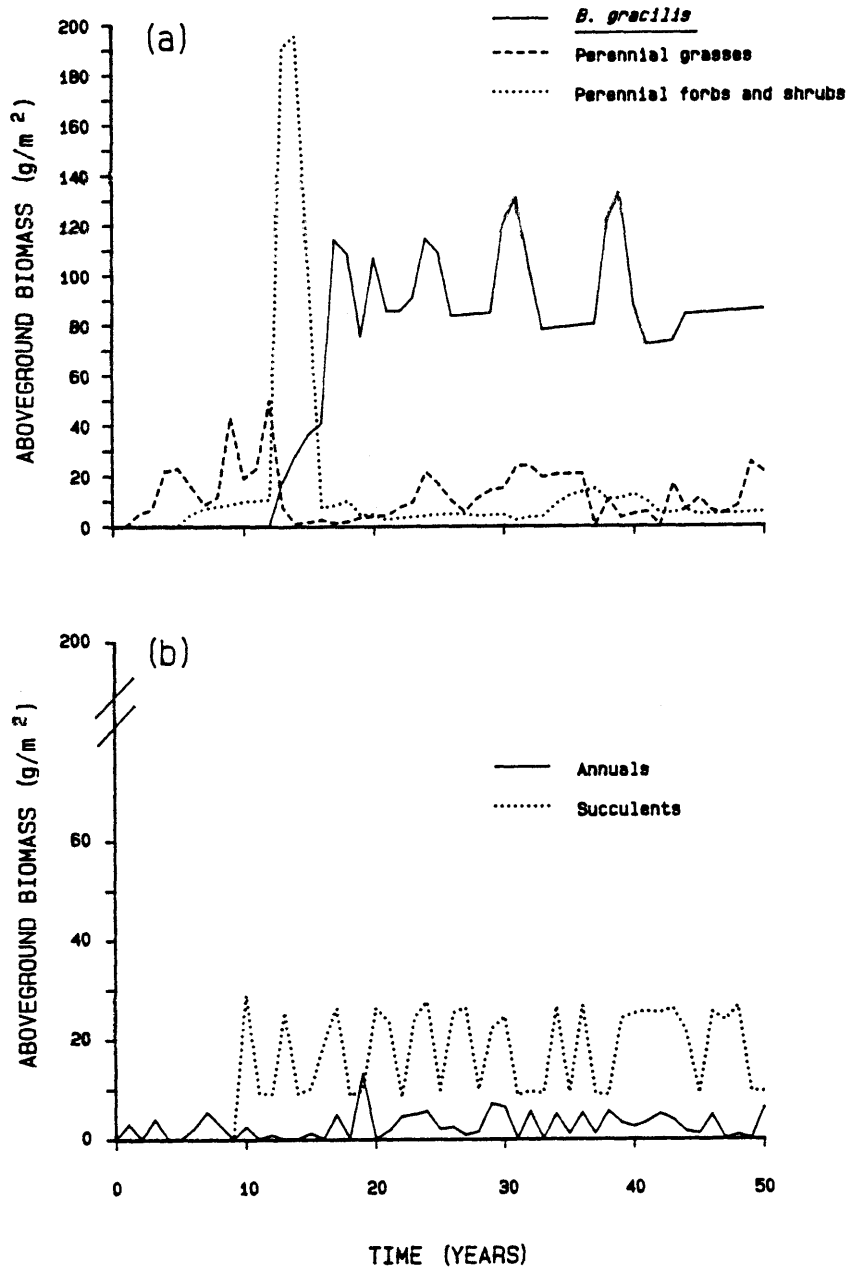


Fig. 4.6. Aboveground biomass of plants on one plot for 50 years for (a) *B. gracilis*, other perennial grasses, and perennial forbs and shrubs (b) annuals and succulents.

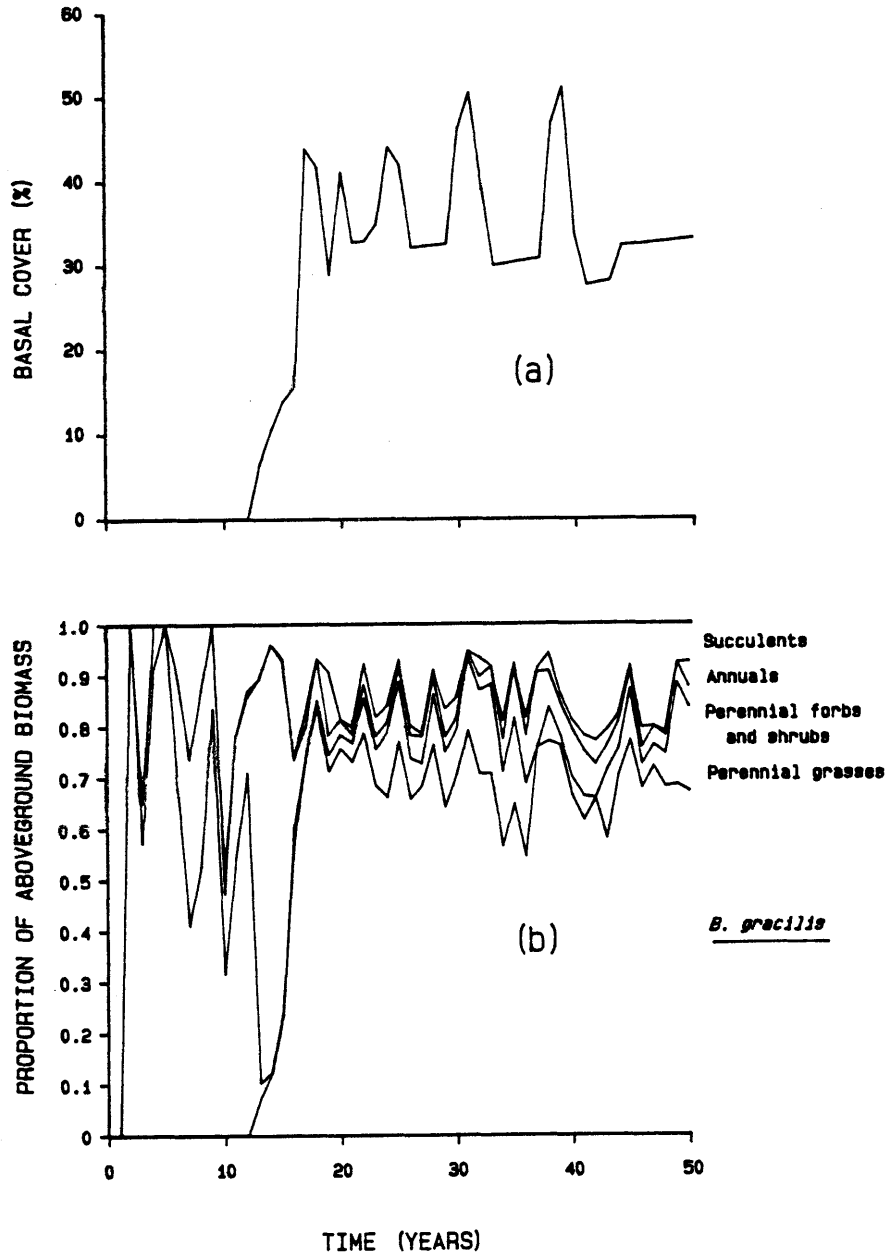


Fig. 4.7. (a) Basal cover of *B. gracilis* on one plot for 50 years. (b) Proportion of the aboveground biomass attributed to five resource-groups on one plot for 50 years.

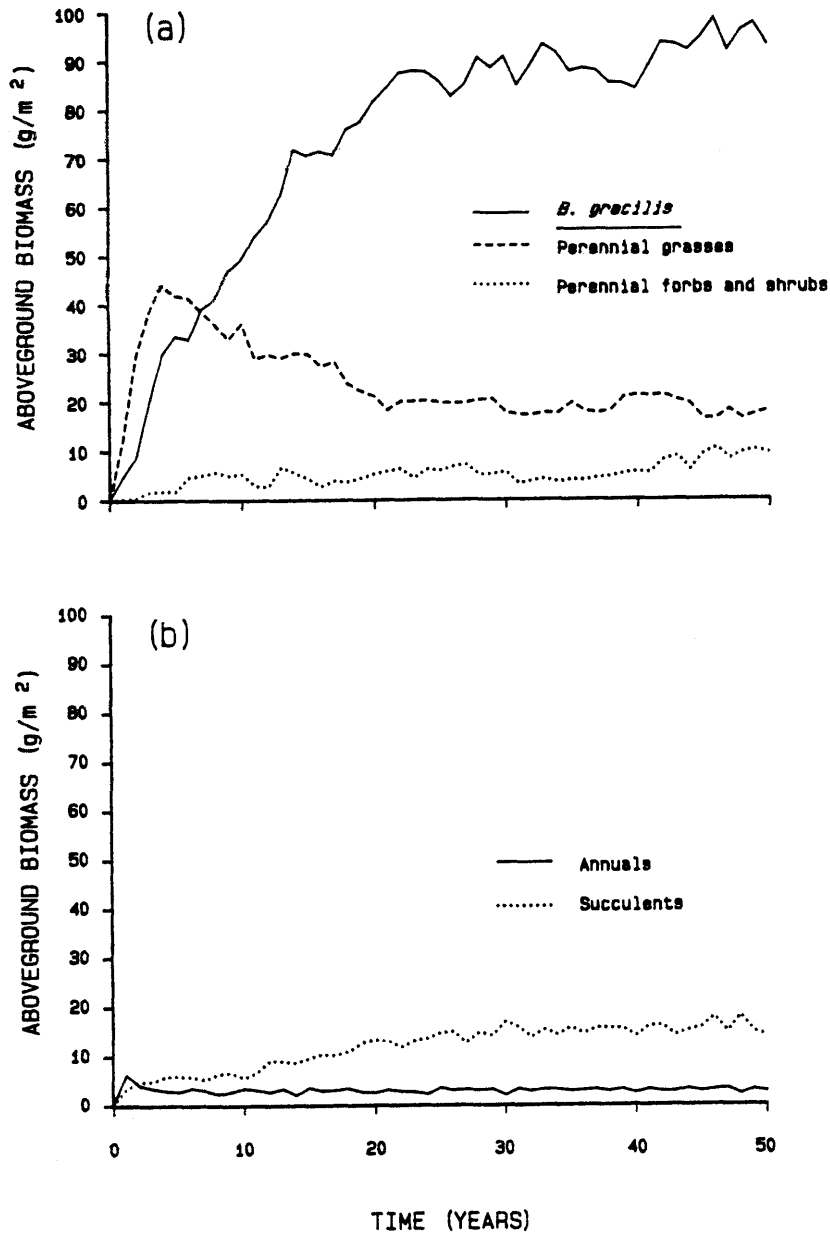


Fig. 4.8. Average aboveground biomass of plants on 50 plots for 50 years for (a) *B. gracilis*, other perennial grasses, and perennial forbs and shrubs (b) annuals and succulents.

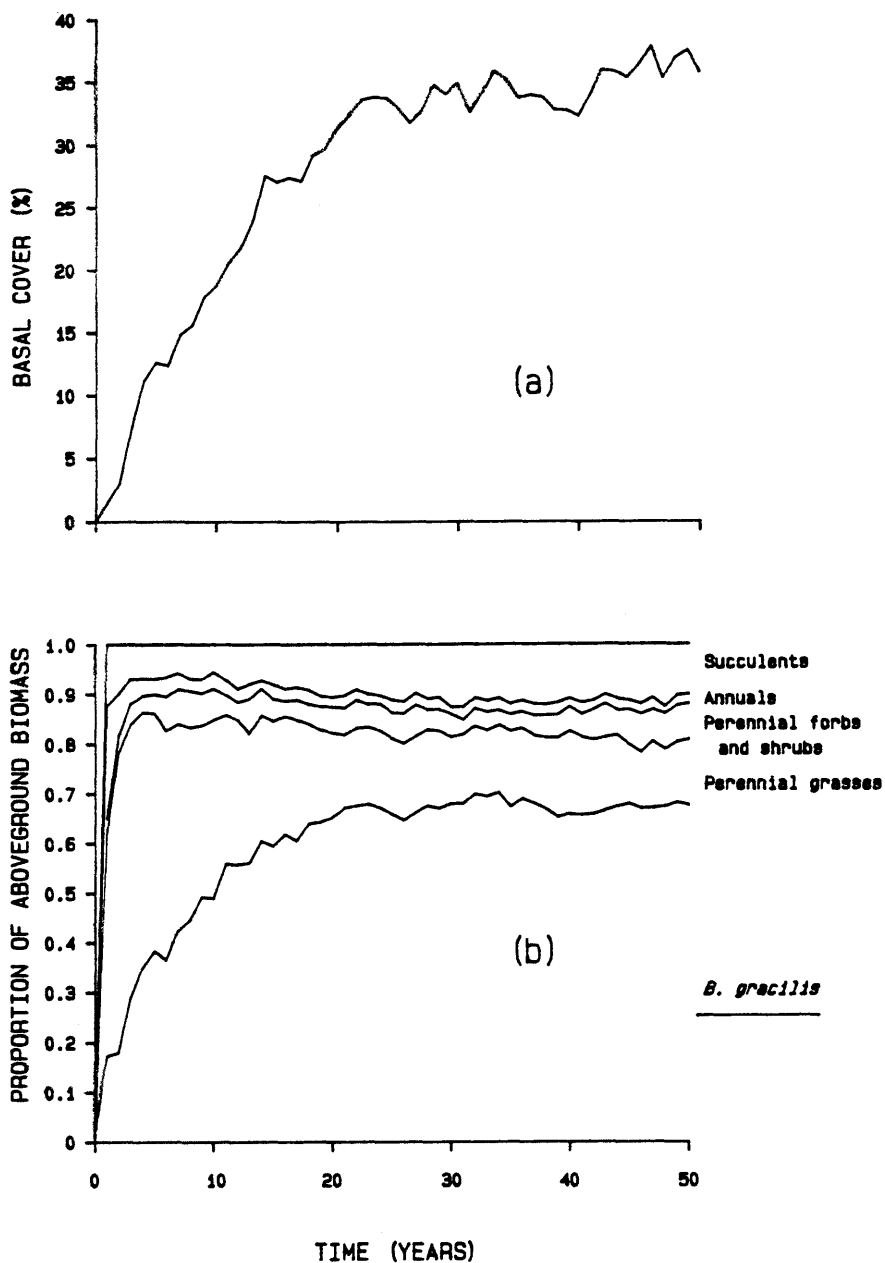


Fig. 4.9. (a) Average basal cover of *B. gracilis* on 50 plots for 50 years. (b) Proportion of the aboveground biomass attributed to five resource-groups on the average of 50 plots for 50 years.

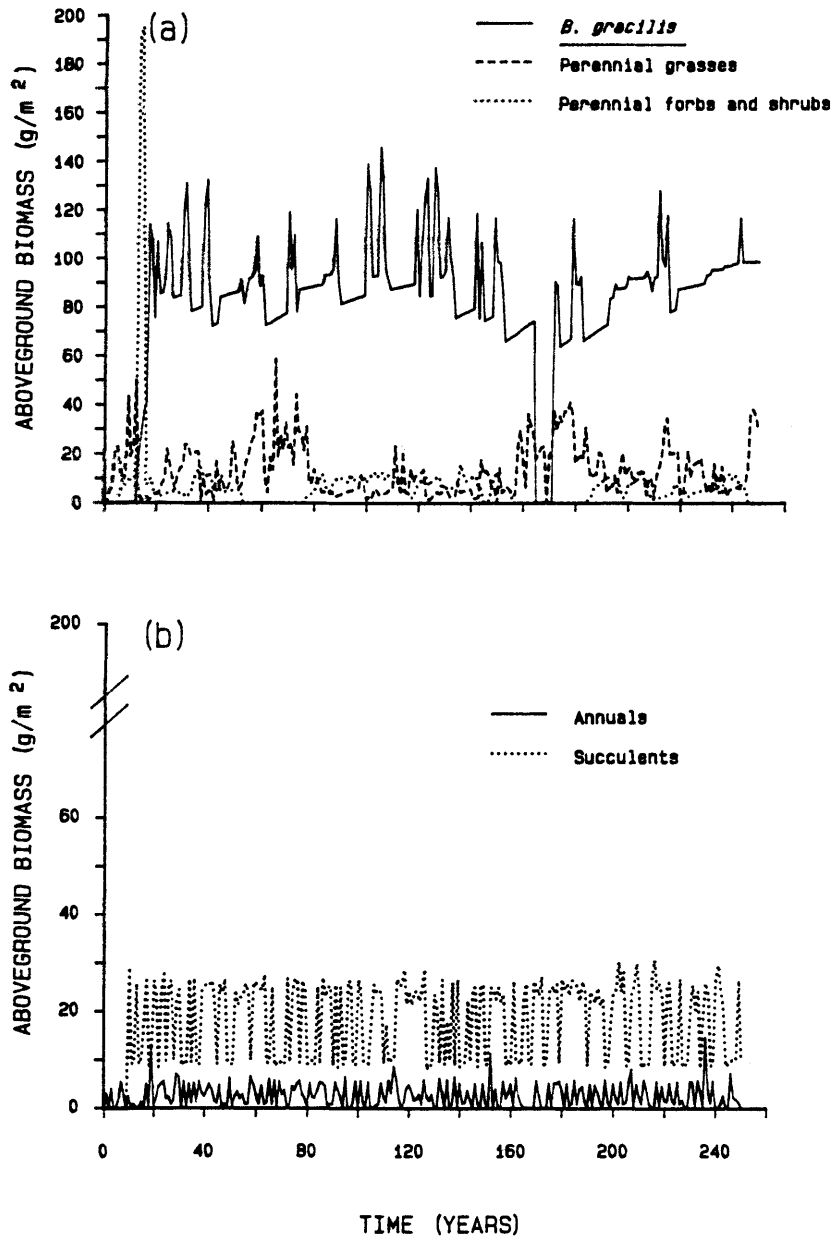


Fig. 4.10. Aboveground biomass of plants on one plot for 250 years for (a) *B. gracilis*, other perennial grasses, and perennial forbs and shrubs (b) annuals and succulents.

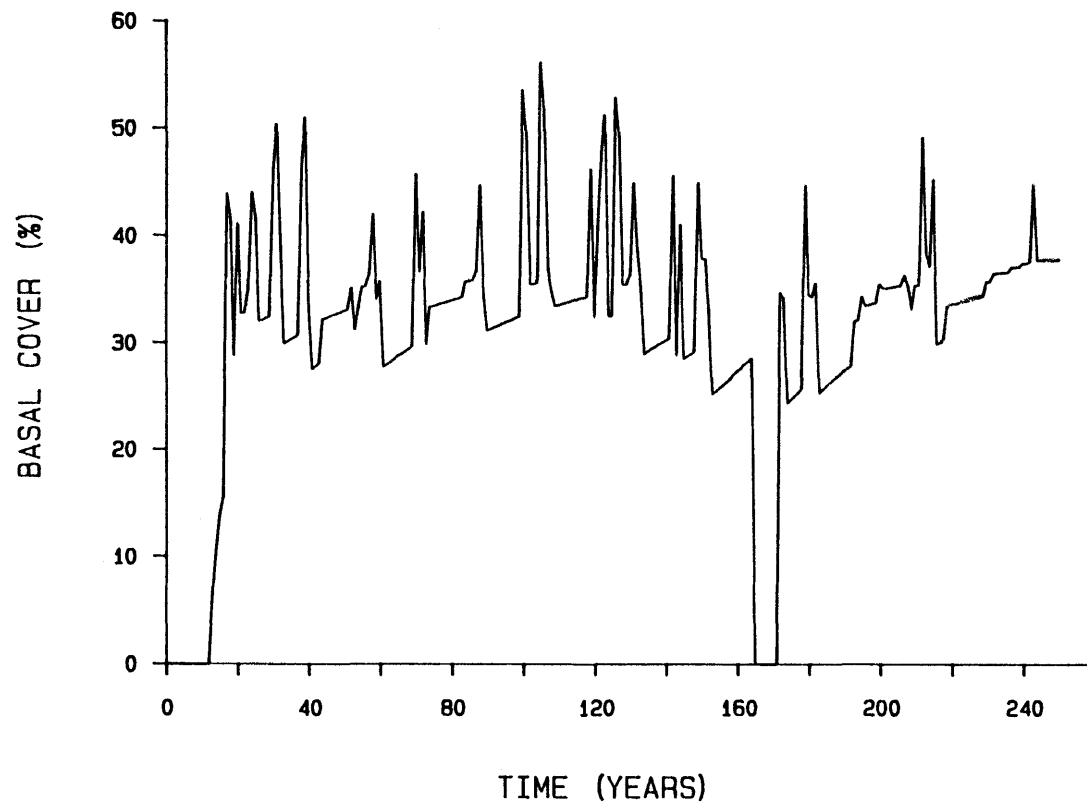


Fig. 4.11. Basal cover of *B. gracilis* on one plot for 250 years.

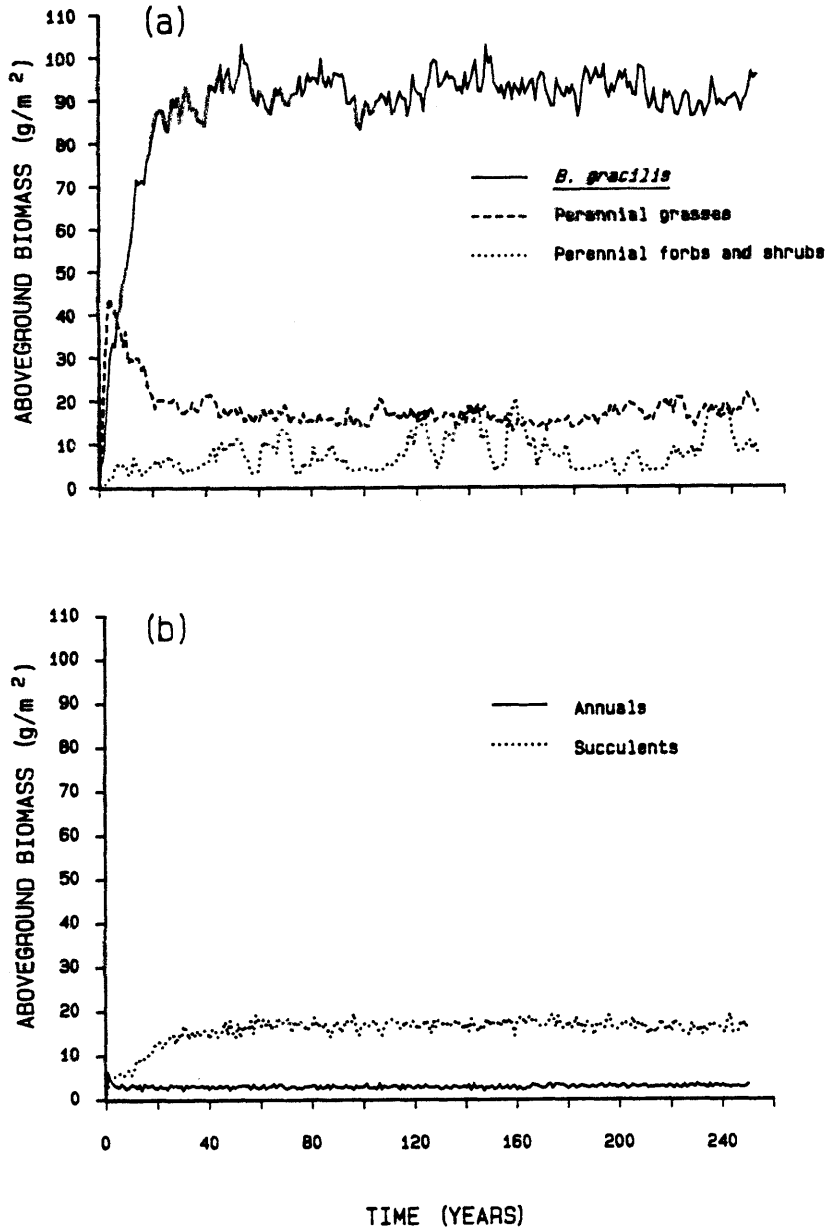


Fig. 4.12. Average aboveground biomass of plants on 50 plots for 250 years for (a) *B. gracilis*, other perennial grasses, and perennial forbs and shrubs (b) annuals and succulents.

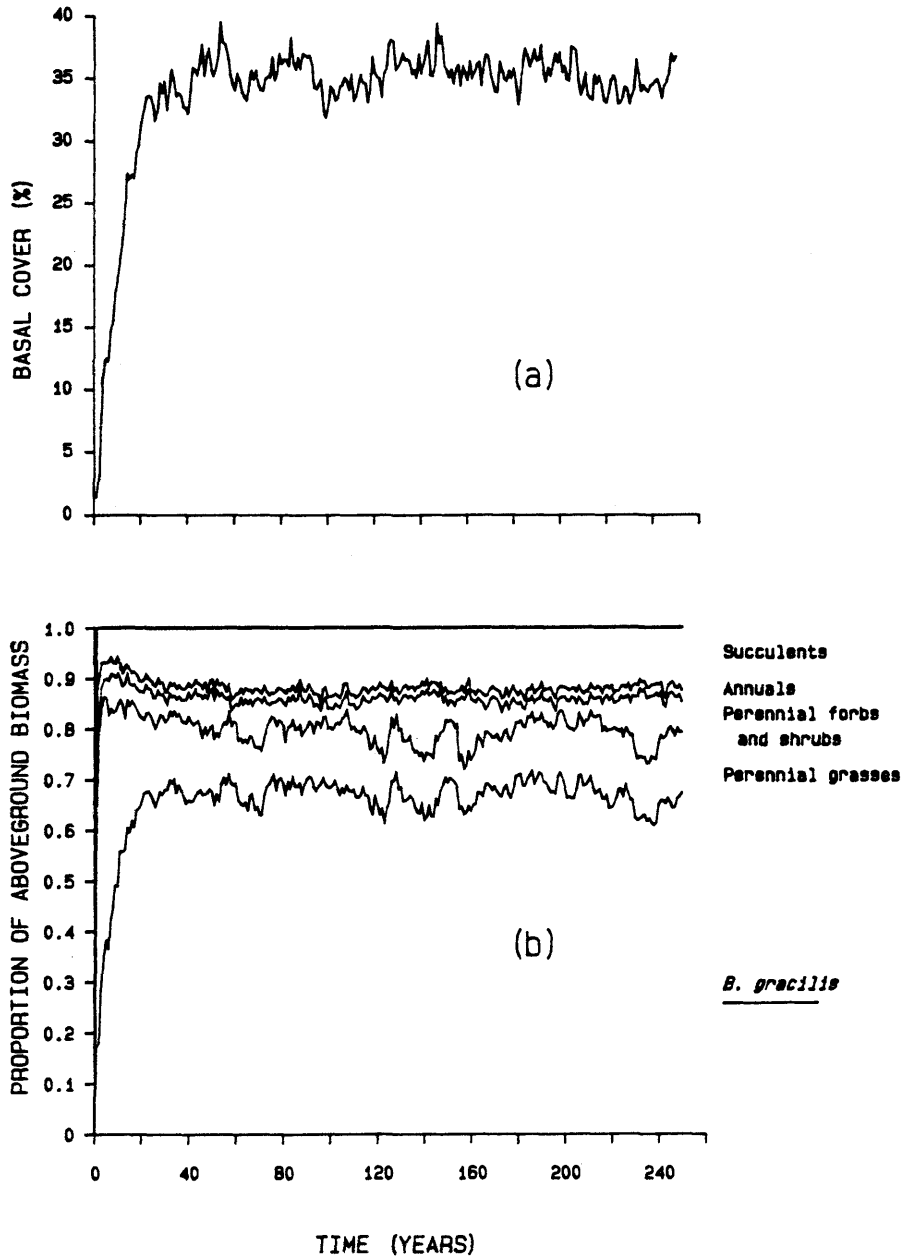


Fig. 4.13. (a) Average basal cover of *B. gracilis* on 50 plots for 250 years. (b) Average proportion of the aboveground biomass attributed to five resource-groups on 50 plots for 250 years.

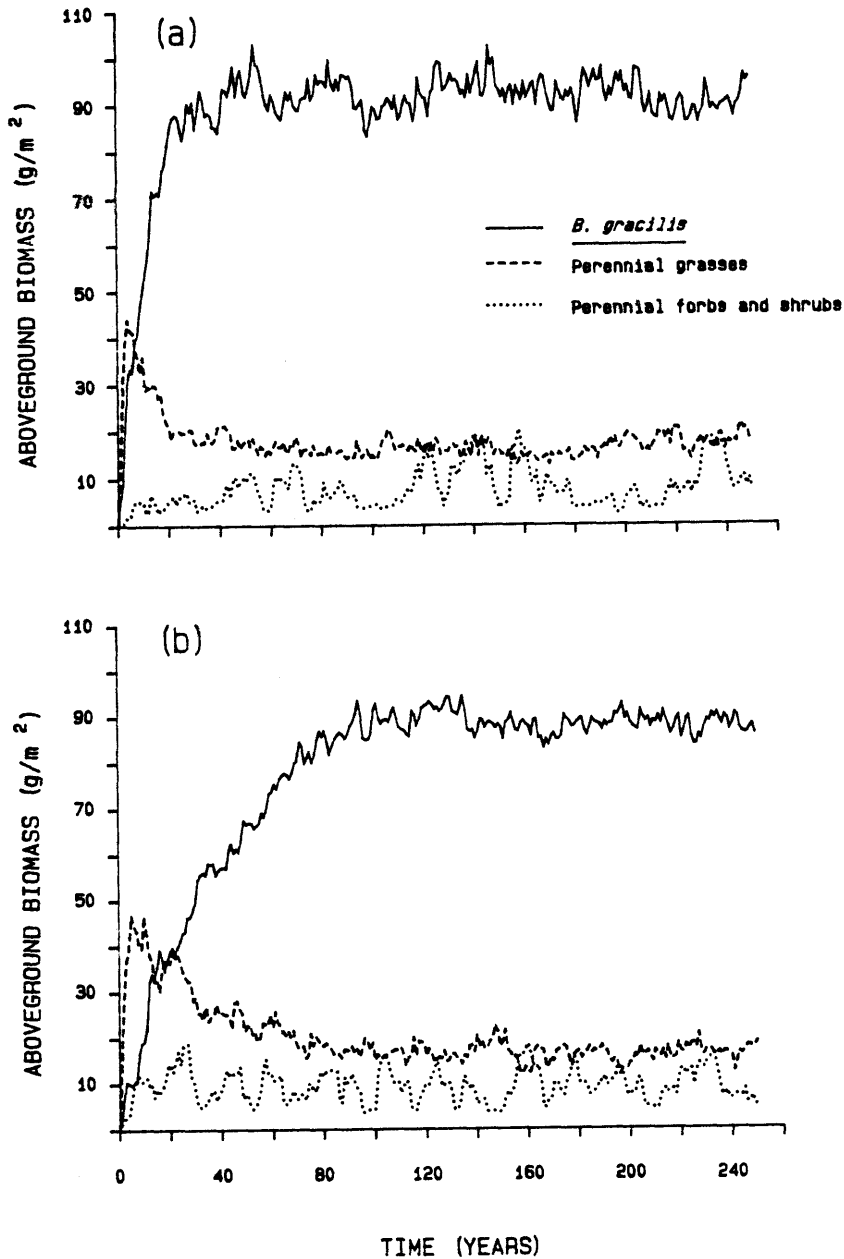


Fig. 4.14. Average aboveground biomass of 50 plots for 250 years for three resource-groups and two conditions of *B. gracilis* seed availability (a) seeds always present (b) seeds have a probability of being present.

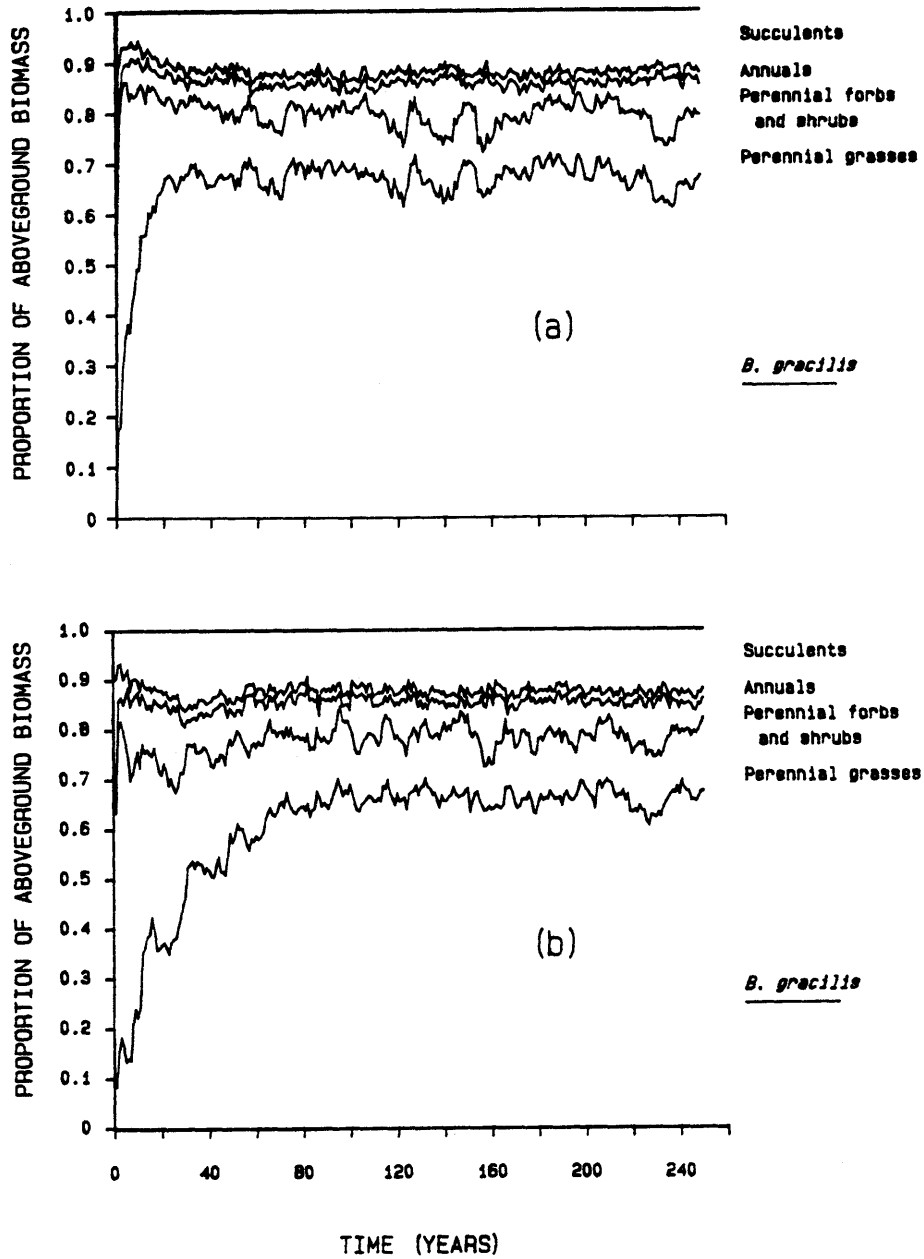


Fig. 4.15. Average proportion of the aboveground biomass attributed to five resource-groups on 50 plots for 250 years for two conditions of B. gracilis seed availability (a) seeds always present (b) seeds have a probability of being present on the plot.

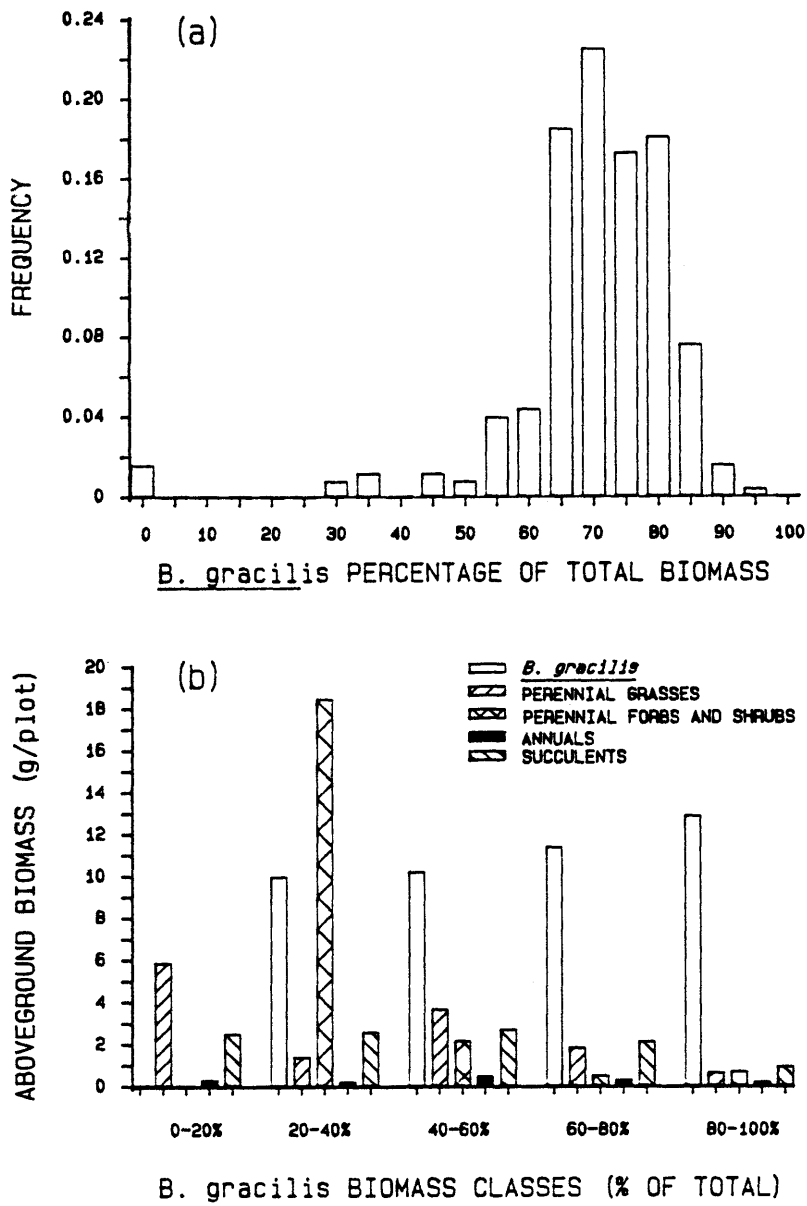
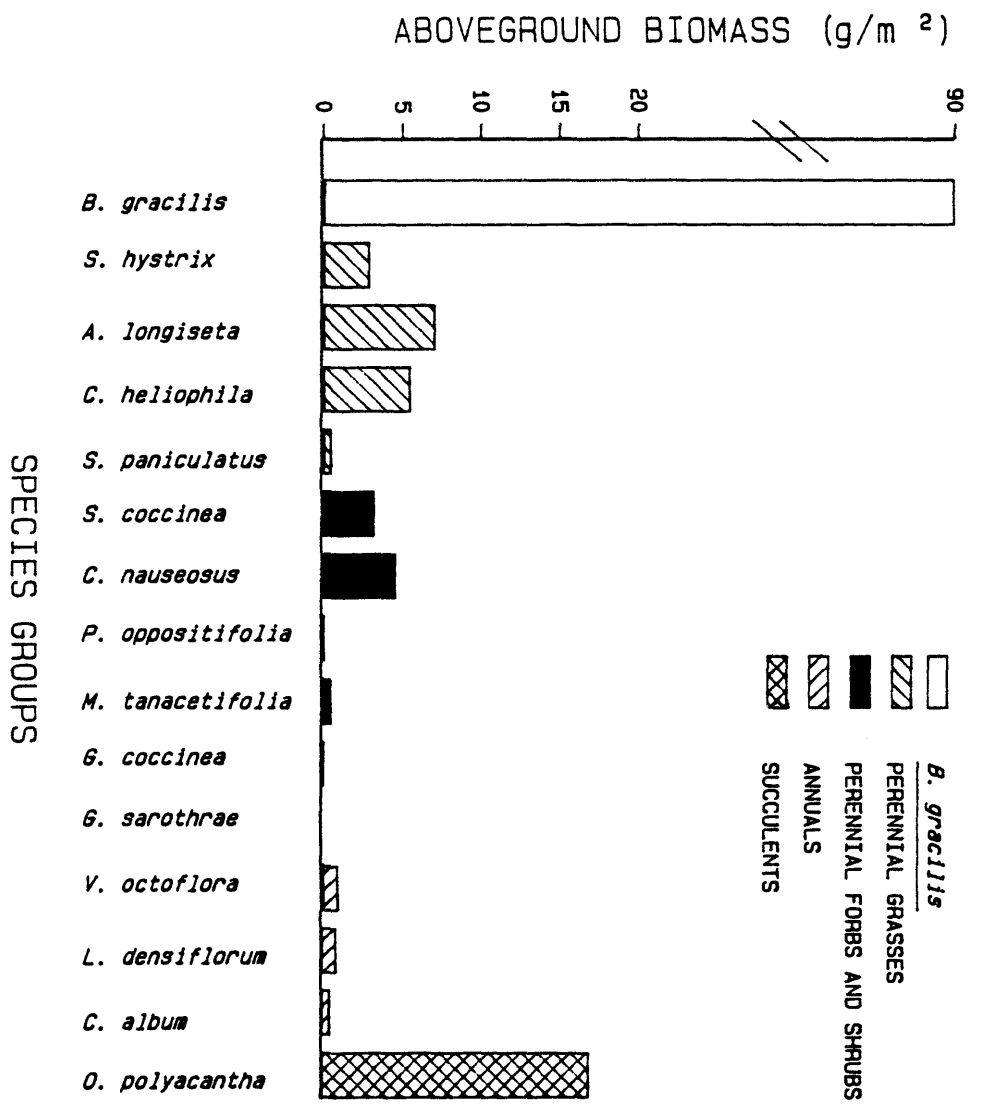


Fig. 4.16. (a) Frequency of occurrence of plots with 0-100% of the aboveground biomass attributed to *B. gracilis*. (b) Aboveground biomass (g/plot) of five resource-groups on five types of plots based on the percentage of the biomass attributed to *B. gracilis*.

Fig. 4.17. Average aboveground biomass (g/m²) of fifteen species-groups on a simulated landscape.



V. SUMMARY AND CONCLUSIONS

Previous conceptualizations of succession in shortgrass plant communities focused on the effects of large disturbances with the conclusion that the dominant plant species, blue grama [Bouteloua gracilis (H.B.K.) Lag. ex Griffiths] recovers very slowly after a disturbance or not at all (Hyder et al 1971, Reichardt 1982). The theory of gap-phase dynamics based on the importance of small, frequently-occurring disturbances that affect an individual of the dominant species (Watt 1947) provides an alternative to a conceptual model of plant communities that focuses on the effects of large disturbances. My overall objective was to apply a gap dynamics approach to shortgrass plant communities with the hypothesis that the death of a full-size B. gracilis plant results in a gap in the belowground resource space and initiates the successional processes of gap dynamics.

My first objective was to evaluate the effects of three small, patch-producing disturbances on B. gracilis-dominated plant communities. I developed a spatially-explicit simulation model to evaluate the effects of cattle fecal pats, western harvester ant mounds, and small animal burrows on the cover and abundance of B. gracilis. The size distributions and rates of occurrence determined from field

data and from the literature for B. gracilis plants and for the three disturbance types were incorporated into the simulation model. Plots were simulated for three topographic positions and three grazing intensities.

Propagating the effects of cattle fecal pats, western harvester ant mounds, and burrows from small animals through time using the simulation model suggested that B. gracilis is able to recover after small disturbances. The accumulation of the effects of small disturbances through time should result in a decrease in B. gracilis if recovery does not occur. However, the results from a field study (Milchunas et al 1988) indicated an increase in the cover of B. gracilis over the past 48 years of heavy grazing at the CPER. The effects of these disturbances were dependent on topographic position and grazing intensity; the largest amounts of B. gracilis were affected on slopes and lowlands compared to uplands.

My second objective was to evaluate the short-term successional dynamics on small disturbances. I conducted a field study to evaluate the effects of three types of disturbances (artificially-produced plots, western harvester ant mounds, and burrows from small animals) and their associated characteristics on the recovery of plants. The disturbance characteristics of size, seasonality, and location by soil texture were studied.

The species composition on the two naturally-occurring disturbances (western harvester ant mounds and burrows from

small animals) were similar one year after the disturbances occurred, and were different from the composition on the artificially produced disturbances. The high density and cover of perennials on ant mounds and animal burrows indicated that perennial organs, such as rhizomes of C. heliophila and tap roots of S. coccinea, were not killed by the clipping activity of harvester ants or the pile of soil from burrowing animals.

In contrast to ant mounds and animal burrows, the majority of the cover on the artificially produced disturbances for both sites, and most sizes and dates, was attributed to annuals while comparable densities of annuals and perennials were found. Annuals and perennials responded similarly to the effects of seasonality, but they responded differently to disturbance size. The density of annuals was not affected by disturbance size while the effects of competition by plants surrounding the plots on the growth of annuals was indicated by the significantly smaller cover values on the smallest compared to the largest plots.

Most of the perennials on the plots produced artificially were the result of vegetative growth by C. heliophila, B. dactyloides and S. coccinea. The recovery of C. heliophila by rhizomes and B. dactyloides by stolons occurred as ingrowth from the edge of the plots; therefore significantly larger density and cover values of perennial grasses were found on the smallest compared to the largest plots for most dates and both sites. The cover and density

of the perennial forb, S. coccinea, was highest in the center of the largest plots, or the farthest distance from potential competitive interactions with plants surrounding the plots.

My third objective was to evaluate the long-term successional dynamics on small disturbances and the time required for B. gracilis to recover after a disturbance. I developed a gap dynamics simulation model based on the belowground gap in the resource space that results when an individual B. gracilis plant dies. Three types of small disturbances were incorporated into the model based on their frequencies of occurrence: cattle fecal pats, western harvester ant mounds, and burrows from small animals.

The aboveground biomass on the simulated plots was dominated by B. gracilis through time and space. The relative proportion of the aboveground biomass and the average biomass values for each species were comparable to the composition of shortgrass plant communities (Sims et al 1978). The average biomass values by species were not affected by differences in the availability of B. gracilis seeds. However, the time required for B. gracilis to recover after a disturbance and dominate the biomass was increased from 20 years when B. gracilis seeds were always present to 65 years when the presence of seeds was a function of annual precipitation. The faster recovery time of B. gracilis in the model than observed experimentally on large disturbances suggests that processes associated with

the recovery of B. gracilis, such as seed dispersal, may be scale-dependent.

Therefore, a gap dynamics conceptualization of shortgrass plant communities provides a promising alternative to a conceptual model that emphasizes the effects of large-scale disturbances. Although further experimental work is required to provide support for my hypothesis, the initial results suggest that gap processes are important to this community.

The gap dynamics approach has been used extensively in temperate and tropical forests, and the successful extension of the approach to a semiarid grassland may indicate that similar processes are occurring across different types of plant communities. Although disturbances are common to many ecological systems, occur across many spatial and temporal scales, and are continuous over all levels of organization, a theory of disturbance is lacking (Pickett and White 1985). The theory of gap dynamics may provide a conceptual framework to evaluate the relationships between plant communities and their disturbance regimes, and the theory may synthesize information about successional dynamics across different plant communities.

Experimental work conducted in forests on processes associated with the production and recolonization of gaps may be applicable to future research in shortgrass communities. Studies in forests have evaluated the effects of the characteristics of the gap, such as size, shape, and

orientation with respect to light, on its microenvironment and the resulting recovery of plants (Bazzaz 1984). The physiological adaptations of plants to gaps have also been studied (Bazzaz and Pickett 1980, Pickett 1983, Brokaw 1985) as well as the partitioning of gaps of different spatial distributions and sizes by tree species has been proposed as a mechanism of resource partitioning to account for species richness (Denslow 1980).

Applying the research that has been conducted in forests to shortgrass communities may result in the identification of species that are dependent on gaps for their continued existence through time. Other possibilities are the identification of processes that are scale-dependent, such as the processes associated with the recovery of B. gracilis.

Experimental studies of the long-term successional dynamics on small-scale disturbances are necessary to determine if gap processes are operating in shortgrass plant communities. The relationship between the spatial scale of the disturbance and physical and biological processes that may affect the establishment, growth and death of plants also needs to be evaluated experimentally.

LITERATURE CITED

- Bazzaz, F. A. 1984. Dynamics of wet tropical forests and their species strategies. Pages 233-243 in E. Medina, H. A. Mooney, and C. Vazquez-Yanes, editors. Physiological ecology of plants of the wet tropics. Dr. W. Junk, The Hague, Pudoc, Wageningen.
- Bazzaz, F. A., and S. T. A. Pickett. 1980. The physiological ecology of tropical succession: A comparative review. Annual Review of Ecology and Systematics 11:287-310.
- Brokaw, N. V. L. 1985. Gap-phase regeneration in a tropical forest. Ecology 66:682-687.
- Denslow, J. S. 1980. Gap partitioning among tropical rainforest trees. Biotropica 12:(Supplement)47-55.
- Hyder, D. N., A. C. Everson, and R. E. Bement. 1971. Seedling morphology and seeding failures with blue grama. Journal of Range Management 24:287-292.
- McGregor, R. L. 1986. Flora of the Great Plains. University Press of Kansas, Lawrence, Kansas.
- Milchunas, D. G., W. K. Lauenroth, P. L. Chapman, and M. K. Kazempour. 1988. Plant communities in relation to grazing, topography, and precipitation in a semiarid grassland. Ecology (submitted).
- Pickett, S. T. A. 1983. Differential adaptation of tropical species to canopy gaps and its role in community dynamics. Tropical Ecology 24:68-84.
- Pickett, S. T. A., and P. S. White. 1985. Patch dynamics: A synthesis. Pages 371-384. in S. T. A. Pickett and P. S. White, editors. The ecology of natural disturbances and patch dynamics. Academic Press, Orlando, Florida.
- Reichhardt, K. L. 1982. Succession of abandoned fields on the shortgrass prairie, northeastern Colorado. Southwestern Naturalist 27:299-304.

- Sims, P. L., J. S. Singh, W. K. Lauenroth. 1978. The structure and function of ten western North American grasslands. I. Abiotic and vegetational characteristics. *Journal of Ecology* 66:251-285.
- Watt, A. S. 1947. Pattern and process in the plant community. *Journal of Ecology* 35:1-22.

APPENDIX I
SPATIAL DISTRIBUTION OF Bouteloua gracilis ROOTS
AND THE EFFECTS OF COMPETITION

Introduction

Belowground processes are a particularly important component of grassland systems. Estimates of the contribution of belowground net primary production to net primary production range from 85% for a shortgrass steppe (Sims and Singh 1978) to 50% for a tallgrass prairie (Kucera et al 1967). Plant community structure, especially following disturbances, may be dependent on competition for belowground resources.

In the shortgrass steppe and other semiarid grasslands, soil water is the most frequent control on plant growth and community structure due to the low and variable patterns of precipitation (Noy-Meir 1973, Lauenroth et al 1978). Shortgrass steppe plant communities of the central and southern Great Plains of the United States are dominated by the perennial grass, blue grama [Bouteloua gracilis (H.B.K.) Lag. ex Griffiths]. The rooting structure of B. gracilis, its interactions with neighboring plants, and its ability to exploit resources are important in determining plant community structure following disturbances.

Approximately 80% of the aboveground production at many sites in the shortgrass region is attributed to B. gracilis. The strongest competitive interactions for belowground resources most likely occurs between a B. gracilis plant and neighboring grasses due to their similar morphology. The distribution of roots of neighboring B. gracilis plants and the distance between plants are important with respect to overlap in the root systems and the potential competitive interactions among plants. A number of studies have been conducted in shortgrass communities to evaluate total (Bartos and Sims 1974) and functional root biomass with depth (Singh and Coleman 1974). The spatial distribution of the functional roots associated with individual B. gracilis plants and the effects of neighboring grasses on the distribution have not been evaluated.

The objectives of this study were to evaluate: 1) the spatial distribution of roots of B. gracilis plants, 2) the effects of intra-lifeform competition on the rooting pattern, 3) the overlap in root systems among neighboring B. gracilis plants, 4) the relationship between the distribution of functional roots of a B. gracilis plant with the distribution of the total root biomass.

Methods

The study was conducted at the Central Plains Experimental Range (CPER). The CPER is located in northcentral Colorado approximately 60 km northeast of Fort

Collins (40° 49' N latitude, 107° 47' W longitude). Mean annual precipitation is 311 mm (sd=79 mm) and mean monthly temperatures range from -5°C in January to 22°C in July. Moderate grazing by cattle occurs throughout the area.

In 1982, ten B. gracilis plants were randomly selected within a temporary exclosure. Five of these were randomly selected as controls. Each of the five remaining plants occupied the center of a 1 m radius circle within which all other grass individuals were removed by clipping below the soil surface. The removals continued on a regular basis until the plants were labeled with the radioactive isotope ^{14}C in July, 1985.

The labeling procedure was adapted to field conditions from Milchunas et al (1985). Clear plastic tents supported by aluminum tubing were placed over each of the ten B. gracilis plants. The tents were secured at the base with soil to prevent $^{14}\text{CO}_2$ leakage during the labeling period. After an initial drawdown of CO_2 , approximately 3.7×10^5 Bq ^{14}C per gram of aboveground plant tissue was released into the tent. The time necessary to reach the plant's CO_2 compensation point was estimated by monitoring atmospheric $^{14}\text{CO}_2$ in the tents with a thin-window GM meter. When the ^{14}C level no longer declined, unlabeled CO_2 was released in the tent. Three drawdowns after the release of the $^{14}\text{CO}_2$ resulted in an uptake efficiency of approximately 95%. The tents were manually shaken to promote airflow and the

temperature inside the tents was monitored throughout the two hour labeling period.

Sampling did not begin until at least four weeks after labeling to allow the incorporation of labile ^{14}C into structural compounds. Preliminary sampling was performed to establish the maximum distance from the plant (30 cm) and maximum depth (90 cm) of labeled B. gracilis roots. Full design sampling was conducted by dividing the aboveground portion of each plant into two equal parts and sampling the region surrounding one half of each plant. Two adjacent 5 cm-diameter cores were taken to a depth of 90 cm at each of four distances: in the center of each plant, 5, 15 and 30 cm from the edge of the plant. Three replicates at each distance were obtained by coring at 0° , 90° and 180° from a point in the center of the plant. Each core was separated into depth increments of 0-10, 10-25, 25-50, and 50-90 cm.

Roots were separated from the soil using a hydropneumatic elutriation system that uses air and water pressure to deposit roots on a fine mesh screen (Smucker et al 1982). Root material was dried at 100°C , weighed, and ground through a micro-Wiley mill to pass a 40-mesh screen. Plant material was combusted in a Packard Model 306 tri-carb sample oxidizer using a Carbosorb CO_2 trap and Permaflour cocktail. ^{14}C activity was determined by liquid scintillation counting. Data are reported on an ash-free, quench, and background-corrected basis.

The DPM/cm³ for each depth and distance from a plant was calculated and summed to obtain a total DPM for the plant. The percentage of the total DPM at each depth and distance location was used to determine the location of labeled roots for plants with and without neighboring grass plants.

The overlap in the root systems of neighboring B. gracilis plants was evaluated using the location of the labeled roots and average distance between plants based on the size distribution and basal cover of B. gracilis plants from Chapter 2. The proportion of roots attributed to each plant at each location was based on the overlap in the distribution of labeled roots for two adjacent plants.

Results and Discussion

The spatial distribution of roots from individual B. gracilis plants were found to extend to 30 cm from the edge of a plant and to depths of 90 cm (Table A1.1). A large proportion of the labeled roots on control plots (> 76%) was found directly beneath and at the edge of the plant in the upper 10 cm of the soil. The percentages of roots at the remaining depths and distances from the plant were not significantly different from each other.

The relatively fast response of B. gracilis to small rainfall events (≤ 5 mm) has been suggested to influence its persistence in shortgrass plant communities (Sala and Lauenroth 1982), and the concentration of B. gracilis roots

near the soil surface is important in its ability to respond to rainfall events that affect only the upper soil layers. Although most of the precipitation events in the shortgrass steppe are small (70%), most of the total precipitation is due to events larger than 10 mm (59%) (Sala and Lauenroth 1982). The extension of the root system to depths of 90 cm would also allow B. gracilis plants to utilize deeper water stores that result from large rainfall events.

A genetic constraint on the spatial distribution of the roots of B. gracilis plants was indicated since the location of the labeled roots for plants with and without neighboring grasses was not significantly different (Fig. A1.1). The root distributions were unaffected by the differences in basal cover of the plants (average of removals=750 cm²; average of controls=516 cm²). Differences in B. gracilis rooting patterns as a result of changes in levels of competition may occur on a smaller scale than could be identified by my sampling scheme.

Factors related to soil type, including bulk density, texture, and impediments, may influence root depth and spatial extension. Soil texture has been found to affect the rooting density with depth of B. gracilis roots (Weaver and Darland 1949, Fox et al 1953), although effects on the horizontal and vertical spatial distribution were not evaluated. The results of this study suggest that the morphology of the root system of B. gracilis plants is

constrained genetically; therefore, full-size B. gracilis plants within a site will have similar root distributions.

The relatively small average distance (10 cm) between neighboring B. gracilis plants compared to the spatial distribution of their roots suggests there is a large degree of overlap in rooting systems between two plants. The greatest amount of overlap, and the greatest potential for competitive interactions, occurred beneath the plants for depths from 10-50 cm, and by definition, for all depths in the space between the plants (Fig. A1.2a). Most of the roots beneath a plant and within 10 cm of the soil surface (87%) were roots from that plant.

The root system of a B. gracilis plant may interact with the roots of a number of other B. gracilis plants. The total volume occupied by the roots of an average full-size B. gracilis plant with a basal cover of 320 cm² is 0.45 m³. The roots of at least four other B. gracilis plants of average size and separated by average distances of 10 cm may occur within the volume of soil associated with the roots of this plant.

The total amount of roots at each location between two B. gracilis plants indicated the spatial heterogeneity of root densities within a depth in the soil profile as well as among depths (Fig. A1.2b). Areas of relatively low root densities were found at the soil surface between the plants, and beneath the plants at the other depths. The microsite variability in root densities of B. gracilis may be a result

of differences in resource availability, morphological constraints on B. gracilis rooting patterns, or a combination of factors. Experimental studies are necessary to differentiate between these possibilities. Similar results on the spatial heterogeneity in root biomass for grass species have been found in the Patagonian arid steppe community (Soriano et al 1987).

The majority of the total root biomass (labeled and unlabeled) for the control and removal plots was found in the upper 10 cm of the soil profile (>70%) while the upper 25 cm contained greater than 87% of the total sampled root biomass (Table A1.2). These results are comparable to previous estimates for the location of the total root biomass in the shortgrass community (Bartos and Sims 1974, Singh and Coleman 1974). The distribution of total root biomass did not represent the distribution of labeled roots, even when neighboring grasses were removed. The distribution of labeled roots and total root biomass were not similar for plants with (Figs. A1.1a, A1.3a) or without neighboring plants (Figs. A1.1b, A1.3b). Neighboring grass plants had important contributions to biomass for the control plots, while large quantities of dead roots, presumably from the neighboring grass plants that had been removed, were found during an excavation of the removal plots (Lee 1988).

LITERATURE CITED

- Bartos, D. L., and P. L. Sims. 1974. Root dynamics of a shortgrass ecosystem. *Journal of Range Management* 27:33-36.
- Fox, R. L., J. E. Weaver, and R. C. Lipps. 1953. Influence of certain soil-profile characteristics upon the distribution of roots of grasses. *Agronomy Journal* 45:583-589.
- Kucera, C. L., R. C. Dahlman, and M. R. Koelling. 1967. Total net productivity and turnover on an energy basis for tallgrass prairie. *Ecology* 48:536-541.
- Lauenroth, W. K., J. L. Dodd, and P. L. Sims. 1978. The effects of water- and nitrogen-induced stresses on plant community structure in a semiarid grassland. *Oecologia (Berlin)* 36:211-222.
- Lee, C. A. 1988. The spatial distribution of roots for three plants life-forms in the shortgrass steppe. M.S. Thesis. Colorado State University, Fort Collins, Colorado. (in prep.).
- McGregor, R. L. 1986. *Flora of the Great Plains*. University Press of Kansas, Lawrence, Kansas.
- Milchunas, D. G., W. K. Lauenroth, J. S. Singh, C. V. Cole, and H. H. Hunt. 1985. Root turnover and production by ¹⁴C dilution: Implications of carbon partitioning in plants. *Plant and Soil* 88:353-365.
- Noy-Meir, I. 1973. Desert ecosystems: Environment and producers. *Annual Review of Ecology and Systematics* 4:25-52.
- Sala, O. E., and W. K. Lauenroth. 1982. Small rainfall events: An ecological role in semiarid regions. *Oecologia(Berlin)* 53:301-304.
- Sims, P. L., and J. S. Singh. 1978. The structure and function of ten western North American grasslands. III. Net primary production, turnover, and efficiencies of energy capture and water use. *Journal of Ecology* 66:573-597.

- Singh, J. S., and D. C. Coleman. 1974. Distribution of photo-assimilated ^{14}C in the root system of a shortgrass prairie. *Journal of Ecology* 62:359-365.
- Smucker, A. J. M., S. L. McBurney, and A. K. Srivastava. 1982. Quantitative separation of roots from compacted soil profiles by the hydropneumatic elutriation system. *Agronomy Journal* 74:500-503.
- Sokal, R. R., and F. J. Rolff. 1981. *Biometry*. Second Edition, Freeman, New York.
- Soriano, A., R. A. Golluscio, and E. Satorre. 1987. Spatial heterogeneity of the root system of grasses in the Patagonian arid steppe. *Bulletin of the Torrey Botanical Club* (in press).
- Weaver, J. E., and R. W. Darland. 1949. Soil-root relationships of certain native grasses in various soil types. *Ecological Monographs* 19:303-338.

Table A1.1. Labeled roots (% of total DPM/cm³) of B. gracilis plants with neighboring grasses (controls) by depth and distance from the plant.^{1,2}

DEPTH (cm)	ACTIVITY (% of total DPM/cm ³)			
	DISTANCE FROM PLANT EDGE (cm)			
	0	5	15	30
0-10	55.9 ^a	21.8 ^b	2.8	1.8
10-25	1.8	6.2	0.2	<0.1
25-50	0.2	0.8	0.0	1.4
50-90	1.5	2.8	2.4	0.4

- 1 Significance determined using a two-way analysis of variance; Tukey's Q values were used to compute least significant ranges (Sokal and Rolff 1981)
- 2 Values not sharing a common superscript are significantly different (p<0.05)

Table A1.2. Root biomass ($\text{g} \times 10^{-3}/\text{cm}^3$) for B. gracilis plants with (controls) and without neighboring grasses (removals).

CONTROL PLANTS

DEPTH (cm)	DISTANCE FROM PLANT EDGE (cm)			
	0	5	15	30
0-10	11.5	8.0	15.8	19.3
10-25	4.1	2.6	2.4	3.3
25-50	1.1	1.8	1.6	1.6
50-90	1.0	1.0	0.7	1.2

PLANTS WITH REMOVALS

DEPTH (cm)	DISTANCE FROM PLANT EDGE (cm)			
	0	5	15	30
0-10	31.3	7.9	9.6	14.0
10-25	2.3	5.1	4.6	3.0
25-50	2.0	1.8	1.4	2.3
50-90	1.0	0.9	0.6	1.1

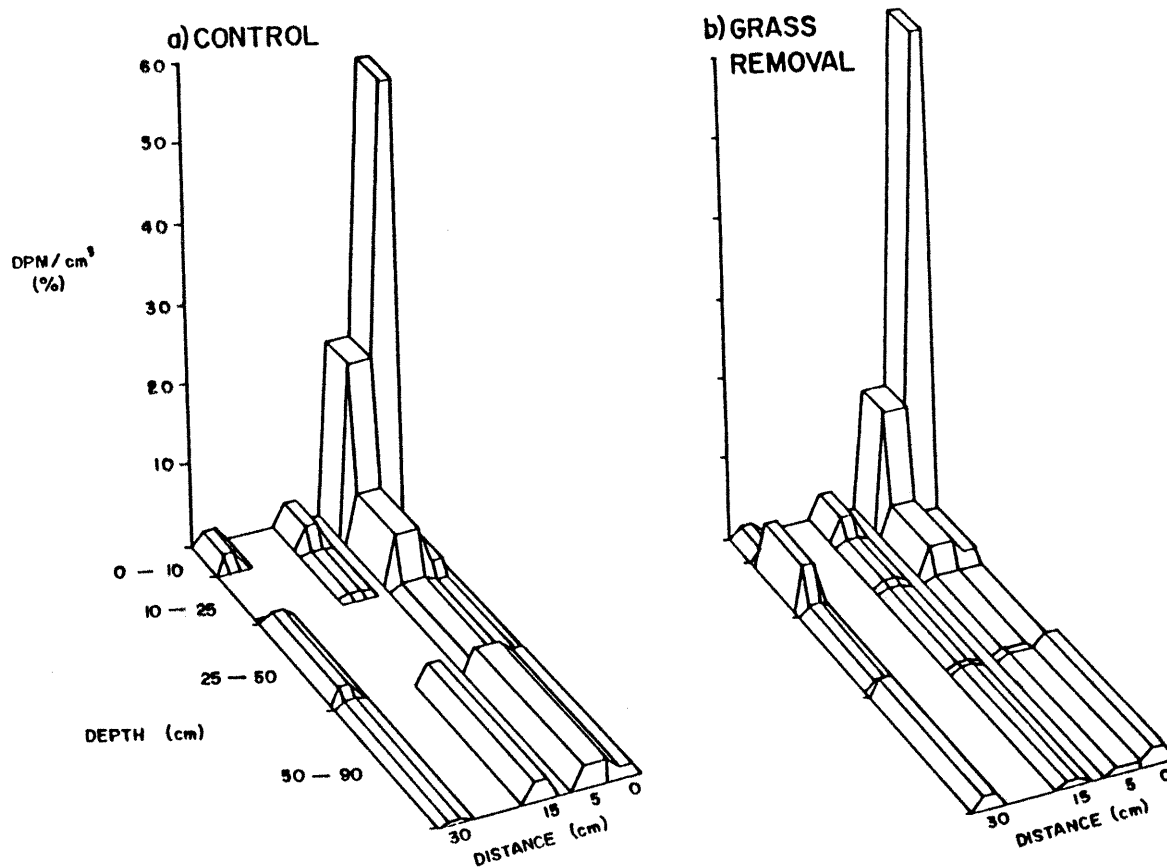


Fig. A1.1. Location of labeled roots (% of total DPM/cm³) by depth and distance for (a) control plants and (b) plants with neighboring grasses removed.

a)	DISTANCE FROM PLANT I (cm)		
	0	5	10
DEPTH (cm)	PLANT I		PLANT II
0-10	87	50	13
10-25	50	50	50
25-50	50	50	50
50-90	36	50	64

b)	DISTANCE FROM PLANT I (cm)		
	0	5	10
DEPTH (cm)	PLANT I		PLANT II
0-10	64.4	43.6	64.4
10-25	3.5	12.4	3.5
25-50	0.3	1.6	0.3
50-90	4.1	5.7	4.1

Fig. A1.2. Overlap of labeled roots for two *B. gracilis* plants separated by 10 cm. The distribution of roots for each plant is from Table 1.1. The values for the 10 cm distance were estimated using values from the 5 and 15 cm distances. (a) Amount of roots (% of total activity) attributed to Plant I at each depth and distance location from Plant I. (b) Location of total root densities (total activity) for two plants.

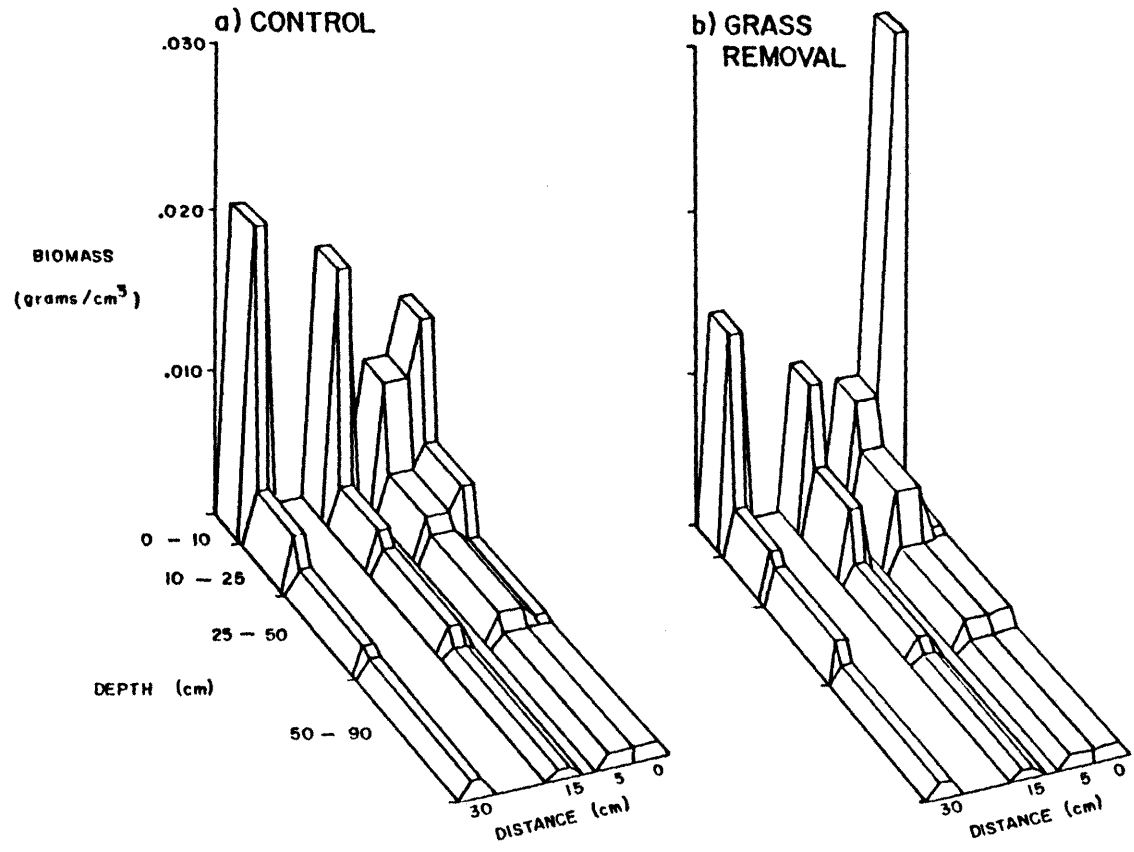


Fig. A1.3. Location of root biomass (g/cm³) by depth and distance for (a) control plants and (b) plants with neighboring grasses removed.

APPENDIX II.

SPATIAL AND TEMPORAL VARIATION IN THE SEED BANK OF A SEMIARID GRASSLAND

Introduction

The seed bank of a plant community represents the "memory" of previous conditions (Templeton and Levin 1979), and an important component of the potential of the community to respond to conditions in the present and future. The recovery of a plant community after disturbances is related to the germination and establishment of seedlings, although in some communities vegetative reproduction by perennial plants is another important process (eg. Platt 1979). Characteristics of disturbances and the storage of germinable seeds vary in both space and time (King 1976, Thompson and Grime 1979, Sousa 1984, Thompson 1986). Patterns of recolonization on disturbed areas are a function of the characteristics of the disturbance and the dynamics of the pool of propagules of which the seed bank is an important part.

Few studies have been conducted on the storage of seeds in semiarid grasslands, and particularly in shortgrass communities (Weaver and Mueller 1942, Lippert and Hopkins 1950). The variability of the seed bank through space and time has not been evaluated. The interaction between the

effects of soil texture on plant community composition (Anderson 1983), and the low and variable patterns of precipitation found in semiarid regions (Noy-Meir 1973, Sala and Lauenroth 1982) leads to the potential for spatial and temporal variability in processes important to the storage of germinable seeds. The objectives of this study were to evaluate the spatial variability in the seed bank of shortgrass plant communities by considering sites with the same climatic conditions but differing in soil texture, and to characterize the seasonal and between-year temporal dynamics of the seed bank.

Methods

This study was conducted at the Central Plains Experimental Range (CPER). The CPER is located in northcentral Colorado approximately 60 km northeast of Fort Collins (40° 49' N latitude, 107° 47' W longitude). Mean annual precipitation over the past 45 years is 311 mm (sd=79 mm) and mean monthly temperatures range from -5° C in January to 22° C in July. Moderate grazing by cattle occurs throughout the site.

Two locations differing in soil texture were chosen to study the germinable seeds in the seed bank. A coarse-textured site on a sandy loam soil and a fine-textured site on a clay to clay loam soil were selected. Plant communities at both sites are dominated by the perennial grass, blue grama [Bouteloua gracilis (H.B.K.) Lag. ex

Griffiths. Nomenclature follows McGregor 1986)].

Aboveground cover of all plants ranges from 40-45% of which 25-35% is B. gracilis. A number of grasses, succulents, shrubs and forbs account for the remainder. The co-dominance of buffalograss [Buchloe dactyloides (Nutt.) Engelm.] and the relatively few shrubs on the fine-textured site are the major differences between the two plant communities.

Fifteen randomly located soil samples were taken at each of the two sites on eight sampling dates over two years. Sampling began July 1, 1984 and continued at two-month intervals until November, and through the 1985 growing season from March 1 to November 1. Each sample consisted of two 7.5 cm-diameter soil cores taken to a depth of 5 cm. One core of each sample was taken within plant cover and one was taken in an adjacent bare area to account for storage differences due to plant structure.

The samples were sieved using a 1 cm-mesh screen to remove plant material, allowed to air dry, and refrigerated for seven days at approximately 0° C. Each sample was spread in a 1 cm-deep layer over a potting soil-sand mixture in plastic trays in a greenhouse maintained at suitable conditions for germination. The samples were watered daily and 33% Hoagland's solution was applied once a week. Seedlings were counted by species at weekly intervals for twelve weeks. Once a seedling was identified it was removed from the tray. The total number of seedlings/m² for the fifteen samples for each date were calculated. The number

of seedlings/m² also were calculated for three species-groups: (1) annual grasses and forbs, (2) perennial grasses, and (3) perennial forbs, shrubs and succulents.

The composition of the plant communities at each site was evaluated using fifty 0.25 m² quadrats randomly positioned on transects at each of the two sites. The number of individuals were counted and the percentage cover by species was estimated. The sampling was conducted in early June and late July (1985) to correspond to the peak standing crop for the cool and warm season species.

Jaccard coefficients of similarity were used to compare the composition of the plant communities and the composition of the germinable seeds in the seed bank (Bray and Curtis 1957). Density and cover values of each of the four groups of species relative to the total were used to calculate the coefficients of similarity.

Results

Perennial grass density and cover as a percent of total vegetation was greater than 60% on both the fine- and coarse-textured sites (Table A2.1). This is typical of shortgrass plant communities of North America (Sims et al 1978). The composition of the perennial grass species on the two sites were similar. Differences were found between the two groups of species that contributed small amounts to the cover and density of the communities. Annuals were significantly higher on the fine-textured site, while the

cover and density of perennial forbs, shrubs and succulents were significantly higher on the coarse-textured site.

Although the composition of the plant communities was similar, there were differences in the composition of the seeds produced (Table A2.1). Most of the seeds produced on the fine-textured site were from annual plants and most of the seeds produced on the coarse-textured site were from perennial grasses. However, the composition of the seed banks across the eight sampling dates was similar for both sites, indicating little spatial variability in the storage of germinable seeds.

A close correspondence was not found between the composition of the seed bank and the composition of the community for either site (Table A2.2). High similarity values were found between the composition of the seed bank and the seeds produced, but the groups of species with the high values were different for the two sites. Perennial forbs, shrubs and succulents had a high similarity value for the coarse-textured site, while high similarity values were found for annuals and perennial grasses at the fine-textured site.

Seasonality was a more important factor in the dynamics of the seed bank than site differences. The number of seedlings was not significantly different between sites for the four groupings of species, while a significant difference was found between dates for the total number of seedlings and the number of annual seedlings (Table A2.3).

For example, a difference of 2626 seedlings/m² was observed between the September and November (1984) samples from the coarse-textured site. A significant difference in the number of seedlings was not found between years, although the largest number of seedlings for 1984 was found in September, and for 1985 the largest numbers were found in May and July.

Seedlings on each date were primarily from annuals. This resulted in a high similarity between the trends for the number of annual seedlings and the total number of seedlings (Table A2.3). Differences between the two sites were primarily due to the number of sixweeks fescue [Vulpia octoflora = Festuca octoflora (Walt.) Rydb.] seedlings (Table A2.4). Significant seasonal differences were found in the storage of seeds from annual plants. The large numbers of annual seedlings found in the September (1984), May and July (1985) samples were due to two species: V. octoflora and pepperweed (Lepidium densiflorum Schrad.). Seedlings of these species were found in all of the samples for these dates, indicating a relatively homogeneous spatial distribution. Seedling dynamics of these species were similar for both plant communities (Table A2.4).

Relatively few perennial grass seedlings emerged from the seed bank (Table A2.3). A consistent component of the seed bank was the warm season grass, sand dropseed [Sporobolus cryptandrus (Torr.) A. Gray] (Table A2.4). There was little variability in the number of perennial

grass seedlings with several exceptions. Relatively large numbers of seedlings were found in the May and November (1985) samples from the fine-textured site; primarily due to the numbers of B. dactyloides seedlings (Table A2.4). There was a clumped distribution of B. dactyloides seedlings; greater than 80% emerged from less than 20% of the samples for all dates. The greater number of seedlings from the fine-textured site reflects the greater relative abundance of B. dactyloides in that plant community compared to the coarse-textured site.

A relatively large number of perennial grass seedlings also was found for the November (1985) sampling date for the coarse-textured site as a result of a relatively large number of B. gracilis seedlings (Table A2.4). Differences in the number of seedlings that emerged for the two sites reflects the significantly larger number of B. gracilis seeds produced in 1985 on the coarse-textured site than on the fine-textured site (Coffin et al 1987).

The fewest number of seedlings of the three species-groups were found for the perennial forbs, shrubs and succulents group (Table A2.3). Seedlings of a number of species occurred infrequently, with a clumped distribution within the sites. Shrub seedlings were not found for any of the sampling dates.

Discussion

In shortgrass communities, disturbances occur over a wide range of spatial and temporal scales (Chapter 2). The interaction between the spatial and temporal variability of the seed bank with the variability of disturbances will have an important influence on the initial colonization of disturbed areas. In this study, temporal variability was more important to the dynamics of the seed bank than spatial variability.

Spatial differences between sites differing in soil texture were attributed primarily to the dynamics of the seeds of annual plants. Differences between the sites in processes such as seed consumption or storage potential are indicated. The spatial distribution of plants in the communities also may be important to the variability in the number of stored seeds. The clumped distribution of B. dactyloides seeds may be related to the limited dispersal of the relatively large seeds located in the foliage of the plants near the soil surface. The clumped distribution of perennial forb seeds and the lack of shrub seeds may be attributed to the sparse distribution of perennial forb and shrub plants in the community and a limited dispersal of seeds.

Temporal differences were found between 1984 and 1985, and seasonally within years. Precipitation and temperature have been found to influence the timing of seed production and dispersal in shortgrass plant communities (Dickinson and

Dodd 1976). The monthly precipitation and average monthly temperatures for 1984 and 1985 as compared to the long-term averages at the CPER indicate the variability inherent in these two factors (Fig. A2.1a,b). This variability may be reflected in the seed bank as a shift in the timing of the peak number of seedlings that emerged. The seasonal variability in number of stored seeds indicates the transient state of most of the species in the seed bank (Thompson and Grime 1979). Seeds of many grassland species appear to germinate as soon as their soil moisture and temperature requirements are met rather than forming a large persistent seed bank (Roberts 1986). A more intensive sampling of the landscape may have revealed the persistence of seeds for species that occurred infrequently and in small numbers. The range of values found in this study compares with previous estimates of the seed bank [638 seeds/m² (Weaver and Mueller 1942) and 761 seeds/m² (Lippert and Hopkins 1950)] for shortgrass communities based on a single sampling date.

Seeds of annual species were found to comprise the majority of the seeds in the seed bank. Successional studies in the shortgrass steppe indicate that annuals are important in early successional stages (Shantz 1917, Judd and Jackson 1939, Costello 1944, Judd 1974). The persistence of the perennial grass, *S. cryptandrus*, in the seed bank may be important to its ability to recover after disturbances (Costello 1944). *Sporobolus cryptandrus* is typically a

minor component of shortgrass plant communities and the abundance of its seeds in the seed bank has been noted previously (Weaver and Mueller 1942).

The dominant species in shortgrass plant communities, B. gracilis, recovers either very slowly after large disturbances or not at all (Riegel 1941, Hyder et al 1975, Briske and Wilson 1977). This has been attributed to a specific set of microenvironmental conditions that must be present for B. gracilis seed germination and establishment (Briske and Wilson 1977; 1978, Wilson and Briske 1979). Other important factors may be the relatively few B. gracilis seeds stored in the soil, and the seasonal and year-to-year variability in the number of germinable seeds (Table A2.4).

The poor correspondence between the relative abundances of species-groups in the seed bank and in the plant community is similar to the results of other studies (Champness and Morris 1948, Major and Pyott 1966, Thompson and Grime 1979, Thompson 1986). An extensive set of greenhouse conditions as described in Roberts (1981) and Major and Pyott (1966) would have been necessary for the germination of all of the stored, germinable seeds for a direct comparison with the plant community composition; however, further attempts to germinate more seeds from the samples used in this study resulted in few additional seedlings indicating that the majority of the seeds germinated initially.

LITERATURE CITED

- Anderson, M. D. 1983. Soil and vegetation pattern on shortgrass catenas. M. S. Thesis. Colorado State University, Fort Collins, Colorado, USA.
- Bray, J. R., and J. T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs* 27:325-349.
- Briske, D. D., and A. M. Wilson. 1977. Temperature effects on adventitious root development in blue grama seedlings. *Journal of Range Management* 30:276-280.
- Briske, D. D., and A. M. Wilson. 1978. Moisture and temperature requirements for adventitious root development in blue grama seedlings. *Journal of Range Management* 31:174-178.
- Champness, S. S., and K. Morris. 1948. Populations of buried viable seeds in relation to contrasting pasture and soil types. *Journal of Ecology* 36:149-173.
- Coffin, D. P., R. L. Dougherty, and W. K. Lauenroth. 1987. Influences of soil texture and vegetation structure on seed dynamics at a shortgrass site. Abstracts of the 40th Annual Meeting, The Society for Range Management, Boise, Idaho.
- Costello, D. F. 1944. Natural revegetation of abandoned plowed land in the mixed prairie association of northeastern Colorado. *Ecology* 25:312-326.
- Dickinson, C. E., and J. L. Dodd. 1976. Phenological pattern in shortgrass prairie. *American Midland Naturalist* 96:367-378.
- Hyder, D. N., R. E. Bement, E. E. Remmenga, and D. F. Hervey. 1975. Ecological responses of native plants and guidelines for management of shortgrass range. United States Department of Agriculture-Agricultural Research Service Technical Bulletin 1503.
- Judd, I. B. 1974. Plant succession of old fields in the Dust Bowl. *Southwestern Naturalist* 19:227-239.

- Judd, I. B., and M. L. Jackson. 1939. Natural succession of vegetation on abandoned farmland in the Rosebud soil area of western Nebraska. *American Society of Agronomy Journal* 39:541-547.
- King, T. J. 1976. The viable seed contents of ant-hill and pasture soil. *New Phytologist* 77:143-147.
- Lippert, R. D., and H. H. Hopkins. 1950. Study of viable seeds in various habitats in Mixed Prairie. *Transactions of the Kansas Academy of Sciences* 53:355-364.
- Major, J., and W. T. Pyott. 1966. Buried, viable seeds in two California bunchgrass sites and their bearing on the definition of flora. *Vegetatio* 13:253-282.
- McGregor, R. L. 1986. *Flora of the Great Plains*. University Press of Kansas, Lawrence, Kansas.
- Noy-Meir, I. 1973. Desert ecosystems: Environment and producers. *Annual Review of Ecology and Systematics* 4:25-52.
- Platt, W. J. 1979. The colonization and formation of equilibrium plant species associations on badger disturbances in a tall-grass prairie. *Ecological Monographs* 45:285-305.
- Riegel, A. 1941. Life history habits of blue grama. *Kansas Academy of Sciences Transactions* 44:76-83.
- Roberts, H. A. 1981. Seed banks in soils. *Advances in Applied Biology* 6:1-55.
- Roberts, H. A. 1986. Seed persistence in soil and seasonal emergence in plant species from different habitats. *Journal of Applied Ecology* 23:639-656.
- Sala, O. E., and W. K. Lauenroth. 1982. Small rainfall events: An ecological role in semiarid regions. *Oecologia (Berlin)* 53:301-304.
- Shantz, H. L. 1917. Plant succession on abandoned roads in eastern Colorado. *Journal of Ecology* 5:19-42.
- Sims, P.L., J. S. Singh, and W. K. Lauenroth. 1978. The structure and function of ten western North American grasslands. I. Abiotic and vegetational characteristics. *Journal of Ecology* 66:251-285.

- Sousa, W. P. 1984. The role of disturbances in natural communities. *Annual Review of Ecology and Systematics* 15:353-391.
- Templeton, A. R., and D. A. Levin. 1979. Evolutionary consequences of seed pools. *American Naturalist* 114:232-249.
- Thompson, K., and J. P. Grime. 1979. Seasonal variation in the seed banks of herbaceous species in ten contrasting habitats. *Journal of Ecology* 67:893-921.
- Thompson, K. 1986. Small-scale heterogeneity in the seed bank of an acidic grassland. *Journal of Ecology* 74:733-738.
- Weaver, J. E., and I. M. Mueller. 1942. Role of seedlings in recovery of Midwestern ranges from drought. *Ecology* 23:275-294.
- Wilson, A. M., and D. D. Briske. 1979. Seminal and adventitious root growth of blue grama seedlings on the Central Plains. *Journal of Range Management* 32:205-213.

Table A2.1. Plant community composition and seed production in 1985, and storage of germinable seeds in the seed bank by functional groups for two shortgrass sites with coefficients of similarity among sites.

	ANNUALS	PERENNIAL GRASSES	PERENNIAL FORBS, SHRUBS AND SUCCULENTS	TOTAL
<hr/>				
PLANT COMMUNITY COMPOSITION ¹ -----				
<u>DENSITY</u> (no/m ²)				
COARSE-TEXTURED	14.1	81.3	16.4	11.8
FINE-TEXTURED	40.5*	85.6	7.9*	134.1*
	[.59]	[.94]	[.57]	[.82]
<u>COVER</u> (percent)				
COARSE-TEXTURED	1.0	38.1	6.9	45.9
FINE-TEXTURED	2.0*	37.6	4.3*	43.8
	[.64]	[.98]	[.79]	[.95]
<hr/>				
SEED PRODUCTION ^{2,3} -----				
(No-m ⁻² -y)				
COARSE-TEXTURED	297	2127	61	2485
FINE-TEXTURED	1776*	476*	55	2307
	[.27]	[.39]	[.98]	[.35]
<hr/>				
SEED BANK ⁴ -----				
<u>DENSITY</u> (no/m ²)				
COARSE-TEXTURED	928	190	26	1144
FINE-TEXTURED	553	185	45	783
	[.93]	[.82]	[.57]	[.89]
<hr/>				
* denotes significance at p<0.05				
[] similarity coefficient among sites				
1 statistical significance determined by analysis of variance				
2 from Coffin et al (1987)				
3 statistical significance determined using t-test				
4 average of eight sampling dates				

Table A2.2. Coefficients of similarity by functional groups for the storage of germinable seeds with the plant community and seed production for two sites.

	ANNUALS	PERENNIAL GRASSES	PERENNIAL FORBS, SHRUBS AND SUCCULENTS	TOTAL
<hr/>				
COARSE-TEXTURED SITE				

PLANT COMMUNITY VS SEED BANK	.27	.36	.27	.31
SEED PRODUCTION VS SEED BANK	.26	.32	.96	.31
<hr/>				
FINE-TEXTURED SITE				

PLANT COMMUNITY VS SEED BANK	.59	.54	.99	.46
SEED PRODUCTION VS SEED BANK	.96	.94	.59	.94
<hr/>				

Table A2.3. Number of seedlings/m² by functional group for eight sampling dates from 1984-1985 and two sites by soil texture.¹

	ANNUALS*	PERENNIAL GRASSES	PERENNIAL FORBS, SHRUBS AND SUCCULENTS	TOTAL*
	(no/m ²)	(no/m ²)	(no/m ²)	(no/m ²)
JULY (1984)				
Coarse-textured	196	204	0	400
Fine-textured	219	166	23	408
SEPTEMBER (1984)				
Coarse-textured	2642	91	15	2748
Fine-textured	1728	143	53	1924
NOVEMBER (1984)				
Coarse-textured	8	76	38	122
Fine-textured	16	128	8	152
MARCH (1985)				
Coarse-textured	249	181	23	452
Fine-textured	242	174	38	454
MAY (1985)				
Coarse-textured	1509	143	45	1697
Fine-textured	830	355	60	1245
JULY (1985)				
Coarse-textured	2219	23	68	2310
Fine-textured	876	68	45	989
SEPTEMBER (1985)				
Coarse-textured	234	204	8	446
Fine-textured	166	106	38	310
NOVEMBER (1985)				
Coarse-textured	370	596	8	974
Fine-textured	347	340	98	785

* denotes significance at $p < 0.05$ for the effects of date
 1 statistical significance determined using Kruskal-Wallis one-way analysis of variance

Table A2.4. Number of seedlings/m² of five species for eight sampling dates from 1984-1985 and two sites by soil texture.

DATE AND SITE	<u>V. octoflora</u> (no/m ²)	<u>L. densiflorum</u> (no/m ²)	<u>S. cryptandrus</u> (no/m ²)	<u>B. dactyloides</u> (no/m ²)	<u>B. gracilis</u> (no/m ²)
<u>JULY (1984)</u>					
Coarse-textured	241	60	407	0	0
Fine-textured	317	45	121	136	0
<u>SEPTEMBER (1984)</u>					
Coarse-textured	4285	694	91	0	0
Fine-textured	2294	649	30	181	0
<u>NOVEMBER (1984)</u>					
Coarse-textured	15	45	106	15	0
Fine-textured	0	0	181	151	0
<u>MARCH (1985)</u>					
Coarse-textured	5	181	226	60	0
Fine-textured	15	211	181	151	0
<u>MAY (1985)</u>					
Coarse-textured	2279	347	15	0	0
Fine-textured	800	287	15	589	0
<u>JULY (1985)</u>					
Coarse-textured	3305	830	45	0	0
Fine-textured	1192	423	45	45	0
<u>SEPTEMBER (1985)</u>					
Coarse-textured	181	121	121	15	211
Fine-textured	91	75	45	151	0
<u>NOVEMBER (1985)</u>					
Coarse-textured	483	91	498	0	649
Fine-textured	317	196	151	453	45

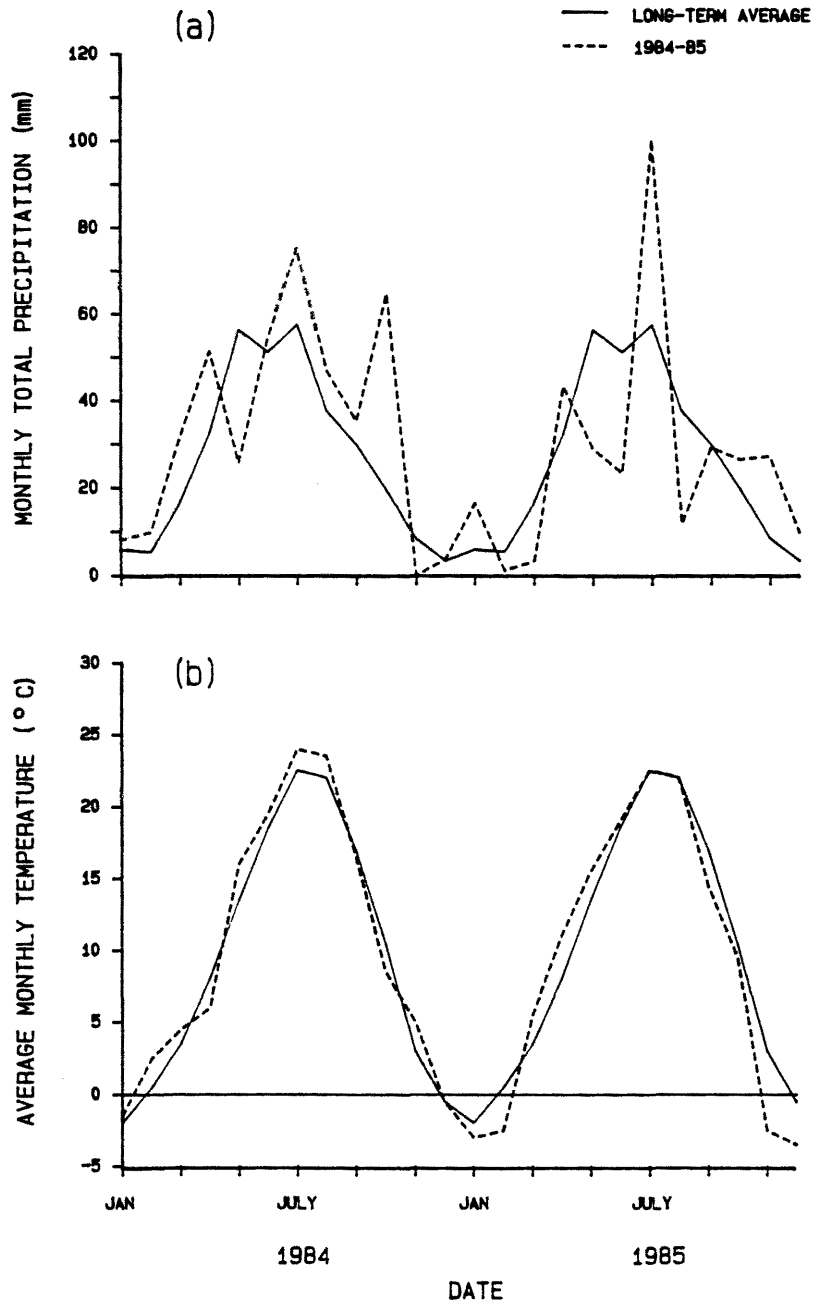


Fig. A2.1. (a) Long-term average and 1984-1985 monthly total precipitation (mm) at the Central Plains Experimental Range. (b) Long-term average and 1984-1985 average monthly temperatures ($^{\circ}\text{C}$) at the Central Plains Experimental Range.

APPENDIX III.

GAP MODEL SENSITIVITY ANALYSIS

Introduction

The objective of the sensitivity analysis was to evaluate the relative response of the model results (output variables) to variability in the values of the parameters.

Eight output variables were chosen to represent the dynamics of the model. Two of the output variables were based on the time required for one Bouteloua gracilis plant to dominate the biomass on the plot by achieving 90% of its maximum size. The first recovery time (1) began at the start of the simulation and included the establishment and growth of a B. gracilis plant. The second recovery time (2) began when B. gracilis plants entered the plot and only included the growth of a plant. The remaining output variables were the biomass variables for the five resource-groups averaged over the time period of each simulation. The perennial forb and shrub group was divided into two sub-groups based on growth rates: slow- and fast-growing plants.

Thirty parameters were chosen from the 109 parameters in the model based on the model structure and their potential effect on the output variables. The parameters can be grouped into five general categories: probabilities associated with seedling establishment, coefficients for

determining the size of the resource space from annual precipitation, growth rates, resource requirements, and the proportion of the resource space associated with each resource-group (Table A3.1).

Sampling Design

A total of 1002 simulations was conducted for 150 years each. A value for each parameter was obtained for each simulation by sampling from a distribution. I assumed the parameter values were uniformly distributed since this type of distribution contains the least amount of bias if only the range of values is known (Tiwari and Hobbie 1976). I assumed the minimum and maximum values of the parameters were approximately 10% below and above the nominal value (Table A3.1). A stratified random, or Latin hypercube, sampling design was used to ensure adequate sampling of the distributions with fewer simulations than would be required for Monte Carlo sampling (McKay et al 1979). Each distribution was divided into three regions of equal area for the sampling; therefore, each region was sampled 334 times for the analysis. At the end of each simulation, the two recovery times of B. gracilis and the average biomass of the resource-groups were calculated.

Statistical Design

A number of statistical analyses have been used in the sensitivity analysis of simulation models, including partial

correlation coefficients, linear regression, and analysis of variance (Rose 1983). The choice of the analysis to use is dependent in part on the objectives of the analysis and the number of parameters to be included. Although analyses such as partial correlation coefficients allow the effects of a large number of parameters to be evaluated, the effects of interactions between parameters on the output variables can not be investigated (Rose 1983). A full factorial analysis of variance does allow the evaluation of interactions, but the number of parameters that can be included in the analysis is limited. The difficulty in interpreting the higher-order interactions has led to the use of a fractional factorial analysis of variance (Steinhorst et al 1978), which also allows more parameters to be included in the analysis than for a full factorial design. Regardless of the statistical analysis chosen, the assumptions underlying these analyses (eg. normality and linear model) may not be valid for the results from a simulation model; therefore the interpretation of the analysis is limited to a ranking of the parameters based on the sensitivity of the output variables to changes in the values of the parameters.

Because of the large number of parameters (30) to be evaluated in the sensitivity analysis for each of the eight output variables, partial correlation coefficients were used as a screening device to determine the nine parameters that each output variable was most sensitive to. The four parameters with the highest absolute value of the partial

correlation coefficients were chosen for each output variable. The remaining five parameters were chosen for their largest expected effects on the output variables due to interactions with other parameters based on the structure of the model. These parameters were then evaluated for the effects of interactions using a fractional factorial analysis of variance that excluded higher-order interactions (> 2-way). The parameters were grouped into three classes of comparable sensitivity based on the F-value associated with each parameter since that value represents the amount of variability in the output variable that is explained by a parameter. The relative sensitivity of the output variables was determined using the magnitude of the F-values for the parameters associated with each output variable.

Results and Discussion

In general, the output variables were relatively insensitive to variability in the parameters. The absolute value of the partial correlation coefficients calculated between each output variable and each parameter were relatively small (0.0003 - 0.474), and most of the parameters for the eight output variables were classified in the sensitivity class with the smallest relative effect (class 3) based on the F-values from the analysis of variance (Table A3.2). The parameters included in the analysis of variance that are not shown in Table A3.2 are

those in which the model results were relatively insensitive compared to the other parameters.

The output variables and the corresponding parameters were chosen based on the objectives and structure of the model. An analysis with a different set of objectives, output variables, and parameters, or a wider range of values for the parameters may have resulted in different conclusions. A relatively small set of parameters (30) was chosen from the total number of parameters in the model (109), and it is possible that higher-order interactions may be important between parameters that were not included in the analysis.

The biomass of B. gracilis, perennial grasses, and annuals were the most sensitive output variables based on their large F-values (>81). The two recovery times of B. gracilis, and the biomass of succulents were of intermediate sensitivity while the biomass values of slow- and fast-growing perennial forbs were relatively insensitive to variability in these parameters.

The two recovery times of B. gracilis were most sensitive to changes in the growth rate of B. gracilis (GBOGR). Parameters associated with the resource requirements of B. gracilis (RBOGR), the size of the resource space in a not extreme precipitation year (SLOP2, YINT2), and the growth and requirements of perennial grasses (RGRASS, GGRASS) were also important. The biomass of B. gracilis was primarily sensitive to parameters associated

with resource requirements and availability of B. gracilis (RBOGR, YINT2, PBOGR, SLOP2). The biomass values of the remaining resource-groups were primarily sensitive to parameters associated with each group, such as the proportion of the resource space partitioned to annuals and the biomass of annuals. Parameters associated with B. gracilis (RBOGR, PBOGR) or with the size of the resource space (YINT2, SLOP2) were also important. Two output variables were sensitive to the probabilities associated with seed availability: the biomass of fast-growing perennial forbs and the biomass of annuals. In several cases, parameters that were not important as main effects were important as interactions with other parameters (ex. YINT2 and the two recovery times of B. gracilis).

Conclusions

The basis of the conceptual and simulation models of gap dynamics in shortgrass communities is the relationship between the availability and use of belowground resources, and the belowground gaps produced by the death of B. gracilis plants. Although the model results were relatively insensitive to the parameters used in the sensitivity analysis, the results were most sensitive to parameters associated with this relationship. Therefore, experimental research should focus on the availability and use of belowground resources by the resource-groups, and in particular by B. gracilis.

LITERATURE CITED

- McKay, M. D., W. J. Conover, and R. J. Beckman. 1979. A comparison of three methods for selecting values of input variables in the analysis of output from a computer code. *Technometrics* 21:239-245.
- Rose, K. A. 1983. A simulation comparison and evaluation of parameter sensitivity methods applicable to large models. Pages 129-140 in W. K. Lauenroth, G. V. Skogerbee, and M. Flug, editors. *Analysis of ecological systems: State-of-the-art in ecological modelling*. Elsevier Scientific Publishing Co. New York.
- Steinhorst, R. K., H. W. Hunt, G. S. Innis, and K. P. Hatdock. 1978. Sensitivity analysis of the ELM model. Pages 231-255 in G. S. Innis, editor. *Grassland simulation model*. Ecological Studies 26. Springer-Verlag. New York.
- Tiwari, J. L., and J. E. Hobbie. 1976. Random differential equations as models of ecosystems: Monte Carlo simulation approach. *Mathematical Biosciences* 28:25-44.

Table A3.1. Sensitivity analysis parameter values

OUTPUT VARIABLE	CODE NAME	MINIMUM VALUE	NOMINAL VALUE	MAXIMUM VALUE
SEEDLING ESTABLISHMENT PROBABILITIES				
<u>B. gracilis</u>	SBOGR	0.113	0.125	0.138
Perennial grasses	SGRASS	0.440	0.490	0.540
Slow-growing perennial shrubs and forbs	SLFB	0.016	0.018	0.020
Fast-growing perennial forbs	SSFB	0.065	0.072	0.079
Annuals	SANNU	0.360	0.400	0.440
Succulents	SOPPO	0.018	0.020	0.022
COEFFICIENTS FOR SIZE OF RESOURCE SPACE				
Below-average precipitation				
y-intercept	YINT1	0.072	0.080	0.088
slope	SLOP1	0.0036	0.004	0.0044
Not extreme precipitation				
y-intercept	YINT2	0.00084	0.00093	0.00102
slope	SLOP2	0.63842	0.70935	0.78029
Above-average precipitation				
y-intercept	YINT3	0.522	0.580	0.638
slope	SLOP3	0.0036	0.004	0.0044
GROWTH RATES				
<u>B. gracilis</u>	GBOGR	0.427	0.474	0.521
Perennial grasses	GGRASS	0.427	0.474	0.521
Slow-growing perennial shrubs and forbs	GLFB	0.427	0.474	0.521
Fast-growing perennial forbs	GSFB	0.663	0.737	0.811
Annuals	GANNU	0.894	0.941	1.000
Succulents	GOPPO	0.260	0.289	0.318

Table A3.1. (continued)

OUTPUT VARIABLE	CODE NAME	MINIMUM VALUE	NOMINAL VALUE	MAXIMUM VALUE
<hr/>				
RESOURCE REQUIREMENTS PER INDIVIDUAL				
<hr/>				
<u>B. gracilis</u>	RBOGR	0.459	0.510	0.561
Perennial grasses	RGRASS	0.188	0.209	0.230
Slow-growing perennial shrubs and forbs	RLFB	0.162	0.180	0.198
Fast-growing perennial forbs	RSFB	0.162	0.180	0.198
Annuals	RANNU	0.0378	0.042	0.0462
Succulents	ROPP0	0.2034	0.226	0.2486
PROPORTION OF RESOURCE SPACE				
<hr/>				
<u>B. gracilis</u>	PBOGR	0.459	0.510	0.561
Perennial grasses	PGRASS	0.063	0.070	0.077
Slow-growing perennial shrubs and forbs	PLFB	0.243	0.270	0.297
Fast-growing perennial forbs	PSFB	0.009	0.010	0.011
Annuals	PANNU	0.063	0.070	0.077
Succulents	POPPO	0.063	0.070	0.077
<hr/>				

Table A3.2. Sensitivity classes and F-values of parameters for eight output variables from analysis of variance

OUTPUT VARIABLE AND PARAMETERS	SENSITIVITY ¹ CLASS	F-VALUE
RECOVERY TIME (1)		
GBOGR	2	19.095
RBOGR	3	5.188
RGRASS x PBOGR	3	4.905
SLOP2 x YINT2	3	4.450
GGRASS x SLOP2	3	4.203

RECOVERY TIME (2)		
GBOGR	2	16.392
RBOGR	3	6.166
RBOGR x YINT2	3	4.694

<u>B. gracilis</u> BIOMASS		
RBOGR	1	118.405
YINT2	2	48.015
PBOGR	3	14.475
SLOP2	3	9.180
PLFB	3	4.603

PERENNIAL GRASSES BIOMASS		
YINT2	1	81.462
RBOGR	3	12.268
SLOP2	3	9.356
SLOP2 x YINT2	3	5.222
RGRASS	3	4.868
SLOP2 x GGRASS	3	4.776

SLOW-GROWING PERENNIAL FORBS BIOMASS		
RBOGR	3	4.044

1 SENSITIVITY CLASSES	1	F-VALUE > 75
	2	15 < F-VALUE <= 75
	3	4 < F-VALUE <= 15

Table A3.2. (continued)

OUTPUT VARIABLE AND PARAMETERS	SENSITIVITY ¹ CLASS	F-VALUE
FAST-GROWING PERENNIAL FORBS BIOMASS		
RBOGR	3	11.562
YINT2	3	10.321
RSFB	3	9.965
SSFB	3	8.314
GBOGR x YINT2	3	6.197
SLOP2 x PSFB	3	5.492
GSFB	3	4.397

ANNUALS BIOMASS		
PANNU	1	106.397
YINT2	1	93.968
RANNU	2	42.820
SANNU	2	29.869
PBOGR	2	25.244
SLOP2	2	20.541
GANNU	3	7.430
SANNU x SLOP2	3	4.304

SUCCULENTS BIOMASS		
POPPO	2	50.357
YINT2	2	34.811
PBOGR	3	12.872
PLFB	3	11.621
SLOP2	3	6.281

1 SENSITIVITY CLASSES	1	F-VALUE > 75
	2	15 < F-VALUE <= 75
	3	4 < F-VALUE <= 15

APPENDIX IV

GAP MODEL DOCUMENTATION

Introduction

The documentation of the gap model (STEPPE) of Chapter 4 is separated into two parts. The first part describes the conceptual model of gap dynamics for a semiarid grassland, and the general structure of the model. The second part consists of the FORTRAN code of the model.

Conceptual Model of Gap Dynamics in a Semiarid Grassland

The gap dynamics conceptualization of plant communities focuses on the resource space associated with individual plants in the community. The conceptual model of gap dynamics for shortgrass communities is based on belowground resource space with a focus on the gaps produced by the death of Bouteloua gracilis plants. The model associates a particular proportion of resource space with individual species or groups of species. The proportion associated with a species or group is a function of its root distribution with depth, the distribution of resources with depth, and the temporal variability of both distributions.

The distributions of resources is based on the average distribution of soil water availability with depth in the soil profile (Fig. A4.1a) since soil water is the major

control on plant growth and community structure in semiarid grasslands (Noy-Meir 1973, Lauenroth et al 1978). The initial increase in resources with depth is the result of high evaporation rates at the soil surface. This initial increase is followed by a gradual decrease in resources with depth as the penetration of the soil water resource declines (Sala and Lauenroth 1985).

The root distributions with depth (Fig. A4.1b) were approximated by grouping the more than 300 plant species that may occur in shortgrass communities into five resource-groups based on similar life histories and spatial distributions of root biomass: B. gracilis, other perennial grasses and sedges besides B. gracilis, perennial forbs and shrubs, annual grasses and forbs, and succulents (Weaver 1919; 1958, Turner and Costello 1942, Coupland and Johnson 1965, Dougherty 1986, Lee 1988, Appendix I). The distribution of roots for each group, or the distribution of potential resource use, is shown as a proportion of the total root biomass, or total resource use, with depth (Fig. A4.1b).

The product of the resource abundance (Fig. A4.1a) and potential resource use distributions (Fig. A4.1b) represents the partitioning of the available resources by the groups (Fig. A4.2). The area between the curves represents the proportion of the resources that are associated with each group, or the resource space for that group (Table A4.1).

I assumed the shape of the potential resource use curves are constant through time, although the proportion of the resources available to each group varies with plant growth, death and establishment. Resources that are not used by one group are available to the other groups depending on the similarity in the distribution of roots and the morphology of the root systems. I hypothesized that B. gracilis plants were not able to use resources associated with other groups. This hypothesis is supported by the lack of response of the spatial distribution of B. gracilis roots to the removal of neighboring plants (Appendix I). Resources not used by B. gracilis plants are available to other groups except succulents. Perennial grasses, perennial forbs and shrubs, and annuals have roots at similar depths in the soil profile as B. gracilis while the roots of succulents are concentrated near the soil surface where few B. gracilis roots are found. Because of the spatial overlap in the location of perennial grass, perennial forb and shrub, and annual roots, I assumed that resources not used by one of these groups are available to the other two groups. Resources associated with succulents are not available to other groups and succulents can not use resources of the other groups.

I assumed the resource abundance curve (Fig. A4.1a) varied with the amount of annual precipitation. Most of the precipitation events at the CPER are small events (<5 mm), while most of the precipitation is contributed by a few

large rainfall events (Sala and Lauenroth 1982). The important difference between average years and wet or dry years is the number of large events (≥ 20 mm). In above-average precipitation years there are typically more large events and in below-average precipitation years there are fewer large events than in average years (Bourgeron et al 1987). The result is that the difference in the resource abundance curves for these three general conditions is in the deep soil layers rather than at the soil surface (Fig. A4.3). Therefore, in years of above-average precipitation the resource-group with a large proportion of its roots in the deep soil layers (perennial forbs and shrubs) is affected more by the increase in resources than the other groups. In years of below-average precipitation, shallow-rooted groups (*B. gracilis* and succulents) are affected less by the decrease in resources than the other groups.

Simulation Model Structure

The STEPPE model simulates the establishment, growth and death of individual plants on a small plot through time on an annual time step. The five resource-groups were divided into fifteen species-groups based on similar life history characteristics and responses to environmental factors (Table A4.2). Fifteen groups were used to account for differences between perennials (forbs and shrubs), annuals (grasses and forbs), and short- and long-lived perennial grasses, forbs and shrubs. A representative

species is used for each of the groups. The size and age of all plants on the plot within each of the fifteen groups are kept track of through time (Fig. A4.4a). The effects of the three driving variables (precipitation, temperature and disturbances) and information flow within and among species-groups on the establishment, growth or mortality of plants on the plot are specific to each group. A generalized Forrester diagram is shown for two representative species in Figure A4.4b.

The size of the plot is an important component of gap dynamics models (Shugart and West 1979). A plot size that is too small will prevent plants from reaching their maximal size while a plot size that is too large will not result in gap-phase replacement since the death of an individual has an insignificant effect on the dynamics of plants on the plot. In forests, aboveground resources are important and the most appropriate plot size is that of a typical large-canopy dominant tree (Shugart 1984). In semiarid grasslands, belowground resources are important; therefore the plot size was based on the belowground resource space associated with a full-size plant of the dominant species, B. gracilis. I assumed the plot size was represented by the total surface area of a full-size B. gracilis plant because of the relationship between surface area and rooting volume of B. gracilis plants (Appendix I). A B. gracilis plant was defined as all tillers currently connected by a crown.

The plot size was estimated in the following way:

The size distribution and basal cover of B. gracilis plants for three topographic positions in a heavily grazed pasture (Chapter 2) were used to estimate the total surface area of a full-size B. gracilis plant. I assumed that a landscape dominated by B. gracilis could be partitioned into equal-sized cells, each containing one B. gracilis plant. The size of a cell, or the plot size, was calculated for each topographic position by dividing the surface area of the full-sized plant by the basal cover of B. gracilis (Table A4.3). I defined a full-size plant as the size that excluded the upper 10% of each frequency distribution. The average plot size for the three locations was 0.1217 m².

FORTRAN Code Documentation

The following pages contain a documentation of the FORTRAN code for the STEPPE model. The code for the MAIN program is followed by the code for the subroutines.


```

PROGRAM STEPPE
COMMON /GRASSL/ NPLANT(50),SIZE(499),IAGE(499),KSPRT(50),NEWTR(50),
1DBHMAX(50),SWTCH(5),RINIT(50),JTEMP(50),RTMAX(50)
COMMON /PARAM/ AAA(50,2),GMORT(50),NGRPID(50),RESRQ(50),NSPD(499),
1AGEMX(50),RESPROP(50),EQIND(50),RGR(50),REGEN(50),NDIST(50)
COMMON /CONST/ NSPEC,APPT,SDPPT,ATEMP,SDTEMP,NGRP
COMMON /DEAD/ NOGRO(499),NTEMP(499)
COMMON /COUNT/ NTOT,NYEAR,KPRNT,KPLOT,ICHECK,MCHECK
COMMON /TEMP/ DTEMP(499),ITEMP(499),DROPT(499),RTOPT(499),
1SUMRT(50),NEWPL(50),JCHECK(50),RESPONSER(50),TEMPR(50),MTEMP(499)
COMMON /PLANTS/ BOGR(1000),SIHY(1000),ARLO(1000),CAHE(1000),
1SCPA(1000),SPCO(1000),CHNA(1000),WFL(1000),WSLL(1000),
2XATA(1000),GACO(1000),GUSA(1000),VUOC(1000),XEDE(1000),CHAL(1000),
3OPPO(1000)
COMMON /RGROUPS/ RBOGR(1000),RGRASS(1000),RFORBL(1000),
1RFORBS(1000),RANNUA(1000),ROPO(1000),XPPT(1000),XTEMP(1000)
COMMON /TPLANT/ TBOGR,TSIHY,TARLO,TCAHE,TSCPA,TSPCO,TCHNA,TWFL,
1TWSLL,TXATA,TGACO,TGUSA,TVUOC,TXEDE,TCHAL,TOPO
COMMON /TREST/ TRBOGR,TRGRASS,TRFORBL,TRFORBS,TRANNUA,TROPPO,
1TXPPT,XTTEMP
COMMON /ENVP/ YPPT,YTEMP
COMMON /SENS/ PARMV(3,40),YOUT(8),XMIN(30),XMAX(30),XNOM(30)
COMMON /SCOUNT/ NCHECK,LYR,KCHECK
C FILE TGROUP IS OUTPUT FILE OF RESOURCE USE BY SPECIES-GROUPS
C FILE RGROUP IS OUTPUT FILE OF RESOURCE USE BY RESOURCE-GROUPS
OPEN (UNIT=8, FILE='D:RGROUP.OUT')
OPEN (UNIT=11, FILE='D:TGROUP.OUT')
C.....
C.....INPUT CONTROL PARAMETERS, SITE CHARACTERISTICS, AND
C.....INDIVIDUAL SPECIES INFORMATION
C.....
CALL INPUT
C 10 STARTS NEXT PLOT
IPLT=0
10 CONTINUE
C INITIALIZE PLOT AT BARE PLOT STAGE
CALL PLOTIN (IPLT)
WRITE (6,30) IPLT
DO 5002 IJ=1,8
YOUT(IJ)=0.0
5002 CONTINUE
C MCHECK AND M ARE USED IN PAT RECOLON. FUNCTION
MCHECK=0
M=0
C ICHECK AND K ARE USED IN MOUND RECOLON. FUNCTION
ICHECK=0
K=0
C NCHECK, KCHECK AND LYR ARE USED IN SENSITIVITY ANALYSIS AND
C MODEL OUTPUT FOR BLUE GRAMA RECOVERY TIMES
NCHECK=0
KCHECK=0
LYR=0
KYR=0

```

```

C   START OF EACH YEAR
      DO 20 KK=1,NYEAR
        KYR=KK
C   DETERMINE PPT AND TEMP VALUES ASSUMING TRUNCATED NORMAL DISTRIBUTIONS
C..... PRECIPITATION
C   THE AVERAGE ANNUAL PPT AT THE CPER FOR 38 YEARS OF DATA IS 311 mm
C   (SALA AND LAUENROTH 1982). THE STANDARD DEVIATION (79.4 mm) WAS
C   BASED ON 42 YEARS OF PPT DATA OVER THE SAME TIME PERIOD FROM
C   THE GREELEY WEATHER STATION. I ASSUMED A SIMILAR DISTRIBUTION OF
C   PPT AT THE CPER AS FOR GREELEY, AND SCALED THE STANDARD DEVIATION
C   TO THE MEAN. I ASSUMED THE PPT VALUES HAD A TRUNCATED NORMAL
C   DISTRIBUTION WITH VALUES RANGING FROM 105-520 mm.
C..... TEMPERATURE
C   THE AVERAGE DAILY MAXIMUM TEMPERATURE (24.5°C) DURING THE GROWING
C   SEASON (APRIL 1-SEPT. 30) WAS OBTAINED FROM A DISTRIBUTION BASED
C   ON MORE THAN 20 YEARS OF DATA FROM THE CPER (JAMESON 1969).
C   THE TEMPERATURE VALUES ARE USED TO DETERMINE THE EFFECTS OF
C   TEMPERATURE ON PLANT GROWTH RATES IN THE GROW ROUTINE. A TRUNCATED
C   NORMAL DISTRIBUTION IS USED WITH VALUES RANGING FROM 15-35°C. THE
C   STANDARD DEVIATION (1.0°C) WAS SCALED TO THE MEAN BASED ON THE
C   DISTRIBUTION OF TEMPERATURE VALUES FROM THE GREELEY WEATHER STATION
C   FOR 33 YEARS OF DATA OVER THE SAME TIME PERIOD.
C
      U1=RANDU(1)
      U2=RANDU(1)
      PI=3.1415927
      RPPT=((( -2*ALOG(U1))**0.5)*SIN(PI*2*U2))
      RTEMP=((( -2*ALOG(U1))**0.5)*COS(PI*2*U2))
      APPT=311.0
      SDPPT=79.43
      ATEMP=24.54
      SDTEMP=1.0
      YPPT=APPT+(RPPT*SDPPT)
      YTEMP=ATEMP+(RTEMP*SDTEMP)
      IF (YPPT.LE.105.0) YPPT=105.0
      IF (YPPT.GE.520.0) YPPT=520.0
      IF (YTEMP.LE.15.0) YTEMP=15.0
      IF (YTEMP.GE.35.0) YTEMP=35.0
C..... PLANTS ARE KILLED EACH YEAR BASED ON AGE AND AMOUNT OF GROWTH
      CALL KILL (KYR)
C..... CAN RECOLONIZATION OF PATS/MOUNDS OCCUR THIS YEAR?
C..... PAT AND MOUND RECOLONIZATION PROCEDURES ARE DESCRIBED IN
C..... THE KILL ROUTINE
      IF (MCHECK.EQ.0) GO TO 13
      IF (MCHECK.GT.0) M=M+1
      RANPF=RANDU(1)
      PROBF=0.0975*M + 0.025
C..... PROBF=PROB. OF RECOLONIZATION
      IF (RANPF.GT.PROBF) GO TO 14
C..... NO RECOLONIZATION THIS YEAR
      M=0
      MCHECK=0
C..... RECOLONIZATION OCCURS IF RANPF <= PROBF

```

```

      GO TO 12
C    CALCULATE NO. OF YEARS ANT MOUND WILL HAVE ANTS AND THEREFORE
C    PLANT RECOVERY CAN NOT OCCUR
13   IF (ICHECK .EQ. 0) GO TO 12
      IF (ICHECK .GT. 0 .AND. K .LT. 1) GO TO 22
      IF (ICHECK .GT. 0 .AND. K .GE. 1) GO TO 33
22   RAN=RANU(1)
      NAYR=RAN*(40-20)+20.5
33   IF (K .LE. NAYR) K=K+1
      IF (K .GT. 0 .AND. K .LT. NAYR) GO TO 14
      IF (K .GE. NAYR) ICHECK=0
      K=0
C..... SEEDLINGS GERMINATE EACH YEAR BASED ON SPECIES REQUIREMENTS
C..... AND SITE CHARACTERISTICS
12   CONTINUE
      CALL RECRUIT (KYR)
C..... CALCULATE AMOUNT OF GROWTH FOR EACH PLANT BASED ON RESOURCES/PPT,
C..... AND TEMPERATURE
14   CONTINUE
      CALL GROW (KYR,IPL0T)
15   CONTINUE
20   CONTINUE
C.....CHECK FOR COMPLETION OF LAST PLOT
C.....
      IF (IPL0T.NE.KPLOT) GO TO 10
      CLOSE (UNIT=8)
      CLOSE (UNIT=11)
      STOP
30  FORMAT (/, ' PLOT NUMBER ',I4)
      END

```

SUBROUTINE INPUT

C.....

C.....SUBROUTINE INPUT CONTAINS ALL INPUT STATEMENTS TO THE MODEL

C.....

```

COMMON /GRASSL/ NPLANT(50),SIZE(499),IAGE(499),KSPRT(50),NEWTR(50),
1DBHMAX(50),SWTCH(5),RINIT(50),JTEMP(50),RTMAX(50)
COMMON /PARAM/ AAA(50,2),GMORT(50),NGRPID(50),RESRQ(50),NSPD(499),
1AGEMX(50),RESPROP(50),EQIND(50),RGR(50),REGEN(50),NDIST(50)
COMMON /CONST/ NSPEC,APPT,SDPPT,ATEMP,SDTEMP,NGRP
COMMON /DEAD/ NOGRO(499),NTEMP(499)
COMMON /COUNT/ NTOT,NYEAR,KPRNT,KPLOT,ICHECK,MCHECK
COMMON /TEMP/ DTEMP(499),ITEMP(499),DROPT(499),RTOPT(499),
1SUMRT(50),NEWPL(50),JCHECK(50),RESPONSER(50),TEMPR(50),MTEMP(499)

```

C.....

```

OPEN (UNIT=5, FILE='MODAT.FOR')

```

C.....KPLOT - NUMBER OF PLOTS TO BE SIMULATED

C.....NYEAR - NUMBER OF YEARS EACH PLOT WILL BE RUN

```

READ (5,20) KPLOT,NYEAR

```

20 FORMAT (6X,I3,8X,I4)

```

WRITE (6,30) KPLOT,NYEAR

```

30 FORMAT ('OPLOTS = ',I3,' YEARS = ',I4)

C.....NSPEC - NUMBER OF SPECIES; NGRP-NO. RESOURCE GROUPS

```

READ (5,130) NSPEC,NGRP

```

130 FORMAT (I2,1X,I2)

```

WRITE (6,135) NSPEC,NGRP

```

135 FORMAT ('ONO. SPECIES = ',I2,' NO. RES. GROUPS = ',I2)

C.....INPUT INDIVIDUAL SPECIES INFORMATION

C.....THE DESCRIPTIONS OF THESE PARAMETERS ARE IN THE SUBROUTINES

C.....WHERE THEY ARE USED.

C.....

C.....AAA - SPECIES NAME

C.....REGEN- PROBABILITIES OF REGENERATION

C.....RINIT- INITIAL SIZE OF SEEDLINGS

C.....AGEMX - MAXIMUM AGE OF SPECIES

C.....NDIST - DISTURBANCE RESPONSE CLASS

C.....RTMAX- MAXIMUM GROWTH INCREMENT

C.....JTEMP - TEMPERATURE RESPONSE CLASSES

C.....NGRPID - RESOURCE GROUP ID

C.....RGR - GROWTH RATE

C.....GMORT - MORTALITY RESPONSE TO LIMITING RESOURCES

C.....RESPROP - PROPORTION OF RESOURCE SPACE USED PER GROUP

C.....RESRQ - RESOURCES REQUIRED PER INDIVIDUAL BY RESOURCE GROUP

```

J=1

```

```

DO 200 K=1,NGRP

```

```

READ (5,*) RGR(J),RESPROP(J),RESRQ(J)

```

```

WRITE (6,*) RGR(J),RESPROP(J),RESRQ(J)

```

```

J=J+1

```

200 CONTINUE

```

J=1

```

```

DO 100 K=1,NSPEC

```

```

READ (5,140) (AAA(J,I),I=1,2),REGEN(J),RINIT(J),AGEMX(J),NDIST(J)

```

```

1,RTMAX(J),JTEMP(J),NGRPID(J),GMORT(J)

```

```

WRITE (6,150) (AAA(J,I),I=1,2),REGEN(J),RINIT(J),AGEMX(J),NDIST(J)

```

```
      1,RTMAX(J),JTEMP(J),NGRPID(J),GMORT(J)
      J=J+1
100 CONTINUE
110 CONTINUE
      CLOSE (UNIT=5)
      RETURN
140 FORMAT (2A2,1X,F6.4,2X,F4.2,2X,F4.1,1X,I1,1X,F4.1,1X,I1,1X,I1,1X,
      1F5.3,1X,F7.5,2X,F5.3,1X,F5.3)
150 FORMAT (' ',2A2,1X,F6.4,2X,F4.2,2X,F4.1,1X,I1,1X,F4.1,1X,I1,1X,I1,
      11X,F5.3,1X,F7.5,2X,F5.3,1X,F5.3)
      END
```

SUBROUTINE PLOTIN (IPLLOT)

C.....

C.....SUBROUTINE PLOTIN INITIALIZES VARIABLES TO START FROM BARE PLOT.

C.....

```

COMMON /GRASSL/ NPLANT(50),SIZE(499),IAGE(499),KSPRT(50),NEWTR(50),
1DBHMAX(50),SWTCH(5),RINIT(50),JTEMP(50),RTMAX(50)
COMMON /PARAM/ AAA(50,2),GMORT(50),NGRPID(50),RESRQ(50),NSPD(499),
1AGEMX(50),RESPROP(50),EQIND(50),RGR(50),REGEN(50),NDIST(50)
COMMON /CONST/ NSPEC,APPT,SDPPT,ATEMP,SDTEMP,NGRP
COMMON /DEAD/ NOGRO(499),NTEMP(499)
COMMON /COUNT/ NTOT,NYEAR,KPRNT,KPLOT,ICHECK,MCHECK
COMMON /TEMP/ DTEMP(499),ITEMP(499),DROPT(499),RTOPT(499),
1SUMRT(50),NEWPL(50),JCHECK(50),RESPONSER(50),TEMPR(50),MTEMP(499)

```

C.....

C.....NTREES CONTAINS NUMBER OF PLANTS OF EACH SPECIES

C.....DBH CONTAINS SIZE OF EACH PLANT RELATIVE TO A FULL-SIZE PLANT

C.....

C.....NOGRO IS USED TO FLAG THE PLANTS THAT ARE SLOW GROWERS

C.....KSPRT IS USED TO FLAG THE SPECIES THAT CAN SPROUT

C.....IAGE CONTAINS THE AGE OF EACH PLANT

C.....

C.....

C.....INITIALIZE ARRAYS TO ZERO

C.....

```

IPLLOT=IPLLOT+1
DO 10 I=1,NSPEC
  NPLANT(I)=0
  SIZE(I)=0.
  NOGRO(I)=0
  KSPRT(I)=1
  IAGE(I)=0
10 CONTINUE
  NSPE1=NSPEC+1
  DO 20 I=NSPE1,499
    SIZE(I)=0.
    NOGRO(I)=0
    IAGE(I)=0
20 CONTINUE
  RETURN
END

```

SUBROUTINE KILL (KYR)

C*****
C
C THREE SOURCES OF MORTALITY ARE POSSIBLE IN THE KILL ROUTINE
C BASED ON INFORMATION FROM SHUGART (1984), AND ARE SPECIFIC TO
C EACH SPECIES-GROUP (TABLE 2)
C 1. EACH SPECIES-GROUP HAS AN AGE-INDEPENDENT INTRINSIC LIKELIHOOD
C OF MORTALITY SINCE A CERTAIN PERCENTAGE OF A COHORT GROWING UNDER
C OPTIMUM CONDITIONS WILL NOT REACH THE MAXIMUM AGE (AGEMX).
C THIS MORTALITY IS REPRESENTED BY THE PROBABILITY THAT A PLANT WILL
C BE DEAD BY THE n th YEAR: $P_n = 1 - (1 - \text{EPS})^n$, WHERE P_n IS THE PROBABILITY
C OF MORTALITY BY YEAR n , AND EPS IS THE ANNUAL MORTALITY PROBABILITY.
C I ASSUMED THAT 1% OF A COHORT WILL REACH THE MAXIMUM AGE; THUS THE
C PROBABILITY OF MORTALITY (EPS) EQUALS $4.605/\text{AGEMX}$. THE MAXIMUM AGE
C OF EACH SPECIES-GROUP WAS APPROXIMATED USING LONGEVITY DATA FOR
C SIMILAR SPECIES FROM OTHER PLANT COMMUNITIES SINCE THE MAXIMUM AGE
C OF SHORTGRASS PLANTS IS UNKNOWN. THE MAXIMUM AGE OF LONG-LIVED PERENNIAL
C GRASSES (25 Y) WAS BASED ON DATA FOR *Bouteloua eriopoda* WHERE
C SEVERAL CLUMPS SURVIVED FOR 20 YEARS AND ONE CLUMP SURVIVED FOR
C 27 YEARS IN A SEMI-DESERT GRASSLAND (WRIGHT 1972). THE MAXIMUM
C AGE OF SHORT-LIVED PERENNIAL GRASSES AND FORBS (10 Y) WAS ESTIMATED
C FROM DATA ON A NUMBER OF GRASSES WITH LIFESPANS RANGING FROM 6-14 Y
C (NELSON 1934, CANFIELD 1957, WRIGHT 1972). I ASSUMED SHORT-LIVED
C PERENNIAL FORBS HAVE A SIMILAR LONGEVITY AS SHORT-LIVED PERENNIAL
C GRASSES. THE MAXIMUM AGE OF LONG-LIVED PERENNIAL FORBS AND SHRUBS
C (35 Y) WAS BASED ON THE MAXIMUM AGE OF A PRAIRIE FORB IN ILLINOIS,
C *Liatris aspera* (34 Y) (KERSTER 1968).
C
C 2. I ASSUMED THAT SLOW-GROWING PLANTS HAVE A GREATER RISK OF DEATH
C BECAUSE OF A GREATER VULNERABILITY TO DISEASE, INSECTS AND SEVERE
C ENVIRONMENTAL CONDITIONS. A SLOW-GROWING INDIVIDUAL WAS DEFINED AS A
C PLANT HAVING A GROWTH RATE LESS THAN 5% OF ITS MAXIMUM RATE FOR TWO
C CONSECUTIVE YEARS. MAXIMUM GROWTH RATES WERE APPROXIMATED AS 90% OF
C THE INTRINSIC RATE OF GROWTH. THE PROBABILITY OF MORTALITY (0.368)
C RESULTS IN A SLOW-GROWING PLANT HAVING A 1% CHANCE OF SURVIVING
C TEN YEARS. THIS IS THE SAME PROBABILITY USED IN THE FOREST MODELS
C (SHUGART 1984).
C *Bouteloua gracilis* AND *O. polyacantha* WERE EXCLUDED FROM THE FIRST
C TWO SOURCES OF MORTALITY BECAUSE I ASSUMED THAT THE CLONAL GROWTH
C EXHIBITED BY PLANTS OF THESE SPECIES WOULD MORE LIKELY RESULT IN
C PARTS OF PLANTS DYING (TILLERS OF *B. gracilis* AND CLADODES OF
C *O. polyacantha*) DUE TO SLOW GROWTH OR AN INTRINSIC LIKELIHOOD OF
C MORTALITY RATHER THAN THE ENTIRE PLANT. THE MORTALITY OF *B. gracilis*
C CLUMPS OCCURS ONLY AS A RESULT OF INSUFFICIENT RESOURCES IN THE
C GROW ROUTINE OR FROM DISTURBANCES, WHILE THE MORTALITY OF *O. polyacantha*
C ALSO INCLUDES A PROBABILITY BASED ON GROWING SEASON PPT. I ASSUMED
C THE DECREASE IN FREQUENCY OF *O. polyacantha* CLUMPS WITH HIGH AMOUNTS
C OF GROWING SEASON PPT FROM FIELD DATA (DOUGHERTY 1986) REPRESENTS THE
C PROBABILITY OF DEATH FOR A CLUMP IN A YEAR WITH THAT AMOUNT OF PPT.
C
C 3. THE THIRD SOURCE OF MORTALITY IS DUE TO DISTURBANCES. THE EFFECTS
C OF CATTLE FECAL PATS, WESTERN HARVESTER ANT MOUNDS, AND BURROWS FROM
C SMALL ANIMALS ARE INCORPORATED INTO THE MODEL BASED ON THEIR

C FREQUENCIES OF OCCURRENCE FROM CHAPTER 2 FOR A MODERATELY GRAZED
C SWALE.

C (a) THE PROBABILITY OF A FECAL PAT OCCURRING ON THE PLOT (PFEC) IS
C 0.0022185/Y. ONCE A PAT IS DEPOSITED ON A PLOT, THERE IS A PROBABILITY
C (RBPAT=0.025) THAT IT WILL EITHER DECOMPOSE OR BE PHYSICALLY REMOVED
C FROM THE PLOT DUE TO CATTLE ACTIVITY SHORTLY AFTER DEPOSITION. THIS
C IS BASED ON THE ESTIMATE THAT 1 IN 20 PAT EVENTS WILL NOT REMAIN ON
C THE PLOT. IF THE PAT IS REMOVED, *B. gracilis* PLANTS AND SPECIES-
C GROUPS COMPOSED PRIMARILY OF LOW-GROWING PLANTS ARE NOT KILLED.
C HOWEVER, PATS THAT REMAIN ON THE PLOT RESULT IN THE DEATH OF THESE
C PLANTS. IN THE CASE OF *B. gracilis*, I ASSUMED A FECAL PAT THAT
C REMAINS ON A PLOT ALWAYS KILLS THE ENTIRE PLANT (CHAPTER 2), AND THAT
C EVEN WHEN PATS ARE ON THE PLOT FOR A SHORT TIME IT IS ALWAYS SUFFICIENT
C TO KILL ANNUAL PLANTS AND THE SEEDLINGS OF SHRUBS, FORBS AND SOME
C GRASSES. I ALSO ASSUMED *O. polyacantha* CLUMPS, AND SHRUBS, FORBS,
C AND SOME GRASSES LARGER THAN SEEDLINGS ARE NOT AFFECTED BY FECAL
C PATS.

C BECAUSE OF THE RELATIVELY SLOW AVERAGE RATE OF DECOMPOSITION OF FECAL
C PATS IN SHORTGRASS COMMUNITIES (LUSSENHOP ET AL 1982), I ASSUMED
C THE TIME WHEN RECOLONIZATION BEGINS ON THE PLOT IS DESCRIBED BY A
C PROBABILITY DISTRIBUTION IN WHICH THE PROBABILITY OF COLONIZATION
C INCREASES WITH TIME AFTER THE EVENT. $PROBF=0.0975*M +0.025$ WHERE
C THE VALUES OF PROBF RANGE FROM 0.025 WHEN $M=0.0$ TO 1.0 WHEN $M=1.0$.
C (THIS OCCURS IN THE MAIN PROGRAM)

C

C (b) THE PROB. OF A WESTERN HARVESTER ANT MOUND OCCURRING ON
C THE PLOT (PANT) IS 0.0000197.

C I ASSUMED THE PRESENCE OF A WESTERN HARVESTER ANT MOUND ON THE
C PLOT RESULTS IN THE DEATH OF ALL PLANTS, EXCEPT SHRUBS AND SOME
C PERENNIAL GRASSES. I BASED THIS ASSUMPTION ON THE PHYSICAL STATURE
C OF THE PLANTS AND FIELD OBSERVATIONS OF THE NEST SELECTION PROCESS
C BY HARVESTER ANTS.

C THE RECOVERY OF PLANTS BEGINS 20-40 YEARS AFTER THE ANT MOUND IS
C INITIATED. THE NUMBER OF YEARS IS UNIFORMLY DISTRIBUTED. THE TIME
C FOR RECOVERY TO BEGIN IS BASED ON THE ESTIMATED TIME THAT ANTS
C OCCUPY A PARTICULAR NEST SITE CALCULATED FROM AN ANALYSIS OF MOUND
C TURNOVER TIMES. THE TOTAL NUMBER OF MOUNDS AT DIFFERENT STAGES OF
C DEVELOPMENT IN A 2.5 HA LIGHTLY GRAZED PASTURE WAS USED TO CALCULATE
C ANT MOUND TURNOVER TIMES. MOUND CONSTRUCTION INVOLVES THREE STAGES
C IN WHICH THE SIZE OF THE MOUND INCREASES THROUGH TIME UNTIL THE FULL-
C SIZE STAGE IS REACHED (COLE 1932). AN ANALYSIS BASED ON THE NUMBER
C OF MOUNDS IN EACH STAGE WAS USED TO ESTIMATE THE NUMBER OF YEARS A
C MOUND WOULD REMAIN IN A STAGE, AND THE TOTAL NUMBER OF YEARS THAT
C PLANT GROWTH WOULD BE PROHIBITED ON THE MOUND DUE TO ANT ACTIVITY.

C

C (c) THE PROB. OF A SMALL ANIMAL BURROW OCCURRING ON A PLOT (PAB)
C IS 0.0000061. I ASSUMED THE PILE OF SOIL PRODUCED BY SMALL BURROWING
C ANIMALS ALWAYS KILLS ALL PLANTS ON THE PLOT AND RECOLONIZATION IS
C POSSIBLE IMMEDIATELY BASED ON DATA FROM CHAPTER 3.

C
C
C
C


```

COMMON /GRASSL/ NPLANT(50),SZE(499),IAGE(499),KSPRT(50),NEWTR(50),
1DBHMAX(50),SWTCH(5),RINIT(50),JTEMP(50),RTMAX(50)
COMMON /PARAM/ AAA(50,2),GMORT(50),NGRPID(50),RESRQ(50),NSPD(499),
1AGEMX(50),RESPROP(50),EQIND(50),RGR(50),REGEN(50),NDIST(50)
COMMON /CONST/ NSPEC,APPT,SDPPT,ATEMP,SDTEMP,NGRP
COMMON /DEAD/ NOGRO(499),NTEMP(499)
COMMON /COUNT/ NTOT,NYEAR,KPRNT,KPLOT,ICHECK,MCHECK
COMMON /TEMP/ DTEMP(499),ITEMP(499),DROPT(499),RTOPT(499),
1SUMRT(50),NEWPL(50),JCHECK(50),RESPONSER(50),TEMPR(50),MTEMP(499)
COMMON /ENVP/ YPPT,YTEMP

```

C.....

C.....SUBROUTINE KILL DETERMINES WHICH PLANTS SHOULD DIE BASED ON

C.....MAXIMUM AGE, DISTURBANCES AND SLOW GROWTH.

C.....

KNT=0

C PROBABILITIES OF DISTURBANCE EACH YEAR

C BASED ON NO. EVENTS IN MODERATELY GRAZED SWALES

PFEC=0.0022185

PANT=0.0000197

PAB=0.0000061

RANUNI=RANDU(1)

RANC=RANDU(1)

DO 30 I=1,NSPEC

IF (NPLANT(I).EQ.0) KSPRT(I)=0

IF (NPLANT(I).EQ.0) GO TO 30

NL=KNT+1

NU=NPLANT(I)+KNT

DO 20 K=NL,NU

C KILL OPUNTIA BASED ON HIGH PPT IN GROWING SEASON

IF (I.EQ.16 .AND. YPPT.GE.335) GO TO 121

GO TO 122

121 CONTINUE

C PROB. OF ENTIRE CLUMP DYING

GSPPT=YPPT*0.864

PROBDO=ABS((-0.0217*GSPPT+6.260491)/100)

RNUNI=RANDU(1)

IF (RNUNI.LE.PROBDO) GO TO 10

122 CONTINUE

C CHECK IF A DISTURBANCE OCCURRED THAT YEAR

C ADJUST NO. INDIVS/SPECIES-GROUP BASED ON DISTURBANCE TYPE

IF (RANUNI .LE. PAB) GO TO 10

IF (RANUNI .LE. PANT) ICHECK=1

IF (RANUNI .LE. PANT.AND.(NDIST(I).EQ.1.OR.NDIST(I).EQ.2.OR.

1 NDIST(I).EQ.4)) GO TO 10

IF (RANUNI .LE. PANT.AND.(NDIST(I).EQ.3.AND.SZE(K).LE..05))

1 GO TO 10

IF (RANUNI .LE. PANT) GO TO 20

IF (RANUNI .LE. PFEC) MCHECK=1

IF (RANUNI.LE.PFEC.AND.NDIST(I).EQ.4) GO TO 25

IF (RANUNI.LE.PFEC.AND.NDIST(I).EQ.1) GO TO 35

IF (RANUNI.LE.PFEC.AND.NDIST(I).EQ.2) GO TO 10

IF (RANUNI.LE.PFEC.AND.(NDIST(I).EQ.3.AND.SZE(K).LE..05))

1 GO TO 10

```

        IF (RANUN.LE.PFEC.AND.(NDIST(I).EQ.3.AND.SZE(K).GT.05))
1  GO TO 25
        GO TO 25
35  RNPAT=RANDU(1)
        RBPAT=0.025
C   WILL PAT EVENT STAY LONG ENOUGH TO KILL BLUE GRAMA?
        IF (RNPAT.LE.RBPAT) GO TO 25
        IF (RNPAT.GT.RBPAT) GO TO 10
25  CONTINUE
C..... KILL PLANTS BASED ON PROBABILITY THAT ONLY 1% REACH MAXIMUM AGE.
C   BLUE GRAMA AND OPUNTIA ARE EXCLUDED FROM THIS MORTALITY TYPE
        IF (I.EQ. 1 .OR. I.EQ. 16) GO TO 20
        EPS=4.605/AGEMX(I)
        RANP=RANDU(1)
        IF (RANP.LE.EPS) GO TO 120
C..... CHECK IF PLANT HAS BEEN FLAGGED AS A SLOW GROWER.
C..... SLOW GROWTH MUST OCCUR FOR TWO YEARS FOR A PLANT TO BE
C..... FLAGGED. ONLY 1% WILL SURVIVE FOR 10 YEARS.
C.....
        IF (I.EQ. 16) GO TO 20
        IF (NOGRO(K).GT.-2) GO TO 20
        RANG=RANDU(1)
        IF (RANG.GT.0.368) GO TO 20
        GO TO 120
10  CONTINUE
        GO TO 120
120 NPLANT(I)=NPLANT(I)-1
C..... CHECK IF DEAD PLANT CAN GROW VEGETATIVELY BASED ON ITS SP-GROUP.
C..... SET KSPRT = -1 FOR A SPECIES TO SPROUT.
C   EACH ELIGIBLE SPECIES-GROUP HAS A 90% CHANCE OF REGROWTH VEGETATIVELY.
        PSPR=0.90
        RANU=RANDU(1)
        IF ((I.EQ. 4 .OR. I.EQ. 6) .AND. RANU.LE. PSPR) KSPRT(I)=-1
        SZE(K)=-1.0
20  CONTINUE
        KNT=NU
        JSP=NGRPID(I)
30  CONTINUE
C.....REWRITE DIAMETERS AND AGES TO ELIMINATE DEAD PLANTS
        K=0
        DO 40 I=1,499
            IF (SZE(I).EQ.0.) GO TO 50
            IF (SZE(I).LT.0.) GO TO 40
            K=K+1
            SZE(K)=SZE(I)
            IAGE(K)=IAGE(I)
            NSPD(K)=NSPD(I)
            NOGRO(K)=NOGRO(I)
40  CONTINUE
50  NTOT=K
        IF (NTOT.EQ.0) RETURN
        NTOT1=K+1
        DO 60 I=NTOT1,NU

```

```
      SIZE(I)=0.  
      IAGE(I)=0  
      NSPD(I)=NSPD(I)  
      NOGRO(I)=0  
60  CONTINUE  
      RETURN  
      END
```

SUBROUTINE RECRUIT (KYR)

C*****
C.....
C.....SUBROUTINE TO CONTROL THE ESTABLISHMENT OF PLANTS
C BY SEEDLINGS OR VEGETATIVE PROPAGATION.
C SEEDS OF ALL SPECIES-GROUPS ARE PRESENT ON THE PLOT AND RESOURCES
C ARE AVAILABLE FOR ESTABLISHMENT EVERY YEAR. THE PROBABILITY THAT
C A SEEDLING WILL BECOME ESTABLISHED FOR GROUP I (REGEN(I)) IS BASED
C EITHER ON SUITABLE
C MICROENVIRONMENTAL CONDITIONS OCCURRING OR THE RELATIVE ABUNDANCE
C OF SEEDS ON THE PLOT. THE ESTABLISHMENT OF *B. gracilis* SEEDLINGS
C IS BASED ON THE PROBABILITY (0.125) THAT A RESTRICTIVE SET OF
C MICROENVIRONMENTAL CONDITIONS REQUIRED FOR GERMINATION AND
C ESTABLISHMENT WILL OCCUR EACH YEAR (BRISKE AND WILSON 1977,
C LAUENROTH ET AL 1987). IN YEARS IN WHICH *B. gracilis* SEEDLINGS DO
C BECOME ESTABLISHED, 1-3 SEEDLINGS ARE ADDED TO THE PLOT AT THE
C ESTIMATED SIZE OF A ONE-YEAR-OLD PLANT (APPROXIMATELY 23 TILLERS),
C WHICH I ASSUMED WAS EQUIVALENT TO 1/20th OF THE SIZE OF A
C FULL-SIZE PLANT.
C I ASSUMED FOR THE OTHER SPECIES-GROUPS THAT FAVORABLE CONDITIONS
C FOR ESTABLISHMENT OCCUR SOMETIME DURING EVERY YEAR. THE PROBABILITY
C OF SEEDLING ESTABLISHMENT FOR EACH SPECIES-GROUP IS BASED ON THE
C RELATIVE ABUNDANCE OF SEEDS PRODUCED BY EACH GROUP FROM SEED
C PRODUCTION DATA FOR A MODERATELY GRAZED UPLAND SITE IN 1985 (COFFIN
C ET AL 1987). I ASSUMED THAT 1-5 SPECIES-GROUPS HAVE SEEDLINGS
C ESTABLISHED EACH YEAR WITH 1-3 SEEDLINGS BEING ADDED TO THE PLOT
C FOR EACH GROUP. SEEDLING SIZE IS BASED ON THE ESTIMATED SIZE OF
C A ONE-YEAR-OLD PLANT AND RANGES FROM 0.022g TO 2.25g. I ASSUMED
C THAT A ONE-YEAR-OLD PLANT WAS EQUIVALENT TO 1/20th THE SIZE OF A
C FULL-SIZE PLANT FOR ALL SPECIES-GROUPS EXCEPT *O. polyacantha*. I
C ASSUMED THAT 75% OF THE SIZE OF A MATURE CLADODE, OR 1/6th THE
C SIZE OF A MATURE CLUMP REPRESENTS A ONE-YEAR-OLD CLUMP.
C*****
C
C SUBROUTINE SPROUT IS CALLED FROM THE ADD ROUTINE. VEGETATIVE
C PROPAGATION IS POSSIBLE IN THE SPROUT ROUTINE FOR TWO SPECIES-
C GROUPS. THE MAJORITY OF GRASSES AND SEDGES IN THE *C. HELIOPHILA*
C GROUP RECOVER FROM RHIZOMES WHILE *S. coccinea*, THE MOST IMPORTANT
C FORB IN THAT GROUP, RECOVERS FROM DEEP TAP ROOTS. I ASSUMED THERE
C IS A 90% CHANCE OF REGROWTH IF A PLANT FROM THESE GROUPS IS
C KILLED EITHER BY A DISTURBANCE, THE EFFECTS OF A SLOW GROWTH RATE,
C OR DUE TO AN INTRINSIC LIKELIHOOD OF MORTALITY (DEATH PROCESSES
C CONTAINED IN THE KILL ROUTINE). THIS IS BASED ON FIELD STUDIES
C OF PLANT RECOVERY ON SMALL DISTURBANCES (CHAPTER 3), AND I
C ASSUMED A SIMILAR RECOVERY FOR THE OTHER TWO SOURCES (SLOW GROWTH
C AND INTRINSIC LIKELIHOOD).
C
C*****
C
C
C
C
C

```

COMMON /GRASSL/ NPLANT(50),SZE(499),IAGE(499),KSPRT(50),NEWTR(50),
1DBHMAX(50),SWTCH(5),RINIT(50),JTEMP(50),RTMAX(50)
COMMON /PARAM/ AAA(50,2),GMORT(50),NGRPID(50),RESRQ(50),NSPD(499),
1IAGEMX(50),RESPROP(50),EQIND(50),RGR(50),REGEN(50),NDIST(50)
COMMON /CONST/ NSPEC,APPT,SDPPT,ATEMP,SDTEMP,NGRP
COMMON /DEAD/ NOGRO(499),NTEMP(499)
COMMON /COUNT/ NTOT,NYEAR,KPRNT,KPLOT,ICHECK,MCHECK
COMMON /TEMP/ DTEMP(499),ITEMP(499),DROPT(499),RTOPT(499),
1SUMRT(50),NEWPL(50),JCHECK(50),RESPONSER(50),TEMPR(50),MTEMP(499)
COMMON /ENVP/ YPPT,YTEMP
C WILL BLUE GRAMA BECOME ESTABLISHED THIS YEAR?
C IF YES, ADD 1-3 SEEDLINGS TO THE PLOT
  RANUNI=RANDU(1)
  IF (RANUNI .GT. REGEN(1)) GO TO 100
  RANUNI=RANDU(1)
  NTRAN=RANUNI*3 + 1
C FILL TEMPORARY ARRAYS WITH OLD PLANTS ONLY
  NTOT=0
  DO 3 I=1,NSPEC
    IF (NPLANT(I) .EQ. 0) GO TO 3
    NTOT=NTOT+NPLANT(I)
3 CONTINUE
  DO 10 I=1,NTOT
    ITEMP(I)=IAGE(I)
    DTEMP(I)=SZE(I)
    MTEMP(I)=NSPD(I)
    NTEMP(I)=NOGRO(I)
10 CONTINUE
  NSP=1
  NSUM=0
  NSUM=NSUM+NPLANT(1)
  NL=NSUM+1
  NUP=NTOT
  DO 60 J=1,NTRAN
    NTOT=NTOT+1
    IF (NTOT .LE. 499) GO TO 50
    WRITE (6,40)
40 FORMAT ('1 THE NUMBER OF PLANTS HAS EXCEEDED 499')
    STOP
50 NSUM=NSUM+1
  NPLANT(NSP)=NPLANT(NSP)+1
  ITEMP(NSUM)=0
  DTEMP(NSUM)=0.05
  MTEMP(NSUM)=1
  NTEMP(NSUM)=0
60 CONTINUE
C ADD NEW PLANTS TO ARRAYS
  IF (NL .GT. NUP) GO TO 80
  N1=NSUM+1
  DO 70 L=NL,NUP
    ITEMP(N1)=IAGE(L)
    DTEMP(N1)=SZE(L)
    MTEMP(N1)=NSPD(L)

```

```

      NTEMP(N1)=NOGRO(L)
      N1=N1+1
70  CONTINUE
C   REINITIALIZE ORIGINAL AGE AND SIZE ARRAYS TO INCLUDE NEW PLANTS
80  DO 90 I=1,NTOT
      IAGE(I)=ITEMP(I)
      SIZE(I)=DTEMP(I)
      NSPD(I)=MTEMP(I)
      NOGRO(I)=NTEMP(I)
90  CONTINUE
100 CONTINUE
C
C   REDO ABOVE PROCEDURE FOR OTHER PLANTS
C
C   PLANT FROM 1-5 SPECIES
      RANUNI=RANDU(1)
      NPLANT=RANUNI*5+1
      DO 200 JK=1,NPLANT
        NTOT=0
        DO 13 I=1,NSPEC
          IF (NPLANT(I) .EQ. 0) GO TO 13
          NTOT=NTOT+NPLANT(I)
13  CONTINUE
C   FILL TEMP ARRAYS WITH OLD PLANTS ONLY FIRST
      DO 110 I=1,NTOT
        ITEMP(I)=IAGE(I)
        DTEMP(I)=SIZE(I)
        MTEMP(I)=NSPD(I)
        NTEMP(I)=NOGRO(I)
110 CONTINUE
C   DETERMINE SPECIES TO PLANT (ALL ARE ELIGIBLE EXCEPT BLUE GRAMA)
      RANUNI=RANDU(1)
      DO 120 I=2,NSPEC
        IF (RANUNI .LE. REGEN(I)) GO TO 125
120 CONTINUE
C   DETERMINE NO. SEEDLINGS TO PLANT FROM 1-3
125 CONTINUE
      NSP=I
      RANUNI=RANDU(1)
      MPLANT=RANUNI*3 + 1
C   IS THERE ROOM FOR MORE INDIVIDUALS?
      NSUM=0
      DO 130 I=1,NSP
130  NSUM=NSUM+NPLANT(I)
        NL=NSUM+1
        NUP=NTOT
        DO 140 J=1,MPLANT
          NTOT=NTOT+1
          IF (NTOT .LE. 499) GO TO 160
          WRITE (6,150)
150  FORMAT ('1 THE NUMBER OF PLANTS HAS EXCEEDED 499')
          STOP
160  NSUM=NSUM+1

```

```
      NPLANT(NSP)=NPLANT(NSP)+1
      ITEMP(NSUM)=0
      DTEMP(NSUM)=RINIT(NSP)
      MTEMP(NSUM)=NSP
      NTEMP(NSUM)=0
140  CONTINUE
      IF (NL .GT. NUP) GO TO 180
      N1=NSUM+1
      DO 170 L=NL,NUP
          ITEMP(N1)=IAGE(L)
          DTEMP(N1)=SZE(L)
          MTEMP(N1)=NSPD(L)
          NTEMP(N1)=NOGRO(L)
          N1=N1+1
170  CONTINUE
C    REINITIALIZE ORIGINAL ARRAYS TO INCLUDE NEW PLANTS
180  DO 190 I=1,NTOT
          IAGE(I)=ITEMP(I)
          SZE(I)=DTEMP(I)
          NSPD(I)=MTEMP(I)
          NOGRO(I)=NTEMP(I)
190  CONTINUE
200  CONTINUE
C    CALL SUBROUTINE SPROUT TO CHECK IF ANY SPECIES ARE ELIGIBLE TO SPROUT
      CALL SPROUT (KYR)
C    INCREMENT AGES
      DO 210 I=1,NTOT
          IAGE(I)=IAGE(I)+1
210  CONTINUE
      RETURN
      END
```

SUBROUTINE SPROUT (KYR)

C.....

C.....SUBROUTINE SPROUT CHECKS WHICH SPECIES ARE ELIGIBLE TO SPROUT

C.....BASED ON THE PLANTS THAT HAVE DIED THAT YEAR

C.....

```

COMMON /GRASSL/ NPLANT(50),SIZE(499),IAGE(499),KSPRT(50),NEWTR(50),
1DBHMAX(50),SWTCH(5),RINIT(50),JTEMP(50),RTMAX(50)
COMMON /PARAM/ AAA(50,2),GMORT(50),NGRPID(50),RESRQ(50),NSPD(499),
1AGEMX(50),RESPROP(50),EQIND(50),RGR(50),REGEN(50),NDIST(50)
COMMON /CONST/ NSPEC,APPT,SDPPT,ATEMP,SDTEMP,NGRP
COMMON /DEAD/ NOGRO(499),NTEMP(499)
COMMON /COUNT/ NTOT,NYEAR,KPRNT,KPLOT,ICHECK,MCHECK
COMMON /TEMP/ DTEMP(499),ITEMP(499),DROPT(499),RTOPT(499),
1SUMRT(50),NEWPL(50),JCHECK(50),RESPONSER(50),TEMPR(50),MTEMP(499)
COMMON /ENVP/ YPPT,YTEMP

```

C.....

C.....

C.....SUM TOTAL NUMBER OF PLANTS

C.....

```

NTOT=0
DO 10 I=1,NSPEC
IF (NPLANT(I).EQ.0) GO TO 10
NTOT=NTOT+NPLANT(I)

```

10 CONTINUE

C.....

C.....DETERMINE WHICH SPECIES CAN SPROUT

C.....

```

NW=0
DO 20 I=1,NSPEC
IF (KSPRT(I).GE.0) GO TO 20
NW=NW+1
NEWTR(NW)=I

```

20 CONTINUE

C.....CHECK FOR PLANTS AVAILABLE TO GROW VEGETATIVELY

C.....

```

IF (NW.EQ.0) GO TO 125
DO 30 J=1,NTOT
ITEMP(J)=IAGE(J)
DTEMP(J)=SIZE(J)
MTEMP(J)=NSPD(J)
NTEMP(J)=NOGRO(J)

```

30 CONTINUE

C SINCE ONLY AGSM, CAHE, AND SPCO ARE CAPABLE OF DOING THIS,

C ALL WILL GROW VEGETATIVELY IF KILLED WITH 0-3 INDIVIDUALS

C ADDED PER SPECIES OF INITIAL SIZE IN RINIT ARRAY

```

DO 120 I=1,NW
NSPC=NEWTR(I)
NSUM=0
DO 50 J=1,NSPC

```

50 NSUM=NSUM+NPLANT(J)

C DETERMINE NO. SPROUTS FROM 0-3

```

RANUNI=RANDU(1)
NSPRT=RANUNI*3

```



```

NL=NSUM+1
NUP=NTOT
DO 60 J=1,NSPRT
  NSUM=NSUM+1
  NPLANT(NSPC)=NPLANT(NSPC)+1
  NTOT=NTOT+1
  IF (NTOT .LE. 499) GO TO 80
  WRITE (6,70)
70  FORMAT ('1 THE NUMBER OF PLANTS HAS EXCEEDED 499')
  STOP
80  ITEMP(NSUM)=0
  DTEMP(NSUM)=RINIT(NSPC)
  MTEMP(NSUM)=NSPC
  NTEMP(NSUM)=0
60  CONTINUE
  IF (NL .GT. NUP) GO TO 100
  N1=NSUM+1
  DO 90 J=NL,NUP
    DTEMP(N1)=SZE(J)
    ITEMP(N1)=IAGE(J)
    MTEMP(N1)=NSPD(J)
    NTEMP(N1)=NOGRO(J)
    N1=N1+1
90  CONTINUE
C  REINITIALIZE ORIGINAL ARRAYS TO INCLUDE NEW SPROUTS
100 DO 110 L=1,NTOT
  IAGE(L)=ITEMP(L)
  NOGRO(L)=NTEMP(L)
  NSPD(L)=MTEMP(L)
  SZE(L)=DTEMP(L)
110 CONTINUE
120 CONTINUE
125 CONTINUE
C  REINITIALIZE SPROUT SWITCH FOR EACH SPECIES
  DO 130 I=1,NSPEC
    KSPRT(I)=1
130 CONTINUE
  RETURN
  END

```

SUBROUTINE GROW (KYR,IPLT)

```

C*****
C.....
C.....SUBROUTINE TO CALCULATE THE GROWTH INCREMENT FOR EACH PLANT
C ANNUAL INCREASE IN SIZE OF EACH PLANT IS A FUNCTION OF ITS
C OPTIMUM GROWTH RATE, THE EFFECTS OF PPT AND TEMPERATURE, AND
C INTERACTIONS WITH OTHER PLANTS FOR BELOWGROUND RESOURCES.
C THE OPTIMUM GROWTH RATE IS USED TO CALCULATE THE AMOUNT OF
C RESOURCES REQUIRED BY EACH INDIVIDUAL IN EACH RESOURCE GROUP.
C PPT AND THE EFFECTS OF OTHER PLANTS ARE USED TO CALCULATE THE
C AMOUNT OF RESOURCES AVAILABLE TO EACH GROUP. THE ACTUAL GROWTH
C RATE FOR EACH INDIVIDUAL IS A FUNCTION OF THE RELATIONSHIP BETWEEN
C THE RESOURCES REQUIRED TO SUSTAIN THE OPTIMUM GROWTH RATE AND THE
C RESOURCES AVAILABLE TO THE PLANT. THIS RELATIONSHIP IS MEDIATED BY
C THE EFFECTS OF TEMPERATURE.
C*****
COMMON /GRASSL/ NPLANT(50),SZE(499),IAGE(499),KSPRT(50),NEWTR(50),
1DBHMAX(50),SWTCH(5),RINIT(50),JTEMP(50),RTMAX(50)
COMMON /PARAM/ AAA(50,2),GMORT(50),NGRPID(50),RESRQ(50),NSPD(499),
1AGEMX(50),RESPROP(50),EQIND(50),RGR(50),REGEN(50),NDIST(50)
COMMON /CONST/ NSPEC,APPT,SDPPT,ATEMP,SDTEMP,NGRP
COMMON /DEAD/ NOGRO(499),NTEMP(499)
COMMON /COUNT/ NTOT,NYEAR,KPRNT,KPLOT,ICHECK,MCHECK
COMMON /TEMP/ DTEMP(499),ITEMP(499),DROPT(499),RTOPT(499),
1SUMRT(50),NEWPL(50),JCHECK(50),RESPONSER(50),TEMPR(50),MTEMP(499)
COMMON /PLANTS/ BOGR(1000),SIHY(1000),ARLO(1000),CAHE(1000),
1SCPA(1000),SPCO(1000),CHNA(1000),WFL(1000),WSLL(1000),
2XATA(1000),GACO(1000),GUSA(1000),VUOC(1000),XEDE(1000),CHAL(1000),
SOPPO(1000)
COMMON /RGROUPS/ RBOGR(1000),RGRASS(1000),RFORBL(1000),
1RFORBS(1000),RANNUA(1000),ROPPO(1000),XPPT(1000),XTEMP(1000)
COMMON /RESOURCE/ TPROP(20),RPROP(10)
COMMON /ENVP/ YPPT,YTEMP
COMMON /SENST/ PARMV(3,40),YOUT(8),XMIN(30),XMAX(30),XNOM(30)
COMMON /SCOUNT/ NCHECK,L,YR,KCHECK
DIMENSION DIFF(50),RESPOND(50),TRESR(50),JCHECK1(50),SUMR(50),
1TRESPROP(50),TRGR(50),PROBM(50),TPROBM(50),TRS(50),SUM(50)
C.....
C THE RESOURCES AVAILABLE TO EACH RESOURCE GROUP (TRS(I)) ARE CALCULATED
C BASED ON ANNUAL PPT (YPPT) USING A STEP FUNCTION TO ACCOUNT FOR THE
C EFFECTS OF PPT ON THE DISTRIBUTION OF SOIL WATER, AND THE DIFFERENT
C SPATIAL DISTRIBUTIONS OF ROOTS FOR THE RESOURCE-GROUPS
C.....
C I ASSUMED THAT 80% OF THE YEARS AT THE CPER DO NOT HAVE EXTREME AMOUNTS
C OF PPT, 10% ARE DRY YEARS, AND 10% ARE WET YEARS. THEREFORE, A NOT
C EXTREME YEAR RANGES FROM 205-420 MM.
PPTMIN=205
PPTMAX=420
DO 30 I=1,NGRP
C IN NOT EXTREME YEARS, THE PROPORTIONAL CHANGE IN THE RESOURCE SPACE
C FOR EACH GROUP IS:
IF ((YPPT .GE. PPTMIN) .AND. (YPPT .LE. PPTMAX)) TRS(I)=(0.00093*
1YPPT)+0.70935

```

C TRS(I)=1.0 IN AN AVERAGE YEAR (311 MM). THE VALUES OF TRS(I) RANGE
 C FROM 0.9 FOR THE MINIMUM PPT VALUE (205 MM) TO 1.1 FOR THE MAXIMUM
 C PPT VALUE (420 MM).
 C IN DRY YEARS (<205 MM), THE SAME EQUATION IS USED FOR GROUPS THAT OBTAIN
 C MOST OF THEIR RESOURCES IN RELATIVELY SHALLOW LAYERS OF THE SOIL PROFILE
 C (B. gracilis AND SUCCULENTS).

IF (YPPT .LT. PPTMIN.AND.((I.EQ.1).OR.(I.EQ.6))) TRS(I)=(0.00093*
 1YPPT)+0.70935

C THE PROPORTIONAL CHANGE IN THE SPACE FOR ALL OTHER GROUPS IS:

IF (YPPT.LT.PPTMIN.AND.((I.EQ.2).OR.(I.EQ.3).OR.(I.EQ.4).OR.
 1(I.EQ.5))) TRS(I)=0.004*YPPT+0.08

C THE RESULT IS FEWER RESOURCES FOR A GIVEN PPT AMOUNT FOR SPECIES THAT
 C OBTAIN MOST OF THEIR RESOURCES DEEPER IN THE SOIL PROFILE THAN
 C B. gracilis AND SUCCULENTS. I ASSUMED THE MINIMUM VALUE OF TRS(I) IN
 C THIS CASE WAS 0.50, OR 50% OF THE PROPORTIONAL CHANGE IN AN AVERAGE
 C PPT YEAR.

C
 C A SIMILAR EQUATION IS USED IN WET YEARS (>420 MM) TO DISTINGUISH SPECIES
 C THAT OBTAIN A LARGE PROPORTION OF THEIR RESOURCES FROM DEEP SOIL LAYERS:

IF (YPPT.GT.PPTMAX.AND.((I.EQ.3).OR.(I.EQ.4))) TRS(I)=(0.004
 1*YPPT)-0.58

C I ASSUMED THE MINIMUM VALUE OF TRS(I) IN THIS CASE WAS 1.5, OR 150%
 C OF THE PROPORTIONAL CHANGE IN A YEAR WITH AVERAGE PPT.

C THE FIRST EQUATION IS USED FOR THE REMAINING GROUPS:

IF (YPPT.GT.PPTMAX.AND.((I.EQ.1).OR.(I.EQ.2).OR.(I.EQ.5).OR.
 1(I.EQ.6))) TRS(I)=(0.00093*YPPT)+0.70935

30 CONTINUE

C.....

C TEMPERATURE RESPONSE

C
 C PARABOLIC CURVES ARE USED TO DETERMINE THE EFFECT OF TEMPERATURE ON
 C GROWTH RATES. SEPARATE CURVES ARE USED FOR COOL AND WARM SEASON PLANTS
 C AND SUCCULENTS (WILLIAMS AND MARKLEY 1973, SALISBURY AND ROSS 1978,
 C MONSON ET AL 1983):

C

DO 410 I=1,NSPEC

IF (JTEMP(I) .EQ. 1) TEMPR(I)=(0.1014*(YTEMP+2)-0.00257*
 1 (YTEMP+2)**2)

IF (JTEMP(I) .EQ. 2) TEMPR(I)=(0.1014*(YTEMP-11)-0.00257*
 1 (YTEMP-11)**2)

IF (JTEMP(I) .EQ. 3) TEMPR(I)=(0.1014*(YTEMP-11)-0.00257*
 1 (YTEMP-11)**2)

IF (TEMPR(I).LE.0.05) TEMPR(I)=0.05

IF (TEMPR(I).GE.1.0) TEMPR(I)=1.0

410 CONTINUE

C

C JTEMP(I) INDICATES COOL (1), WARM (2), OR SUCCULENTS (3); YTEMP IS
 C THE CURRENT YEAR'S TEMPERATURE (FROM THE INPUT ROUTINE); TEMPR(I)
 C IS THE TEMPERATURE RESPONSE. THE COOL SEASON CURVE HAS A MAXIMUM
 C OF 1.0 WHEN YTEMP=20°C, AND THE WARM SEASON/SUCCULENTS CURVE HAS A
 C MAXIMUM OF 1.0 WHEN YTEMP=32°C.

C

C.....

```

C
C
C
C   INITIALIZE PARAMETERS AT THE START OF EACH YEAR FOR COMPARING RESOURCE
C   REQUIREMENTS IF GROWING AT OPTIMUM RATES, WITH RESOURCE AVAILABILITY
C
      DO 6 I=1,NSPEC
          TPROBM(I)=0.0
6   CONTINUE
      DO 7 I=1,NGRP
          SUMRT(I)=0.0
          DIFF(I)=0.0
          EQIND(I)=0.0
          PROBM(I)=0.0
          IF (NEWPL(I).EQ.0) JCHECK(I)=0
7   CONTINUE
      NT=0
      NEWP=0
C
C   THE NEXT SERIES OF CODE CALCULATES THE NUMBER OF INDIVIDUALS IN
C   EACH RESOURCE-GROUP (NEWPL(I) BASED ON THE NUMBER IN EACH SPECIES
C   -GROUP (NPLANT(I)).
C   THIS IS NECESSARY SINCE THE GROWTH ROUTINE IS BASED ON RESOURCE,
C   NOT SPECIES-GROUPS.
C
      DO 10 I=1,NSPEC-1
          IF (I .EQ. 1) NEWP=NPLANT(I)
          IF (NGRPID(I) .EQ. NGRPID(I+1)) GO TO 12
          IF (NGRPID(I) .NE. NGRPID(I+1)) GO TO 14
12   NEWP=NEWP+NPLANT(I+1)
          GO TO 9
14   NT=NT+1
          NEWPL(NT)=NEWP
          NEWP=NPLANT(I+1)
9   CONTINUE
10  CONTINUE
      NT=NT+1
      NEWPL(NT)=NEWP
C   NGRPID(I)= ID NUMBER FOR EACH RESOURCE GROUP
C   NPLANT(I)= NO. PLANTS IN EACH SPECIES-GROUP
C   NGRP=NO. RESOURCE GROUPS
C   NEWPL(I)=# INDIVS. PER RESOURCE GROUP
C
C.....
C   PROCEDURE TO DETERMINE GROWTH INCREMENTS
C
C   STEP 1. CALCULATE TOTAL RESOURCES REQUIRED FOR EACH RESOURCE GROUP
C           IF ALL INDIVIDUALS GROW AT OPTIMUM RATE
C
C   A NATURAL GROWTH FUNCTION IS USED TO REPRESENT THE OPTIMUM GROWTH OF
C   EACH PLANT THROUGH TIME
      NL=1
      DO 80 I=1,NGRP

```

```

C   SKIP THE LOOP FOR A RESOURCE GROUP IF IT CONTAINS 0 PLANTS
      IF (NEWPL(I) .EQ. 0) GO TO 80
      NU=NL+(NEWPL(I)-1)
      SUMRT(I)=0.
      DO 70 J=NL,NU
          DROPT(J)=RGR(I)*(1.0-SZE(J))
          RTOPT(J)=SZE(J)+DROPT(J)
          MSP=NSPD(J)
          SUMRT(I)=SUMRT(I)+RTOPT(J)
70  CONTINUE
      NL=NL+NEWPL(I)
80  CONTINUE
C   DROPT(J) IS THE OPTIMUM GROWTH RATE FOR A PLANT, RGR(I) IS THE INTRINSIC
C   RATE OF GROWTH, AND SZE(J) IS THE SIZE OF THE PLANT RELATIVE TO A FULL-
C   SIZE PLANT. INTRINSIC GROWTH RATES FOR EACH SPECIES-GROUP WERE ESTIMATED
C   BY THE NUMBER OF YEARS REQUIRED FOR AN INDIVIDUAL TO REACH ITS FULL-SIZE
C   WHILE GROWING UNDER OPTIMUM CONDITIONS.
C
C.....
C
C   STEP 2. FOR EACH RESOURCE-GROUP, THE EQUIVALENT NUMBER OF FULL-SIZE
C   INDIVIDUALS (EQIND(I) THAT CAN BE SUPPORTED BY THE AVAILABLE
C   RESOURCES ARE CALCULATED USING THE PROPORTION OF THE RESOURCE
C   SPACE ASSOCIATED WITH A GROUP (RESPROP(I)), THE SIZE OF THE
C   RESOURCE SPACE BASED ON ANNUAL PPT (TRS(I)), AND THE RESOURCE
C   REQUIREMENT FOR A FULL-SIZE INDIVIDUAL OF THAT GROUP (RESRQ(I)).
C   (TABLE A4.1)
C   RESOURCES THAT ARE NOT USED BY PLANTS IN ONE GROUP
C   MAY BE AVAILABLE TO OTHER GROUPS DEPENDING ON THE MORPHOLOGY
C   OF THE ROOT SYSTEMS AND THE SPATIAL OVERLAP WITH ROOTS OF OTHER
C   PLANTS. I HYPOTHEZED THAT B. gracilis PLANTS ARE NOT ABLE TO
C   USE RESOURCES ASSOCIATED WITH OTHER GROUPS. THIS HYPOTHESIS IS
C   SUPPORTED BY THE LACK OF RESPONSE OF THE SPATIAL DISTRIBUTION
C   OF B. gracilis ROOTS TO THE REMOVAL OF NEIGHBORING PLANTS
C   (APPENDIX I). RESOURCES NOT USED BY B. gracilis PLANTS ARE
C   AVAILABLE TO OTHER GROUPS EXCEPT SUCCULENTS. PERENNIAL GRASSES,
C   PERENNIAL FORBS AND SHRUBS, AND ANNUALS HAVE ROOTS AT SIMILAR
C   DEPTHS IN THE SOIL PROFILE AS B. gracilis WHILE THE ROOTS OF
C   SUCCULENTS ARE CONCENTRATED NEAR THE SOIL SURFACE WHERE FEW
C   B. gracilis ROOTS ARE FOUND. BECAUSE OF THE SPATIAL OVERLAP IN
C   THE LOCATION OF PERENNIAL GRASS, PERENNIAL FORB AND SHRUB, AND
C   ANNUAL ROOTS, I ASSUMED THAT RESOURCES NOT USED BY ONE OF THESE
C   GROUPS ARE AVAILABLE TO THE OTHER TWO GROUPS. I ASSUMED THAT
C   PERENNIALS OBTAIN THE RESOURCES FIRST, AND IT IS DETERMINED
C   RANDOMLY AS TO GRASSES OR FORBS AND SHRUBS. THE REMAINING
C   RESOURCES ARE THEN AVAILABLE TO THE OTHER PERENNIAL GROUP, AND
C   THEN TO ANNUALS. RESOURCES ASSOCIATED WITH SUCCULENTS ARE NOT
C   AVAILABLE TO OTHER GROUPS AND SUCCULENTS CAN NOT USE RESOURCES
C   THE OTHER GROUPS.
C.....
C
C   INITIALIZE REMAINING RESOURCES (REM) FOR EACH GROUP TO 0

```

```

    REM1=0.0
    REM2=0.0
    REM3=0.0
    REM4=0.0
    REMRES=0.0
C   CALCULATE EXTRA RESOURCES (REMRES) FIRST IF NO PLANTS ARE IN A GROUP
    IF (NEWPL(1).EQ.0) REM1=RESPROP(1)*TRS(1)
    IF (NEWPL(2).EQ.0) REM2=RESPROP(2)*TRS(2)
    IF (NEWPL(3).EQ.0) REM3=RESPROP(3)*TRS(3)
    IF (NEWPL(4).EQ.0) REM4=RESPROP(4)*TRS(4)
    REMRES=REM1+REM2+REM3+REM4
C   SKIP THIS SECTION IF NO BLUE GRAMA PLANTS
    IF (NEWPL(1).EQ.0) GO TO 300
        EQIND(1)=RESPROP(1)*TRS(1)/RESRQ(1)
        DIFF(1)=SUMRT(1)/EQIND(1)
        IF (SUMRT(1).LT.EQIND(1)) REMRES=(1.0-SUMRT(1)/EQIND(1))
    1 *RESPROP(1)*TRS(1)+REMRES
300 CONTINUE
    RANUNI=RANU(1)
    IRAN=RANUNI*(4-2)+2.5
    IF (NEWPL(IRAN).EQ.0) GO TO 380
        EQIND(IRAN)=(RESPROP(IRAN)+REMRES)*TRS(IRAN)/RESRQ(IRAN)
        DIFF(IRAN)=SUMRT(IRAN)/EQIND(IRAN)
        IF (SUMRT(IRAN).LT.EQIND(IRAN)) REMRES=(1.0-SUMRT(IRAN)/
    1 EQIND(IRAN))*((RESPROP(IRAN)+REMRES)*TRS(IRAN))
        IF (SUMRT(IRAN).GE.EQIND(IRAN)) REMRES=0.0
380 CONTINUE
800 RANUNI=RANU(1)
    JIRAN=RANUNI*(4-2)+2.5
    IF (JIRAN.EQ.0) GO TO 800
    IF (NEWPL(JIRAN).EQ.0) GO TO 302
        EQIND(JIRAN)=(RESPROP(JIRAN)+REMRES)*TRS(JIRAN)/RESRQ(JIRAN)
        DIFF(JIRAN)=SUMRT(JIRAN)/EQIND(JIRAN)
        IF (SUMRT(JIRAN).LT.EQIND(JIRAN)) REMRES=(1.0-SUMRT(JIRAN)/
    1 EQIND(JIRAN))*((RESPROP(JIRAN)+REMRES)*TRS(JIRAN))
        IF (SUMRT(JIRAN).GE.EQIND(JIRAN)) REMRES=0.0
302 CONTINUE
    IF ((IRAN.EQ.2.AND.JIRAN.EQ.3).OR.(IRAN.EQ.3.AND.JIRAN.EQ.2)) KIRAN=4
    IF ((IRAN.EQ.3.AND.JIRAN.EQ.4).OR.(IRAN.EQ.4.AND.JIRAN.EQ.3)) KIRAN=2
    IF ((IRAN.EQ.2.AND.JIRAN.EQ.4).OR.(IRAN.EQ.4.AND.JIRAN.EQ.2)) KIRAN=3
    IF (NEWPL(KIRAN).EQ.0) GO TO 310
        EQIND(KIRAN)=(RESPROP(KIRAN)+REMRES)*TRS(KIRAN)/RESRQ(KIRAN)
        DIFF(KIRAN)=SUMRT(KIRAN)/EQIND(KIRAN)
        IF (SUMRT(KIRAN).LT.EQIND(KIRAN)) REMRES=(1.0-SUMRT(KIRAN)/
    1 EQIND(KIRAN))*((RESPROP(KIRAN)+REMRES)*TRS(KIRAN))
        IF (SUMRT(KIRAN).GE.EQIND(KIRAN)) REMRES=0.0
310 CONTINUE
    IF (NEWPL(5).EQ.0) GO TO 315
        EQIND(5)=(RESPROP(5)+REMRES)*TRS(5)/RESRQ(5)
        DIFF(5)=SUMRT(5)/EQIND(5)
315 IF (NEWPL(6).EQ.0) GO TO 320
        EQIND(6)=RESPROP(6)*TRS(6)/RESRQ(6)
        DIFF(6)=SUMRT(6)/EQIND(6)

```

```

320 CONTINUE
      IPROBM=0
      KNT=0
C
C
C.....
C THE COMMON SITUATIONS ENCOUNTERED IN ALLOCATING RESOURCES FOR PLANT
C GROWTH ARE:
C 1. RESOURCES REQUIRED BY PLANTS IN A GROUP ARE LESS THAN THOSE
C AVAILABLE
C 2. RESOURCES REQUIRED ARE GREATER THAN THOSE AVAILABLE
C
C.....
      DO 150 I=1,NGRP
          IF (NEWPL(I) .EQ. 0) JCHECK(I)=0
          IF (NEWPL(I) .EQ. 0) GO TO 150
          NL=KNT+1
          NU=NEWPL(I)+KNT
C.....
C CASE 1.
C IF SUFFICIENT RESOURCES ARE AVAILABLE FOR ALL INDIVIDUALS IN A
C RESOURCE-GROUP TO GROW AT THEIR OPTIMUM RATE (IE. SUMRT(I) <= EQIND(I)),
C THEN A LOGISTIC FUNCTION IS USED TO DETERMINE THE RESPONSE (RESPONER).
C IF RESOURCES ARE NOT SUFFICIENT FOR OPTIMUM GROWTH, THEN PLANTS MAY
C BE KILLED AND REDUCTIONS MADE IN THE GROWTH RATES.
C
          IF (SUMRT(I) .LE. EQIND(I)) GO TO 110
          IF (SUMRT(I) .GT. EQIND(I)) GO TO 120
110 CONTINUE
C
C CONVERT SUMRT(I) TO PROPORTION OF EQIND(I)
C
          JCHECK(I)=0
          SCHECK=SUMRT(I)/EQIND(I)
          IF (EQIND(I) .LE. 0.0) SCHECK=1.0
          REFFECT=0.95/(1+99*EXP(-10.5*SCHECK))
          RESPONER(I)=1-REFFECT
C THIS FUNCTION HAS A MAXIMUMJ OF 0.99 WHEN SCHECK=0.0 AND A MINIMUM
C OF 0.05 WHEN SCHECK=1.0.
C
          GO TO 145
C
C CASE 2. RESOURCES ARE NOT SUFFICIENT FOR OPTIMUM GROWTH OF ALL
C INDIVIDUALS
C
120 CONTINUE
C
C THE EFFECT OF INSUFFICIENT RESOURCES ON PLANT GROWTH (RESPONER(I))
C IS BASED ON THE PROPORTION OF THE AMOUNT OF RESOURCES REQUIRED TO
C THE AMOUNT AVAILABLE (DIFF(I)).
          RESPONER(I)=1/DIFF(I)
          JCHECK(I)=JCHECK(I)+1
C JCHECK=NO. CONCURRENT YEARS THAT RESOURCES ARE INSUFFICIENT

```

```

140  CONTINUE
C    THE NUMBER OF PLANTS KILLED IN A GROUP (IPROBM) IS ALSO BASED ON THIS
C    PROPORTION (DIFF(I)):
      IPROBM=((1-(1/DIFF(I)))*NEWPL(I))
C    THE PROBABILITY OF MORTALITY IS INVERSELY RELATED TO PLANT SIZE;
C    THEREFORE, THE SMALLEST PLANTS ARE KILLED FIRST UNTIL THE TOTAL
C    NO. TO BE KILLED IS REACHED.
C
C    CLONAL PLANTS HAVE ADDITIONAL CONSTRAINTS ON THEIR GROWTH IF PLANTS
C    ARE NOT KILLED HERE, OR IF THIS IS THE FIRST YEAR THAT RESOURCES
C    ARE INSUFFICIENT. A PROBABILITY OF MORTALITY (AMORT) IS CALCULATED
C    BASED ON THE NO. OF YEARS (JCHECK(I)) THAT RESOURCES ARE LIMITING.
C    IF MORTALITY OCCURS, THEN THE NO. OF PLANTS KILLED (IPROBM) IS 90%
C    OF THE PLANTS IN THE GROUP. THIS SOURCE OF MORTALITY OCCURS MOST
C    FREQUENTLY WHEN TWO B. gracilis PLANTS OF COMPARABLE SIZE OCCUR ON
C    A PLOT WITH A COMBINED RESOURCE REQUIREMENT SMALL ENOUGH THAT BOTH
C    PLANTS SURVIVE INDEFINITELY IF THE ONLY SOURCE OF MORTALITY IS BASED
C    ON THE PREVIOUS EQUATION FOR ALL GROUPS.
C
      IF (I.EQ.1 .OR. I.EQ.6) GO TO 141
      GO TO 190
141  IF (IPROBM.GT.0 .OR. JCHECK(I).LE.1) GO TO 190
      RANUNI=RANDU(1)
      AMORT=0.04*(JCHECK(I)**2)
      IF (AMORT.GE.1.0) AMORT=1.0
      IF (RANUNI .LE. AMORT) IPROBM=0.9*NEWPL(I)
      IF (IPROBM .LT. 1) PROBM(I)=2.0
C    PROBM(I) IS A FLAG TO INDICATE THAT PLANTS WERE NOT KILLED
190  CONTINUE
      NU=NEWPL(I)+KNT
      IF (JCHECK(I) .LE. 1 ) GO TO 145
      IF (NEWPL(I).EQ.1) GO TO 711
C    DO NOT SORT BOGR OR OPPO! THIS ORDER NEEDED FOR REDUCTIONS
C    IF CLONAL PLANTS ARE NOT KILLED THEN THE CLUMPS ARE REDUCED IN SIZE
C    AT 900
      IF ((I.EQ.1 .OR. I.EQ.6).AND. PROBM(I).EQ.2.0) GO TO 900
C    SORT BY SMALLEST PLANTS FIRST WITHIN EACH RESOURCE GROUP SINCE
C    SMALLEST PLANTS ARE KILLED FIRST
      DO 155 J=NL,NEWPL(I)+KNT-1
        K=J
        L=K+1
        DO 755 II=L,NEWPL(I)+KNT
          IF (SZE(K).GT.SZE(II)) K=II
755  CONTINUE
      T=SZE(J)
      SZE(J)=SZE(K)
      SZE(K)=T
      NS=IAGE(J)
      IAGE(J)=IAGE(K)
      IAGE(K)=NS
      NR=NOGRO(J)
      NOGRO(J)=NOGRO(K)
      NOGRO(K)=NR

```



```

      NQ=NSPD(J)
      NSPD(J)=NSPD(K)
      NSPD(K)=NQ
155  CONTINUE
711  CONTINUE
C
C
C.....AFTER PLANTS WITHIN GROUPS ARE SORTED, KILL YOUNGEST FIRST UP TO IPROBM
C   AT 810
      GO TO 810
C.....
C   REDUCTION OF CLUMPS OF CLONAL PLANTS IF PLANTS WERE NOT KILLED
C   B. gracilis CLUMPS ARE REDUCED BY KILLING TILLERS WHILE
C   SUCCULENTS ARE REDUCED BY KILLING CLADODES. THE SIZES OF THE CLUMPS
C   ARE REDUCED UNTIL RESOURCE REQUIREMENTS ARE APPROX. EQUAL TO
C   AVAILABILITY. SMALL PLANTS SUFFER A GREATER PROPORTIONAL REDUCTION
C   THAN LARGE PLANTS.
C.....
900  CONTINUE
      OVERSHT=SUMRT(I)-EQIND(I)
      J=NL
      SET=0.
      DO 910 K=1,NEWPL(I)
        IF (I.EQ.1) ISP=1
        IF (I.EQ.6) ISP=16
        PERC=RTOPT(J)/SUMRT(I)
        IF (SET .GT. 0) PERC=SET
        IF (PERC .EQ. 0.5) GO TO 915
        IF (NEWPL(I) .EQ. 1) PERC=0.0
        GO TO 925
915  RANUNI=RANDU(1)
      SET=1.0-RANUNI
      PERC=RANUNI
925  TINC=(1.0-PERC)*OVERSHT
      SZE(J)=RTOPT(J)-(((1.0-TEMPR(ISP))*TINC)+TINC)
      IF (SZE(J) .LE. 0.0) GO TO 920
      IF (SZE(J) .GT. 0.0) GO TO 930
920  SZE(J)=-1.0
      NPLANT(ISP)=NPLANT(ISP)-1
930  J=J+1
910  CONTINUE
      GO TO 145
810  IF (IPROBM.LT.1) GO TO 703
C   REMOVE THE DEAD PLANTS FROM THE ARRAYS
      J=NL
      DO 156 K=1,IPROBM
        SZE(J)=-1.0
        ISP=NSPD(J)
        NPLANT(ISP)=NPLANT(ISP)-1
C   75% CHANCE OF VEGETATIVE REGROWTH FOR TWO SPECIES-GROUPS IF DEATH
C   OCCURS AS A RESULT OF INSUFFICIENT RESOURCES (CAHE, SPCO)
      RMORT=0.75
      RANUNI=RANDU(1)

```

```

          IF ((NSPD(J).EQ.4.OR.NSPD(J).EQ. 6) .AND. RANUNI .LE. RMORT)
1 KSPRT(ISP)=-1
          J=J+1
156 CONTINUE
703 CONTINUE
          IF ((I.EQ.1.OR.I.EQ.6).AND.PROBM(I).EQ.2.0) GO TO 145
          IF (NEWPL(I).EQ.1) GO TO 145
C
C RESORT ALL RESOURCE GROUPS, EXCEPT CLONAL PLANTS, BY SPECIES CODE
C ALSO, SET PARAMETERS NEEDED FOR SPECIES-GROUPS FROM VALUES OF
C RESOURCE GROUPS
C
          DO 157 J=NL,NEWPL(I)+KNT-1
              K=J
              L=K+1
              DO 757 II=L,NEWPL(I)+KNT
                  IF (NSPD(K) .GT. NSPD(II)) K=II
757 CONTINUE
                  T=SIZE(J)
                  SIZE(J)=SIZE(K)
                  SIZE(K)=T
                  NS=IAGE(J)
                  IAGE(J)=IAGE(K)
                  IAGE(K)=NS
                  NR=NOGRO(J)
                  NOGRO(J)=NOGRO(K)
                  NOGRO(K)=NR
                  NQ=NSPD(J)
                  NSPD(J)=NSPD(K)
                  NSPD(K)=NQ
157 CONTINUE
145 CONTINUE
          KNT=NU
150 CONTINUE
          I=1
          DO 160 J=1,NSPEC
              IF (NGRPID(J) .EQ. 1) GO TO 170
              I=I+1
              RESPOND(J)=RESPONSER(I)
              TPROBM(J)=PROBM(I)
              TRESPROP(J)=RESPROP(I)
              TRESR(J)=RESRQ(I)
              TRGR(J)=RGR(I)
              GO TO 180
170 RESPOND(J)=RESPONSER(I)
              TRESPROP(J)=RESPROP(I)
              TPROBM(J)=PROBM(I)
              TRESR(J)=RESRQ(I)
              TRGR(J)=RGR(I)
180 CONTINUE
160 CONTINUE
C
C REWRITE SIZES AND AGES TO ELIMINATE DEAD PLANTS

```

```

C
      K=0
      DO 220 I=1,499
        IF (SZE(I) .EQ. 0.0) GO TO 230
        IF (SZE(I) .LT. 0.0) GO TO 220
        K=K+1
        SZE(K)=SZE(I)
        IAGE(K)=IAGE(I)
        NSPD(K)=NSPD(I)
        NOGRO(K)=NOGRO(I)
220  CONTINUE
230  NTOT=K
      IF (NTOT .EQ. 0) RETURN
      NTOT1=K+1
      DO 240 I=NTOT1,NU
        SZE(I)=0.0
        IAGE(I)=0
        NOGRO(I)=0
        NSPD(I)=NSPD(I)
240  CONTINUE
C.....
C  CALCULATE ACTUAL GROWTH INCREMENTS
C
      NL=1
      DO 420 I=1,NSPEC
        TPROP(I)=0.0
        SUM(I)=0.0
        PROP=0.0
        IF (NPLANT(I) .EQ. 0) GO TO 420
        IF (I.EQ.1.AND.(NCHECK.EQ.0.AND.NPLANT(I).GT.0)) GO TO 610
        GO TO 620
610  CONTINUE
        NCHECK=1
        LYR=KYR
        IF (NCHECK.GT.0) NCHECK=1
620  CONTINUE
        NU=NL+NPLANT(I)-1
        DO 430 J=NL,NU
C  REDUCE OPTIMUM GROWTH INCREMENT FOR RESOURCES AND TEMPERATURE
        IF ((I.EQ.1 .OR. I.EQ.16).AND.TPROBM(I).EQ.2.0) GO TO 421
        IF (SZE(J).GT.1.0) SZE(J)=1.0
        OPT=TRGR(I)*(1.0-SZE(J))
        DINC=OPT*RESPOND(I)*TEMPR(I)
        SZE(J)=SZE(J)+DINC
        GO TO 424
421  IF (I.EQ.16 .AND. YPPT.GE.314.0) GO TO 423
        GO TO 424
423  CONTINUE
C  O. polyacantha CLUMPS ARE REDUCED FURTHER IN SIZE IN YEARS OF ABOVE-
C  AVERAGE PPT BASED ON THE NEGATIVE RESPONSE OF THIS SPECIES TO
C  RELATIVELY HIGH AMOUNTS OF PPT DURING THE GROWING SEASON (DOUGHERTY
C  1986). I ASSUMED THAT 86% OF THE ANNUAL PPT OCCURS DURING THE GROWING
C  SEASON (APRIL 1-SEPT. 30). THE FUNCTION IS BASED ON CHANGES IN DENSITY

```

```

C   OF O. polyacantha CLADODES WITH GROWING SEASON PPT FROM DATA COLLECTED
C   NEAR MILES CITY, MT. I ASSUMED A SIMILAR RELATIONSHIP FOR
C   O. polyacantha AT THE CPER SINCE PPT PATTERNS ARE SIMILAR AT THE TWO
C   SITES.
C
      GSPPT=YPPT*0.864
      PROPDO=ABS(-.0025*GSYPPT+0.677533)
      SIZE(J)=SIZE(J)-SIZE(J)*PROPDO
424  IF (I.EQ.1) GO TO 630
      GO TO 640
C.....
C   CALCULATION OF B. gracilis RECOVERY TIME TO 90% OF A FULL-SIZE CLUMP
C_
630  CONTINUE
      IF (KCHECK.GT.0 .OR. SIZE(J).LT.0.90) GO TO 640
      YOUT(1)=KYR
      KSET=KYR-LYR
      YOUT(2)=KSET
      KCHECK=1
      IF (KCHECK.GT.0) KCHECK=1
640  CONTINUE
      SUM(I)=SUM(I)+SIZE(J)
      PROP=SIZE(J)/(TRESPROP(I)/TRESR(I))
      PROP1=PROP*TRESPROP(I)
      TPROP(I)=TPROP(I)+PROP1
C   COMPARE GROWTH INCREMENT WITH MAXIMUM INCREMENT
C   PLANT IS FLAGGED AS SLOW GROWER IF INCREMENT IS < 5% OF ITS MAXIMUM
C   GROWTH RATE
      IF (DINC .GE. .05*RTMAX(I)) NOGRO(J)=0
      IF (DINC .LT. .05*RTMAX(I)) NOGRO(J)=NOGRO(J)-1
430  CONTINUE
      NL=NL+NPLANT(I)
      IF (KYR .EQ. NYEAR) JCHECK1(I)=0
420  CONTINUE
      IF (KYR .EQ. NYEAR) GO TO 499
      GO TO 600
499  CONTINUE
      DO 500 I=1,NGRP
          JCHECK(I)=0
500  CONTINUE
600  CONTINUE
C   COMPUTE TOTAL PROPORTION OF RESOURCE SPACE USED BY EACH RESOURCE GROUP
      NT=0
      TEWP=0.0
      DO 520 I=1,NSPEC-1
          IF (I.EQ.1) TEWP=TPROP(I)
          IF (NGRPID(I).EQ.NGRPID(I+1)) GO TO 522
          IF (NGRPID(I).NE.NGRPID(I+1)) GO TO 524
522  TEWP=TEWP+TPROP(I+1)
          GO TO 529
524  NT=NT+1
          RPROP(NT)=TEWP
          TEWP=TPROP(I+1)

```

529 CONTINUE

520 CONTINUE

NT=NT+1

RPROP(NT)=TEWP

C COMPUTE PROPORTION OF RESOURCES USED BY EACH SPECIES AT NYEAR (1000)
 C FOR STATISTICAL DISTRIBUTION OF LANDSCAPE
 C THESE PROPORTIONS ARE BASED ON THE BIOMASS/INDIVIDUAL (EX. 12.096),
 C THE PROPORTION OF THE RESOURCE SPACE USED BY EACH GROUP THAT YEAR,
 C AND THE RESOURCE REQUIREMENT OF A FULL-SIZE INDIVIDUAL (EX. 0.512).

C

C CONVERSION FACTORS ARE USED TO CONVERT DATA FROM THE MODEL (IN
 C TERMS OF PROPORTIONS) TO A FORM COMPARABLE TO DATA COLLECTED IN
 C THE FIELD (BIOMASS, DENSITY AND COVER). IN ORDER TO DETERMINE THE
 C CONVERSION FACTORS, IT WAS NECESSARY TO ACCUMMULATE DATA FROM
 C FIELD STUDIES CONDUCTED IN DIFFERENT PASTURES AND OVER DIFFERENT
 C YEARS, AND ASSUME THE VALUES ARE COMPARABLE. THE PROPORTION OF
 C THE RESOURCE SPACE USED BY EACH GROUP IN A YEAR IS CONVERTED TO
 C THE EQUIVALENT BIOMASS, DENSITY AND COVER OF FULL-SIZE PLANTS
 C ON THE PLOT.

C THE BIOMASS OF A FULL-SIZE PLANT FOR MOST SPECIES-GROUPS WAS
 C ESTIMATED USING FIELD DATA FOR THE YEARS 1984-1986. BIOMASS
 C VALUES (G/M^2) WERE OBTAINED FROM A MODERATELY GRAZED SWALE
 C AND DENSITY VALUES (NO/M^2) WERE OBTAINED FROM A HEAVILY
 C GRAZED SWALE (LAUENROTH AND MILCHUNAS UNPUBL.) (TABLE A4.3).
 C I ASSUMED THE BIOMASS OF A PLANT FOR EACH SPECIES-GROUP
 C CALCULATED FROM THE FIELD DATA REPRESENTS THE BIOMASS OF A
 C FULL-SIZE PLANT (TABLE A4.4). THE BIOMASS OF A FORB PLANT
 C CALCULATED FROM THE FIELD DATA WAS USED FOR ALL SHORT-LIVED
 C FORBS AND ANNUALS, WHILE THE BIOMASS OF A S. COCCINEA PLANT
 C WAS USED FOR ALL LONG-LIVED FORBS. THE BIOMASS OF A SHRUB
 C PLANT WAS USED FOR THE C. NAUSEOSUS GROUP. THE BIOMASS OF A
 C GRASS PLANT WAS USED FOR ALL PERENNIAL GRASS GROUPS EXCEPT
 C C. HELIOPHILA, WHICH WAS ESTIMATED SEPARATELY IN THE FIELD.

C

C THE BIOMASS AND DENSITY VALUES FOR G. SAROTHRAE WERE OBTAINED
 C FROM FIELD DATA FOR AN UNGRAZED UPLAND IN 1984 (LAUENROTH
 C AND MILCHUNAS UNPUBL.). THE BIOMASS OF A FULL-SIZED
 C O. POLYACANTHA CLUMP (15.0 g) WAS ESTIMATED USING THE
 C DENSITY OF CLADODES ($12/M^2$) AND BIOMASS PER CLADODE (3g)
 C FROM DOUGHERTY (1986), AND THE DENSITY OF CLUMPS ($2.52/M^2$)
 C FROM CHAPTER 3 FOR SITES ON MODERATELY GRAZED PASTURES.
 C THE BIOMASS OF A FULL-SIZE CLUMP OF B. GRACILIS (12/096g)
 C WAS CALCULATED USING FIELD DATA FOR A MODERATELY GRAZED
 C SWALE AVERAGED OVER THREE YEARS (1984-1986) (LAUENROTH
 C AND MILCHUNAS UNPUBL.)

C

C THESE VALUES ARE THEN STORED IN AN ASCII FILE FOR ANALYSIS

C

IF (KYR.LT.NYEAR) GO TO 590
 TPROP(1)=TPROP(1)*12.096/.51
 TPROP(2)=TPROP(2)*3.0548/.209
 TPROP(3)=TPROP(3)*3.0548/.209
 TPROP(4)=TPROP(4)*1.3985/.209

```
TPROP(5)=TPROP(5)*3.0548/.209
TPROP(6)=TPROP(6)*.7067/.18
TPROP(7)=TPROP(7)*19.726/.18
TPROP(8)=TPROP(8)*2.126/.18
TPROP(9)=TPROP(9)*19.726/.18
TPROP(10)=TPROP(10)*.429/.18
TPROP(11)=TPROP(11)*.429/.18
TPROP(12)=TPROP(12)*2.126/.18
TPROP(13)=TPROP(13)*.429/.042
TPROP(14)=TPROP(14)*.429/.042
TPROP(15)=TPROP(15)*.429/.042
TPROP(16)=TPROP(16)*15.0/.309
RPROP(1)=TPROP(1)
RPROP(2)=TPROP(2)+TPROP(3)+TPROP(4)+TPROP(5)
RPROP(3)=TPROP(6)+TPROP(7)+TPROP(8)+TPROP(9)
RPROP(4)=TPROP(10)+TPROP(11)+TPROP(12)
RPROP(5)=TPROP(13)+TPROP(14)+TPROP(15)
RPROP(6)=TPROP(16)
YOUT(3)=RPROP(1)
YOUT(4)=RPROP(2)
YOUT(5)=RPROP(3)
YOUT(6)=RPROP(4)
YOUT(7)=RPROP(5)
YOUT(8)=RPROP(6)
WRITE (11,1000) (TPROP(I),I=1,NSPEC)
1000 FORMAT (16(F7.4,1X))
      WRITE (8,1301) (YOUT(I),I=1,8)
1301 FORMAT (8(F8.4,1X))
590 CONTINUE
      RETURN
      END
```

LITERATURE CITED

- Bourgeron, P. S., W. K. Lauenroth, W. J. Parton, G. Zimmerman. 1987. Analysis of precipitation in the shortgrass region of North America: Implications for the soil-plant system. *Journal of Ecology* (submitted).
- Briske, D. D., and A. M. Wilson. 1977. Temperature effects on adventitious root development in blue grama seedlings. *Journal of Range Management* 30:276-280.
- Briske, D. D., and A. M. Wilson. 1978. Moisture and temperature requirements for adventitious root development in blue grama seedlings. *Journal of Range Management* 31:174-178.
- Canfield, R. H. 1957. Reproduction and life span of some perennial grasses of southern Arizona. *Journal of Range Management* 10:199-203.
- Coffin, D. P., R. L. Dougherty, and W. K. Lauenroth. 1987. Influences of soil texture and vegetation structure on seed dynamics of a shortgrass site. Abstracts of the 40th Annual Meeting, The Society for Range Management, Boise, Idaho.
- Cole, A. C., Jr. 1932. The rebuilding of mounds of the ant, Pogonomyrex occidentalis Cress. *Ohio Journal of Science* 32:245-246.
- Coupland, R. T., and R. E. Johnson. 1965. Rooting characteristics of native grassland species in Saskatchewan. *Journal of Ecology* 53:475-507.
- Dickinson, C. E., and J. L. Dodd. 1976. Phenological pattern in the shortgrass prairie. *American Midland Naturalist* 96(2):367-378.
- Dougherty, R. L. 1986. The soil water resource of Opuntia polyacantha in semiarid grasslands. Ph.D. Dissertation. Colorado State University, Fort Collins, Colorado.
- Jameson, D. A. 1969. General description of the Pawnee Site. United States International Biological Program Technical Report Number 1.

- Kerster, H. W. 1968. Population age structure of the prairie forb, Liatris aspera. *Bioscience* 18(5):430-432.
- Lauenroth, W. K., J. L. Dodd, and P. L. Sims. 1978. The effects of water- and nitrogen-induced stresses on plant community structure in a semiarid grassland. *Oecologia* (Berlin) 36:211-222.
- Lauenroth, W. K., O. E. Sala, and T. B. Kirchner. 1987. Soil water dynamics and the establishment of seedlings of Bouteloua gracilis in the shortgrass steppe: A simulation analysis. Abstracts of the 40th Annual Meeting, The Society for Range Management. Boise, Idaho.
- Lee, C. A. 1988. The spatial distribution of roots for three plant life-forms in the shortgrass steppe. M.S. Thesis. Colorado State University, Fort Collins, Colorado. (in prep.)
- Lussenhop, J., D. T. Wisklow, R. Kumar, and J. E. Lloyd. 1982. Increasing the rate of cattle dung decomposition by nitrogen fertilization. *Journal of Range Management* 35:249-250.
- McGregor, R. L. 1986. *Flora of the Great Plains*. University Press of Kansas, Lawrence, Kansas.
- Monson, R. K., R. O. Littlejohn, Jr., and G. J. Williams. III. 1983. Photosynthetic adaptation to temperature in four species from the Colorado shortgrass steppe: a physiological model for coexistence. *Oecologia*(Berlin) 58:43-51.
- Nelson, E. 1934. The influence of precipitation and grazing upon black grama grass range. United States Department of Agriculture Technical Bulletin Number 409.
- Noy-Meir, I. 1973. Desert ecosystems: Environment and producers. *Annual Review of Ecology and Systematics* 4:25-51.
- Sala, O. E., and W. K. Lauenroth. 1982. Small rainfall events: An ecological role in semiarid regions. *Oecologia* (Berlin) 53:301-304.
- Sala, O. E., and W. K. Lauenroth. 1985. Root profiles and the ecological effect of light rainshowers in arid and semiarid regions. *American Midland Naturalist* 114:406-408.

- Salisbury, F. B., and C. W. Ross. 1978. Plant physiology. Wadsworth Publishing Co., Inc. Belmont, CA.
- Shugart, H. H., and D. C. West. 1979. Size and pattern of simulated forest stands. *Forest Science* 25(1):120-122.
- Shugart, H. H. 1984. A theory of forest dynamics. Springer-Verlag. New York.
- Turner, G. T., and D. F. Costello. 1942. Ecological aspects of the prickly pear problem in Eastern Colorado. *Ecology* 23:419-426.
- Weaver, J. E. 1919. The ecological relations of roots. Carnegie Institute of Washington Publications.
- Weaver, J. E. 1958. Classification of root systems of forbs of grassland and a consideration of their significance. *Ecology* 39:393-401.
- Williams, G. J. III., and J. L. Markley. 1973. The photosynthetic pathway type of North American shortgrass prairie species and some ecological implications. *Photosynthetica* 7:262-270.
- Wilson, A. M., and D. D. Briske. 1979. Seminal and adventitious root growth of blue grama seedlings on the Central Plains. *Journal of Range Management* 32:205-213.
- Wright, R. G. 1972. A demographic study of a semi-desert grassland. Ph.D. Dissertation. Colorado State University, Fort Collins, Colorado.

Table A4.1. Model parameters for resource-groups

RESOURCE-GROUP	PROPORTION ¹ OF RESOURCE SPACE ON A PLOT	DENSITY ² (NO/PLOT)	PROPORTION ³ OF RESOURCE SPACE TO SUPPORT ONE PLANT
<i>B. gracilis</i>	0.51	1.00	0.510
PERENNIAL GRASSES	0.07	0.33	0.209
PERENNIAL FORBS AND SHRUBS	0.28	1.56	0.180
ANNUAL GRASSES AND FORBS	0.07	1.67	0.042
SUCCULENTS	0.07	0.31	0.226

1 based on Fig. A4.1b

2 from Chapter 3

3 proportion of resource space/density

Table A4.2. Model Parameters for the fifteen species-groups

RESOURCE- AND SPECIES-GROUPS ¹	AGEMAX (years)	MAXIMUM GROWTH RATE	DISTURBANCE ² CLASS	SEED ESTABL. PROB.	SEEDLING SIZE (g)	VEG. OR CLONAL GROWTH	GROWTH RATE	TEMP. ³ CLASS	BIOMASS ⁴ (g/plant)
<u>Bouteloua gracilis</u> (H.B.K.)Lag. ex Griffiths	NA	NA	1	0.125	0.605	Y	0.474	1	12.096
PERENNIAL GRASSES									
<u>Aristida purpurea</u> Nutt. var. <u>longiseta</u>	25	0.426	3	0.170	0.153	N	0.474	1	3.055
<u>Carex heliophila</u> Mack.	25	0.426	1	0.120	0.070	Y	0.474	2	1.399
<u>Sitanion hystrix</u> (Nutt.)J.G. Sm.	10	0.426	3	0.190	0.153	N	0.474	2	3.055
<u>Schedonnardus</u>									
<u>paniculatus</u> (Nutt.)Trel.	10	0.426	1	0.010	0.153	N	0.474	1	3.055
PERENNIAL FORBS AND SHRUBS									
FORBS									
<u>Sphaeralcea coccinea</u> (Pursh)Rydb.	35	0.426	2	0.015	0.035	Y	0.474	2	0.707
<u>Picrodeniopsis</u>									
<u>oppositifolia</u> (Nutt.)Rydb.	35	0.426	2	0.001	0.106	N	0.474	1	0.707
<u>Machaeranthera</u>									
<u>tanacetifolia</u> (H.B.K.)Nees	10	0.663	2	0.060	0.022	N	0.737	1	0.429
<u>Gaura coccinea</u> Pursh	10	0.663	2	0.011	0.022	N	0.737	2	0.429
SHRUBS									
<u>Chrysothamnus</u>									
<u>nauseosus</u> (Pall.)Britt.	35	0.426	3	0.002	0.986	N	0.474	2	19.726
<u>Gutierrezia sarothrae</u> (Pursh)Britt. and Rusby	10	0.663	3	0.001	0.106	N	0.737	2	2.126

1 Nomenclature follows McGregor (1986)

2 Disturbance Class
 1 = low-statured perennial grasses
 2 = perennial forbs and annuals
 3 = shrubs and bunchgrasses

NA = Not Applicable 4 = succulents

3 Temperature Class
 1 Warm season and succulents
 2 Cool season

4 from Lauenroth and Milchunas (unpubl.),
 Dougherty (1986), Chapter 3

Table A4.2. (continued)

RESOURCE- AND SPECIES-GROUPS ¹	AGEMAX (years)	MAXIMUM GROWTH RATE	DISTUR- BANCE ² CLASS	SEED ESTABL. PROB.	SEEDLING SIZE (g)	VEG. OR CLONAL GROWTH	GROWTH RATE	TEMP. ³ CLASS	BIOMASS ⁴ (g/plant)
ANNUAL GRASSES AND FORBS									
GRASSES									
<u>Vulpia octoflora</u> (Walt.) Rydb.	1	0.852	2	0.170	0.022	N	0.947	2	0.429
FORBS									
<u>Chenopodium album</u> L.	1	0.852	2	0.170	0.022	N	0.947	1	0.429
<u>Lepidium densiflorum</u> Schrad.	1	0.852	2	0.170	0.022	N	0.947	2	0.429
SUCCULENTS									
<u>Opuntia polyacantha</u> Haw.	NA	NA	4	0.020	2.250	Y	0.289	1	15.000

1 Nomenclature follows McGregor (1986)

2 Disturbance Class 1 = low-statured perennial grasses

2 = perennial forbs and annuals

3 = shrubs and bunchgrasses

NA = Not Applicable

4 = succulents

3 Temperature Class

1 Warm season and succulents

2 Cool season

4 from Lauenroth and Milchunas (unpubl.), Dougherty (1986), Chapter 3

Table A4.3. Basal cover, surface area and total area of full-size B. gracilis plants for three topographic positions

TOPOGRAPHIC POSITION	BASAL ¹ COVER (%)	FULL-SIZE ² PLANT SIZE (m ²)	TOTAL ³ AREA FOR A FULL-SIZE PLANT (m ²)
UPLANDS	24.3	0.030	0.1235
SLOPES	23.0	0.028	0.1217
LOWLANDS	31.7	0.038	0.1199

- 1 Average of lightly, moderately and heavily grazed pastures from Chapter 2
 2 from Chapter 2 for a heavily grazed pasture
 3 full-size plant size/basal cover/100

Table A4.4. Biomass and density values from field data used to calculate the biomass per full-size plant on a plot

SPECIES	BIOMASS ¹ (g/m ²)	DENSITY ¹ (no/m ²)	BIOMASS/PLANT (g/plant)
FORBS	4.508	10.50	0.429
<u>S. coccinea</u>	5.300	7.50	0.707
SHRUBS	6.904	0.35	19.726
GRASSES	4.124	1.35	3.055
<u>C. heliophila</u>	1.888	1.35	1.399
<u>G. sarothrae</u>	2.381	1.12	2.126

1 Lauenroth and Milchunas (unpubl.)

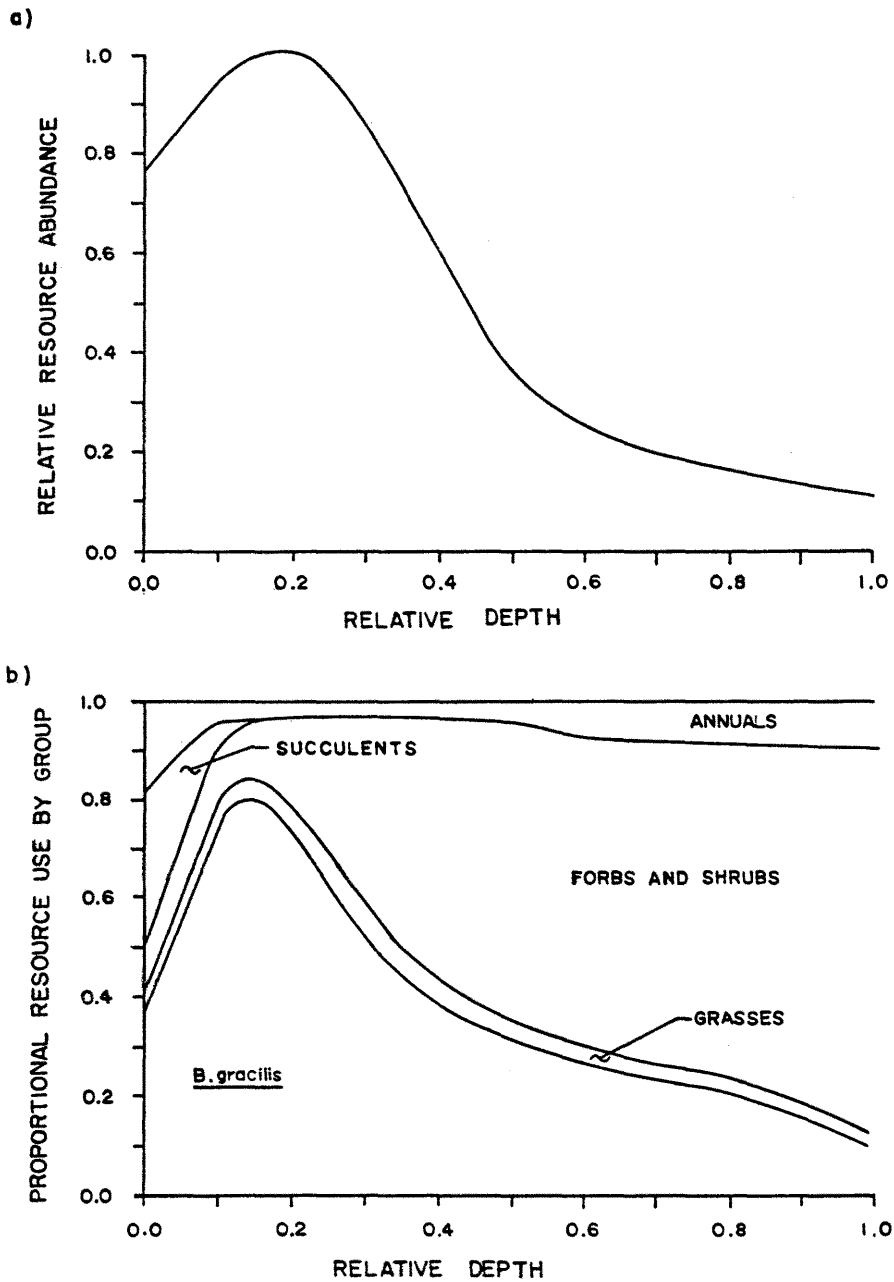


Fig. A4.1. (a) Distribution of soil water resources with depth in the soil profile. (b) Distribution of resource use as a proportion of the total for five resource-groups with depth in the soil profile.

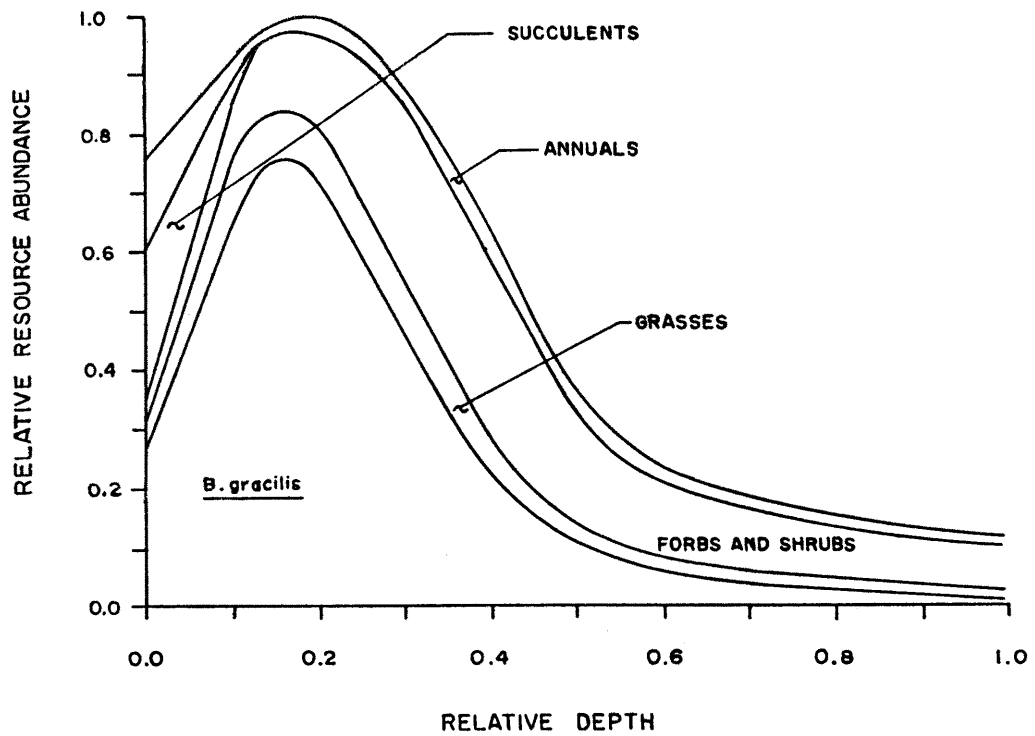


Fig. A4.2. Distribution of resource use with depth in the soil profile as a proportion of the total resources available for five resource-groups.

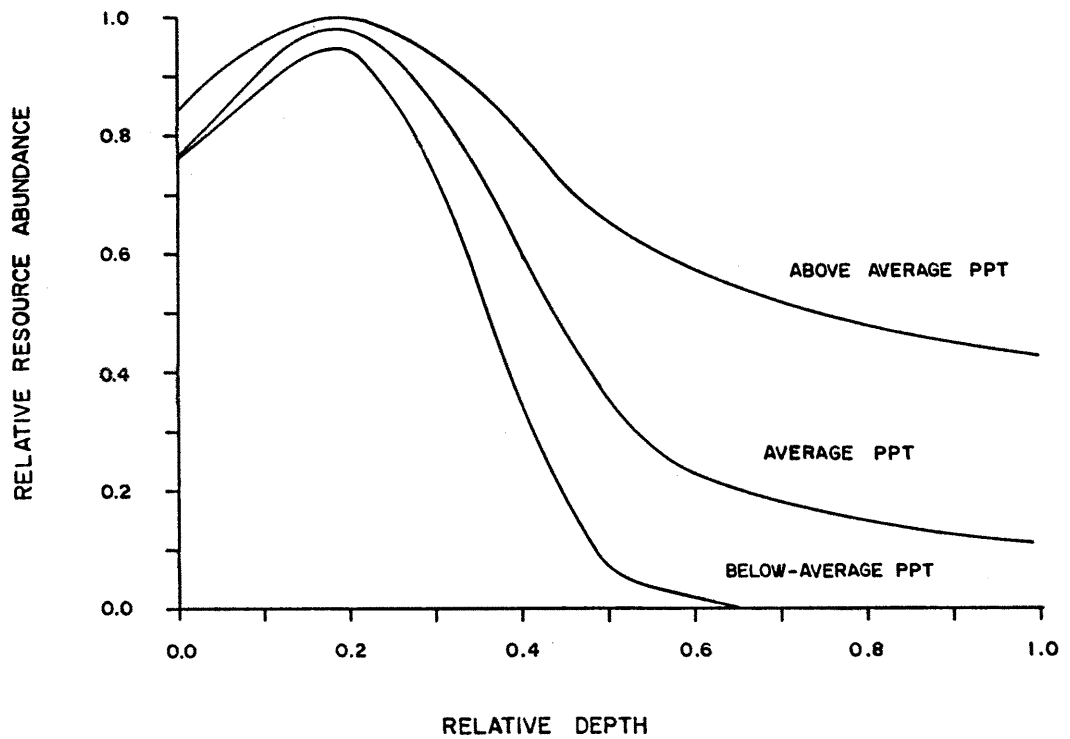


Fig. A4.3. Distribution of soil water resources with depth for three conditions of annual precipitation.

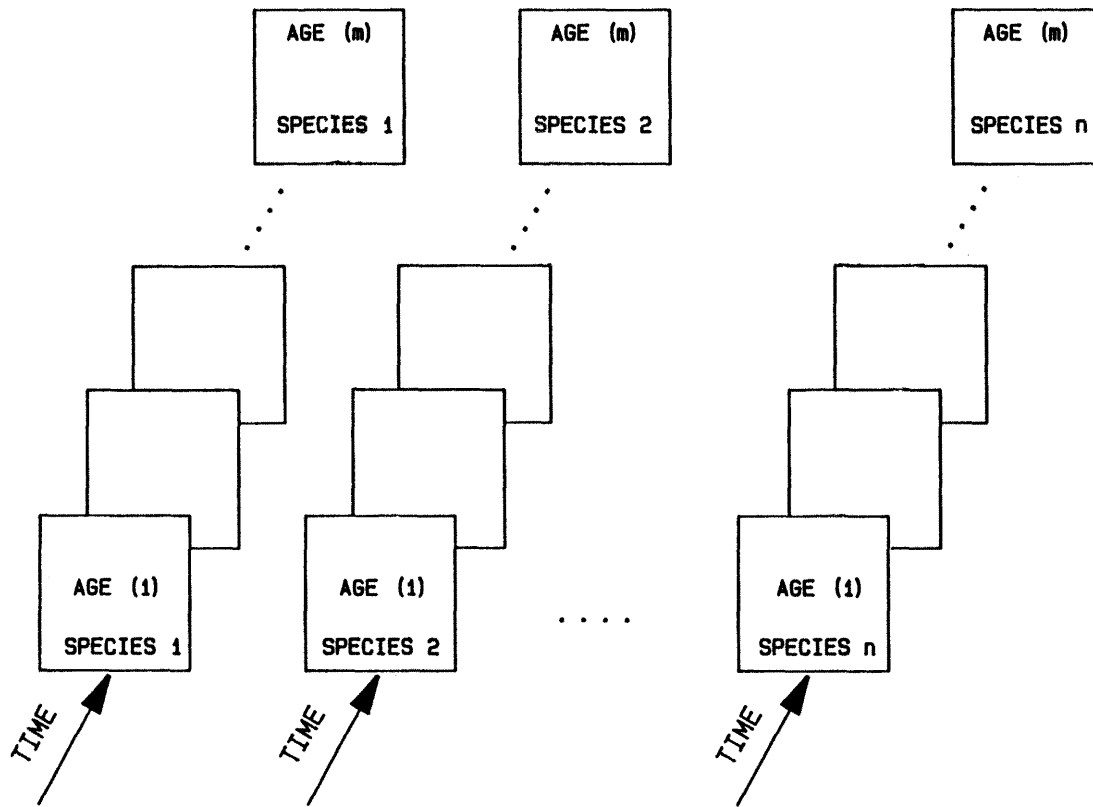
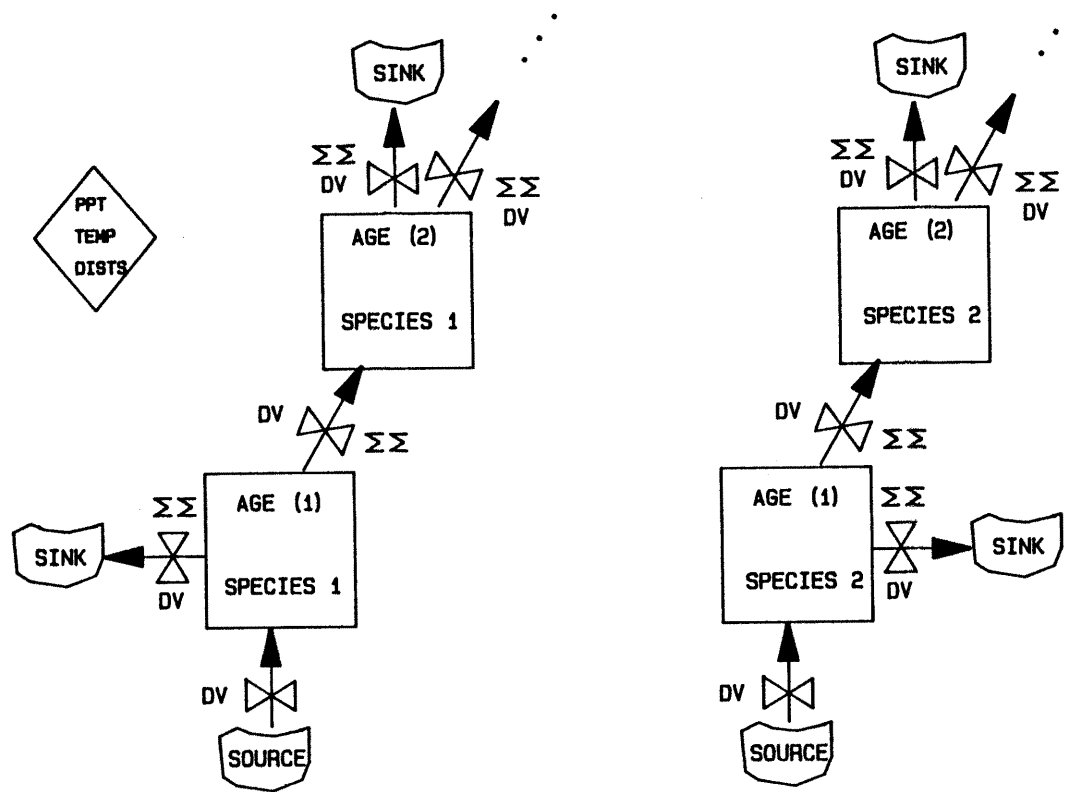


Fig. A4.4a. Diagram for $n=15$ species-groups through time for plants in 1 to m age classes.



PPT = PRECIPITATION
 TEMP = TEMPERATURE
 DISTS = DISTURBANCES

DV INFORMATION FLOW FROM DRIVING VARIABLES
 $\sum_{i=1}^n \sum_{j=1}^m$ INFORMATION FLOW FROM $i=1$ TO n SPECIES
 AND $j=1$ TO m AGE CLASSES

Fig. A4.4b. Generalized Forrester diagram for two representative species-groups.