

**PLANT COMMUNITY DYNAMICS GOVERNED BY RED  
HARVESTER ANT (*POGONOMYRMEX BARBATUS*) ACTIVITIES  
AND THEIR ROLE AS DROUGHT REFUGIA  
IN A SEMI-ARID SAVANNA**

A Dissertation

by

NANCY CAROL NICOLAI

Submitted to the Office of Graduate Studies of  
Texas A&M University  
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

August 2005

Major Subject: Rangeland Ecology and Management

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## ABSTRACT

Plant Community Dynamics Governed by Red Harvester Ant (*Pogonomyrmex barbatus*)

Activities and Their Role as Drought Refugia in a Semi-arid Savanna. (August 2005)

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This study examined modifications made by *Pogonomyrmex barbatus*, by their processes of granivory and nest construction, to forb and grass dynamics under large-scale disturbances of fire, recent drought and long-term, large-mammalian herbivory using comparative studies, field experimental manipulations, and a simulation model on the Edwards Plateau, Texas. Ant nests are refugia for grass survival during extreme droughts as demonstrated during the drought of 1998 to 2002. Significantly greater cover of grasses and lower abundance and cover of forbs was found beside nests compared with surrounding habitat throughout the drought and recovery. Grasses near nests may be the seed source for surrounding habitats during recovery.

Seeds were differentially collected among most forbs and grasses despite seed abundance. Harvest was significantly reduced in the fall relative to spring. During preference experiments, harvest differences were found between grazing treatments for two of four species, but only during the spring. High lipid content seeds were unpreferred in fall compared to high protein and carbohydrate content seeds.

Granivory influences on seedling establishment were studied by comparing seedling recruitment among sown and naturally occurring seeds excluded and open to foragers. Exclosures were placed in three nest densities and two burn treatments. Seeds in exclosures produced significantly more seedlings than open arenas only during the first year of drought recovery. Densities of grasses and annual forbs were higher in open arenas the second year

due to indirect effects of granivory. By reducing seeds ants release seedlings from competition. Sown seedling abundance was unaffected by colony density and fire.

Colony density and distribution were influenced by topography, soil types, soil depth and woody cover, but not by historical grazing treatments. Cleared vegetation on nest disks impacted less than 1% of total surface area and losses were compensated by greater basal cover of grasses next to disks compared to surrounding habitats. Foraging areas influenced 17.3-73.6% of surface area and could diminish seed populations for potential seedlings.

Model results agree with experimental observations that communities may be modified by *P. barbatus* presence due to differential responses of grass species to interaction between nests or granivory and rainfall amounts.

## **DEDICATION**

I dedicate this dissertation to my parents, Dr. Art and Mrs. Glennis Nicolai, and to those whose inspiration and encouragement led me to pursue sound science, Boyd Collier, Leroy McClenaghan Jr., Jeffrey Lovich, Jane Belnap, Elena Fink, A. Christina Longbrake, the wildlife biologists at the California Energy Commission, and Jon Atwood. They showed me that field ecology is meaningful in today's pursuit of conserving our natural heritage.

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## CHAPTER I

### INTRODUCTION

Natural disturbances are drivers in the dynamics of plant communities. Biotic agents contribute to disturbance regimes and may influence community functioning and potential for restoration following disturbances. Animals can be important by facilitating, inhibiting or altering the trajectory of plant population dynamics. Seed-harvester ants, of the genus *Pogonomyrmex*, exhibit two biotic processes demonstrated to be influential in arid plant communities; collection of seed for food and construction of nests with a cleared disk (MacMahon et al. 2000). They occur in North American savannas that are highly dynamic ecosystems largely controlled by a disturbance regime of extremes and variability of precipitation, frequent fires, and large mammalian herbivory (Amos and Gehlbach 1988, Smeins and Merrill 1988, Bazzaz 1996, Fuhlendorf and Smeins 1997, Frost 1998, Fuhlendorf et al. 2001). Dynamics of these savannas may be locally modified by the processes of *Pogonomyrmex* activities. This study focused on seed collection and nest disks and their affects on the dynamics of herbaceous species subject to a recent drought, historical grazing, and fire.

Harvester ants and herbaceous plants interact by many mechanisms, some negative (herbivory/predation) and some positive (facilitation/competitive release). Most of what we know of harvester ant influences on plant communities comes from research in deserts on seed predation. Harvester ants primarily gather small seeds from herbaceous plants after the seeds have fallen to the ground. Seed predation influences recruitment and population densities of plants (Brown et al. 1979; Davidson et al. 1984; Hobbs, 1985 and Rissing, 1986), and differential selection of seed causes changes in desert communities structure by reducing abundance of the preferred species (Inouye et al. 1980, Hobbs 1985). Furthermore, these studies found that plant species diversity increases due to the competitive release of

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This dissertation follows the style of Ecology.

uncommon species as a result of harvester ant reduction of abundant winter annual seeds.

Although less extensively studied, prairies can have high rates of harvester ant seed predation which favors plants that are dependent upon vegetative reproduction for persistence (McGowan 1969, Marshall and Jain 1970, Pulliam and Brand 1975, Louda 1989). In California grasslands there are conflicting results on the relative importance of seed predation on plant community composition (Hobbs 1985, Hobbs and Mooney 1995, Brown and Human 1997, Peters et al. 2005). It is uncertain under what environmental factors seed predation becomes significant. Additionally, limited information exists on selective seed predation, and, on seasonal or annual variation in predation pressure (Rice 1989). Although most studies show that large quantities of seeds are harvested, few studies demonstrate resultant alterations in plant populations or communities.

Several species of *Pogonomyrmex* create bare soil disks of approximately one-meter in diameter by clearing all vegetation on their nests (Rissing 1988, Whitford and DiMarco 1995, Wagner et al. 1997, MacMahon et al. 2000). *Pogonomyrmex* species have been considered a disturbance agent in rangelands because total land surface cleared by ants has been reported to be as high as 18% (Wight and Nichols 1966, Kirkham and Fisser 1972). However, plants surrounding harvester ant disks are larger and produce more seeds than those in surrounding habitats which perhaps offsets losses (Golley and Gentry 1964, Rissing 1986, Whitford 1988). In addition, vegetation composition often differs from areas adjacent to disks. Shrub and perennial dicot richness is lower while grass richness is higher (Rissing 1986, Soule and Knapp 1996, Lei 1999).

Disturbances transform landscapes into a mosaic of patches of different sizes and ages which results in a pattern of differing abundances and distributions in organisms (Paine 1966 and Sousa 1984). Patches are recognized as an important component of landscape ecology because they confer a heterogeneous landscape with diverse species dynamics, and population and community stability (Forman and Godron 1986). Smaller patches generally are created by small, frequent disturbances such as small mammal diggings, ant mounds, and patch grazing. These are imbedded in disturbances that are larger in aerial extent and are less

frequent, such as drought. These smaller scale phenomenon can influence the composition, structure and dynamics of nearby vegetation (Collins and Barber 1985, Whiticker and Detling 1988, Cloudsley-Thompson 1996, Carson and Root 1999).

*Pogonomyrmex* disks and nests could influence vegetation in two ways, the provision of more productive soils and the creation of gaps in existing vegetation. Their nests are unique patches in terms of soil chemistry, texture, moisture, and mycorrhizal communities compared to surrounding soils (Carlson and Whitford 1991, McGinley et al. 1994, Whitford and DiMarco 1995, Carson and Root 1999, MacMahon et al. 2000, Boulton et al. 2003). Furthermore, the disk, as a disruption of vegetation cover, is a patch that could be one of many possible gaps essential in grasslands as sites for seed germination and seedling establishment, while providing a competitive advantage to adult plants growing next to the disk (Evans 1975, Huntly and Inouye 1988, Coffin and Lauenroth 1989, Belsky 1992, Cheplick 1998, del-Val and Crawley 2005) .

If the impact of large-scale disturbances differs among ant-created patches, then the number and arrangement of the patches and the dispersal capabilities of plants among patches may determine plant population resistance or resilience (Palmer et al. 1996). The extent to which the patches created by *Pogonomyrmex* by nest construction interacts with large-scale disturbances to influence herbaceous composition and dynamics of grasslands is unknown.

Prior to European settlement, natural herbivory, periodic fires and weather variability were major driving factors in maintaining the liveoak savanna parkland of the Edwards Plateau of Texas (Smeins and Merrill 1988, Fuhlendorf et al. 2001). Suppression of fire, demise of large, free-roaming herbivores and introduction of confined grazing by livestock greatly transformed the structure and composition of these parklands (Amos and Gehlbach 1988, Smeins and Merrill 1988, Fuhlendorf and Smeins 1997, Knapp 1998). Fire suppression leads to woody plant encroachment and confined, intense grazing produces a vegetation community of shortgrasses and other species more tolerant of high levels of herbivory than the less grazing tolerant large bunchgrasses (Smeins and Merrill 1988,

Fuhlendorf 1996, Hendrickson 1996, Briske and Hendrickson 1998). These shortgrass communities often have greater gaps allowing for early successional species to become established and ultimately result in maintenance of an early successional community.

Climate extremes are a dominant, large-scale disturbance affecting vegetation change on the Edwards Plateau (Fuhlendorf 1996, Fuhlendorf and Smeins 1997). Droughts reduce basal areas of individual grasses, reduce populations of large bunchgrasses and perennial dicots, allow early successional species to fill gaps formed by the die-off, and change the dominant species to ones that are more drought resistant.

Natural fires typically maintain grassland structure on the Edwards Plateau since they inhibit expansion of tree and shrub species by killing seedlings (Collins and Barber 1985, Collins 1987, Knapp 1998, Taylor 2001). Frost (1998) estimates that the Edwards Plateau historically burned every one to six years.

*Pogonomyrmex* species may cause significant changes in this dynamic community by creating local patches of differential seed harvest and by constructing nests which provide habitats for plant establishment and survival. Since *Pogonomyrmex* can have distinct effects on plant community structure and dynamics, understanding the ways these effects are expressed is essential to understanding the role of ants in the response of plants to disturbance regimes. Experimental studies of these effects of harvester ants on community dynamics have not been conducted in many ecosystems where they occur, including the semi-arid savanna parklands of the Edwards Plateau, Texas. This study examined the interactions between seed collection and nest construction by the red harvester ant, *Pogonomyrmex barbatus*.

*Pogonomyrmex barbatus* is one of the few species of harvester ants that build large, cleared disks on the nest (MacMahon et al. 2000). They forage nearly all year, except during the coldest months of winter; thus, harvester ants can harvest crops of spring through late fall-dispersed seed (MacMahon et al. 2000). *Pogonomyrmex barbatus* could impact communities by harvesting a large number of seeds from the seed rain and by creating patches of cleared vegetation. Comparative studies (Chapters II and III), field experimental

manipulations (Chapters IV and V), and simulation models (Chapter VI) were used to test the results of seed gathering and disk construction (small-scale processes) and their interaction with historical, large-herbivore grazing, spring fire and weather variation (large-scale processes) on grassland dicots and grasses in a semi-arid savanna parkland on the Edwards Plateau.

Distribution and density data for this species are lacking for Edwards Plateau communities; thus the first four objectives of this study (Chapter II) were:

- (1) to determine the occurrence of harvester ant species on the Sonora Research Station,
- (2) to describe distribution of *P. barbatus* in woody compared to herbaceous habitats,
- (3) to determine density of nests in relation to historical grazing regimes, soil type, parent soil material and slope, and
- (4) to assess area of influence of nests and foraging ranges on vegetation dynamics in differing historical grazing regimes.

A study was designed to assess the influence of *P. barbatus* nest construction and its interaction with historical large herbivore grazing on grass and dicot structure and potential recovery following drought by comparing disk margins with adjacent habitat to address the following hypotheses (Chapter III):

- (1) perennial and annual grass and dicot species density and cover are comparable between disk margin and away from the disk across long-term (approximately 50 years) ungrazed and light and heavily grazed pastures now recovering from a recent drought,
- (2) water infiltration rates are similar on disks, disk margins and away from the disk,
- (3) drought refugia affects will decrease at a higher rainfall location (Kerr Wildlife Management Area) in light and heavily grazed treatments compared to the Sonora Research Station, and
- (4) following drought, seedling distributions will be aggregated near ant nests.

Manipulative field experiments were conducted to investigate selection and harvest of seeds by *P. barbatus* as influenced by season and by the differences between seed diversity and availability caused by successional stage due to grazing history (Chapter IV). Specific hypotheses were:

- (1) foragers will collect species of seeds in relation to their availability,
- (2) they will prefer late successional species regardless of their habitat's grazing history or season, and
- (3) they will select seeds with high protein levels in the spring and high carbohydrate levels in the fall.

To understand whether seed collection (Chapter IV) effects seedling establishment and interacts with large-scale disturbances, a manipulative field experiment was conducted to test the following hypotheses (Chapter V):

- (1) densities of naturally occurring dicot and grass seedlings are comparable among three densities of *P. barbatus* colonies, presence or absence of seed predation and between burned and unburned treatments,
- (2) density of seeded perennial dicot and grass seedlings sown from equal quantities of seed is comparable among the experimental treatments, and
- (3) seedling densities will be similar among years.

The objective of the simulation model is to determine the long-term effects of *P. barbatus* seed harvest and nest construction under variable rainfall (the primary driver of the ecosystem) on density of selected grass species at three distances from the nest. The model is used to test the following hypotheses;

- (1) density of *Bouteloua curtipendula* and *Hilaria belangeri* increases at the tasks zone during colony maturity (Figure 20A and B between m and d) and decreases when the colony dies (Figure 20A and B at d) with normal and low rainfall treatments, but remain unchanged in high rainfall (Figure 20A and B). A third species, *Stipa leucotricha*, will decrease at the tasks zone (Figure 20C between m and d). During colony maturity, seed harvest effects are highest at the tasks zone,

variable depending on species in the foraging zone (Figure 20D) and nonexistent in the unoccupied zone (Figure 20E), and

(2) during colony maturity, grass density is higher at the tasks zone compared with the other two zones for *Bouteloua curtipendula* and *Hilaria belangeri* and lower for *Stipa leucotricha*.

## CHAPTER II

# THE DISTRIBUTION AND ABUNDANCE OF RED HARVESTER ANT COLONIES IN A SEMI-ARID SAVANNA ON THE EDWARDS PLATEAU, TEXAS AND ITS IMPLICATION FOR ANT-PLANT INTERACTIONS

### Introduction

Harvester ants, a group of over 150 species, primarily collect and store seeds for food (MacMahon et al. 2000). Half the species belong to the genus *Pogonomyrmex* (subfamily Myrmicinae), which are large individuals, occurring sympatrically with smaller harvester ants of the genera *Pheidole*, *Messor*, *Aphaenogaster* and *Solenopsis* (Cole 1968, Tabor 1998). There are 291 species of ants in Texas (O'Keefe et al. 2000). The geographic range of thirteen confirmed and unconfirmed seed-harvesting species of ants includes the Sonora Research Station: *Pheidole crassicornis*, *P. dentata*, *P. hyatti*, *P. porcula*, *P. sitarches*, *P. tepicana*, *P. texana*, *Pogonomyrmex barbatus*, *P. imberbicus*, *Solenopsis aurea*, *S. geminata*, *S. molesta*, and *S. xyloni*. The most conspicuous species is *Pogonomyrmex barbatus* because individuals are nearly one centimeter long and they create approximately one-meter diameter, bare soil disks by clearing all vegetation on top of their nests (Rissing 1988, Whitford and DiMarco 1995, Wagner et al. 1997, MacMahon et al. 2000).

In North America, *Pogonomyrmex* species primarily occur in arid and semi-arid climates (Holldobler and Wilson 1990, Johnson 2001). *Pogonomyrmex barbatus* is distributed through most of Mexico north to Arizona, Kansas and Colorado, U. S. A. (Figure 1). They are known to occur in a variety of habitats including grassland, cultivated groves, savanna and along roadways (Tabor 1998). They are usually found in loam to clay loam soils and from low to mid-elevation (<1,500 m) on nearly flat terrain (Tabor 1998, Johnson.



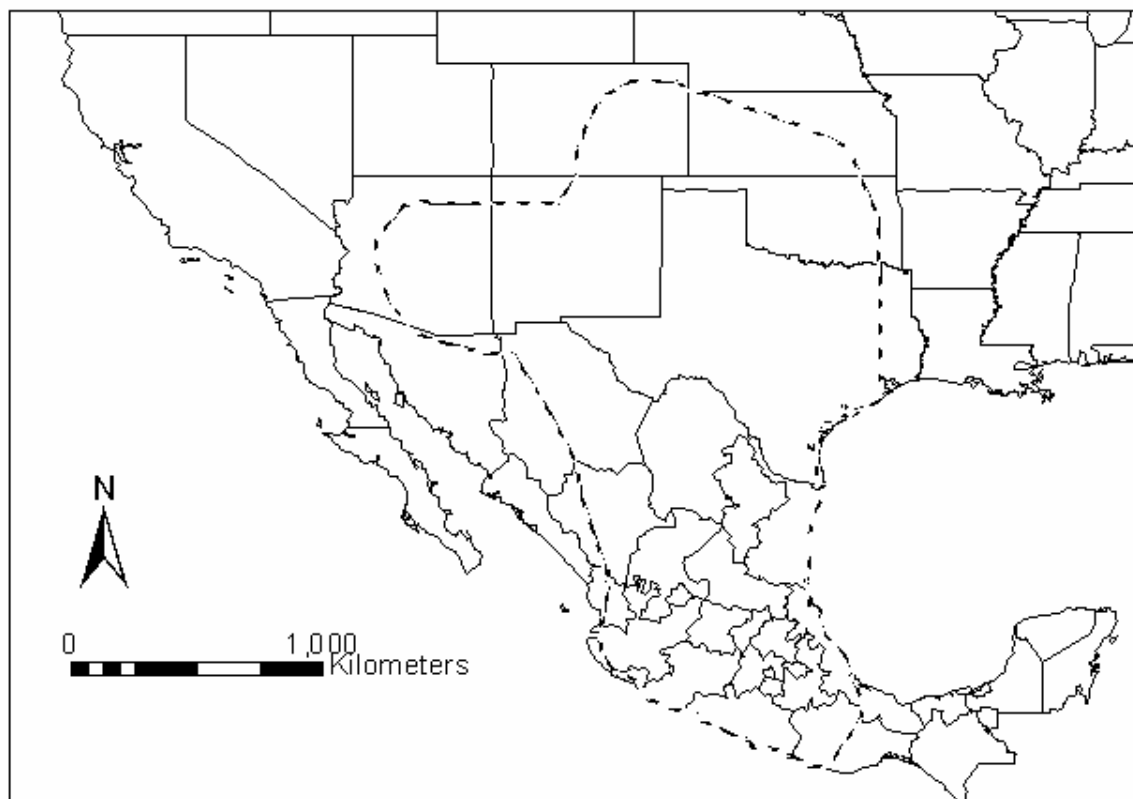


Figure 1. Range of *Pogonomyrmex barbatus* (red harvester ant). Data are from Johnson (2001).

2001). Harvester ant colonies may vary from 20 to 150 per hectare in areas of suitable habitat (Holldobler and Wilson 1990, MacMahon et al. 2000, McIntyre 2003).

Populations of harvester ants do not appear to be affected by livestock grazing (Kerley and Whitford 2000). *Pogonomyrmex* species have been considered a disturbance agent in rangelands (Wight and Nichols 1966, Kirkham and Fisser 1972). Total land surface cleared by *Pogonomyrmex* species have been reported to be as high as 18%, but typically studies find 1-8% (Wight and Nichols 1966, Kirkham and Fisser 1972, Soule and Knapp 1996) where they can impact plant communities by harvesting a large number of seeds from the seed rain as well as by creating patches of cleared vegetation.

Distribution and density data for this species are lacking for Edwards Plateau communities; thus potential impacts to vegetation structure and dynamics from *P. barbatus* are unknown for this region. The objectives of this study were:

- (1) to determine the occurrence of harvester ant species on the Sonora Research Station,
- (2) to describe distribution of *P. barbatus* in woody compared to herbaceous habitat,
- (3) to determine density of nests in relation to historical grazing regimes, soil type, parent soil material and slope, and
- (4) to assess area of influence of nests and foraging ranges on vegetation dynamics in differing historical grazing regimes.

## **Materials and Methods**

### ***Study Area***

Studies were conducted at the 1,404 ha Texas A&M University Agricultural Research Station (Sonora Research Station), Edwards Plateau, which is located 204 km NW of San Antonio, Texas (31 18'N; 100 28'W) at an elevation of 735 m.

The Sonora Research Station is on the Edwards Plateau-Divide, (Gould et al. 1960) which has gently rolling topography with slopes usually from 1% to 4% and soils with high percentages of stone fragments on the surface and in the solum. Weathering produces numerous vertical cracks through the horizontal bands of limestone parent material allowing

for some soil development, tree roots, rodent and armadillo burrows (USDA 1986, Woodruff 1996, Woodruff and Collins 2003).

Two major soil types occur on the study sites, Tarrant and Eckrant (USDA 1968, 1982, Loomis 2003). Tarrant soils are clayey-skeletal, smectitic, thermic Lithic Haplustolls. They are found on slopes and are shallow (3-23 cm deep), clayey, stony soils with limestone fragments 35 to 70% of the soil volume (USDA 1968). Eckrant soils are clayey-skeletal, smectitic, thermic Lithic Haplustolls. They are found on gently undulating to steep slopes, primarily uplands, and are slightly deeper than Tarrant (17-30 cm deep) with stone fragments 40 to 65% of soil volume (USDA 1986). Two less common soils are the Prade and Valera. Prade soils are clayey-skeletal, smectitic, thermic Petrocalcic Calciustolls. They are shallow soils (15-45 cm deep) with much of the soil volume made up of coarse rock fragments. Prade soils occur on level uplands. Valera soils differ because they are moderately deep (25-120 cm). Valera soils are fine, mixed, thermic Petrocalcic Calciustolls. They are found on level to gently sloping topography and consist of clay in the top surface with small limestone fragments making up 15% of soil volume. There is an indurated caliche layer just above the bedrock. Tarrant and Eckrant soils overlay Edwards limestone parent material whereas Prade and Valera soils overlay Buda limestone (USDA 1986). These limestones form soils that are alkaline (8.0 pH) and calcareous (11.0%  $\text{CaCO}_3$  equivalent) (Marshall 1995).

The climate is continental and semi-arid with a bimodal distribution (peaks in May and September) of growing season rainfall. Temperatures average 30<sup>0</sup> C in July and 9<sup>0</sup> C in January (Station Records). Average annual precipitation (1919-2004) is 57.5 cm, but variability between years is great with a range of 35.7 cm and standard deviation of 5.1 cm (Station Records).

Vegetation is potentially mixed-grass, savanna parkland dominated by groves of *Quercus virginiana*, *Q. pungens* var. *vaseyana*, *Juniperus ashei* and *J. pinchotii* in a matrix of mid- and short-grass species (Kuchler 1975, Smeins and Merrill 1988, Hatch et al. 1990). The grassland is dominated by the grasses *Bouteloua curtipendula*, *Stipa leucotricha*,

*Hilaria belangeri*, and *Bouteloua trifida*

From approximately 1870 to 1948, Sonora Research Station and surrounding ranches were grazed by cattle, sheep and goats at high intensities. Grazing changed the herbaceous vegetation from mid-grass species to a few short-grass species with sparse cover. Four grazing intensity research treatments used for this study were established in 1948 into pastures of varying grazing levels; light (16.2 ha/AUY) had two-32 ha replicates, moderate (8.1 ha/AUY) had four-24 ha replicates, heavy (5.4 ha/AUY) had two-32 ha replicates and ungrazed by livestock had two-11 ha replicates (Figure 2). The less intensively grazed treatments were allowed to recover from pre-1948 high intensities. In grazing treatments that have not been burned woody species, primarily *Juniperus*, increase in the absence of fire. As *Juniperus* cover increased a corresponding amount of herbaceous area decreased and stocking rates were adjusted accordingly (Fuhlendorf and Smeins 1997, Taylor 2001). In 1983 the entire Sonora Research Station's stocking rates were reduced to 16.2 ha/AUY. Since 1948 the ungrazed treatment has only been grazed by native herbivores. The light grazing treatment was burned in 1999 and *Juniperus* and *Prosopis* were mechanically removed from it in 1969.

***Ant Community Composition***

The harvester ant community was sampled by randomly establishing one 24 m<sup>2</sup> array in perennial grassland in three pastures (Figure 2). An array consisted of 24 pitfall traps, each 1 m apart. A pitfall trap (500 ml volume, 12 cm tall and 9 cm diameter) was filled with propylene glycol to kill and preserve specimens (Nazzi et al. 1989). Traps were buried so the tops were left flush with the soil surface. They were left undisturbed for seven consecutive days, June 5-11, 2002. All ants were collected daily, placed in alcohol for preservation, and identified to genus. Additionally, individuals of *Pogonomyrmex barbatus* were collected from their nests throughout the Sonora Research Station to confirm identification of this species and to collect voucher specimens subsequently stored in

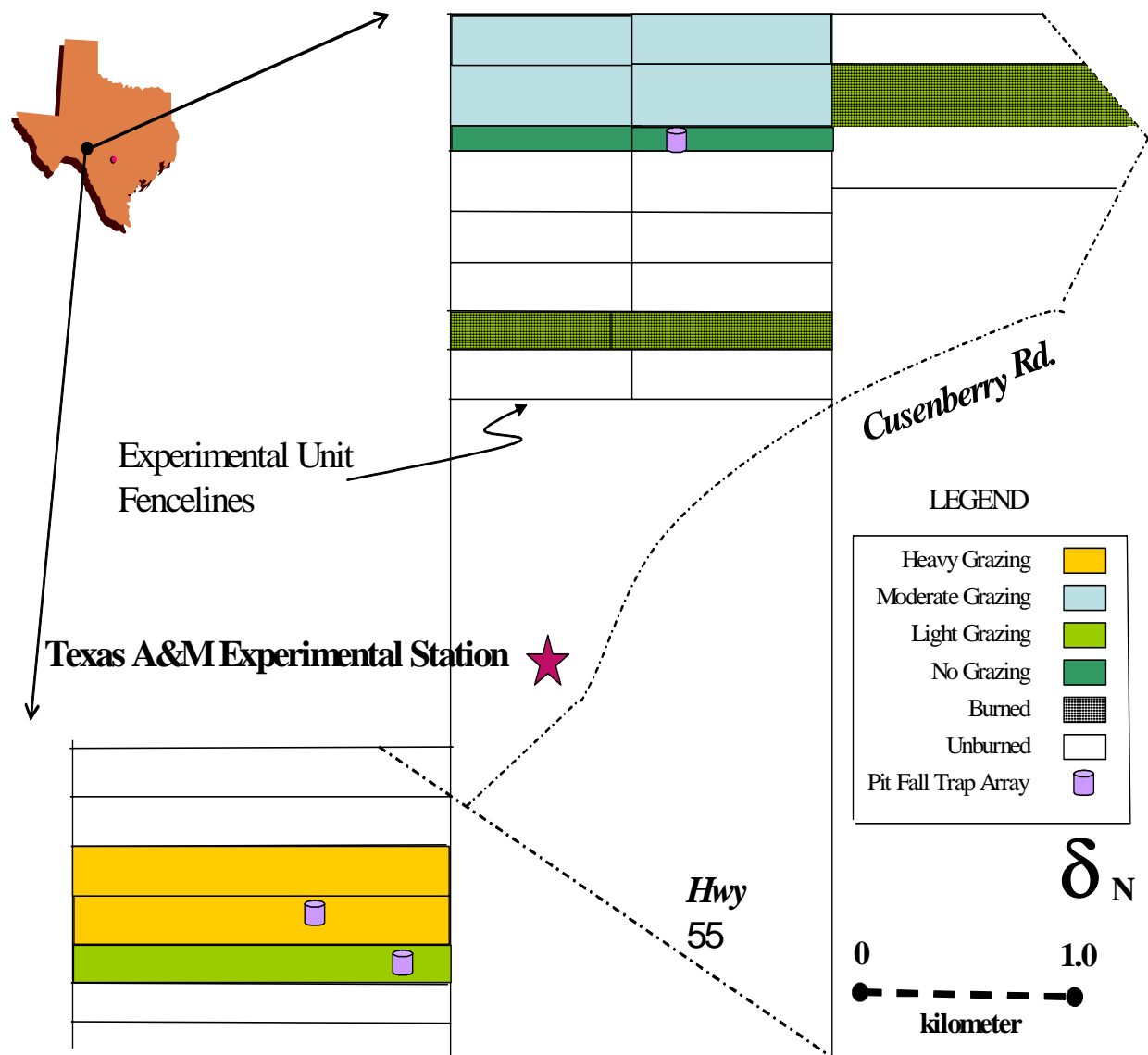


Figure 2. Map of the Texas A&M University Research Station showing unburned and prescribed burn treatments 1997-2002, heavy, moderate, light and ungrazed treatments, and locations of pitfall trap arrays for sampling ants.

The Entomology Museum, Department of Entomology, Texas A&M University. Nomenclature for ant species follows O'Keefe et al. (2000).

Nests were never found away from tree canopies. As a result, the distribution of nests under woody cover was compared to open habitats by conducting a survey for the presence of nests in these two habitat types across the Sonora Research Station. The entire Sonora Research Station was set up in a 2,200 ha grid of 10 ha cells. Using the center of each grid as a location, ten randomly chosen locations were searched August 19-20, 2003. Locations occurred in five moderately grazed, three lightly grazed, and two heavily grazed pastures. Observations showed nests were not found on rock slabs, streambeds, and temporary pools, therefore these areas were eliminated from search locations. At each location a 2,500 m<sup>2</sup> (50 m x 50 m) area was chosen in woody cover and another 2,500 m<sup>2</sup> area was selected in an open habitat. Data collected were number of *P. barbatus* nests in each habitat type.

The density of *P. barbatus* colonies was determined by conducting surveys across four grazing treatments each with two replicate pastures: light (32 ha each), moderate (24 ha each), heavy (32 ha each) and ungrazed (11 ha each) (Figure 2). Surveys consisted of 15 to 30 parallel transects walked approximately 10 m apart from one end of the pasture to the other; pasture length was from 850 m to 1,700 m. Number and length of transects varied depending upon size of pasture. Surveys were conducted throughout the summer of 2001 and spring 2002. Active *P. barbatus* nests were given an individual number, marked in the field and recorded. Active nests were determined by: (1) presence of ants, (2) presence of fresh nest debris, and (3) dead ants in spider webs. Grazing treatment and percent slope were recorded for each nest. Parent soil material was recorded at subsamples of 285 of a total of 411 nests. Soil parent material was determined by the type of exposed limestone fragment in or adjacent to the nest and percent slope was determined across the surface of the nest. Soil type was identified by overlaying soil maps over approximate nest localities (Loomis 2003).

A subset of ten nests in each of three grazing treatments (ungrazed, light and heavy) was randomly selected to determine soil depth at nests. Soil depth was measured by driving

a 1 cm diameter steel rod into the soil at three locations on the bare soil disk, at the entrance, 3 cm from the entrance and 40 cm from the entrance. The mean of the three measurements was used as the soil depth for the nest.

The presence of *P. barbatus* entirely in open habitat indicated that comparisons of density within grazing treatments should be adjusted to accord for unoccupied woody cover. Available habitat was determined with aerial photographs taken of the Sonora Research Station by the Texas Forest Service in August 2002, at 16,000 m scale. Two replicated pastures of heavy, light and ungrazed treatments were used by registering a grid of 16 control points and georeferencing with topographic maps of 1:24000 in UTM projections. Results were affected by color distortion, thus an independent classification across each image was used.

Each image was classified with ARCGIS Spatial Analyst that classified pixel values and then checked with visual examination of the photos. Analyses were based on 400 dbi resolution at 1m pixel and pixels were classified as woody cover, open habitat, or developed. Woody cover had a continuous canopy of at least 3 shrubs or small trees. Developed areas, such as buildings, were excluded. The amount of woody cover and open habitat were calculated from the number of pixels of each type. The amount of open habitat was determined for each replicate of the grazing treatments. Density of *P. barbatus* nests were recalculated to number per hectare of open habitat.

#### ***Area of Nest Impact***

The amount of cleared area on top of *P. barbatus* nests was determined for three grazing treatments, heavy, light and ungrazed. Data were collected on the diameter of the cleared area on top of the nest (hereafter called nest disk) from a subset of twenty nests while conducting *P. barbatus* nest surveys in 2001-2002. Nest disk diameter was converted to area m<sup>2</sup> using a circular formula because disks are nearly circular (Figure 3).

All vegetation was recorded on nest disks using a circular quadrat and data were collected from seven concentric rings which were 15 cm wide, and extended from the nest disk center, past the nest margin to 105 cm. Vegetation was not sampled under woody plants

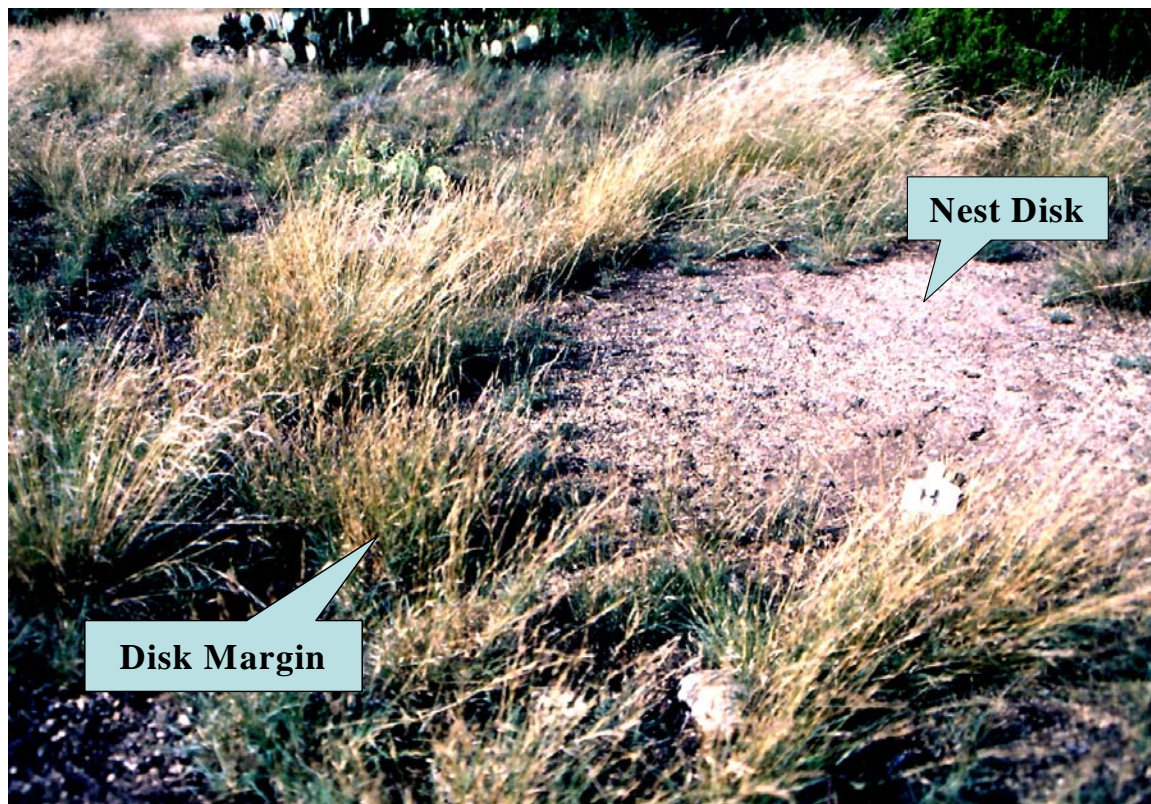


Figure 3. Photograph of a *Pogonomyrmex barbatus* nest showing the circular nest disk and the encircling disk margin of dense, tall grasses. The Sonora Research Station, July 2003.



or in rock outcrops because vegetation varies markedly from the remaining herbaceous community. The nest disk contains the 15 cm concentric rings on the cleared area, whereas the disk margin contains the rings that have high basal and aerial cover of perennial grasses on the outer margin of the nest disk. Vegetation data from the 15 cm concentric rings that encompassed the disk margin were grouped together for analysis. Area of disk margin was calculated using a circular formula since most encircle the nest disk.

The amount of foraging area by *P. barbatus* colonies was determined for three grazing treatments, heavy, light and ungrazed. In June 2003 two replicates of each treatment were sampled with 31 colonies in heavy, 56 in light and 20 in ungrazed for a total of 107 colonies. *Pogonomyrmex barbatus* create cleared foraging trails that are easily found and workers can be seen following the trail to their foraging area. Trails are curved and twisted slightly, thus linear distance to the foraging area is shorter than the trail. Nests have 2 to 5 trails radiating out from the nest in varying directions and workers use these trails throughout the year to go to their foraging areas (Gordon 1995, Gordon and Kulig 1996). Included in the colony's foraging area is the end of the trail, next to the nest disk, and a band on either side of the trail which overlaps band widths on adjacent trails, thus over a season the entire area surrounding a nest is searched. At each colony, length to foraging area was measured on the longest foraging trail with workers. Foraging areas were calculated using a circular formula since the mean distance to foraging areas is the radius of a circle, centered on the nest entrance, that encompassed the entire foraging area during a season.

### ***Data Analyses***

Number of nests in woody compared to open habitats was analyzed with a one-way treatment in a completely randomized design. Distributions of nest data were highly skewed because woody cover had no nests, therefore a nonparametric Mann-Whitney U test was conducted (Zar 1996).

Percent slope and soil depth at nests was compared among grazing treatments with a one-way treatment in a randomized complete design analysis of variance (ANOVA) for each variable (Zar 1996). Due to resource constraints soil depth was not gathered in the

moderately grazed pasture. Data for percent slope and soil depths at nests were non-normal and the variances among factors were unequal, therefore analyses were performed on square root transformations of the data. Differences among grazing treatments were tested using the least statistical difference test for post-hoc comparisons (Zar 1996).

Relative frequencies of nests in Buda or Edwards limestone soil parent material, among four grazing treatments, were analyzed with a 2 X 4 Chi-square goodness of fit test (Zar 1996). Relative frequencies among five soil types and among four grazing treatments were compared with a 5 X 4 Chi-square goodness of fit analysis.

Nest densities in available open habitat were compared among grazing treatments using a one-way treatment in a completely randomized design ANOVA. Due to inequality of variances, even after data transformations, nonparametric statistics (Kruskal-Wallis) were used for the analysis. Each pasture had varying amounts of open habitat largely due to past fire, brush clearing and grazing history. To determine if nest densities were related to amount of available habitat, the relationship between hectares of open habitat in a pasture and densities of ant nests was examined with Spearman's Rank Correlation.

## **Results**

### ***Ant Community in Grassland***

Five harvester ant species were found in the grasslands of the Sonora Research Station (Table 1). The largest, *Pogonomyrmex barbatus*, occurs commonly, albeit at low densities (Table 2). It has two color morphologies: a dark burnished-red and a lighter orange-red. The remaining four harvester ants were small species. Included are: two species of *Pheidole*, a species of *Epebomyrmex*, and *Solenopsis molesta* (Table 1).

### ***Density and Distribution of Pogonomyrmex barbatus***

*Pogonomyrmex barbatus* nests were found exclusively in open habitat ( $8.8 \text{ ha}^{-1}$ , S.D. = 3.7) compared to woody cover ( $0.0 \text{ ha}^{-1}$ , S.D. = 0.0) (Mann-Whitney U = 0.0,  $p < .001$ ,  $n = 20$ ).

Ninety percent of *P. barbatus* nests were found on nearly flat topography with slopes less than 5% and all were less than 15%. Although nests occurred on relatively flat

Table 1. Ant species collected from three pitfall trapping arrays at the Sonora Research Station, June 5-11, 2002. Blank rows indicate that the species was not captured in that array. Harvester ant species are designated with an \*.

Array 1	Array 2	Array 3
<i>Pogonomyrmex barbatus</i> *	<i>Pogonomyrmex barbatus</i> *	<i>Pogonomyrmex barbatus</i> *
<i>Ephebomyrmex</i> spp. probably <i>imberbicus</i> *	--	--
<i>Pheidole</i> spp. 1 *	<i>Pheidole</i> spp. 1 *	--
<i>Pheidole</i> spp. 2 *	<i>Pheidole</i> spp. 2 *	--
--	<i>Solenopsis molesta</i> *	<i>Solenopsis molesta</i> *
--	<i>Odontomachus</i> spp.	<i>Odontomachus</i> spp.
<i>Dorymyrmex</i> spp.	--	--
<i>Monomorium</i> spp.	--	--
--	<i>Paratrechina</i> spp.	<i>Paratrechina</i> spp.
--	<i>Linepithema</i> spp.	--

Table 2. Mean (95% C.I.) density ha<sup>-1</sup> of *Pogonomyrmex barbatus* nests and mean (95% C.I.) slope (%) and soil depth (cm) at nests in heavy, moderate, light and ungrazed treatments at the Sonora Research Station during summer 2001 and spring 2002. Soil depth and density were unsampled in the moderate grazing treatment. Differing letters indicate significant differences.

Grazing Treatment	Slope (%)	Soil Depth (cm)	Density (ha) in open habitat
Heavy	2.4 (0.3) a	15.2 (6.4) b	3.3 (9.4) a
Moderate	2.7 (0.3) a	uncollected	uncollected
Light	2.7 (0.3) a	8.2 (2.9) a	6.7 (6.4) a
Ungrazed	4.0 (0.7) b	9.5 (3.1) a,b	5.1 (3.1) a

topography, significant differences were found among grazing treatments ( $F = 7.20$ , d.f. = 3,  $p < .001$ ; Table 2) with more nests on steeper slopes in the ungrazed treatment compared to heavy ( $LSD = 0.48$ ,  $p < .001$ ), moderate ( $LSD = 0.33$ ,  $p = .002$ ) and lightly grazed treatments ( $LSD = 0.41$ ,  $p < .001$ ).

Average soil depth at *P. barbatus* nests was 11 cm (2.6 cm 95% C.I.) varying from 3 to 35 cm (Table 2). Grazing treatments were significantly different ( $F = 3.63$ , d.f. = 2,  $p = 0.04$ ). More nests were found in deeper soils in the heavily grazed treatment compared to lightly grazed ( $LSD = 0.98$ ,  $p = 0.02$ ).

Geology and soil type are strongly related, therefore soil type was used as a direct indicator of the soil parent material from which it was derived. (Tarrant and Eckrant soils overlay Edwards limestone parent material whereas Prade and Valera soils overlay Buda limestone.) Examination of the amount of soil types in each grazing treatment showed that more Buda limestone occurs in heavy and lightly grazed treatments compared to more Edwards limestone in moderate and ungrazed treatments. The number of nests reflect this pattern with more nests on Buda limestone in heavy and lightly grazed treatments compared to moderate and ungrazed ( $X^2 = 30.54$ ,  $p < .001$ ,  $n = 285$ ; Figure 4).

Sixty-seven percent of the nests found were located in Eckrant soils; approximately 15% more than if they occurred equally with the relative amount of Eckrant surface area in each treatment (Table 3). But, 1% and 2% of the nests were in Valera and Tarrant-Valera soils, respectively, which is approximately 10% less than the relative amount of these soils in surface area for each treatment (Table 3). Counts of five nests or less were found in the soils Tarrant-Valera, Valera and Tarrant-Eckrant soils and therefore the two Valera soil types were pooled and Tarrant-Eckrant was pooled with Eckrant soil type for Chi-square statistical analysis. Significant differences were found for the combination of grazing treatment and soil type ( $X^2 = 23.88$ ,  $p = .001$ ). Four 2 X 2 Chi-square tests were used to

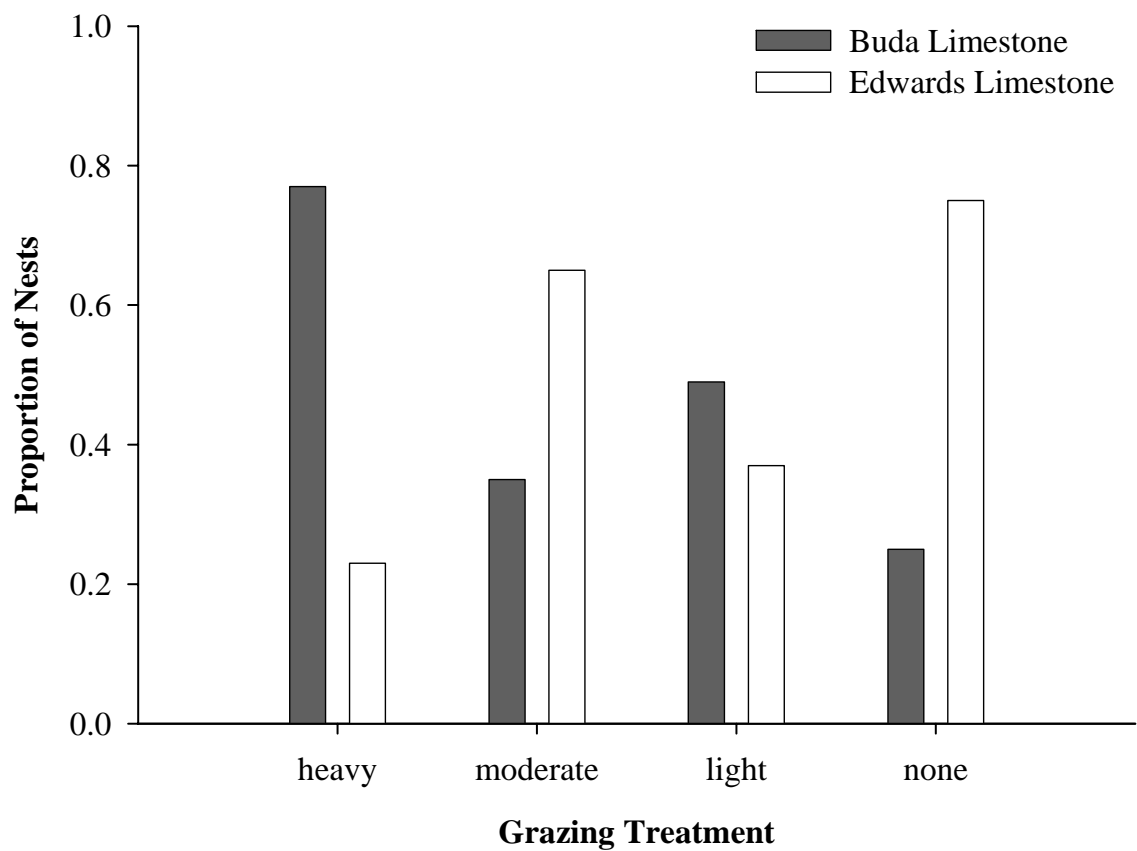


Figure 4. Proportion of *Pogonomyrmex barbatus* nests at Buda and Edwards limestone soil parent material in four grazing treatments, heavy, moderate, light and no grazing at the Sonora Research Station. Numbers above bars are number of nests.

Table 3. Percent of *Pogonomyrmex barbatus* nests and surface area in Eckrant, Prade-Eckrant, Tarrant-Valera, Tarrant-Eckrant and Valera soil types in four grazing treatments, heavy, moderate, light and no grazing at the Sonora Research Station. Numbers in parentheses are number of nests.

Grazing Treatment Unit	Soil Type				
	Eckrant	Prade- Eckrant	Tarrant- Valera	Valera	Tarrant-Eckrant
Heavy Nests	69 (64)	31 (29)	0	0	0
Surface Area	52	25	13	10	0
Moderate Nests	75 (77)	19 (20)	6 (6)	0	0
Surface Area	60	25	15	0	0
Light Nests	59 (103)	30 (52)	0	3 (5)	8 (15)
Surface Area	40	45	0	12	3
None Nests	82 (33)	0	5 (2)	0	13 (5)
Surface Area	75	0	5	0	20
Total Nests	67 (277)	25 (101)	2 (8)	1 (5)	5 (20)

determine whether the probability of nest occurrence was independent of soil type. There were significantly more nests in the Eckrant soil pool, while in contrast, significantly less nests occurred in the Valera pool for each grazing treatment (heavy  $X^2 = 13.17$ ,  $p < .001$ ,  $n = 93$ ; moderate  $X^2 = 82.39$ ,  $p < .001$ ,  $n = 103$ ; light  $X^2 = 110.48$ ,  $p < .001$ ,  $n = 171$ ; none  $X^2 = 32.40$ ,  $p < .001$ ,  $n = 40$ ). Available, open habitat for *P. barbatus* to colonize varied from 41.9 % of a replicate in ungrazed treatments to 50.0% in heavily grazed and up to 84.3% in lightly grazed treatments (Table 4). Density of nests in open habitat were not significantly different among none, light and heavy grazing levels (Kruskal Wallis = 4.19, d.f. = 2,  $p = 0.12$ ; Table 2). Correlation between amount of open habitat in a treatment replicate and nest density was also not significant (Spearman's  $\rho = 0.44$ ,  $p = 0.38$ ,  $n = 6$ ).

#### ***Area of Nest Impact***

Average diameter of *P. barbatus* nest disks was 1.02 m (0.2 m S.D.), with a mean area of 0.817 m<sup>2</sup>. Total percent surface area of a pasture disturbed by *P. barbatus* disks (using mean disk area) was from 0.02% to 0.06% depending on nest density (Table 4). Percentage of pasture with disk margin vegetation varied from 0.03%, in a low density, heavily grazed pasture to 0.06% in a high density, lightly grazed pasture (Table 4). Percentages of surface areas impacted by foraging is much greater than disk and disk margin percentages. Percentage of the available area of a pasture that is colony foraging area is greatest, 73.6%, in pastures with high nest densities and large mean foraging areas (Table 4).

#### **Discussion**

Ten ant species, five of which were species of harvester ants, occur in the semi-arid savanna of Sonora Research Station. The most conspicuous, *Pogonomyrmex barbatus*, was found throughout the study area but natural heterogeneity of the Sonora Research Station affected both *P. barbatus* density and distribution. Its occurrence was influenced by landscape topography, soil types, and vegetation composition which agrees with previous studies of this species (Mangrum 1954, Whitford and DiMarco 1995, Tabor 1998, Johnson 2000a).



Table 4. Total area of *Pogonomyrmex barbatus* disk margins, disks and foraging areas in heavy, light and none grazing treatments at the Sonora Research Station. Area of open habitat per pasture was obtained from aerial photography, August 2002 and hand classified as open habitat. For a description of the calculations for area of disk margin, disk and foraging area see text.

Grazing Treatmnt	Non- wooded, open habitat (m <sup>2</sup> ) (% of total pasture)	No. of nests	Total disk area (m <sup>2</sup> )	Total disk area in open habitat (%)	Total disk margin area (m <sup>2</sup> )	Total disk margin area in open habitat (%)	Total foraging area (m <sup>2</sup> )	Mean foraging area (m <sup>2</sup> ± S.D)	Total foraging area in open habitat (%)
Heavy	195,240 (60.3)	40	32.7	0.02	56.0	0.03	33,752.0	600.5 ±563.3	17.3
Heavy	175,851 (54.3)	79	64.5	0.04	110.6	0.06	47,439.5	843.8 ±1404.7	27
Light	136,444 (84.3)	98	80.1	0.06	225.4	0.16	100,401.0	1024.5 ±1080.6	73.6
Light	136,444 (78.0)	85	69.4	0.05	195.5	0.14	32,478.5	382.1 ±470.9	23.8
None	47,988 (41.9)	27	22.1	0.05	62.1	0.13	23,889.6	884.8 ±1450.4	49.8
None	57,166 (49.9)	21	17.2	0.03	48.3	0.08	10,271.1	489.1 ±1159.2	18

*Pogonomyrmex barbatus* densities are effected by the amount of woody cover because they do not tolerate living under woody canopies (McCook 1880, Mangrum 1954). Nests were never found directly under trees although several nests were found just outside the canopy. In one instance a colony was found in open habitat approximately 6 m away from the edge of the oak motte where it had been observed six months before. Presumably it moved to escape the canopy cover. Woody cover is probably avoided because the temperature under canopies is cooler throughout the day and *Pogonomyrmex* workers reduce foraging behavior leading to lower food intake (Holldobler and Wilson 1990, Romey 2001). Additionally, founding queens may not select shaded areas to start a colony or may have greater survivorship in open areas (Johnson 2000a). Nagel and Rettenmeyer (1973) and DeMers (1993) found new colonies of *Pogonomyrmex occidentalis* only on bare, unvegetated soil and none under trees or shrubs.

Heterogeneity caused by land use indirectly affects *P. barbatus* density because suppression of fire increases woody cover of *Juniperus* and *Quercus* species (Smeins and Merrill 1988, Fuhlendorf et al. 2001). As woody cover increases the amount of available habitat is reduced for this species, thus only grasslands are occupied.

Nevertheless, *P. barbatus* are patchily distributed across available habitat so other factors affect where they occur. Results show that nests are restricted to relatively flat topography (< 8% slope). The ungrazed treatment had similar topography to all other treatments, however, more nests were found on steeper slopes in this treatment relative to the grazed treatments. Although colonies prefer flat topography, they may be restricted to open habitat with slightly steeper slopes than open habitat in grazed treatments due to the high percent cover of woody canopy in the ungrazed treatment (54.1%).

*Pogonomyrmex* dig nests up to 20 m deep and presumably need relatively deep soils to accommodate such large nests (McCook 1880, Tabor 1998, Gordon 1999). At the Sonora Research Station, where nearly all surface soils are less than 0.3 m deep, *P. barbatus* colonies find it difficult to create large nests. Instead, they apparently are able to make nests in soil found in rock cracks which extend vertically and horizontally into bedrock (USDA

1986, Woodruff 1996). An aggregation of 15 nests  $\text{ha}^{-1}$  was found in a replicate of the heavy grazing treatment with soils 20 to 35 cm deep. Densities of nests are approximately 30  $\text{ha}^{-1}$  where nests have been excavated to six meters (Gordon 1999) and McCook (1880) describes nests “... in vast numbers, within a few paces of one another.” where he excavated nests to two meters in depth. Perhaps greater densities of colonies would occur on the Sonora Research Station if there were deeper soils.

There is a high relationship between soil parent material and soil type, however, soils derived from Buda and Edwards limestone are mixed within a few meters. Colony number was high on Buda limestone parent material in an area which was high in Buda limestone. Numbers on Edwards limestone show the same pattern. Both limestones are fractured which is probably the important variable in determining presence of nests because where there are suitably deep cracks, with some soil, colonies can likely occupy these soils. Further study of this variable and its affect on the distribution of *P. barbatus* colonies is needed.

*Pogonomyrmex barbatus* rarely occur in clay soils with few rock fragments on the Sonora Research Station, which is similar to other parts of this species' range where it is restricted to soils with some clay content, or to clays with coarse, rock fragments (Tabor 1998, Johnson 2000a). The closely-related species, *P. rugosus*, is also found in coarse, rocky soils (Johnson 1992). In this study *P. barbatus* occurred in stony clay and clay loam soils. Deep clay soils with few rock fragments may create conditions unsuitable for colonies. Rock fragments in soils increase drainage, infiltration rates and rocks on the surface increase soil temperatures (Munn et al. 1987). Draining water off the nest appears to be important. For example, a few nests were observed with conical nest disks at least 0.25 m high. These nests were near small washes that periodically carry water over the nests. Perhaps producing this slope helps drain water off their disk and away from the nest entrance. Although soils are rocky and shallow with little soil volume to create a nest, colonies may take advantage of the affects of rock fragments which create better habitat conditions in the predominantly clay loams of the study site. Soil type and the fractures in parent material are an important determinant in the location and density of nests.

Lack of correlation between amount of available habitat in a pasture and density of nests may indicate that as woody cover encroaches, harvester ants can crowd into remaining open habitat.. This species tends toward regular spatial arrangement caused by interference between workers of neighboring colonies and adults interfere with juvenile establishment (Holldobler 1976, Gordon 1995, 1999). Using a simulation model of *P. barbatus* demography Johnson (2000b) predicted random spatial patterns among nests at low densities and as populations increased less regular dispersion patterns could occur. Low population density could account for the results of the present study. The density of *P. barbatus* on the Sonora Research Station is lower than other regions where interference may be more important. Instead, at the Sonora Research Station natural heterogeneity factors of slope and soils may be more critical to distribution and abundance.

The disturbance created by cleared areas on nest disks has very little effect on overall loss of vegetation at the Sonora Research Station and impacts less than 1% of the surface of pastures. Losses are compensated by the addition of disk margins with their greater basal and foliar cover of grasses compared to surrounding areas (Table 4). Although compensation by disk margins is less in the heavy grazed treatment because area of the disk margin was 1.4 m<sup>2</sup> while it was 2.3 m<sup>2</sup> in light and ungrazed treatments which is 1.6 times greater than the disk margins at heavily grazed.

In contrast, potential seed losses from foraging areas could greatly diminish seed bank populations for potential seedlings. Large surface areas, 17.3-73.6%, of the grassland community could be impacted depending on nest density and the size of colony foraging areas.

At the landscape scale *P. barbatus* is distributed in open habitats and on mostly flat topography ranging from 0 to 5% slope. Further, their densities may be affected by soil depth as indicated by the higher densities found on a deeper soils patch. Further tests of this hypothesis are needed to determine the importance of soil depth to colony occurrence. They are found in Eckrant, Prade-Eckrant and Tarrant-Eckrant soils, but avoid the deep clays of Valera. Distribution and area of cracks in the limestone parent material, although not

directly measured, must be important to the maintenance of this species on the shallow soils of the Sonora Research Station. Additionally, colonies avoid streambeds, large rock slabs and temporary ponds. Highest nest frequencies were found on Eckrant soils. Densities are unaffected by long-term historical grazing intensity. Large-scale patterns due to variety among woody cover, soil type and topography cause local *P. barbatus* density to differ across the Sonora Research Station. Thus, harvester ant effects on grassland communities and their role in the function of savanna ecosystems depend on colonies' location in the landscape and their density at the local scale.

## CHAPTER III

### SPATIAL AND TEMPORAL INFLUENCES OF HARVESTER ANT NESTS

#### Introduction

The importance of ants as agents of soil change is well documented. Their patches of unique soils often increase biodiversity and plant performance (MacMahon et al. 2000). Within the genus *Pogonomyrmex* there are several species that create approximately one-meter diameter, bare soil disks by clearing all vegetation (Rissing 1988, Whitford and DiMarco 1995, Wagner et al. 1997, MacMahon et al. 2000). Plants on the disk margin, however, tend to be larger and produce more seeds than surrounding habitats (Golley and Gentry 1964, Wight and Nichols 1966, Rissing 1986, Whitford 1988, Soule and Knapp 1996). Vegetation composition often differs from adjacent areas; shrub and perennial dicot richness is lower while grass is higher (Rissing 1986, Soule and Knapp 1996, Lei 1999). Most studies of the vegetation at the edge of disks focus on structure and mechanisms of establishment and often conclude that viable seeds rejected from storage granaries are the primary seed source. However they arrived, the disk and the plants at its margin are a unique patch and, according to patch theory, may affect larger scale dynamics of surrounding vegetation.

Prior to European settlement natural herbivory, periodic fires and weather variability were major driving factors in maintaining the liveoak savanna parkland of the Edwards Plateau of Texas. Suppression of fire, demise of large, free-roaming herbivores and introduction of confined, grazing by livestock transformed the structure of these parklands (Amos and Gehlbach 1988, Smeins and Merrill 1988, Fuhlendorf and Smeins 1997, Knapp 1998). Nevertheless, droughts remain a strong driver in community structure. For many communities, populations and individuals to survive droughts, they must have physiological adaptations or find refuge from the disturbance (Clements 1934, Jacobsen and Kleynhans

1993, Magoulick and Kobza 2003, Fritz and Dodds 2004, Shackelford 2004). By being in a refugia, a place where negative effects of drought are lower than surrounding areas, organisms can avoid the effects of drought (Lancaster and Belyea 1997).

In addition to these ubiquitous large-scale impacts of fire, herbivory, and weather variation, smaller scale phenomena caused by small mammals, birds and insects can influence the composition, structure and patch dynamics of these ecosystems (Collins and Barber 1985, Whiticker and Detling 1988, Cloudsley-Thompson 1996, Carson and Root 1999). *Pogonomyrmex* disks and nests are unique patches in terms of soil chemistry, texture, moisture, and mycorrhizal communities compared to surrounding soils (Carlson and Whitford 1991, McGinley et al. 1994, Whitford and DiMarco 1995, Carson and Root 1999, MacMahon et al. 2000, Boulton et al. 2003). As a result, ant colonies produce patches of differing resource availability for plants. Therefore, vegetation on the disk margin deviates in structure and composition, and could respond differently to disturbances than nearby areas. Droughts remain a strong driver in community structure.

The aim of this study was to understand whether small-scale processes due to *Pogonomyrmex barbatus* nest construction, can interact with large herbivore grazing and weather variation to affect community composition and structure and potential for recovery following drought. A study was designed to assess the influence of *P. barbatus* on vegetation structure and dynamics by comparing disk margins with adjacent habitats during and following a severe drought to address the following hypotheses:

- (1) perennial and annual grass and dicot species composition, density and cover are comparable between disk margins and adjacent vegetation in long-term (approximately 50 years) ungrazed, light and heavily grazed pastures now recovering from a recent drought,
- (2) water infiltration rates are similar on disks, disk margins and away from the disk.,
- (3) after drought, seedling distributions will be aggregated near nests.

## Materials and Methods

### Study Area

The study was conducted at the Texas A&M University Agricultural Research Station (elevation 735 m), Edwards Plateau, Texas (31°18'N; 100°28'W). Vegetation is potentially a mixed-grass, savanna parkland dominated by groves of *Quercus virginiana*, *Q. pungens* var. *vaseyana*, *Juniperus ashei* and *J. pinchotii* in a matrix of mid- and short-grass species. Grassland at the study site is dominated by the grasses *Bouteloua curtipendula*, *Stipa leucotricha*, *Hilaria belangeri*, and *Bouteloua trifida*.

The grassland community is noted for its heterogeneity due to its shallow, rocky limestone-derived soils (Fuhlendorf and Smeins 1998). The study area has been partitioned into three herbivory treatments that were heavily grazed (5.4 ha/AUY; One AUY is the yearly demand rate of oven-dry forage for an animal at 12 kg/day (Glossary Update Task Group, 1988), lightly grazed (16.2 ha/AUY) or ungrazed by livestock from 1948 until 1969. Since 1969 the heavily grazed treatments were changed to light levels. The ungrazed treatment has been continually protected from domestic herbivory since 1948.

The climate is continental and semi-arid with a bimodal distribution (peaks in May and September) of growing season rainfall. Average annual precipitation (1919-2003) is 57.5 cm, but variability between years is great with a range of 35.7 cm and standard deviation of 5.1 cm (Station Records). Station records (within 3 km of study sites) were used to create a Palmer drought severity index (Palmer 1965, Shackelford 2004) for a drought that began with low growing season rainfall in 1997 (Figure 5). It continued with a general pattern of surplus moisture ( $> 1.0$  PDSI) during the winter and deficit moisture ( $< -1.0$  PDSI) during the summer. Although increased rainfall occurred in 1999 little plant recovery occurred (Shackelford 2004). The drought ended July 2002 with a return to above normal precipitation during the growing season that continued into 2003 (Figure 5).

### Methods

To examine the impact of red harvester ant nests on drought recovery in the herbaceous community, sixty established nests were marked and divided among one



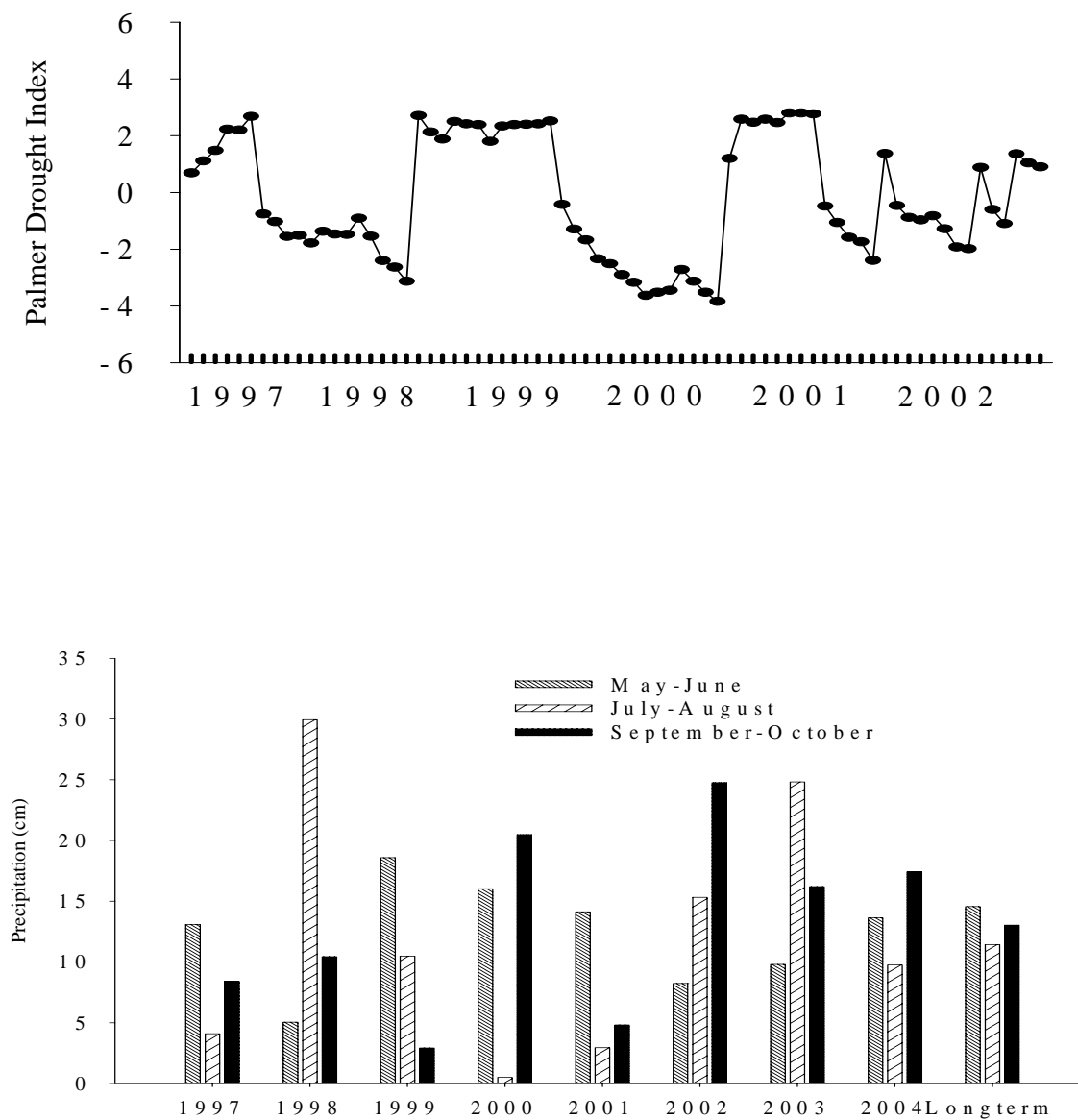


Figure 5. Total monthly precipitation during the growing season for 1997-2004 compared to the long-term average for 1916-1996 at the Sonora Research Station (Station Records). Monthly Palmer drought severity index values for 1997-2002 (Reprinted with permission from Shackelford 2004).

replication each of heavily grazed, lightly grazed or ungrazed treatments. Data were collected at three sampling dates; June 2002, the last month of drought, October 2002, three months after normal rainfall returned, and August 2003, one year later.

All vegetation was recorded on ant disks using a circular quadrat covering the cleared disk and all of its margin. Data were collected in concentric rings 15 cm wide, starting from the nest entrance to 105 cm. Vegetation was also sampled 3 m from the edge of the disk in two random cardinal directions with a 0.50 X 0.50 m quadrat. Vegetation was not sampled under woody plants or in rock outcrops to control for vegetation varying markedly from the herbaceous community at ant nests.

Data collected for each grass species were: number  $\text{m}^{-2}$ , number of inflorescences  $\text{plant}^{-1}$ , percent basal and aerial cover. Data collected for perennial and annual dicots were number  $\text{m}^{-2}$  and percent aerial cover.

Data from 15 cm concentric rings that encompassed the disk margin were grouped together for analysis. Preliminary analysis indicated that disks in heavy grazed treatment consisted of two 15 cm concentric rings (30 cm wide) and disks in light grazed and ungrazed consisted of three 15 cm concentric rings (45 cm wide). The data were pooled within the two or three concentric rings and the resulting area was called the disk margin. Area of the disk margin was 2.3  $\text{m}^2$  in light and ungrazed treatments, and 1.4  $\text{m}^2$  in the heavy grazed. Area of the samples collected 3 m away from the disk was 0.50  $\text{m}^2$  consisting of two 0.25  $\text{m}^2$  samples. Species of grasses sampled were grouped into grazing tolerant, early-successional, species, or grazing intolerant, mid to late-successional species (Figure 6) (Smeins and Merrill 1988, Fuhlendorf and Smeins 1997).

All sample data were converted to  $\text{m}^2$  values for analyses. Data for all grass and dicot variables were non-normal and the variances among factors were unequal. Analyses on perennial grass density were performed on square root transformation and analyses of percent basal cover were performed on logarithmically transformed data. To compare vegetation on the nest margin versus away, a two-way treatment in a randomized complete block design analysis of variance was conducted (Zar 1996). Grazing treatment was not

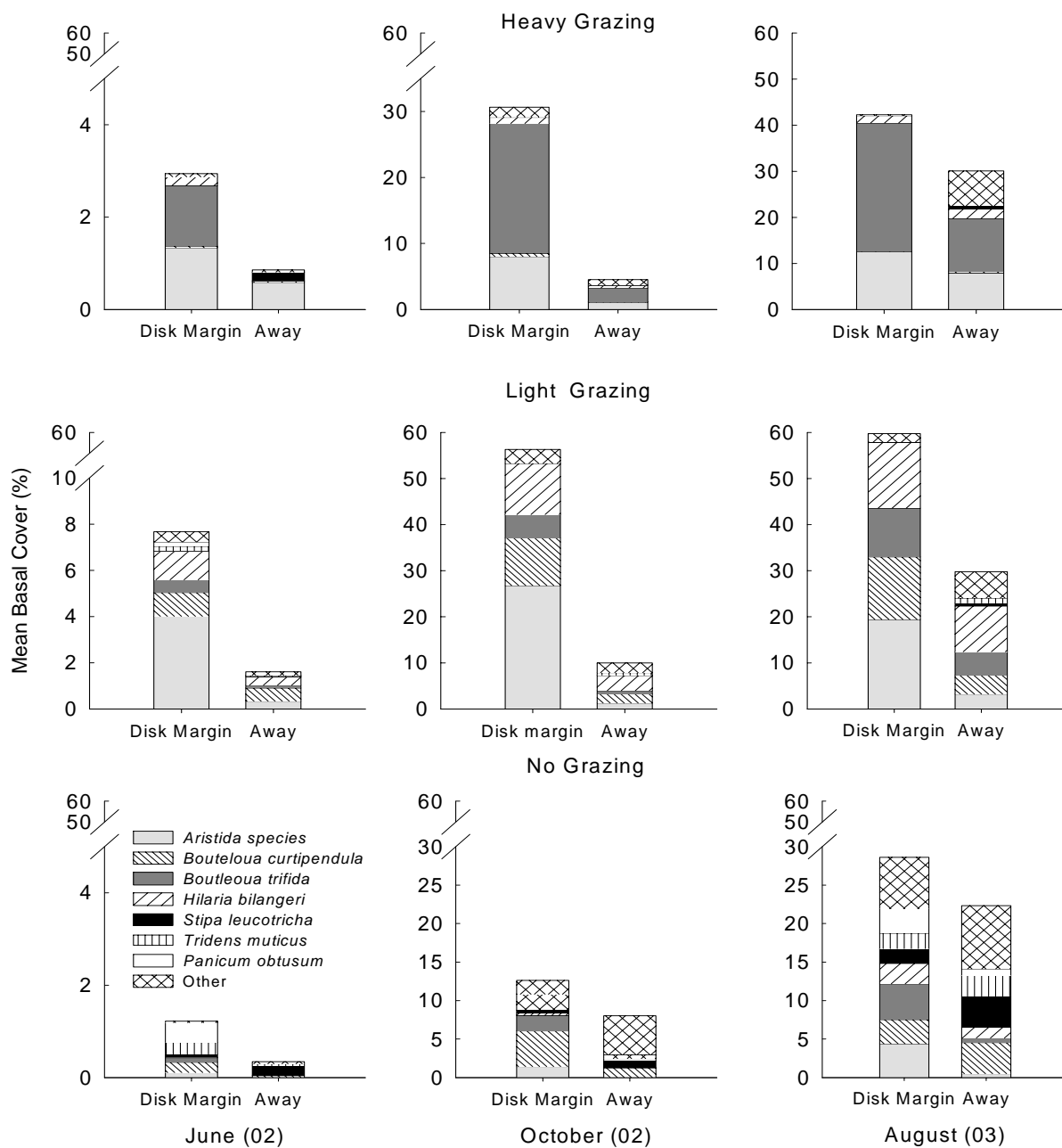


Figure 6. Mean basal cover of grass species in heavy, light and no grazing treatments, at disk margins compared to away, during (June 2002) and after drought (October 2002 and August 2003) at the Sonora Research Station. NOTE: break point in each graph scale varies.

replicated, therefore treatment was analyzed as a block effect. Distributions of data for grass aerial cover, number of inflorescences, perennial dicot cover and density were highly skewed even after transformations, therefore, a two-way treatment in a completely randomized design nonparametric analysis of variance was conducted (Scheirer-Ray-Hare) (Dytham 1999). Non-replicated grazing treatments prevented a statistical analysis for these variables.

### ***Infiltration Rate Methods***

Water infiltration rates were compared in January 2002 at ten nests randomly chosen in a pasture of deferred rotational grazing (moderate level) with no surface rocks, on Tarrant-Eckrant soils, with slopes of 0-1% (USDA 1982, Loomis 2003). Weather conditions were cool and dry with minimal evaporation and nearly dry soils. Three samples were taken at three locations at a nest; at the disk center, the disk margin and 3 m away from the nest where there was sufficient soil to conduct the study for a total of 9 samples per nest.

A metal ring was installed to measure the water infiltration rate in each sample site (Bouwer 1986). The ring, 15 cm in diameter and 18 cm tall, was placed into the soil to a depth of approximately 3 cm. Water was added to the ring to a depth of 18 cm. Infiltration rates were measured every 3 cm until water completely disappeared at the bottom of the ring (12 cm). Water was gently added to dry soils so that no splash effects would occur. Depth to bedrock or large boulders impacts infiltration rate, thus soil depth at each sample site was collected after the tests were completed using a 1 cm diameter bar sharpened at the end.

Analysis on infiltration rate ( $\text{cm}^3/\text{minute}^{-1}$ ) was performed on logarithmically transformed data. Soil depth was used as a covariate in the analyses. To improve numerical accuracy all data were standardized as a z-score. A two-way treatment in a completely randomized design analysis of covariance (ANCOVA) was conducted to compare infiltration rate on the disk, disk margin and away and at four 3 cm time intervals (Zar 1996).

### ***Seedling Spatial Patterns***

One randomly located transect, 1 km long and 15 cm wide, was surveyed for

numbers of grass seedlings in two lightly grazed pastures in July 2004, one year after the drought ended. Total number of grass seedlings were recorded every 15 cm in a 225 cm<sup>2</sup> square along the transect for *Aristida* species, *Bouteloua curtipendula*, *Hilaria belangeri*, *Stipa leucotricha* and *Bouteloua trifida*. At every square presence or absence of nest disk was recorded. Seedlings from seed were counted, however, counts of *H. belangeri* and *S. leucotricha* could be overestimated due to the difficulty of distinguishing between seedlings from seed and from tillering in these species.

Spatial pattern of count data were estimated from the Ripley's K statistic (Ripley 1981);

$$L(t) = n^{-2} A \sum \sum w_{ij}^{-1} I_t(u_{ij})$$

where  $L(t)$  = average number of grass seedlings within distance “t” of a disk along the transect

$n$  = number of plants along the transect

$A$  = length of the transect

$I_t$  = number of samples

$u_{ij}$  = distance between individual plants  $i$  and  $j$

$w_{ij}$  = weighing factor for edge effects at the ends of the transect

$L(t)$  was calculated every 15 cm for distances beginning with  $t = 15$  cm to  $t = 30$  m. Ripley's K spatial statistic was used because it allows spatial patterns to be analyzed at all scales of interest. The spatial pattern of seedling establishment in relation to *P. barbatus* nests may be scale-dependant, with seedlings establishing near nests at small scales but randomly distributed through the pasture at larger scales. The distribution of grass seedlings and *P. barbatus* nests were 1-dimensional because the swath width (15 cm) was very small compared to the transect length (1 km) (O'Driscoll 1998). The distribution of seedlings was tested by comparing the average counts to a distribution created from 100 Monte Carlo results of the number of seedlings.

## Results

In all grazing treatments, grasses on disk margins had significantly greater basal and

aerial cover relative to away areas (Tables 5, 6 and 7). Generally, the number of inflorescences per plant were significantly higher on disk margins compared to away (Tables 5 and 6). In contrast, away areas had significantly higher densities of grass relative to disk margins (Tables 5 and 7) resulting in more small plants away and fewer large plants on the disk margin.

While, in general, all grass variables increased after the drought ended, this varied between disk margin and away, as indicated by the significant interactions in basal cover and density (Table 7, Figure 6). No significant interactions were detected for number of inflorescences and aerial cover (Table 6), although they appear to occur (Figure 6). Interactions preclude main effects comparisons.

The proportion of grazing tolerant, early-successional, species was highest in heavily grazed treatments and lowest in ungrazed, while in contrast the ungrazed treatment was dominated by grazing intolerant, mid to late-successional species (Figure 6). Significantly greater basal cover and density occurred in the grazed treatments (light and heavy) compared to the ungrazed treatment (Tables 5 and 7). Treatment differences were not analyzed for grass aerial cover and number of inflorescences due to their skewed distributions, however, they are moderately correlated with basal cover (Spearman's  $\rho = 0.77$  and  $0.55$ , respectively), which had significant treatment differences, thus aerial cover and number of inflorescences may also be significantly different among treatments. During drought, grass density was 11.4 and 7.7 in heavy, 23.7 and 22.2 in light and 4.3 and 12.5 in ungrazed treatments on disk margin and on away, respectively. However, during recovery density was always higher away compared to disk margins regardless of grazing treatment (Table 5).

By comparing average basal cover among recovery periods and initial average basal cover (measured during drought) ratios could be used to compare relative rate of recovery. Recovery was greatest in ungrazed areas with an increase in October 2002 of 1:10 and in August 2003 of 1:32. Lower rates occurred in light herbivory during corresponding dates (October 2002 1:6; August 2003 1:10), and least in heavy herbivory (October 2002 1:5),

Table 5. Mean (95% C.I.) perennial grass basal cover (%), aerial cover (%), density (number m<sup>-2</sup>), and number of inflorescences plant<sup>-1</sup>, before and after drought, in heavy, light and no grazing treatments, at *Pogonomyrmex barbatus* disk margin and at 3 m away. n=20 nests in June, 2002 15 in October, 2002 and 18 in August, 2003.

Variable Grazing Trtmnt	6/2002 Drought		10/2002 Recovery		8/2003 Recovery	
	Disk Margin	Away	Disk Margin	Away	Disk Margin	Away
Basal Cover						
Heavy	2.95 (0.54)	0.66 (0.20)	30.67 (5.22)	4.53 (0.60)	44.35 (7.36)	30.07 (2.53)
Light	7.48 (0.88)	1.57 (0.15)	55.67 (6.20)	9.52 (0.63)	59.74 (5.42)	29.78 (1.79)
None	1.24 (0.08)	0.35 (0.06)	12.43 (0.97)	8.40 (0.54)	28.60 (0.80)	22.32 (0.74)
Aerial Cover						
Heavy	2.97 (0.79)	1.08 (0.33)	23.57 (4.58)	9.50 (1.26)	111.25 (18.89)	63.19 (6.37)
Light	10.95 (1.31)	3.23 (0.27)	49.82 (3.81)	22.73 (1.30)	126.92 (12.18)	62.00 (3.09)
None	1.22 (0.13)	0.71 (0.08)	44.36 (6.05)	17.43 (1.01)	76.24 (2.16)	57.50 (1.93)
Density						
Heavy	11.38 (2.80)	7.70 (1.81)	22.34 (5.54)	39.73 (5.41)	61.19 (12.39)	73.04 (8.14)
Light	23.65 (2.21)	22.20 (2.04)	26.52 (2.57)	48.42 (4.75)	63.16 (5.97)	74.77 (8.37)
None	4.28 (0.30)	12.47 (1.31)	9.47 (0.54)	28.29 (2.02)	36.27 (1.18)	49.11 (1.58)
Inflorescence plant <sup>-1</sup>						
Heavy	2.55 (1.88)	1.30 (1.25)	9.53 (1.83)	5.67 (0.94)	--	--
Light	23.85 (6.05)	14.35 (3.05)	19.51 (1.65)	19.21 (0.82)	--	--
None	1.88 (0.53)	1.12 (0.04)	12.50 (1.93)	15.96 (0.90)	--	--

Table 6. Effects of the margin of *Pogonomyrmex barbatus* disks and drought on perennial grass variables using Sheirer-Ray-Hare tests. Number of inflorescences not collected in August 2003. P-values are from the chi-square distribution. n=20 nests in June, 15 in October 2002, and 18 in August 2003.

Source of Variation	df	Aerial Cover (%)		Number of Inflorescences plant <sup>-1</sup>	
		SS	SS/MS Total	SS	SS/MS Total <sup>1</sup>
Disk Margin (DM)	1	59902.64	14.90***	1381.18	4.02*
Before & After Drought (D)	2	185892.78	46.22***	2647.30	7.70**
Interaction (DM x D)	2	4930.44	1.23	175.71	0.51
Error	313	614856.76	152.89	37891.78	110.26

\* p = .05; \*\* p = .005; \*\*\* p < .001

1 d.f. = 1 for all sources of variation and error is 216



Table 7. Results of ANOVA tests on the effects of grazing treatments, before and after drought, and *Pogonomyrmex barbatus* disk margin on perennial grass variables. Treatment was block in the two-way treatment in a randomized complete block design. Data are normal, but variances are slightly unequal ( $p = .03$ ).  $n=20$  nests in June, 15 in October 2002, and 18 in August 2003.

Source of Variation	Basal Cover (%)			Density (Number m <sup>-2</sup> )	
	df	MS	F	MS	F
Disk Margin (DM)	1	10.065	94.70***	27.27	20.27***
Before & After Drought (D)	2	36.99	348.01***	187.41	137.12***
Herbivory Treatment	2	5.01	47.12***	42.42	31.03***
Interaction (DM x D)	2	1.08	10.18***	4.26	3.11**
Error	331	0.11		1.371	

\*\*  $p = .004$ ; \*\*\*  $p < .001$

1 d.f. = 313

The dependant variables are estimated numbers of basal cover ( $\log_{10}(X + 1)$ ) and density ( $\sqrt{X + .01}$ ).

except in August 2003 where heavy treatment was higher than light (1:20). *Bouteloua trifida* and *Bouteloua curtipendula* showed the greatest response in all three grazing treatments (Figure 7, Table 8). *Hilaria belangeri* was third; responding well in the ungrazed treatment. Fastest recovery occurred in the no grazing treatment exhibited by all three species having the highest ratios in this treatment (Table 8).

Cover and density of annual dicots were highly affected by season (Table 9). Cool season annuals made up the majority of plants during the drought because there was sufficient winter rainfall for their emergence. Large numbers of annual dicot seedlings emerged after the drought, blanketing the study area. In all grazing treatments, dicots had significantly greater density and cover away from disks relative to disk margins (Tables 9 and 10). Any perennial dicot that survived the drought was usually found away from the disk (Table 9), while, in general, perennial dicot density and cover increased after the drought, this varied between disk margin and away, as indicated by the significant interactions (Table 10).

### ***Infiltration Rates***

*Pogonomyrmex barbatus* disks had significantly greater infiltration rates compared to disk margins and away areas ( $F = 6.35$ , d.f. = 2,  $p = .002$ ; Figure 8). The decline in infiltration rates as water penetrated the soil was typical of water infiltration rates recorded for dry soils (White 1997) and was potentially due to the slowly permeable nature of Tarrant-Eckrant soils ( $F = 6.27$ , d.f. = 3,  $p < .001$ ). No significant interaction was detected between nest area and the soil depth covariate.

### ***Seedling Spatial Patterns***

The spatial distribution of seedling numbers in relation to *P. barbatus* nests were compared with Monte Carlo distributions of seedling and nest counts. Random distribution of grasses in 1-dimensional space was calculated with a bivariate Ripley's  $K(t) = 2t$  where  $t$  was the spatial distance of interest from the nest (O'Driscoll 1998). If the grass seedlings are clustered with *P. barbatus* nests then  $K(t) > 2t$  and if seedlings are regularly spaced away from nests then  $K(t) < 2t$ .

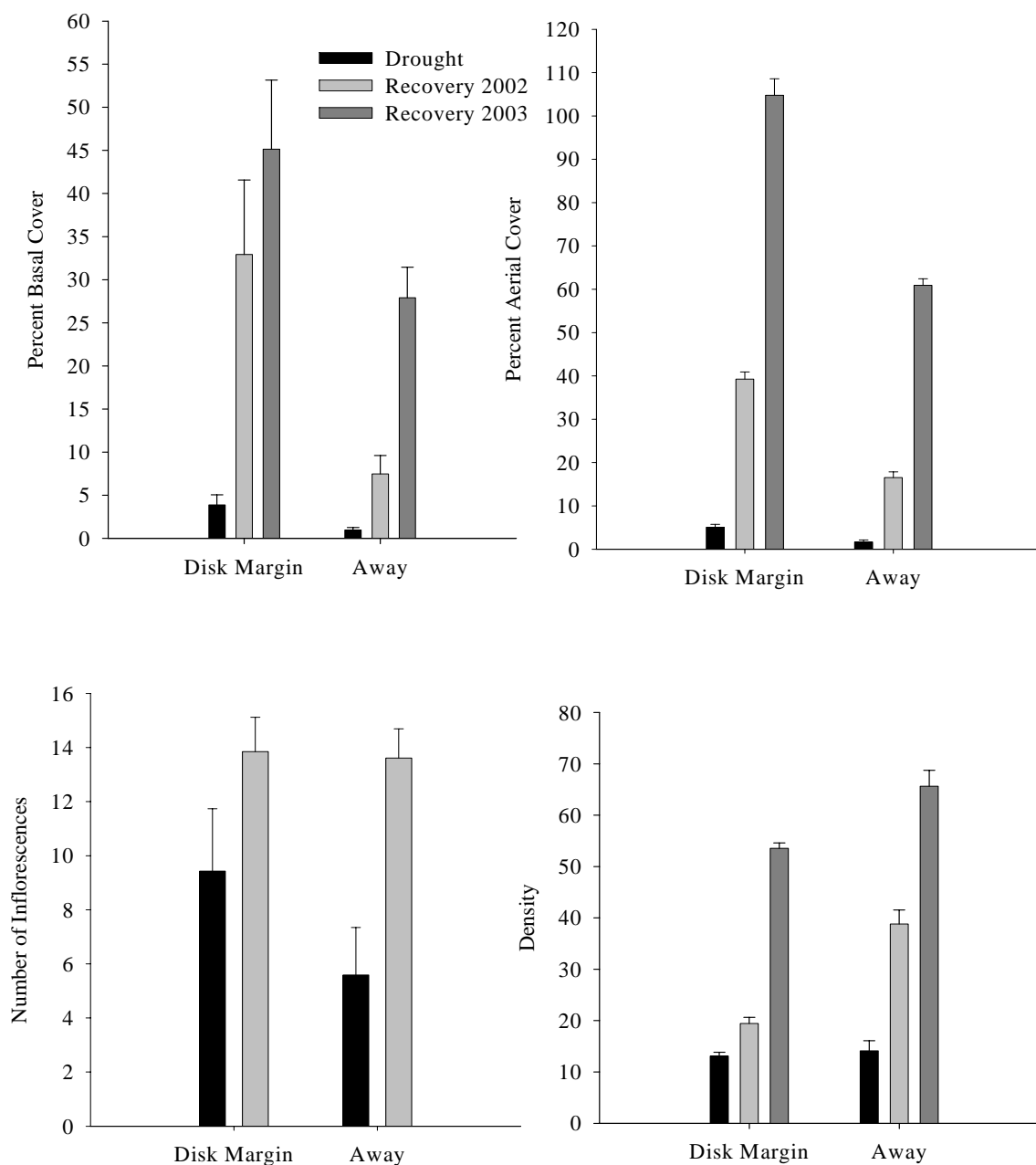


Figure 7. Interactions of perennial grass variables at disk margin compared to away, before and after drought, in pooled grazing treatments at the Sonora Research Station. Number of inflorescences were uncollected in August 2003. Error bars are 95% C.I.

Table 8. Ratios of mean basal cover (%) during drought (June 2002) compared to during recovery (October 2002 and August 2003) for *Bouteloua trifida*, *Hilaria belangeri*, *Bouteloua curtipendula* and the total of the three species at *P. barbatus* disk margins in heavy, light and no grazing treatments at the Sonora Research Station.

	Heavy	Light	None
<i>Bouteloua trifida</i>	1:17:30	1:8:26	1:19:61
<i>Hilaria belangeri</i>	1:7:19	1:9:17	1:32:518
<i>Bouteloua curtipendula</i>	1:11:9	1:8:12	1:23:36
Total of the three species	1:15:28	1:8:17	1:17:56

Table 9. Mean (95% C.I.) perennial and annual forb foliar cover (%) and annual forb density (number m<sup>-2</sup>), before and after drought, in heavy, light and no grazing treatments, at *Pogonomyrmex barbatus* disk margin and at 3 m away. Density data were not collected in October because thousands of seedlings appeared. n = 20 nests in June; 15 in October, 2002 and 18 in August, 2003.

Variable Grazing Trt	6/2002 Drought		10/2002 Recovery		8/2003 Recovery	
	Disk Margin	Away	Disk Margin	Away	Disk Margin	Away
Annual Forb Cover						
Heavy	10.6 (5.72)	11.1 (3.23)	34.0 (8.46)	37.0 (8.09)	0.8 (0.98)	13.7 (3.08)
Light	4.7 (1.41)	6.5 (2.40)	27.9 (6.80)	20.2 (5.06)	0.2 (0.37)	12.0 (4.08)
None	1.1 (0.62)	5.5 (3.82)	25.4 (7.33)	25.4 (7.70)	0.3 (0.37)	1.4 (1.25)
Annual Forb Density						
Heavy	136.1 (42.63)	463.8 (107.78)	—*	--	0.4 (0.36)	28.3 (9.06)
Light	108.2 (34.45)	440.1 (112.17)	--	--	0.1 (0.14)	17.4 (5.99)
None	46.2 (23.00)	271.8 (101.07)	--	--	0.1 (0.23)	4.4 (3.73)
Perennial Forb Cover						
Heavy	0.1 (0.08)	3.4 (3.99)	2.1 (2.78)	12.1 (6.30)	6.2 (5.78)	40.4 (9.75)
Light	0.1 (0.03)	0.8 (1.13)	1.7 (1.29)	7.0 (3.61)	1.1 (1.08)	19.4 (9.05)
None	0.01 (0.02)	0.5 (1.02)	2.9 (3.05)	7.3 (3.98)	3.1 (4.08)	12.1 (6.76)
Perennial Forb Density						
Heavy	0.3 (0.40)	2.2 (1.40)	--	--	1.5 (1.40)	25.4 (9.40)
Light	1.2 (0.90)	1.2 (1.07)	--	--	0.5 (0.61)	8.8 (4.20)
None	0.4 (0.60)	5.9 (4.91)	--	--	0.2 (0.22)	11.7 (7.36)

Table 10. Effects of *Pogonomyrmex barbatus* disk margin and drought on perennial forb variables using Sheirer-Ray-Hare tests. Density uncollected in October 2002. P-values are from the chi-square distribution. n=20 nests in June, 15 in October 2002 and 18 in August 2003.

Source of Variation	df	Perennial Cover (%)		Perennial Density (Number m <sup>-2</sup> )	
		SS	SS/MS Total	SS	SS/MS Total <sup>1</sup>
Disk Margin (DM)	1	15646.37	36.49***	12291	39.00***
Before & After Drought (D)	2	17379.56	40.53***	4743.8	15.05***
Interaction (DM x D)	2	7524.9	17.55***	4643.3	4.74***
Error	313	45404.91	105.9	22750.9	72.2

\*\*\* p < .001

1 df =1 for all sources of variation and error is 216

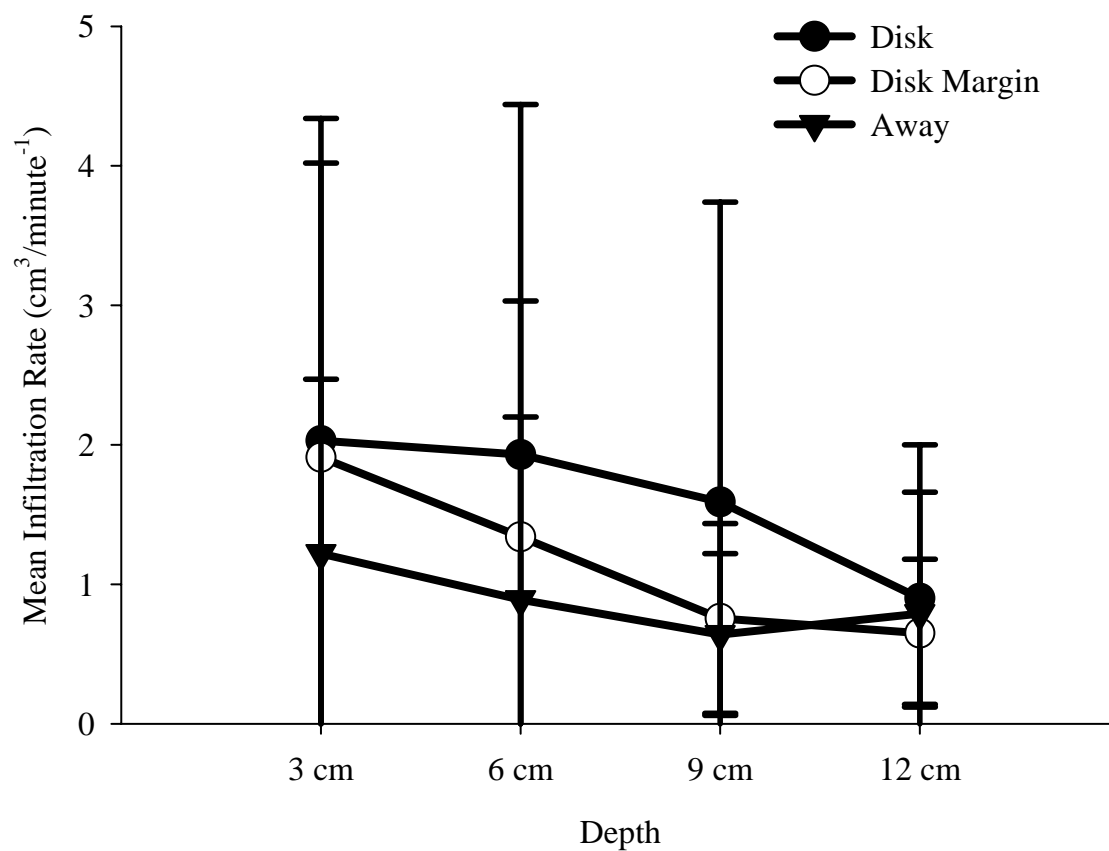


Figure 8. Mean ( $\pm$ S.D.) water infiltration rates (cm/minute) using single-ring infiltrometer at *Pogonomyrmex barbatus* disks, disk margins and away at four water depths 3 cm, 6 cm, 9 cm and final depth at 12 cm. The Sonora Research Station, January 2002. n = 10 nests

Results of the distribution patterns, at various scales, of seedlings compared to *P. barbatus* nests varied among grass species, but generally did not vary between the two pastures. However, seedling counts less than 20 for a pasture transect were not used in the analysis. Clumping between nests and seedlings occurred up to 30 m away from nests for *B. trifida* and *H. belangeri* depending on pasture surveyed (Figures 9 and 10). *B. trifida*, *H. belangeri* and *Aristida* species were clumped near *P. barbatus* nests with first peak clumping occurring at 1.5 m, 2.0 m and 11.5 m respectively (Figures 9 and 10). First peak is considered the maximum between the nest and seedlings while additional peaks may be caused by other processes. A regular pattern of seedlings occurred for *Bouteloua curtipendula* (Figure 9) up to 30 m and a random pattern occurred for *Stipa leucotricha* across all distances from nests (Figure 10).

## Discussion

These results agree with others that vegetation structure and composition often differ between harvester ant disk margins and surrounding vegetation (Costello 1944, Golley and Gentry 1964, Wight and Nichols 1966, Rissing 1986, Whiticker and Detling 1988, Carlson and Whitford 1991, Soule and Knapp 1996, Lei 1999). Perennial grasses had greater basal and aerial cover on disk margins compared to away and perennial dicot cover was lower on disk margins (Golley and Gentry 1964, Wight and Nichols 1966, Rissing 1986, Nowak et al. 1990, Soule and Knapp 1996, Lei 1999). These results suggest that ant nests effects are universally similar, unique patches in many habitat types throughout the ranges of this group of harvester ants.

*Pogonomyrmex barbatus* disk margins are drought refugia. More grasses survive on disk margins during drought (Table 5). Only one instance of a potential refugia maintained by animals is known from termite-created soils around *Acacia aneura* logs (Tongway et al. 1989). The present study shows plant survival is also contingent on species composition because ungrazed treatments consist of larger, late-successional species with deep root



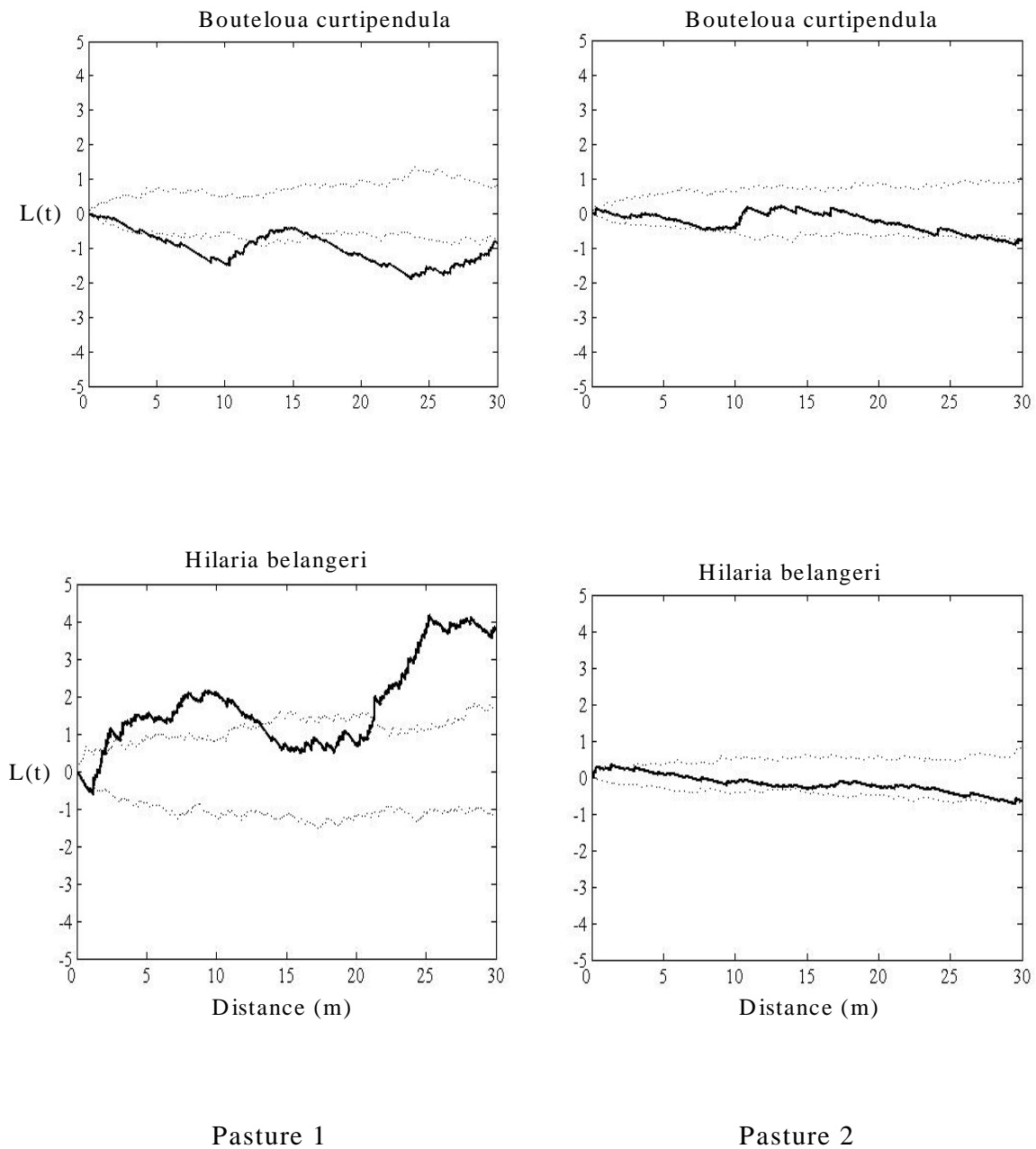


Figure 9. Dispersion pattern between *Bouteloua curtipendula* or *Hilaria belangeri* seedlings and *P. barbatus* nests in replicate pastures. Solid lines are Ripley's K statistical results and dotted lines are Monte Carlo derived 95% confidence limits. Results above C. I. show clumped pattern between seedlings and nests at that distance, results below C. I. show regular pattern and results between C. I. show random.

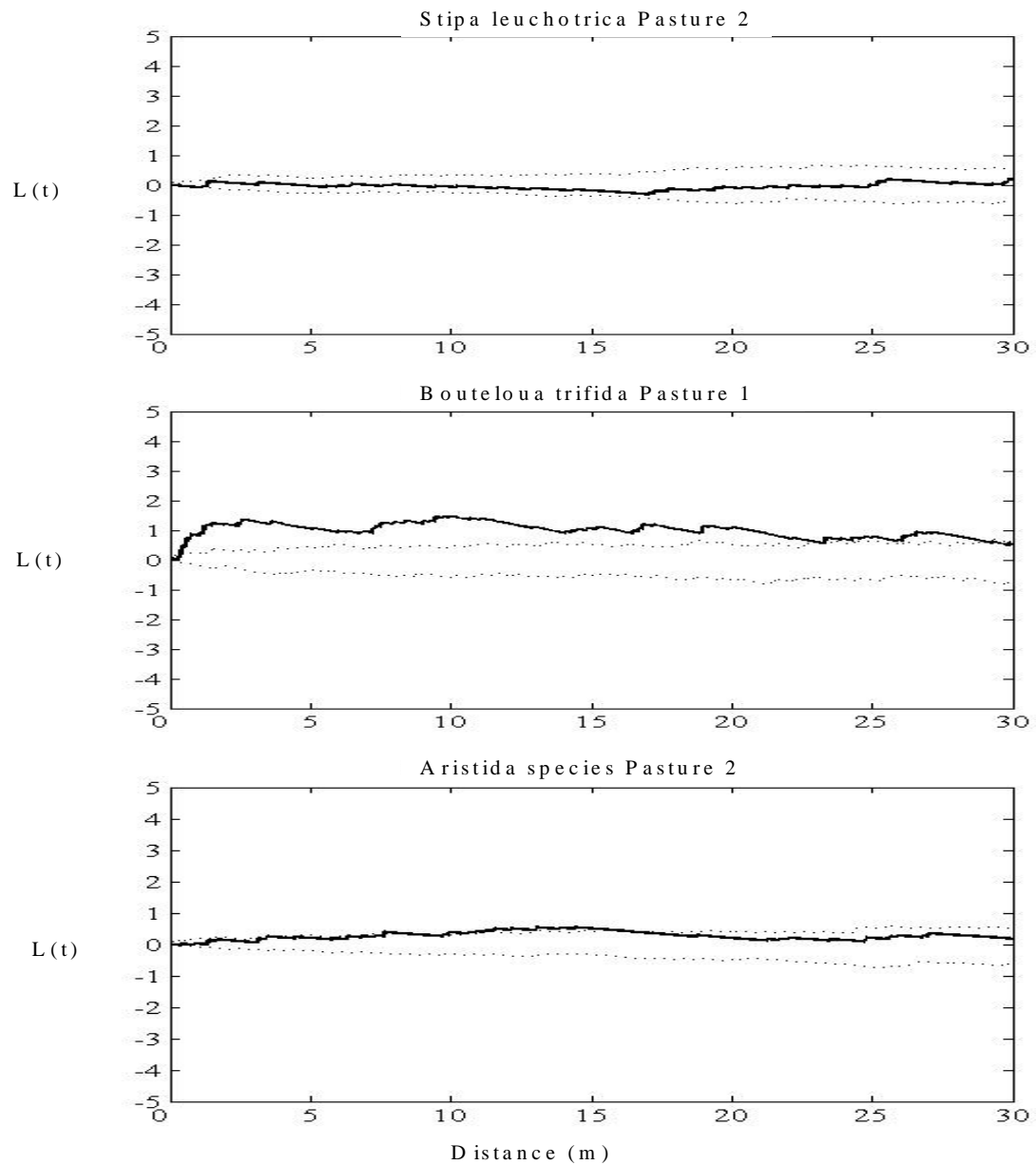


Figure 10. Dispersion pattern between *Stipa leucotricha*, *Bouteloua trifida* or *Aristida* species seedlings. Solid lines are Ripley's K statistical results and dotted lines are Monte Carlo derived 95% confidence limits. Results above C. I. show clumped pattern between seedlings and nests at that distance, results below C. I. show regular pattern and results between C. I. show random. Number of individuals were too small to include in the analyses in both pastures for these species.

systems compared to heavily grazed treatments with smaller, early-successional species often with shallow roots. During drought, larger species maintain themselves by dying back above- ground and sustaining their root systems. During early recovery in the ungrazed treatment, late-successional species returned from their large basal crown, but with only a few new tillers observed, as illustrated by the greater basal cover relative to aerial cover on both margin and away (Table 5). This pattern was exhibited in the grazed treatments, but only on disk margins leading to the hypothesis that all grasses may retain larger root systems on disk margins. Ants may locate nests with deeper soils or at least cracks with soil in them because they need this space for their nests, thus they might choose deeper soils which leads to greater grass production. Moisture could be greater, for a longer period, in nests than away. Whitford and DiMarco (1995) found greater moisture in harvester ant nests than surrounding areas. Additionally, with very little vegetation on the cleared disk moisture may be retained on the disk longer than away areas allowing grasses on the disk margin to forage into the disk and gain more moisture in soil beneath nests than grasses no on the margin. Infiltration rates are a surrogate for moisture availability in soils. The study found that infiltration rates were highest on nest disks but did not differ between disk margin and away, indicating that the moisture the roots are seeking are in the nest. Also that nests can store more water agreeing with studies that show there is greater moisture in harvester ant nests than surrounding soils. If foraging roots aren't clipped by ants maintaining the colony, the nest might provide a patch of higher moisture that allows grasses to survive prolonged droughts longer than grasses in away areas.

Densities were higher away from nests indicating that plant density patterns differ among regions. Individuals are larger on disk margins (Table 5) than away so there are fewer, but larger grasses on the margin. Conversely, there are higher numbers of smaller individual grasses in away areas.

Other studies have shown that species composition, both grasses and dicots, differs between harvester ant disks and the surrounding habitat (Costello 1944, Rissing 1986, Carlson and Whitford 1991, Lei 1999). Previous studies found occurrence among some

species significantly greater on disk margins but generally dicots occurred less often. The present study found species composition unvarying between the margin and away. Instead, composition on the disk reflects past grazing history. The suite of species available for recruitment to the disk margin following drought is determined by the larger-scale disturbance regime of the region. Research with other ant genera, as well as harvester ants, found that disturbances such as fire, flooding, agricultural practices and heavy grazing outweigh disk or nest effects in terms of species composition (Wight and Nichols 1966, Carlson and Whitford 1991, Lewis et al. 1991, Folgarait et al. 2002).

During drought, annual and perennial dicot cover and density were significantly lower on disk margins compared to away in nearly all grazing treatments (Table 5). These findings are supported by other studies on harvester ant disks (Nowak et al. 1990, Whitford and DiMarco 1995, Soule and Knapp 1996, Lei 1999). Nowak et al. (1990) also observed no differences in annual dicot size or density. However during recovery, October 2002, results were similar because fall, annual dicot seedlings blanketed nearly 75% of the ground surface regardless of nest area or grazing treatment. Perhaps pulses of rainfall that cause synchronous germination of common annual dicots may account for these observations. During recovery (October 2002 and August 2003) perennial dicots were significantly higher away compared to disk margins (Table 5). This difference was least in the ungrazed treatment probably due to the overall better conditions of the treatment; perhaps ant disks do not provide differentially better resources for dicots.

Vegetation composition could influence the rate of recovery due to larger, late-successional species recovering faster and conditions being better in ungrazed treatments. For example, both the short-grass, *B. trifida*, and mid-grass, *B. curtipendula*, recovered faster in ungrazed than the heavy grazed. Although grasses in the ungrazed treatment recovered faster than either of the grazing treatments, absolute means of basal cover remained lower than the grazed treatments. In semi-arid savannas, *Juniperus* cover is known to reduce biomass and basal cover of herbaceous vegetation under shrubs (Armentrout and Peiper 1988, Fuhlendorf et al. 1997, Yager and Smeins 1999) and up to 7 m away from

canopy edges (Dye II et al. 1995, Breshears et al. 1997a, Breshears et al. 1997b). Dye II et al. (1995) found herbaceous biomass was significantly reduced away from *Juniperus* canopies in shallow soils where both shrub and grass roots may be competing for resources. Since the canopy cover of woody plants in the ungrazed treatment were high (Chapter II), data were divided between disks in the shade of woody vegetation (40%) and those in sunny locations (60%) because species composition varied. Only five nests were shaded in the heavy treatment and did not vary in composition, and no nests were shaded in the lightly grazed treatment therefore these two treatments were left combined. Differences between the cover of grasses in woody compared to sunny locations were low. In summary, the ungrazed treatment has few, but large grasses due to the greater diversity of late-successional species. During drought its composition leads to greater above-ground die-back with perhaps greater below-ground persistence thus leading to faster recovery when the drought ends. Nevertheless, high *Juniperus* cover may constrain the grasses from achieving greater biomass.

Seedling establishment by *Hilaria belangeri*, *Bouteloua trifida* and *Aristida* species were clumped with *P. barbatus* nests indicating that individuals surviving in disk margins may be the source of recovery immediately after the drought ended. The pattern occurred up to 30 m from nests indicating that seedling establishment from adults at nests may be important for establishing these species in larger areas of disturbance than just near the nest. Alternatively, seedling establishment may occur at safe sites that are located near their parents, and this may be the same habitat as nest sites (Harper 1977).

During droughts, grasses are able to persist and express greater vigor on harvester ant disk margins than in surrounding herbaceous habitats. This pattern occurs in all grazing treatments. Harvester ant nests provide better conditions and can then act as refugia during droughts. Although reproductive output, measured as number of inflorescences, does not differ between margin and away, disks are areas of high grass survivability and thus they may act as foci for community recovery by providing more grass seed than surrounding areas in the herbaceous community. These observations suggest that *P. barbatus* disks may

serve as reservoirs of plant survival and a seed source for recovering vegetation after drought like refugia demonstrated at abiotic sites in semi-arid environments (Tongway et al. 1989, Ludwig and Tongway 1995, Milchunas and Noy-Meir 2002, Shackelford 2004).

**CHAPTER IV**

**INTERACTION BETWEEN GRASSLAND COMPOSITION AND  
SEASON ON SEED PREFERENCE BY RED HARVESTER ANTS  
(*POGONOMYRMEX BARBATUS*, HYMENOPTERA, MYRMICINAE)  
ON THE EDWARDS PLATEAU**

**Introduction**

Animals can play a role in plant recovery after disturbances by facilitating, inhibiting or changing the trajectory of plant population dynamics. Harvester ants are capable of impacting plant demographics by harvesting a large number of seeds (Rissing 1988, Whitford and DiMarco 1995, Wagner et al. 1997, MacMahon et al. 2000) and by differentially selecting some species over others (Hobbs 1985, Crist and MacMahon 1992). The food value of a species of seed depends on the colonies' current requirements for many nutrients and the mix of nutrients present in available food sources (Wheeler 1994, Simpson and Raubenheimer 2001).

Populations of *P. barbatus* are distributed through most of Mexico north to Arizona, Kansas and Colorado, U. S. A. where they can be the most abundant ant species in communities where they occur (Holldobler and Wilson 1990). *Pogonomyrmex barbatus* is capable of impacting communities by harvesting a large number of seeds. They gather food for the colony using foraging trails that radiate from the nest and lead to foraging areas. Foragers primarily gather freshly fallen small seeds from herbaceous plant species, but they also collect insects, feces, soil and parts of vegetation (Tabor 1998). *Pogonomyrmex barbatus* forages nearly all year, except for the coldest months of winter (Gordon 1999, MacMahon et al. 2000). During winter, colonies must feed off stored seed and begin producing new workers (Holldobler and Wilson 1990).

Nourishment obtained by foragers in the spring is passed on to the growing brood and to the queen for reproduction. Protein is used by the queen for egg production and by

larvae for growth, while workers use carbohydrates to sustain their activity (Wheeler 1994). Additional nutrition is required in the spring when the colony produces male and female alates. Queens must obtain sufficient nutrition before they disperse to raise their first brood without feeding (Wheeler 1994). Throughout the year patterns of nutrient acquisition vary depending on the colony's status, that is, its nutritional requirements and reproductive season. Two characteristics of a *P. barbatus* colony's status, spring reproduction (Gordon 1999) and fall seed storage for winter inactivity, could be important factors in seed selection. Intensity of foraging by a colony is not only affected by nutritional requirements but also on climatic conditions and seed abundance (Holldobler 1976, Rissing and Wheeler 1976, Gordon 1991, Lopez et al. 1993).

Seed consumption becomes important to plant populations when it removes seed from the population or causes indirect, differential mortality among competing plants (Brown et al. 1979, Louda 1989, Hulme 1998). Studies in the Sonoran and Chihuahuan Deserts demonstrate that differences in seed selection by harvester ants changes plant community structure by reducing the abundance of preferred species (Inouye et al. 1980, Hobbs 1985) and by increasing plant diversity due to harvesting seeds of the most abundant annual species (Brown et al. 1979, Hobbs 1985, Rissing 1986)

North American savannas are highly dynamic ecosystems, largely controlled by a disturbance regime consisting of herbivory, fire, and variable rainfall, which results in a mosaic of vegetation patches of differing sizes and ages (Smeins and Merrill 1988, Bazzaz 1996, Fuhlendorf and Smeins 1997, Fuhlendorf et al. 2001). Seed recruitment is an important process in the recovery of grasslands and could be important in recovery from large-scale perturbations because seeds survive disturbances underground, or they are dispersed widely from surviving individuals. Recovery from seed could be altered by post-dispersal seed predators both before the disturbance, by altering the populations of seeds destined to survive in soil, and after the disturbance by harvesting freshly dispersed seeds. High granivory rates by ants are reported for California annual grassland (Marshall and Jain 1970), desert grassland (Pulliam and Brand 1975) and Australian cultivated grassland which



results in annual ryegrass (*Lolium rigidum*) becoming extirpated while other annual grass and dicot populations were reduced (McGowan 1969). As part of the reproductive dynamics of grassland populations, seed mortality by predation might affect plant populations recovering from disturbances.

One of the factors responsible for the amount and type of seeds selected is the availability of preferred seeds. Large herbivores can influence grassland composition by the frequency and intensity of herbivory. Heavy, continuous livestock grazing in a liveoak savanna parkland on the Edwards Plateau of Texas results in habitats dominated by grazing resistant short-grasses (Smeins and Merrill 1988, Fuhlendorf and Smeins 1997). These species typically disperse thousands of tiny seeds with little endosperm. In contrast, light herbivory produces a plant community of grazing intolerant mid-grasses that produce fewer seeds with greater endosperm. Harvester ants are known to change seed species preferences depending on the level of grazing (Capon and O'Connor 1990, Milton and Dean 1993). This could lead to deviations in plant species' establishment.

Seed selection by harvester ants can be influenced by seed characteristics; morphology (Davison 1982), size (Davidson 1978, Rissing 1981, Morehead and Feener 1998), seed density (Rissing and Wheeler 1976, Crist and MacMahon 1992, Kunin 1994), chemical properties (Gordon 1999), energy content (Kelrick et al. 1986, Fewell and Harrison 1991), and handling time (Pulliam and Brand 1975, Schoning et al. 2004) as well as status of the colony.

Description of harvester ant patterns of food selection under varying natural conditions improves the ability to determine potential consequences for plant populations and community dynamics. The aim of this study was to describe a pattern of seed choice in the red harvester ant, *Pogonomyrmex barbatus*, following decades of intense herbivory and during the spring and fall, in a liveoak savanna parkland on the Edwards Plateau, Texas. Experiments were conducted to investigate selection and harvest of seed by *P. barbatus* as influenced by the seasonal context of a colony's nutritional requirements and by the differences between seed diversity and availability caused by grazing. Specific hypotheses

were:

- (1) foragers will collect species of seeds in relation to their availability,
- (2) they will prefer late successional species regardless of large herbivore grazing intensity in their habitat or due to season, and
- (3) they will select seeds with high protein levels in the spring and high carbohydrate levels in the fall.

## **Materials and Methods**

### ***Study Site***

Research was conducted at the Texas A&M University Agricultural Research Station, a semi-arid savanna parkland in the western edge of the Edwards Plateau Land Resource Area, Texas (31°18'N; 100°28'W). Mean long-term annual precipitation is 574 mm but variability between years is great, with a range of 357 mm and standard deviation of 51 mm (Station Records). Vegetation at the station is a liveoak, mixed-grass, parkland characterized by groves of *Quercus virginiana*, *Q. pungens* var. *vaseyana*, *Juniperus ashei*, and *J. pinchotii*. Between the groves are grasslands of mid- and short-grass species with a diversity of perennial dicots (Gould et al. 1960, Kuchler 1964, 1975, Smeins and Merrill 1988). The main periods of grass and dicot seed production occur in June and October. However, many dicots and one common grass, *Stipa leucotricha*, set seed in the spring

The study was conducted within two, 11 ha ungrazed exclosures and two, 32 ha continuously grazed pastures. From 1948 to 1983 the grazed pastures were continuously and heavily grazed by domestic herbivores (5.4 ha/AUY; One AUY is the yearly demand rate of oven-dry forage for an animal at 12 kg/day (Group 1988)); since 1983 grazing has been reduced in the continuously grazed pastures, allowing them to begin recovery. The exclosure has had only native herbivores. The two treatments are approximately 2.5 km apart and the study was carried out on the same soils with similar topography. The continuously grazed site was dominated by grass species that tolerate intense herbivory; the short-grasses *Hilaria belangeri* and *Bouteloua trifida*, and three *Aristida* species (Gould 1978, Fuhlendorf and Smeins 1998). Common dicots were *Verbena canescens*, *Plantago rhodosperma* and other

annual species that commonly occur in disturbed places. The ungrazed site was dominated by grazing-intolerant species including the mid-grasses *Bouteloua curtipendula*, *S. leucotricha*, and *Tridens muticus* with a high diversity of perennial dicots such as *Ratibida columnaris*.

The red harvester ant, *Pogonomyrmex barbatus* Smith 1858 (subfamily Myrmicinae), is prevalent at the station, numbering approximately 5.1 colonies ha<sup>-1</sup> in the ungrazed and 3.3 colonies ha<sup>-1</sup> in the continuously grazed sites (Chapter II) which is near the low range of recorded population densities (Crist and Wiens 1996, Gordon 1999). Workers are monomorphic, approximately 1.0 cm long, and have a dark red coloration. Nests are constructed underground with an approximately one-meter diameter, bare soil disk on top (Rissing 1988, Whitford and DiMarco 1995, Wagner et al. 1997, MacMahon et al. 2000). This species primarily gathers small seeds from herbaceous plants after the seeds have fallen to the ground. The term “seed” in this study refers to the propagules, either fruit or seed, dispersed by grasses and dicots found at the Sonora Research Station. Foraging occurs nearly all year except for the coldest months, from November to March. Colonies raise one generation of brood per year and they become adults in April or May depending on adequate rainfall (Gordon 1999).

#### ***Colony Seed Collection and Seed Availability***

Seed collection by returning workers of *P. barbatus* were recorded and compared to composition of vegetation in foraging areas to assess selection of seed species in both continuously grazed and ungrazed sites. To determine whether seeds were collected in similar proportions to seed availability, item retrieval was related to food availability at the end of the foraging trail. Ten colonies were selected randomly from one pasture within each grazing treatment for a total of twenty colonies. In August 2002 thirty returning foragers were intercepted on a cleared trail approximately 1.5 m from the nest entrance and their food item was taken from them. Individuals were caught using a modified dustbuster. This routine was repeated at each colony between 8:00 a.m. and 11:00 a.m. and from 6:00 p.m. to 8:00 p.m., the periods of highest observed daily activity, in one day. Immediately after

collections, the cleared trail was followed until the foraging area was found and it was sampled in a 1 m<sup>2</sup> quadrat for percent aerial cover of each species dispersing seeds. All seeds were stored and identified to species.

Seed preference was calculated by comparing the proportion of the number of seeds per species collected by foragers on the trail, to the proportion available in a foraging area. Seed availability (the density and diversity of seeds that can be harvested by foragers) is a challenge to measure directly at the Sonora Research Station because dispersed seeds are highly variable at scales less than 1 m (Kinucan 1987). To determine the proportion of seed available in a foraging area an indirect measurement was used (hereafter called Availability Index); the median number of seeds on an individual plant was calculated from twenty plants and then multiplied by plant density in the 1m<sup>2</sup> foraging area samples.

Selection among seed species and differences between the grazed and ungrazed treatments were compared using the electivity index which estimates selection independent of availability in the foraging area (Chesson 1983). Selection for a seed species, using the electivity index, is interpreted as the collection of a seed species relative to the average collection of alternative seeds. The electivity index displays selection with a range from -1 to +1, with 0 representing no preference. The electivity index is computed by:

$$E_i = m \alpha_A - 1 / (m - 2) \alpha_A + 1, A = 1, 2, \dots, m,$$

where A is the number of species producing seeds occurring in the foraging area and  $\alpha_A$  is a vector of relative abundance. It is given by

$$\alpha_A = (d_i / f_i) / \sum d_j / f_j, A = 1, 2, \dots, m,$$

where  $d_i$  is the proportion of seeds of species “i” collected from foragers,  $f_i$  is the proportion of seeds of species “i” in the foraging area,  $d_j$  is the proportion of seeds of species “j” collected from foragers and  $f_j$  is the proportion of seeds of species “j” in the foraging area.

For example; at a given nest four species were seeding in the foraging area. The proportion of seeds collected for species “I” or  $d_i$  was 0.74 and the proportion of seeds of species “I” in the foraging area or  $f_i$  was 0.65 for a quotient of 1.14. The sum of the four species’ quotients was 2.29, therefore  $\alpha_A$  was  $1.14/2.29 = 0.50$ . Availability Indices were used to determine the number of seeds in foraging areas. An electivity index was calculated at each colony for every species of seed retrieved from returning foragers. Electivity indices were calculated for species that had overall proportions  $f_i > 1\%$  within a grazing treatment and were found at more than one nest. This was done to avoid erroneous conclusions about species that were rare.

To compare species producing seeds a one-way treatment in a completely randomized design was conducted (Zar 1996). Data were non-normal and variances unequal, therefore nonparametric analysis of variance were used. The grazing areas were not replicated preventing a statistical comparison between treatments.

### ***Seed Selection Experiments***

Four herbaceous species, known to be harvested by *P. barbatus*, were used to directly quantify seed preference under natural seed rain. Species were picked for their high densities during early or late recovery phases after longterm heavy grazing at Sonora Research Station (Smeins and Merrill 1988, Fuhlendorf and Smeins 1997). *Plantago rhodosperma* is an annual that typically disperses seed from March through April and is common during early to mid recovery phases. Three grasses were chosen, *Bouteloua curtipendula*, a mid-grass species common in later phases of recovery; *Aristida* species, a mid-grass occurring during early recovery; and *Hilaria belangeri*, a short-grass, also occurring during early recovery phases. *Plantago rhodosperma* and *Aristida* species were found in the highest proportions in the continuously grazed treatment while *B. curtipendula* was found at highest densities in the ungrazed treatment. Weight of seeds offered included parts of the grass spikelet found attached together by foraging ants including florets, glumes and awns. Mean weight of seeds were; *Hilaria belangeri* 0.17 mg, *Aristida* species 0.26 mg, *Bouteloua curtipendula* 0.05 mg, and *Plantago rhodosperma* 0.06 mg.

Seeds were offered in 168.9 cm<sup>2</sup> area (12.7 X 13.3 cm), 3.5 cm tall, plastic petri dishes with ceiling spackle placed inside to allow ants to freely move in and out of the dishes. Sixty seeds were placed in each dish for a density of 3,529 m<sup>-1</sup>. Density of seed offered to harvester ants were ten times seed rain densities found for the Station (Kinucan 1987). An equal number of seeds (15) of each species was mixed together when offered in a dish.

To determine if selection was made based on nutrient content, commercial non-native seeds were offered which were lentil, brown rice and sesame. Here, nutrient content was defined by the primary metabolic constituent of each species. Nutrients were carbohydrates, lipids and protein and each species had high levels of one nutrient compared to the other two nutrients (Table 11). Harvester ants generally prefer heavier seeds over lighter (Crist and MacMahon 1992). To reduce the weight factor all seeds were ground to similar weights: lentils were 0.39g ( $\pm 0.07$  C.I.), sesame 0.30g ( $\pm 0.01$  C.I.), and brown rice 0.30g ( $\pm 0.05$  C.I.). Twenty seeds of each commercial species were mixed together for a total of 60 seeds, and presented to the ants in the same manner as native species.

Three replicate dishes were placed along an active ant trail approximately 1 m from the edge of the cleared area, on top of the ant nest. Dishes were put in place before the colony became active in the morning. Seeds were offered throughout the foraging time or until five native or six commercial seeds of the most preferred species were left (to minimize effects of depletion).

Seeds were presented to foragers in two continuously-grazed and two ungrazed sites. Commercial seed experiments were conducted on two consecutive days during April 11-14, 2003 and native seeds were presented during May 8-12, 2003. During this time, harvester ants were assumed to be raising their single brood generation for the year. The experiment was repeated in the fall just prior to winter dormancy, when harvester ants were assumed to be gathering seed for the winter. Commercial seeds were presented on two consecutive days during October 22-24, 2003 and native seeds were presented on two consecutive days during October 26-28, 2003.

Table 11. Nutrient content of commercial seeds offered to foraging workers in the seed selection experiment. Average nutrient per 100 g of each seed.

Average Content <sup>1</sup>	Lentil seed (g)	Sesame seed (g)	Brown rice seed (g)
Carbohydrates	57.1	23.5	76.2
Lipids	0.96	49.7	2.68
Protein	28.1	17.7	7.5

1= U. S. Dept of Agriculture 2002

Due to the large number of uncollected seeds during the fall, the distribution of data were highly skewed even after transformations, therefore nonparametric statistics were used for all analyses. Replicate dishes and replicate sites were pooled within grazing treatment and within season. Separate tests were conducted to compare differences between the factors grazing treatment, seed species and season. A one-way treatment in a completely randomized design nonparametric ANOVA (Kruskal-Wallis) was used. Contrasts were conducted to determine differences among species using the Q-statistic test (Zar 1996).

## Results

### *Colony Seed Collection and Seed Availability*

Colonies collected 25 species of seed with 52% species congruence between continuously grazed and ungrazed treatments. Fifteen species were collected without a corresponding seeding species in the 1m<sup>2</sup> foraging areas. Thirteen species comprised >1% of all species found in foraging areas and were found at more than one nest (Table 12).

Seed preference, the relative number of seeds collected by foragers on the trail compared to the relative number occurring in the foraging area was significantly ( $p < .001$ ) different among species. Except for the introduced grass *Eragrostis cilianensis* which changed from not preferred to collected relative to availability, all species were harvested similarly in the two grazing treatments (Figure 11). Four species were preferred, five were not preferred, two were selected in proportion to their Availability Indices and one changed preference between treatments (Figure 11). The most common species in the foraging areas; *Panicum hallii*, *Chaetopappa asteroides*, *Sida abutifolia*, *Bouteloua curtipendula* and *Digitaria cognata* varied in preference (Table 12). Generally, foragers did not choose seed relative to their Availability Index nor did they consistently prefer the most common species.

Selection among seed species independent of availability in the foraging areas was analyzed using the electivity index and was significantly different among species ( $p < .001$ ). No differences were detected between grazing treatments. *Panicum hallii*, a perennial grass,



Table 12. Relative number of seed species, insect parts, plant parts, faeces, and soil particles captured from returning workers and relative foliar cover found at 1m<sup>2</sup> foraging areas, in heavy continuous and ungrazed treatments. The list shows species > 1% of total foliar cover sampled in each treatment's foraging areas and used for further analyses. Species with -- were not found in that treatment. See text for explanation of foliar cover as an availability index.

Seed species	Ungrazed Treatment		Continuous Treatment	
	Ant collection	Foraging areas	Ant collection	Foraging areas
	Relative seed number	Relative foliar cover	Relative seed number	Relative foliar cover
<u>Used in Analyses</u>				
<i>Aristida</i> species	0.003	0.010	0.030	0.171
<i>Bouteloua curtipendula</i>	0.000	0.184	--	--
<i>Bouteloua trifida</i>	0.033	0.000	0.093	0.047
<i>Chaetopappa asteroides</i>	0.010	0.002	0.057	0.215
<i>Croton monanthogynus</i>	0.003	0.048	0.020	0.000
<i>Digitaria cognata</i>	0.033	0.181	0.010	0.000
<i>Eragrostis cilianensis</i>	0.030	0.048	0.000	0.010
<i>Erioneuron pilosum</i>	0.057	0.000	0.010	0.024
<i>Hedeoma drummondii</i>	0.000	0.021	0.000	0.024
<i>Hilaria belangeri</i>	0.027	0.000	0.000	0.020
<i>Panicum hallii</i>	0.270	0.337	0.063	0.153
<i>Sida abutifolia</i>	0.187	0.068	0.270	0.301
<i>Tridens muticus</i>	0.000	0.051	--	--
<u>Unused in Analyses</u>				
<i>Boerhaavia linearis</i>	0.017	0.000	--	--
<i>Bothriochloa barbinodis</i>	0.003	0.019	--	--
<i>Daucus pusillus</i>	0.013	0.000	--	--
<i>Eriochloa sericea</i>	0.020	0.000	--	--
<i>Lepidium austrinum</i>	--	--	0.003	0.000
<i>Panicum obtusum</i>	0.013	0.000	--	--

Table 12. Continued

Seed species	Ungrazed Treatment		Continuous Treatment	
	Ant collection	Foraging areas	Ant collection	Foraging areas
	Relative seed number	Relative foliar cover	Relative seed number	Relative foliar cover
<u>Unused in Analyses</u>				
<i>Plantago helleri</i>	0.020	0.000	0.003	0.000
<i>Ratibida columnifera</i>	0.020	0.004	--	--
<i>Schedonnardus paniculatus</i>	0.003	0.000	0.003	0.010
<i>Scutellaria drummondii</i>	--	--	0.000	0.009
<i>Stipa leucotricha</i>	0.007	0.000	0.003	0.000
<i>Verbena canescens</i>	0.010	0.000	0.090	0.003
unknown species	0.033	0.000	0.023	0.000
Total seeds (number)	0.812 (244.000)		0.680 (204.000)	
faeces	0.003		0.007	
insect parts	0.007		0.017	
<i>Juniperus</i> scales	0.023		0.003	
algae	0.007		--	--
soil	0.147		0.293	
Total other items (number)	0.188 (56.00)		0.320 (96.00)	
Total harvested (number)	1.000 (300.00)		1.000 (300.00)	

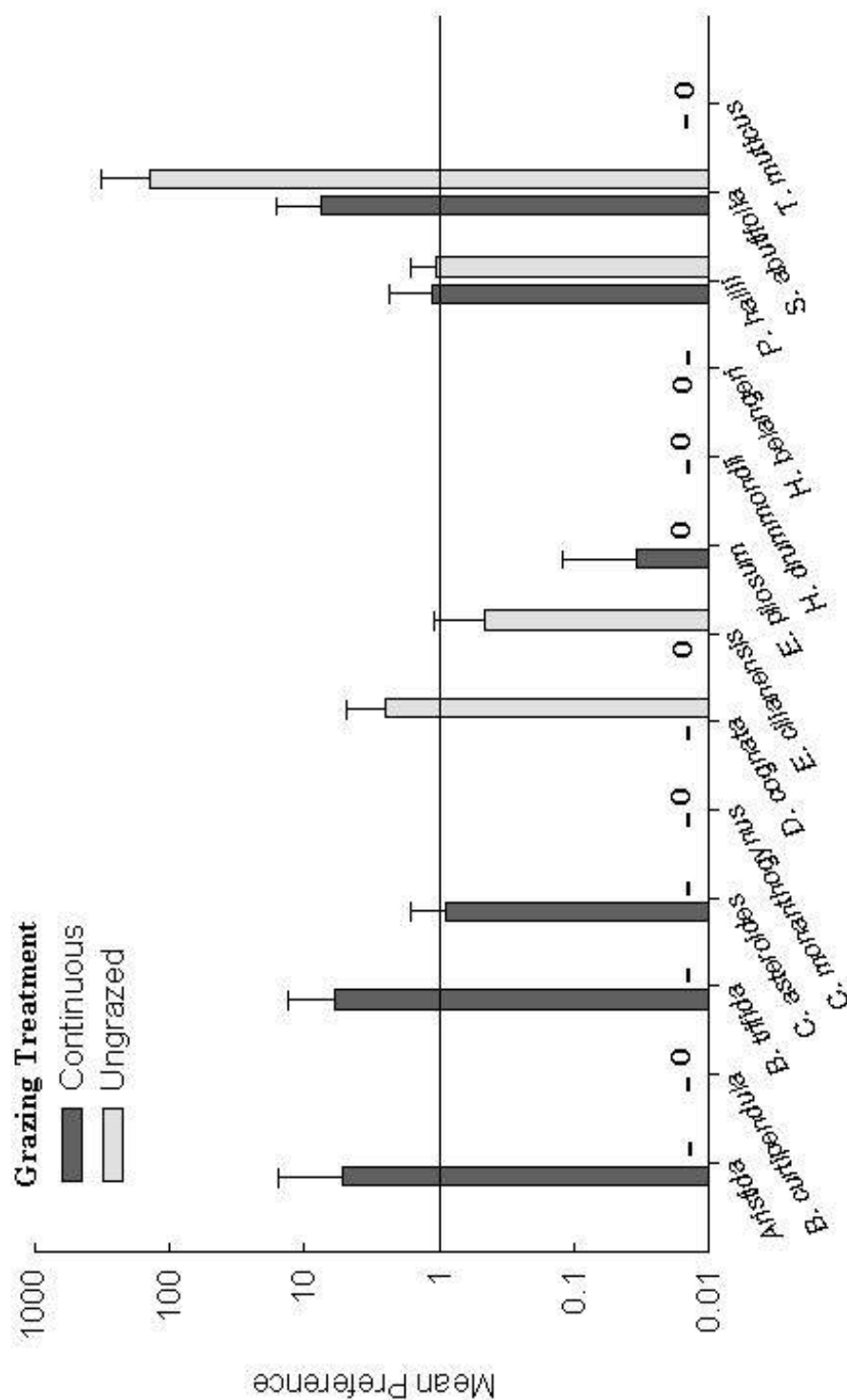


Figure 11. Mean preference of species collected by *Pogonomymex barbatus* colonies in continuous and ungrazed treatments. A preference value of 1 = species collected proportional to availability, a preference value of 0 = unpreferred, a preference value of over 1 = preferred, and a preference value of - = species absent from foraging areas. Sample sizes were 2-12 nests. Error bars are standard deviation.

and *S. abutifolia*, a perennial dicot, were collected in the greatest quantities (100 and 137 seeds, respectively, out of 448). Among species that produce seeds in the foraging areas, eight species were rejected (no seeds harvested), four were harvested in proportion to other species and one, *S. abutifolia*, was selected in greater numbers relative to other species and it is a species commonly found during recovery after longterm heavy grazing (Figure 12). Grazing-intolerant mid-grasses were rejected.

### ***Seed Selection Experiments***

A significantly greater proportion of seeds were harvested from dishes in the spring compared to the fall for both native ( $p < .001$ ) and commercial seeds ( $p < .001$ ) (Figure 13). Both grazing treatments had greater proportions of seeds harvested in the spring (Figure 13). However, individual species varied between seasons. *Bouteloua curtipendula* and *Plantago rhodosperma* were harvested significantly more in the spring, but *Aristida* species and *Hilaria belangeri* were not significantly different (Table 13). Nevertheless, all commercial seed species were harvested significantly more in the spring compared to the fall (Table 13).

The Kruskal-Wallis statistic cannot test for interactions between factors but inspection of the median percent of seeds harvested suggests interaction affects between grazing treatment and season for three of the species (Figure 14). *Bouteloua curtipendula* was harvested more in the continuously grazed compared to the ungrazed treatment in the spring, but, in the fall very few seeds were harvested in either treatment (Figure 14). In contrast, *Aristida* species were harvested about 10% more in ungrazed than continuously grazed treatment in the spring, but fall foragers decreased harvest in the ungrazed treatment and increased harvest in the continuously grazed. Commercial species also showed interaction effects with sesame selected much less in the spring in the continuously grazed treatment (Figure 14).

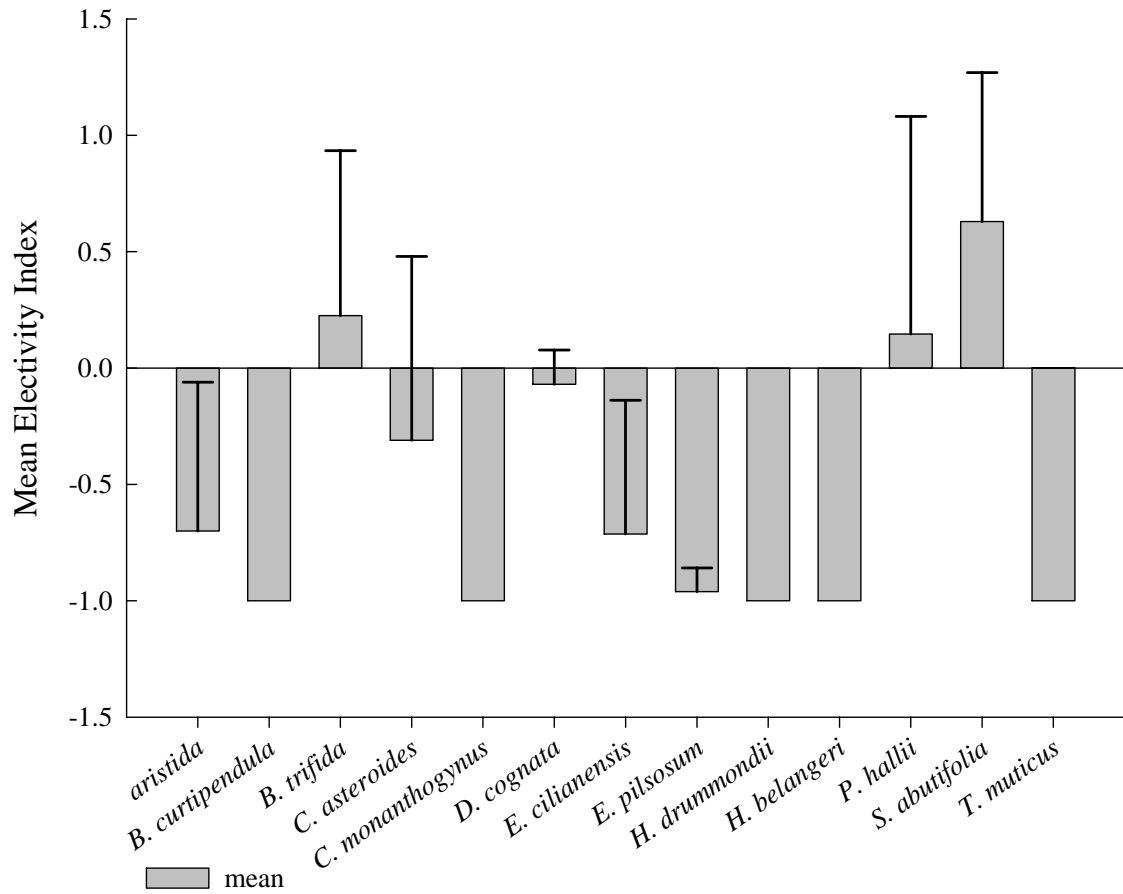


Figure 12. Mean Electivity Index of seed species collected by all twenty colonies in pooled grazing treatments. Index values of 0 = no selection; positive values = selected; negative values = rejected. Error bars are standard deviation.

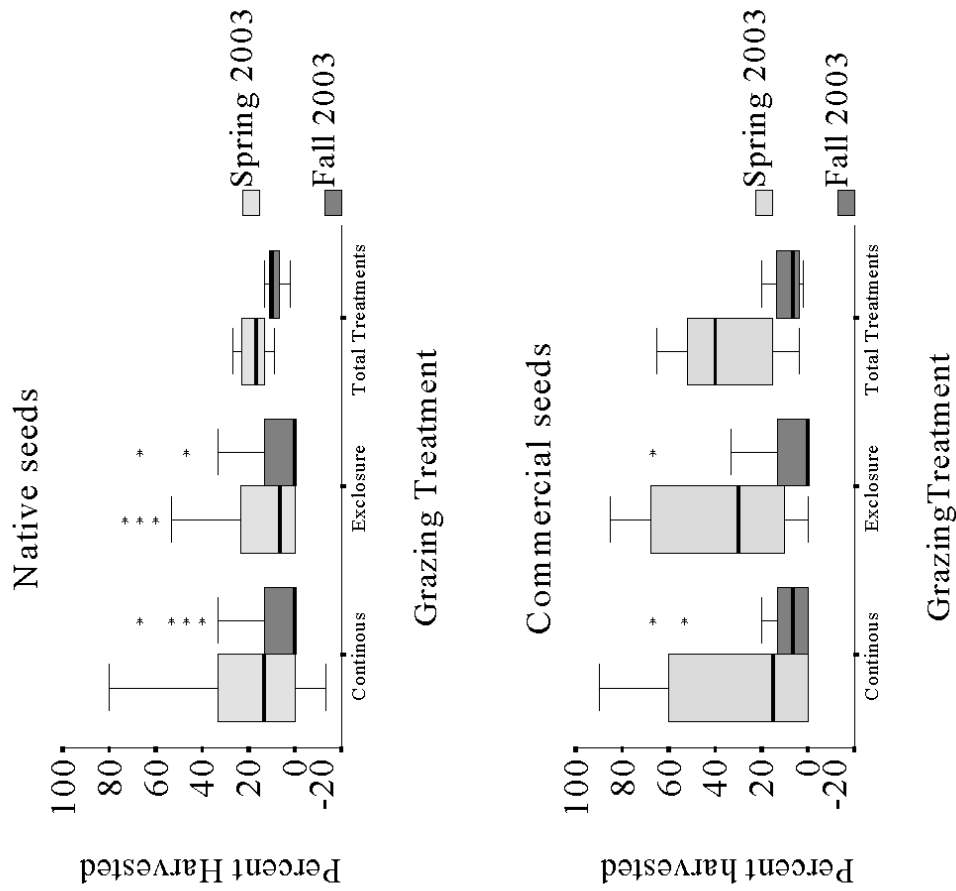


Figure 13. Median with an inter-quartile range that lies 25% and 75% into ranked data of percent of total harvested native and commercial seed from trays by *P. barbatus* during the spring and fall seed selection experiments in heavy continuously grazed, ungrazed and total grazing treatments. Boxes above the median are 25% down the ranked data and boxes below the median are 25% up. Bars represent 75% of the inter-quartile range. Stars above bars are outlier data points.

Table 13. *Pogonomyrmex barbatus* spring and fall seed selection experiments among seed species. Data are percent seed harvested from total presented and are means pooled between grazing treatments. Numbers in parentheses are standard deviation. Species multiple contrasts between spring and fall were conducted by Kruskal-Wallis tests. Spring N = 208 trays, Fall N = 120 trays.

Species	Native		Species	Commercial	
	Spring	Fall		Spring	Fall
<i>Bouteloua</i> <i>curtipendula</i> **	28.33 (24.20)	3.78 (7.77)	sesame*	27.87 (31.82)	7.18 (13.05)
<i>Aristida</i> species	27.31 (22.99)	21.11 (16.62)	lentil**	41.49 (30.98)	13.08 (18.33)
<i>Hilaria</i> <i>belangeri</i>	6.92 (13.97)	6.00 (16.82)	brown rice**	32.55 (26.86)	6.67 (10.99)
<i>Plantago</i> <i>rhodosperma</i> *	10.13 (15.48)	3.11 (5.46)			
Total Species	18.17 (21.83)	8.50 (14.59)	Total Species	33.97 (30.29)	8.97 (14.57)

\*  $p < .05$ , \*\*  $p = .001$

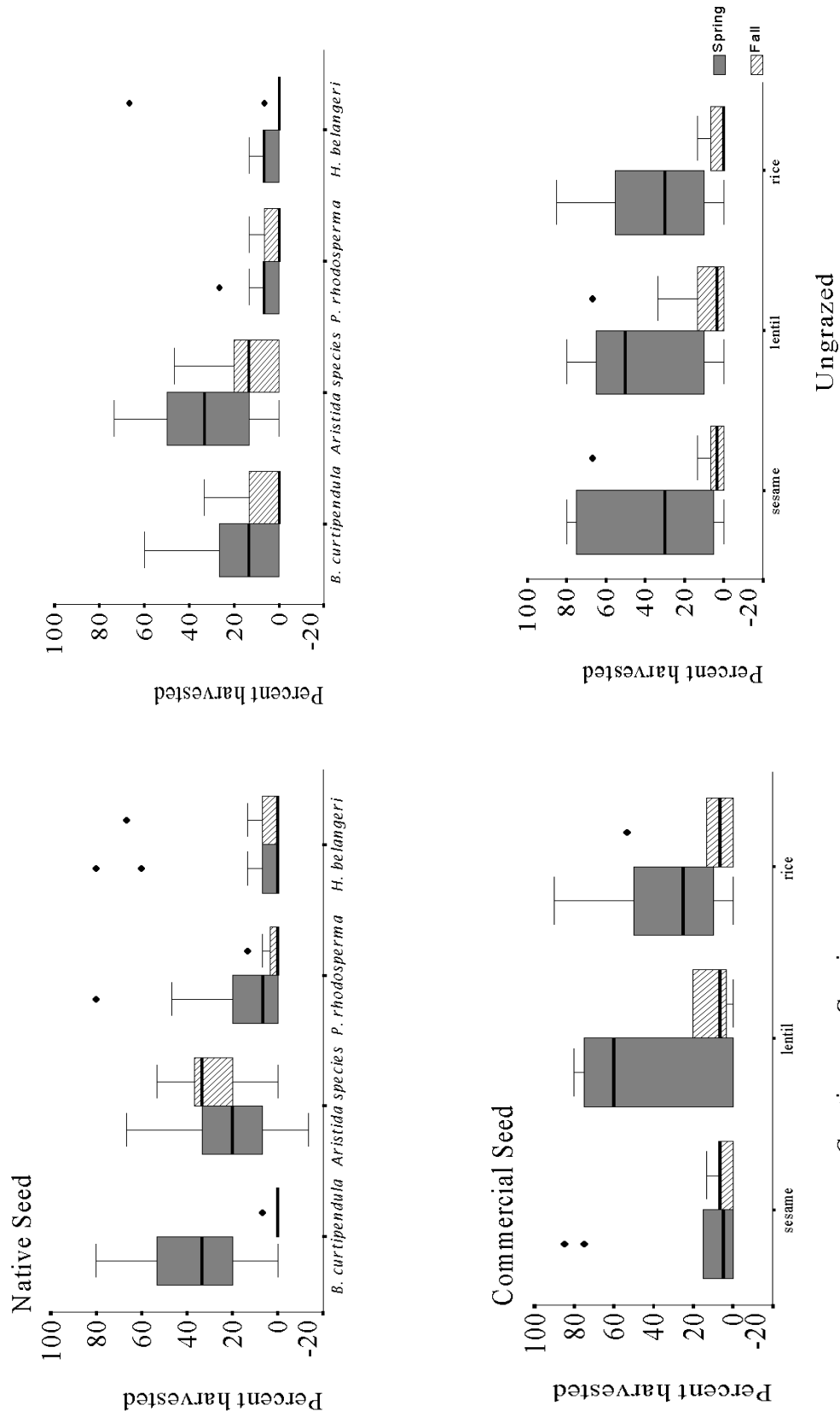


Figure 14. Median with an inter-quartile range that lies 25% and 75% into ranked data of percent of total harvested native and commercial seed from trays by *P. barbatus* during the spring and fall seed selection experiments in heavy continuously grazed and ungrazed treatments. Boxes above the median are 25% down the ranked data and boxes below the median are 25% up. Bars represent 75% of the inter-quartile range. Circles above bars are outlier data points.



Median seed removal between grazing treatments for both native ( $p = 0.23$ ) and commercial seeds ( $p = 0.32$ ) was not significantly different during spring experiments (Figure 13). Grazing treatment data were then pooled and native seed preference was significantly different among species ( $p < .001$ ). Multiple comparison Q-tests (Zar 1996) found the two mid-grasses, *B. curtipendula* and *Aristida* species, were harvested significantly more than *H. belangeri* and *P. rhodosperma* (Figure 15). The late recovery species, *B. curtipendula*, was selected but so was the early recovery *Aristida* species, nevertheless the remaining two early-recovery species were rarely collected. Commercial seeds were selected equally among species ( $p = 0.17$ ; Figure 15), perhaps failing to elicit choice in seed species with varying amounts of protein, carbohydrates and lipids.

Fall experiments again were not significantly different between grazing treatments for both native ( $p = 0.33$ ) and commercial seeds ( $p = 0.39$ ) (Figure 13). Native seeds were significantly different among species ( $p < .001$ ). Multiple comparison Q-tests showed that *Aristida* species were selected significantly more than any other species, and in contrast to spring, *B. curtipendula* was rarely taken and was not significantly different from *H. belangeri* and *P. rhodosperma* (Figure 15). Again, commercial seeds were selected similarly among species ( $p = 0.28$ ; Figure 15).

## Discussion

*Pogonomyrmex barbatus* collected seed differentially among most dicot and grass seed regardless of abundance and availability in natural conditions. Both Electivity Index and Preference values showed similar patterns among species, validating these indices. Species with the highest cover in foraging areas, *P. hallii* and *S. abutifolia*, had mean Availability Indexes of 1 and 138 respectively, and those with lower cover, such as *Aristida* species and *B. curtipendula*, had mean Availability Indices of 5 and 0, respectively, therefore abundance was unimportant in relation to seed preference. Foliar cover and Availability Indices were closely related even though foliar cover is an imprecise measure of grass production primarily due to lack of nutrients needed for reproduction and herbivory.

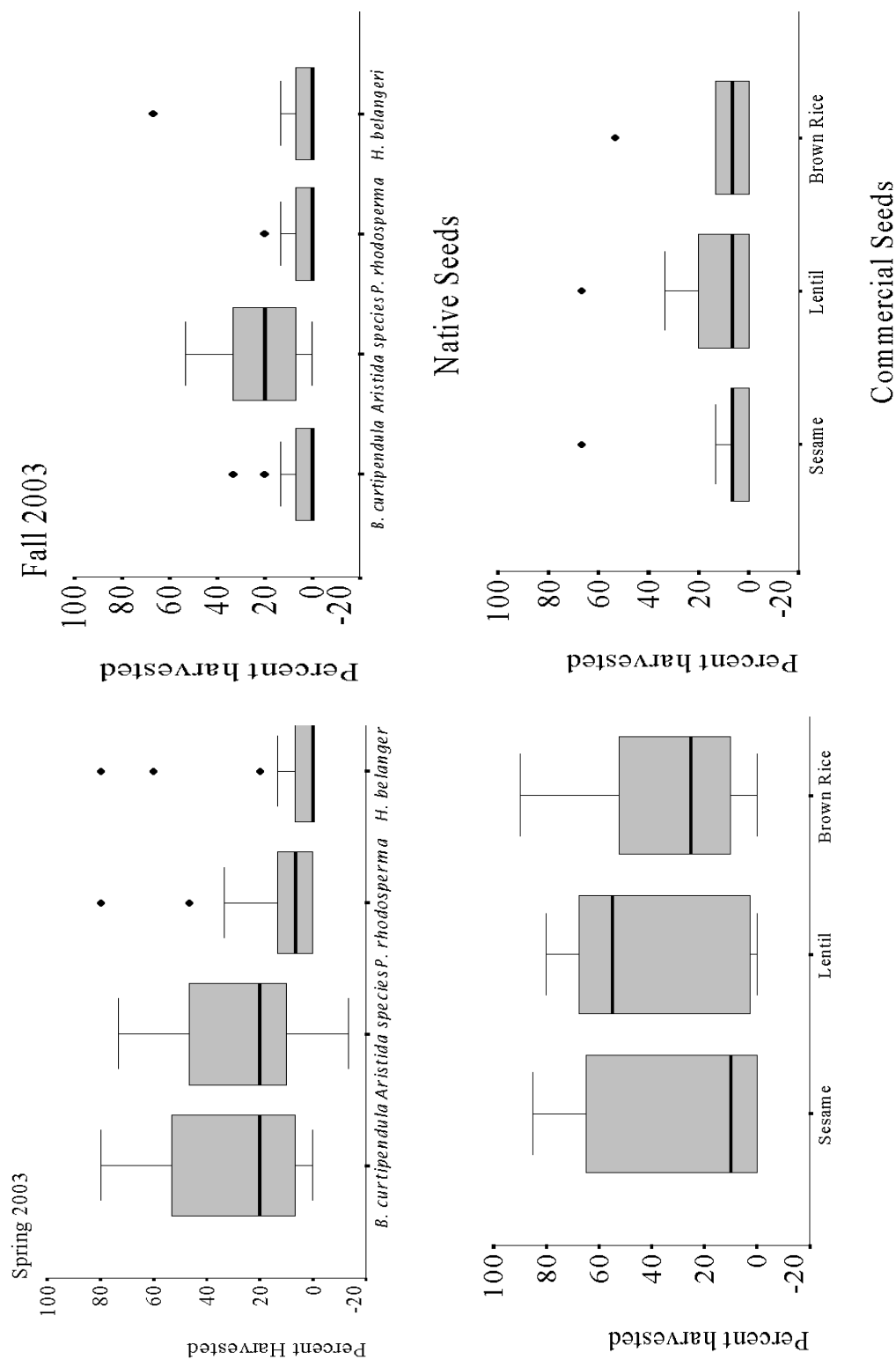


Figure 15. Median with an inter-quartile range that lies 25% and 75% into ranked data of percent of total harvested native and commercial seed from trays by *P. barbatus* during the spring and fall seed selection experiments. Boxes above the median are 25% down the ranked data and boxes below the median are 25% up. Bars represent 75% of the inter-quartile range. Symbols above bars are outlier data points.

A total of 69% of species (used in the analysis) were not collected in relation to their availability. In contrast, previous studies found *Pogonomyrmex* foragers collecting species of seed relative to their availability (Pulliam and Brand 1975, Whitford 1978, Fewell and Harrison 1991, Crist and MacMahon 1992). Some studies have documented comparable patterns of seed selection when overall seed abundance is high (Davidson 1978, Whitford 1978, Hobbs 1985, Wilby and Shachak 2000). Rissing and Wheeler (1976) observed that when abundance is scarce, foragers gather species in relation to their availability. Crist and MacMahon (1992) reasserted this pattern among preferred seed species, but non-preferred species were rarely chosen regardless of their abundance. During the present study, sufficient rainfall and cooler July temperatures resulted in substantial seed production. This higher abundance of seed could have encouraged greater seed selection. High standard deviations in species Availability Indices and Electivity values (Figures 1 and 2) indicate that there was intra-nest variability which could be due to; (1) variation in searching ability of foragers, (2) temporal variability in plant dispersal of seed, and (3) the spatial patchiness of seeds at Sonora Research Station (Kinucan 1987, Louda 1989, Wilby and Shachak 2000). Rare seeds may have much lower opportunity of being found, even if they are preferred (Kunin 1994).

However, some species remain uncollected or are rejected regardless of natural occurrence. It is unknown how harvester ants choose seeds. Leaf-cutter ants of the genus *Acromyrmex* attack many species of plants and they strongly prefer some species over others (Roces 1994). Foragers are capable of discriminating among leaves on the basis of nutrients and odors (Holldobler and Wilson 1990, Roces 1994). However, for both leaf-cutter and harvester ants the basis for the preference of some plant species over others remains unclear.

*Pogonomyrmex barbatus* foragers were selective under spring experimental conditions harvesting 28.33% *B. curtipendula* and 27.31% *Aristida* species significantly more than 10.13% for *P. rhodosperma* or 6.92% for *H. belangeri*. The hypothesis that *B. curtipendula*, a late-recovery species, would be preferred over the other three, early-recovery species, was rejected based on the equally high harvest of *Aristida* species in the

spring; and, the significantly lower harvest of *B. curtipendula* in the fall when it was selected equally with the early-recovery species *H. belangeri* and *P. rhodosperma* (Figure 14). Two mechanisms could be responsible for how foragers selected seeds of *B. curtipendula* more than *H. belangeri* or *P. rhodosperma*. First, harvester ants can select among nutrients presented in solution thus, foragers are capable of choosing seeds relative to their nutritional contents. Secondly, colonies may have experience with the shelf-life of seeds and may choose those with long shelf-life. Shelf-life is important because colonies need stored seeds for their own use and for raising their brood during winter, a time when they are not foraging. Finally, *P. rhodosperma* may not have been harvested because it uses a dispersal mechanism called myxospermy which causes its seed to adhere to soil with a mucilaginous layer when the seed is wetted (Schoning et al. 2004). Myxospermy makes the seed unattractive to ant predators and reduces seed predation rates (Schoning et al. 2004).

Total seed harvest was significantly reduced in the fall relative to spring (Figure 14). Reduced harvest of *B. curtipendula* seeds in the fall could be attributable to lack of a brood because adults are unable to process *B. curtipendula* for nutrients without their brood to do it for them. In the fall, *P. barbatus* behavior is inconsistent with results of previous studies demonstrating that while seed abundance is high there is correspondingly high foraging rates (Wilby and Shachak 2000). The experimental data of this study showed that with increased seed production in October, after fall rains, there was not a corresponding increase in harvest rate. There were no differences among median percent harvest in seeds with known nutrient levels (Table 13), consequently the experiments were unable to reject the third hypothesis that foragers will select seeds with high protein levels in the spring and high carbohydrate levels in the fall. Similar results were reported for other *Pogonomyrmex* species (Kelrick et al. 1986, Fewell and Harrison 1991, Crist and MacMahon 1992). Fewell and Harrison (1991) found that *Pogonomyrmex occidentalis* preferred oats more than millet, sesame and rye seed probably because oats were correlated with the highest energy (joules/minute) content. In the present study, sesame had the highest energy content, but since it was rejected (during the spring, in the heavy grazing treatment) compared to the other two

species no apparent nutrient correlation can explain the result. The importance of carbohydrates versus proteins varies among ant species, however, it is unknown to what extent these nutrients are important to *P. barbatus* (Kay 2002). Nutrients in seeds are accessible to the colony but are constrained by features of the seed (such as myxospermy), foraging constraints (such as predation and competition), and environmental conditions. Separating confounding effects of seed features, secondary compounds and nutritional contents remains difficult.

Grazing treatments differed in vegetation composition with continuously grazed having a much higher proportion of early-recovery species relative to the ungrazed treatment. Nevertheless, for species that were found in both treatments colony preference patterns were similar (Figure 11). Preference differed between grazing treatments only for the non-native grass, *Eragrostis cilianensis* which was the only introduced grass seeding during the experiments (Figure 11). Cover of this species was 4.8% in the ungrazed treatment and was selected equal to its availability, compared to 1.0% cover in the continuously grazed with zero preference, therefore colonies may have more experience with this species in ungrazed sites. No significant differences in median seed harvest were found between grazing treatments in the experiments however, an interaction effect was observed between grazing treatment and season. Sesame was selected significantly less, during spring in the continuously grazed treatment. *Bouteloua curtipendula* was selected significantly more in the continuously grazed than the ungrazed treatment, but only during the spring (Figure 14). Therefore, the hypothesis that the late-recovery species, *B. curtipendula* will be preferred regardless of the grazing treatment was rejected. These results contrast with studies which found differences in harvesting rates for species between grazed and ungrazed treatments (Capon and O'Connor 1990, Milton and Dean 1993). Although Milton and Dean (1993) found that selection varied by level of grazing, it was generally correlated with seed abundance.

Seed selection by *P. barbatus* foragers could modify plant community structure through the effects of seed harvest. Further, recovery after intense grazing could be affected

by seed selection if late-recovery species are chosen. Sites recovering from heavy grazing are dependant on late-recovery species whose seeds are typically short-lived in the seed bank (Kinucan 1987, Louda 1989), therefore, as seeds disperse into grazed sites plant establishment is vulnerable to seed predation by harvester ants. Though only a few late-recovery species may be impacted by *P. barbatus* preference for their seed, these observations suggest that recovery after heavy grazing could be hindered by *P. barbatus* seed selection and rates of harvest in the spring.

## **CHAPTER V**

### **HARVESTER ANT GRANIVORY AND SEEDLING ESTABLISHMENT OF GRASSES AND FORBS IN A SEMI-ARID SAVANNA**

#### **Introduction**

The comparative role that biotic and abiotic agents play in recruitment can be important in our understanding of plant population dynamics and success in community restoration. Recruitment from seed is regulated by number of viable seeds produced, germination conditions, disease, and predation (Shaw 1968). Conditions that occur during the seedling recruitment phase in a plant's life cycle are important in determining the abundance of plant populations (Grubb 1977, Harper 1977). Gaps created by disturbances are essential in grasslands as sites for seed germination and seedling establishment (Evans 1975, Huntly and Inouye 1988, Belsky 1992) while increasing diversity by allowing less competitive species to establish (Coffin and Lauenroth 1989, Cheplick 1998, del-Val and Crawley 2005).

In semi-arid savanna and grassland ecosystems climate, herbivory and fire are major driving factors in plant population dynamics (Amos and Gehlbach 1988, Smeins and Merrill 1988, Bazzaz 1996, Fuhlendorf et al. 2001). Drought, grazing and fire can disrupt vegetation cover which may create gaps for seedling establishment.

Patterns of regeneration are influenced by differences among species' requirements for germination and seedling establishment. Recruitment of seedlings is dependant upon germination of seeds at the appropriate time of year, and upon environmental conditions that provide the best opportunity for growth and development. Germination differs among species, with some species germinating in a wide range of environmental requirements and others in a narrow range (Guterman 1993, Baskin and Baskin 1998). In semi-arid climates seedling establishment coincides with sufficient rainfall and favorable temperatures.

Microhabitat differences that influence the distribution and penetration of water can affect seed germination and seedling establishment, and the probability of a seed's germination depends on the position of the seed in this environment (Guterman 1993, Cheplick 1998, Lauenroth and Aguilera 1998, Petru and Menges 2003).

Fire is also a major abiotic component of savanna ecosystems. Fire can have positive effects on seedling establishment by increasing nitrogen availability, breaking seed dormancy, opening gaps for seed, and increasing light (Keeley 1987, Grubb 1988). However, it can also be detrimental, killing seedlings and seeds and increasing evaporation and temperature of the soil following the fire.

Seed densities may be greatly reduced by post-dispersal seed predators which may result in modified plant populations (Harper 1977). Few studies, however, document alterations in plant communities due to post-dispersal seed predation (Louda 1989, MacMahon et al. 2000).

The harvester ant, *Pogonomyrmex barbatus*, collects post-dispersal seeds from herbaceous species as a food source. Colonies can collect nearly 100% of preferred seed species and high colony densities can remove numerous seeds (Polis 1991, Crist and MacMahon 1992). Nevertheless, most estimates of losses to annual seed production are less than 10% (Pulliam and Brand 1975, Whitford 1978). Seed loss could be compounded where colony foraging areas overlap. However, *P. barbatus* is territorial and adult colonies protect foraging areas (Gordon 1991, Gordon 1993, Gordon 1995).

The predation effects of these ants may be obtained from manipulative field experiments where foragers are totally excluded. In deserts, winter annual density increases where ant and rodent seed predators are removed (Brown et al. 1979, Inouye et al. 1980, Davidson et al. 1984, Rissing 1986). High seed predation rates in prairies favors dominant plants that are dependant upon vegetative reproduction for persistence (McGowan 1969, Marshall and Jain 1970, Pulliam and Brand 1975, Louda 1989). Although most studies show that large quantities of seeds can be harvested, they have not related this removal to reduced recruitment in plant populations. The nature and degree of impact that harvester ants have



on seedling establishment are unclear.

The goal of this research was to learn if the foraging activities and colony density of *P. barbatus* can influence herbaceous seedling establishment. In addition, the impact of prescribed fire on ant foraging and seedling establishment were investigated.

The following hypotheses were addressed:

- (1) densities of naturally occurring dicot and grass seedlings are comparable among three densities of *P. barbatus* colonies, presence or absence of seed predation and between burned and unburned treatments,
- (2) density of seeded perennial dicot and grass seedlings sown from equal quantities of seed is comparable among the experimental treatments, and
- (3) seedling densities will be similar among years.

## **Methods**

### ***Study Site***

The study was conducted at the Texas A&M University Agricultural Research Station (Sonora Research Station), Edwards Plateau, Texas (31° 18'N; 100° 28'W). The Station is at 735 m elevation on gently rolling topography with slopes from 1 to 4%. Soils are shallow (17-30 cm deep) with limestone-derived stone fragments 35 to 70% of soil volume and are Tarrant and Eckrant cobbly silty clay loams (USDA 1968). Valera Clay soils occur on 12% of the site. The climate is continental and semi-arid with a bimodal distribution (June and September peaks) of growing season rainfall. Temperatures average 30° C in July and 9° C in January (Station Records). Average annual precipitation (1919-2004) is 57.5 cm, but variability between years is great with a range of 35.7 cm and standard deviation of 5.1 cm (Station Records). The study began three months after a severe five-year drought ended. Station records were used to create a Palmer drought severity index (Palmer 1965, Shackelford 2004) which shows a general pattern of surplus moisture (Figure 16A) ( $> 1.0$  PDSI) during the winter and deficit moisture ( $< -1.0$  PDSI) during the summer growing season with normal rainfall returning July 2002 (Figure 16A). Annual rainfall was above monthly medians during the study (Figure 16B).

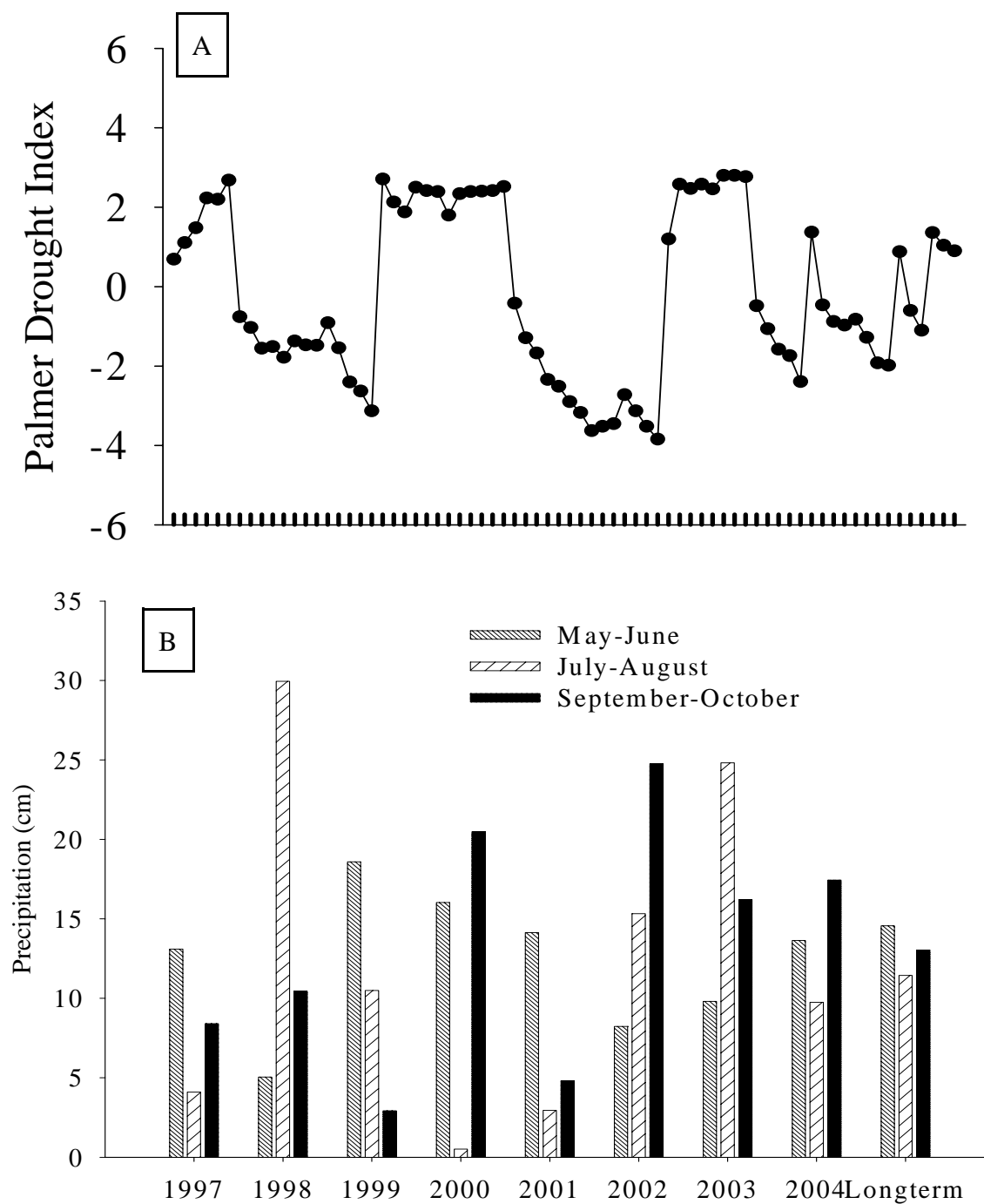


Figure 16. A. Monthly Palmer drought severity index values for 1998-2002 (Reprinted with permission from Shackelford 2004). B. Total monthly precipitation for study period, October 2002-October 2004 and long-term (1919-2004) monthly median precipitation at the Sonora Research Station (Station Records).

Experiments were conducted in a 32.0 ha<sup>-1</sup> pasture with a 55-year history of sheep grazing at 16.2 ha/AUY (one AUY is the yearly demand rate of oven-dry forage for an animal at 12 kg/day (Group 1988).). In 1999 a prescribed summer burn was conducted and in 1969 *Juniperus* and *Prosopis* were mechanically removed. Vegetation is potentially mixed-grass, savanna parkland dominated by groves of *Quercus virginiana*, *Q. pungens* var. *vaseyana*, *Juniperus ashei* and *J. pinchotii* in a matrix of mid- and short-grass species (Kuchler 1964, Smeins and Merrill 1988, Hatch et al. 1990). Grassland at the experimental site is dominated by the grasses *Bouteloua curtipendula*, *Aristida wrightii*, *Aristida purpurea* var. *purpurea*, *Aristida glauca*, *Hilaria belangeri*, and *Bouteloua trifida*. The site was ungrazed during the experiments. Voucher specimens of plants observed in this study were stored in The Tracy Herbarium, Department of Rangeland Ecology and Management, Texas A&M University. Nomenclature for grass species follows Hatch (2001) and for dicots follows Hatch, et al. (1990).

Birds and insects are the primary seed predators at the Sonora Research Station. Granivorous mammals have not been observed, however, six probable small omnivores, such as *Peromyscus attwateri* may be present in low numbers and three recorded medium-sized mammals, *Thomomys bottae*, *Sciurus niger* and *Procyon lotor* are known to consume herbaceous seeds (Museum of Texas Tech University, Texas Tech University and Texas Cooperative Wildlife Collection, Department of Wildlife and Fisheries Sciences, Texas A&M University). Intensity of seed predation by these mammals was expected to be minimal and variable in space and time. Flocks of seed-eating sparrows and other song birds overwinter at the research site. Their distribution is unpredictable and patchy throughout the winter, thus their probable rate of seed intakes could be locally high but widely dispersed. Diversity of seed eating insects is unknown although five species of harvester ants were recorded on the Sonora Research Station (Chapter III).

Aboveground herbivory of seedlings may be intense, but during the study it was low. Observed potential herbivores are, Ensifera (grasshoppers, katydids and crickets), *T. bottae* (gophers), Lagomorpha (black-tailed hares and Audubon cottontail), and *Odocoileus*

*virginianus* (white-tail deer). Common belowground herbivores in grasslands such as scarab beetle larvae (Scarabaeidae), wireworms (Elateridae), nematodes, (Nematoda), and tipulid larvae (Tipulidae) (Curry 1994) could be present, however these micro- and macro-invertebrates, and their impacts, have not been identified at the Sonora Research Station. Herbivory was assumed to influence the experiments equally.

### ***Exclosure Experiments***

To assess the reduction in seedling recruitment by *P. barbatus* foragers an exclosure study was established. Experiments measured the individual and combined effects of three *P. barbatus* nest densities and two burn treatments. The experimental design was a 2 X 2 X 3 nested treatment structure in a randomized block design (Figure 17A). All twelve treatment combinations were assigned to 58 blocks for a total of 116 arenas. Each block was placed randomly at either a *P. barbatus* nest or at a location in a zero nest density region and contained a set of two arenas, an exclosure of flashing and a completely open plot (Figure 17B). Arenas within a block were positioned randomly between 3 and 8 m from the nest with an ant trail going through both arenas. Trails typically circled the exclosure once it was placed and after the first season, trails sometimes turned away from it. In these cases the open arena was shifted to the new trail, but at the identical distance from the nest as previously positioned. This assures similar probability for seeds to be harvested.

Arenas were established in October 2002 and the experiment continued until November 2004. On March 10, 2004, 17 months after the experiment was begun, twenty-nine blocks were burned and 29 were left unburned. The prescribed fire was conducted in two large patches within the study area so that arenas would be burned with a natural intensity.

In each burn treatment three *P. barbatus* nest densities were selected, high, low and zero. High nest densities were considered those locations where foraging areas of neighboring nests overlapped. Nest densities were determined by measuring the number of nests in both numerous and scarce patches. High densities are approximately 22 nests in 1,000 m<sup>2</sup>. Low densities are 9 nests in 1,000 m<sup>2</sup> with minimal overlap of foraging areas. A

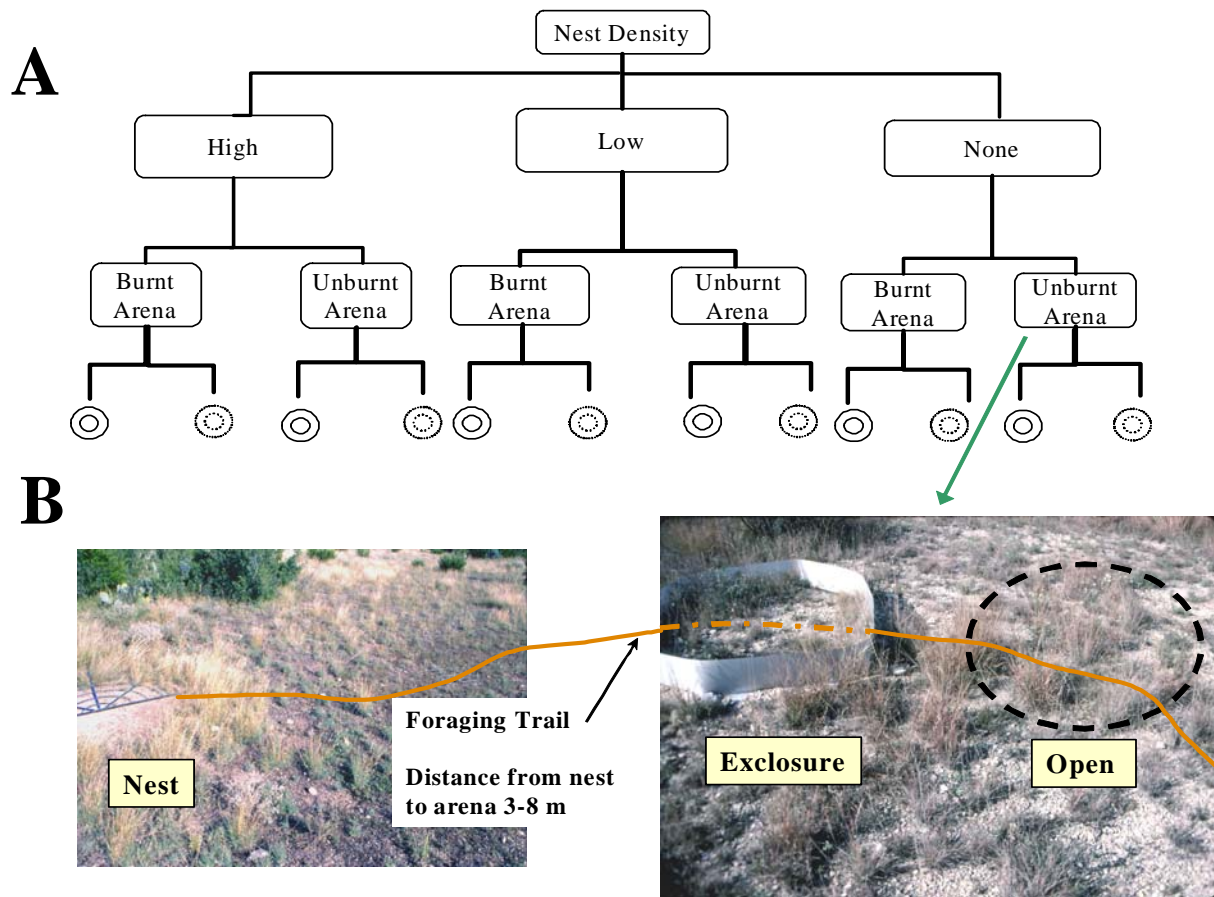


Figure 17. Experimental design of the prescribed burn, foraging removal and colony density treatments at *Pogonomyrmex barbatus* foraging areas at the Sonora Research Station, 2002-2004. A. Treatment design. B. Arena treatments at one nest. The portion of the foraging trail with a dashed line represents a foraging trail cut off by the exclosure.

third density was a location with no nests within 50 m.

In each block, two arenas were created in October 2002. The exclosure arena consisted of aluminum flashing 28 cm tall with a flange 10 cm long at the bottom, directed outward, parallel to the ground (Figure 17B). Flanges were placed flush to the ground to prevent ants from entering and were weighted with rocks while dirt covered the flange and its edges to assure lack of openings. The second treatment was a completely open area allowing access to foraging *P. barbatus* workers. While establishing the arenas, researchers did not step inside the arena thus plants and soil remained undisturbed inside. Each arena was two meters in diameter chosen to (1) assure capturing the variability of vegetation composition in the herbaceous community and to (2) offset shading effects from the flashing. After large rain events exclosures were checked and any openings were covered with soil. Storms occurred infrequently during the experiment and only once, for two weeks, were exclosures open to *P. barbatus* foragers. Additionally, because openings could be too small to detect, bait was placed inside the exclosures to assure that foraging ants were unable to enter. During the baiting, *P. barbatus* workers were never observed inside the exclosures and no bait was removed.

Data in each arena were collected on the number of seedlings from known quantities of sown seed and on the densities of naturally occurring grass and dicot plants. Sown seed species had perennial life history traits and were *Engelmannia pinnatifida*, *Simsia calva*, *Verbena bipinnatifida*, *Thelesperma filifolium* and *Leptochloa dubia*; chosen because they occur in the region and are late-successional species. All species can germinate from spring to fall except *S. calva* and *T. filifolium* which germinate only in spring. Each year new seeds were obtained for the experiment.

Initially, on November 2, 2002, 100 seeds of *L. dubia* were sown in each arena on a 10 cm x 10 cm surface area. This density of seeds approximates high levels in the soil seed bank on the Sonora Research Station (Kinucan 1987). Seeds of *L. dubia* were replaced the following year before fall rainfall occurred (August 3, 2003). Seeds of *E. pinnatifida*, *S. calva*, *V. bipinnatifida*, *T. filifolium* and *L. dubia* (n = 25 per species) were added to arenas

on October 22, 2003 to mimic natural seedfall. An additional mixture of seeds ( $n = 40$  per species) was added on May 23, 2004 because prior environmental conditions failed to produce ample seedling numbers for analyses. This last seed addition represents a 2-fold increase in the known soil seed bank. Each seed addition was placed in a different 10 cm X 10 cm area of the arena.

Seedling establishment was defined as the emergence of first leaves. The number of established seedlings from sown seeds was recorded six times after sufficient rainfall beginning May 1, 2003 until October 22, 2003, when seed would remain dormant until spring, and began again from April 1 to July 10, 2004. Counts of seedlings established from sown seed were ended in July when sufficient numbers of seedlings became established.

Viable seeds could not be visually determined, therefore germination in laboratory conditions was used as an assessment of potential seedling establishment. Twenty-five seeds of each species were germinated in five replicate trays for a total of 125 seeds. Seeds were covered with germination paper and were watered as needed to keep them damp. Germination was defined as the emergence of seedling radicle and data were the proportion of seeds germinating in 14 days.

The number of naturally occurring plants was recorded in July 2003, after sufficient rainfall produced seedlings of natural dicots and grasses, and in May and November 2004 after both spring and fall rainfall periods were completed.

### ***Seed Harvest Experiment***

Percent of total sown seeds harvested by *P. barbatus* were recorded for each species at 20 nests with arena treatments. Eight nests were in burned treatments. Seed harvest was tested by placing 40 seeds (equivalent of  $10,390 \text{ seeds m}^{-1}$ ) in lids 7 cm in diameter; one lid was covered with nylon to prevent ant harvest and the other lid was uncovered to allow ant access to the seed. A pair of covered and uncovered lids was placed inside an enclosure and another pair was placed outside. Seeds were presented to ant foragers for 21 days beginning with the day seeds were sown into arenas for the seedling establishment experiment. Data were the percent of seeds removed.

### **Data Analysis**

A nested design analysis of variance (ANOVA) was used to test differences among treatment means, and the arena was the sample unit. The prescribed burn was conducted in an area large enough to assure several nests would be burned and two randomly assigned areas with zero nest density were burned, therefore ant nest density was nested in burn treatment.

Data were number of established seedlings for each species and, in naturally occurring samples, number of seedlings or young plants for grasses and dicots. Sampling dates after exclosures were positioned were included as a factor in the analysis. Seedling recruitment was low resulting in many instances of zeros in the data, but equalities of variances were improved by log transformation of the data. Only data from July 2004 were used for the sown seed because it was the only date when sufficient numbers of seedlings of *Engelmannia pinnatifida* and *Simsia calva* could be used for ANOVA analyses. The sample sizes of *Leptochloa dubia*, *Verbena bipinnatifida* and *Thelesperma simplicifolium* seedlings remained too low to be used in the ANOVA, however they were included in counts of total species. Contrasts of total and *S. calva* abundance used Least Significance Difference tests. Separate analyses were conducted for seedlings from sown seed and for naturally occurring plants. Data from some naturally occurring species were not normal, even after transformations, therefore non-parametric ANOVA (Kruskal-Wallis) tests were conducted (Zar 1996).

Seed harvest by *P. barbatus* was analyzed with a completely randomized 2 x 2 design ANOVA to compare the proportion of seed removed between arena treatments and lid treatments. Data transformations improved equality of variances and normality for *T. simplicifolium* but, *S. calva* and total seedlings remained non-normal. If seeds fell under lids they were not available and the data were adjusted accordingly.

### **Results**

#### ***Exclosure Experiment - Sown Seed***

Thirty-one percent of the exclosure arenas established seedlings in July 2004 and



open arenas had 21.4%. *Simsia calva* had the highest seedling establishment (27%) in zero nest density treatments. Emergence of seedlings did not occur until rainfall exceeded 5 cm and soils remained moist for several days.

Seedling density was not significantly different between burned and unburned treatments (total seedlings  $F = 3.61$ ,  $p > .06$ ; *S. calva*  $F > 1.92$ ,  $p > .18$  and *Engelmannia pinnatifida*  $F = 2.96$ ,  $p > .11$ ), although trends were lower numbers of seedlings in burned treatments. Burn data were pooled for the remaining analyses. Seedling establishment was significantly higher in exclosures compared to open arenas for all species combined, *S. calva* and *E. pinnatifida* (Table 14, Figure 18). Mean seedling numbers were similar between the arena treatments in zero nest density, indicating that flashing did not affect establishment. Furthermore, nest density significantly changed establishment for total and *S. calva* seedlings (Table 14). Contrasts of total and *S. calva* abundance found significantly more seedlings in the zero nest density treatment compared with either low or high density, suggesting greater seedling establishment in open arenas without the presence of *P. barbatus* compared to open arenas with ants (Figure 18). *Engelmannia pinnatifida* seedlings were not significantly different among nest density treatments.

Additionally, a significant interaction between nest density and arena treatments was observed for total seedlings and *E. pinnatifida* (Table 14). In zero nest density more *E. pinnatifida* seedlings occurred in open compared with exclosure but had the opposite counts in both low and high densities (Figure 18). Total seedlings had greater establishment in exclosures than open treatments where nests were present compared with no differences between arenas in the zero nest density treatment (Figure 18).

Proportion of seeds that germinate under laboratory conditions were high. Mean percent germination for *T. simplicifolium* was 75%, for *V. bipinnatifida* was 70%, for *L. dubia* was 69%, for *S. calva* was 66% and for *E. pinnatifida* was 33%.

#### ***Pogonomyrmex barbatus* Seed Harvest**

Seeds had low percent loss in covered lids that were inaccessible to foraging animals indicating seed loss by factors other than granivory was minimal (Table 15). But, *V.*

Table 14. Effects of ant nest density, burn and arena treatment on number of seedlings m<sup>-1</sup> of *Simsia calva*, *Engelmannia pinnatifida* and all species at the Sonora Research Station. Numbers in parentheses are error d.f.

Source of Variation	df	All Species Establishment		<i>Simsia calva</i> Establishment		<i>Engelmannia pinnatifida</i> Establishment	
		MS	F	MS	F	MS	F
Nest Density	2	9.53	9.95**	5.18	4.99*	0.5	2.48
Arena	1	8.63	9.01*	8.3	7.99*	3.19	15.79*
Nest Density x Arena	2	3	3.14*	2.66	2.56	4.01	19.82**
Error	55	0.76		1.04 (35)		0.20 (11)	

\* p < .05

\*\* p < .001

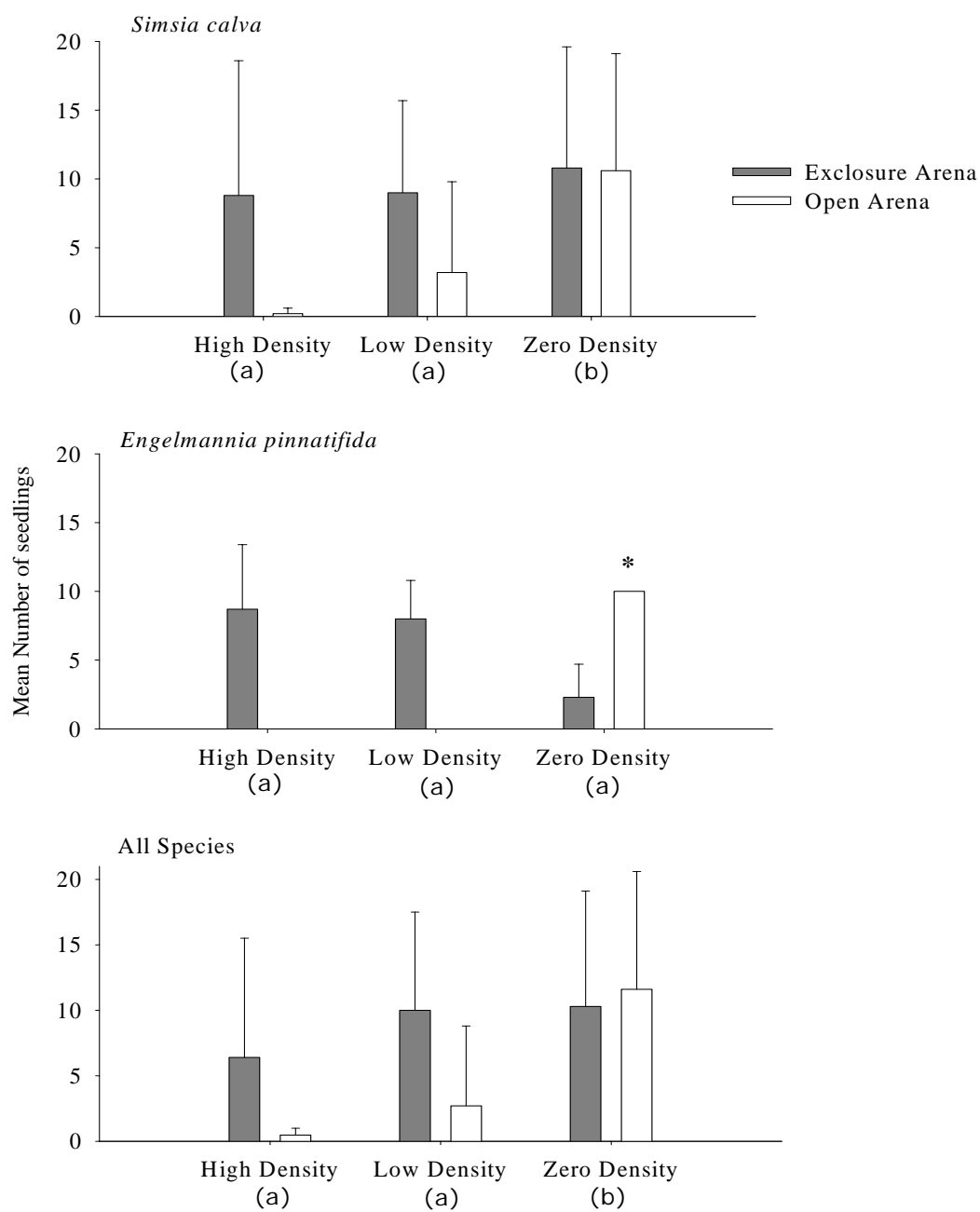


Figure 18. Seedling recruitment from sown seed in ant nest density and arena treatments for *Simsia calva*, *Engelmannia pinnatifida* and all species, July 2004 at the Sonora Research Station. Different letters are significant differences ( $p < .05$ ) for nest density using Least Significant Differences tests. \* indicates data are from one arena. Error bars are S. D.

Table 15. Mean (95% C.I.) percent seed loss by *Pogonomyrmex barbatus* foragers in open arenas compared to other seed losses at exclosure treatments and in covered and uncovered lids at the Sonora Research Station, May 2004. Differences between letters are significant. n = 10 lids per treatment combination.

Species of Seeds	Exclosure		Available	
	Covered Lid	Uncovered Lid	Covered Lid	Uncovered Lid
<i>Leptochloa dubia</i>	15.2 (17.7) <sup>ac</sup>	28.8 (18.9) <sup>bc</sup>	17.3 (24.4) <sup>ad</sup>	81.5 (8.2) <sup>bd</sup>
<i>Verbena bipinnatifida</i>	21.6 (20.0) <sup>ac</sup>	42.8 (19.2) <sup>bc</sup>	50.3 (8.4) <sup>ad</sup>	69.5 (14.2) <sup>bd</sup>
<i>Thelesperma simplicifolium</i>	0.0 (0.0) <sup>ac</sup>	24.0 (23.1) <sup>bc</sup>	9.7 (14.0) <sup>ad</sup>	49.2 (26.3) <sup>bd</sup>
<i>Simsia calva</i>	9.2 (13.7) <sup>ac</sup>	49.6 (26.1) <sup>bc</sup>	11.4 (18.2) <sup>ad</sup>	96.0 (8.0) <sup>bd</sup>
<i>Engelmannia pinnatifida</i>	4.0 (8.9) <sup>ac</sup>	35.2 (18.6) <sup>bc</sup>	0.0 (0.0) <sup>ac</sup>	72.8 (22.7) <sup>bc</sup>

*bipinnatifida* had 21.6% and 50.3% seed losses in enclosure and open arenas, respectively, perhaps due to its flat seeds that may have washed under lids during rainstorms. In uncovered lids enclosures significantly lowered seed loss for four species (*L. dubia*  $F = 14.5$ ,  $p = .001$ ; *V. bipinnatifida*  $F = 8.4$ ,  $p = .007$ ; *T. simplicifolium*  $F = 4.9$ ,  $p = .03$ ; *S. calva*  $F = 9.7$ ,  $p = .004$ ), but not for *E. pinnatifida* ( $F = 0.5$ ,  $p = .47$ ) (Table 15). No differences in percent seed harvest were detected between burned and unburned treatments.

To detect the effect of granivory on seedling establishment in relation to seed germination, the number of seeds harvested by *P. barbatus* was subtracted from the total seed sown and this result was multiplied by the percent of seeds germinating in laboratory conditions. The result was the probability of an individual seed surviving to a seedling under ideal conditions but with granivory. Results ranged from 2.6% for *S. calva* to 38.1% for *T. simplicifolium* (Table 16). Field results were lower for all species except *S. calva* whose percent seedling establishment was equal to probable seedling establishment in low nest densities (Table 16). Where granivory was absent in the zero nest density treatment seedling establishment was much lower than germination reflecting high losses from factors other than granivory such as disease or lack of germination.

#### ***Exclosure Experiment - Natural Seed***

Arenas in the zero nest density treatment were placed at locations at least 50 m from the nearest *P. barbatus* nest. All arenas were placed in similar habitat initially, however, after normal rainfall returned the following year arenas in zero density treatments were discovered to have been placed in habitats that had meager numbers of plant species. Because of this, zero nest density treatments were removed from analyses. Fifteen species of annual dicots, one biannual dicot, 25 perennial dicots, and 14 perennial grasses were found (Table 17). One species of grass that did not survive to identifiable size was included in the counts as unknown grass. The relative abundance of species depended on season and year.

May 2004 had the most seedlings of any sampling period due to favorable

Table 16. Comparison of probable seedling establishment to field establishment from sown seeds in open arenas at the Sonora Research Station, July 2004. Granivory is the mean percent of seed removed from uncovered lids in open arenas. Germination is percent of seeds that germinated in laboratory conditions. Field results are mean percent of seedlings from total seed sown (40 seeds) in open arenas at high, low and zero nest density treatments. Data were pooled for burn treatment.

Species	Granivory (%)	Germination (%)	Probable seedling establishment (%)	Field seedling establishment in nest density treatments (%)		
				High	Low	Zero
<i>Engelmannia pinnatifida</i>	72.8	33.0	9.0	0.0	0	2
<i>Leptochloa dubia</i>	81.5	68.5	12.7	0.2	0	0
<i>Simsia calva</i>	96.0	65.5	2.6	0.2	3	18
<i>Thelesperma filifolium</i>	49.2	75.0	38.1	0.8	0	0
<i>Verbena bipinnatifida</i>	69.5	70.0	21.4	0.2	0	0

Table 17. Plant density of species identified in experimental arenas July 2003, May 2004 and November 2004 at burned and unburned treatments. Density is number m<sup>-1</sup> of seedlings or young plants. November 2004 includes density of adults. Numbers in parentheses are percent of total density. July 2003 treatments were all unburned.

Species	July 2003		May 2004 <sup>1</sup>		November 2004	
	Burned	Unburned	Burned	Unburned	Burned	Unburned
<i>Hilaria belangeri</i>	116.0 (18.4)	65.00	--	--	392.4 (18.5)	536.8 (17.9)
<i>Hedyotis acerosa</i>	--	--	--	--	14.2 (0.7)	295.8 (9.9)
<i>Oxalis drummondii</i>	--	--	--	--	191.0 (9.0)	6.0 (0.2)
<i>Bouteloua trifida</i>	7.0 (1.1)	17.0 (2.7)	--	--	151.3 (7.1)	252.5 (8.4)
<i>Panicum hallii</i>	--	--	--	--	157.8 (7.4)	54.2 (1.8)
<i>Sida abutifolia</i>	11.0 (1.7)	17.0 (2.7)	--	--	122.5 (5.8)	200.0 (6.7)
<i>Aphanostephos skirrhobasis</i>	--	--	--	--	89.5 (4.2)	177.7 (5.9)
<i>B. curtispindula</i>	2.0 (3.3)	29.0 (4.6)	--	--	113.3 (5.3)	174.5 (5.8)
<i>Thelesperma simplicifolium</i>	--	--	0.0	162.7 (1.3)	40.6 (1.9)	168.5 (5.6)
<i>Verbena canescens</i>	--	--	0.0	169.7 (1.4)	57.9 (2.7)	156.9 (5.2)
<i>Aristida</i> species	--	--	0.0	6.7 (0.5)	96.8 (4.6)	108.0 (3.6)
<i>Dyssodia pentachaeta</i>	--	--	--	--	55.0 (2.6)	117.5 (3.9)
<i>Parthenium confertum</i>	--	--	0.0	64.4 (0.5)	74.6 (3.5)	43.5 (1.5)
<i>Erioneuron pilsosum</i>	--	--	--	--	68.3 (3.2)	81.0 (2.7)
<i>Tridens muticus</i>	--	--	--	--	50.7 (2.4)	93.5 (3.1)
<i>Bouteloua hirsuta</i>	4.0 (0.6)	7.0 (1.1)	--	--	3.5 (0.2)	89.5 (3.0)
<i>Ratibida columnaris</i>	83.0 (13.1)	1.0 (0.2)	0.0	7.4 (0.06)	57.5 (2.7)	22.5 (0.8)
<i>Schedonnardus paniculatus</i>	--	--	--	--	57.7 (2.7)	20.0 (0.7)
<i>Stipa leucotricha</i>	--	--	0.0	16.0 (0.1)	55.0 (2.6)	45.0 (1.5)
<i>Croton monanthogynus</i>	4.0 (0.6)	1.0 (0.2)	0.0	2.7 (0.02)	26.3 (1.2)	66.5 (2.2)
<i>Astragalus leptocarpus</i>	--	--	0.0	122.2 (1.0)	28.3 (1.3)	50.0 (1.7)

Table 17. Continued

Species	July 2003		May 2004 <sup>1</sup>		November 2004	
	Burned	Unburned	Burned	Unburned	Burned	Unburned
<i>Digitaria cognata</i>	--	--	--	--	28.2 (1.3)	48.5 (1.6)
<i>Bothriochloa barbinodis</i>	--	--	--	--	11.9 (0.6)	37.5 (1.3)
<i>Dalea nana</i>	6.0 (0.9)	11.0 (1.7)	0.0	7.5 (0.06)	8.4 (0.4)	37.0 (1.2)
<i>Bothriochloa ischaemum</i>	--	--	--	--	25.3 (1.2)	9.5 (0.3)
<i>Mimosa</i> species	--	--	0.0	119.9 (1.0)	0.0	32.0 (1.1)
<i>Eriochloa sericea</i>	--	--	--	--	20.0 (0.9)	0.0
<i>Solanum elaeagnifolium</i>	--	--	--	--	17.0 (0.8)	0.0
<i>Hedeoma drummondii</i>	32.0 (5.1)	21.0 (3.3)	0.0	36.2 (0.3)	14.5 (0.7)	13.2 (0.4)
<i>Xanthocephalum sarothroe</i>	--	--	0.0	1.7 (0.01)	0.0	20.5 (0.7)
<i>Rhynchosia texana</i>	--	--	--	--	12.0 (0.6)	7.0 (0.2)
<i>Hymenoxys oderata</i>	--	--	0.0	81.9 (0.7)	10.0 (0.5)	0.0
<i>Abutilon incanum</i>	--	--	0.0	7.0 (0.06)	5.5 (0.3)	7.5 (0.3)
<i>Panicum obtusum</i>	4.0 (0.6)	4.0 (0.6)	--	--	1.0 (0.1)	0.0
<i>Zexmenia hispida</i>	--	--	--	--	0.0	4.0 (0.1)
<i>Plantago helleri</i>	--	--	0.0	7303.4	--	--
<i>Plantago rhodosperma</i>	--	--	0.0	2033.6 (16.6)	--	--
<i>Chaetopappa asteroides</i>	59.0 (9.3)	18.0 (2.8)	0.0	291.6 (2.4)	--	--
<i>Phlox drummondii</i>	10.0	33.0 (5.2)	--	--	--	--
<i>Chaetopappas bellidifolia</i>	--	—	0.0	574.2 (4.7)	--	--
<i>Evax verna</i>	--	--	0.0	565.8 (4.6)	--	--
unknown grass seedlings	28.0 (4.4)	12.0 (1.9)	--	--	--	--



Table 17. Continued

Species	July 2003		May 2004 <sup>1</sup>		November 2004	
	Burned	Unburned	Burned	Unburned	Burned	Unburned
<i>Scutellaria drummondii</i>	6.0 (0.9)	4.0 (0.6)	0.0	19.0 (0.1)	--	--
<i>Erodium texanum</i>	--	--	0.0	75.1 (0.6)	--	--
<i>Gilia rigidula</i>	--	--	0.0	50.0 (0.4)	--	--
<i>Oenothera speciosa</i>	1.0 (0.2)	1.0 (0.2)	0.0	9.9 (0.08)	--	--
<i>Gaillardia mexicana</i>	--	--	0.0	12.7 (0.1)	--	--
<i>Salvia texana</i>	--	--	0.0	11.0 (0.09)	--	--
<i>Krameria lanceolata</i>	--	--	0.0	7.0 (0.06)	--	--
<i>Oenothera missouriensis</i>	--	--	0.0	7.0 (0.06)	--	--
<i>Thamnosma purpurea</i>	--	--	0.0	5.3 (0.05)	--	--
Total Density	392.0 (62.0)	241.0 (38.0)	0.0	12,245.9 (100)	2,128.9 (41.7)	2,976.6 (58.3)

<sup>1</sup> A prescribed burn was conducted March 10, 2004.

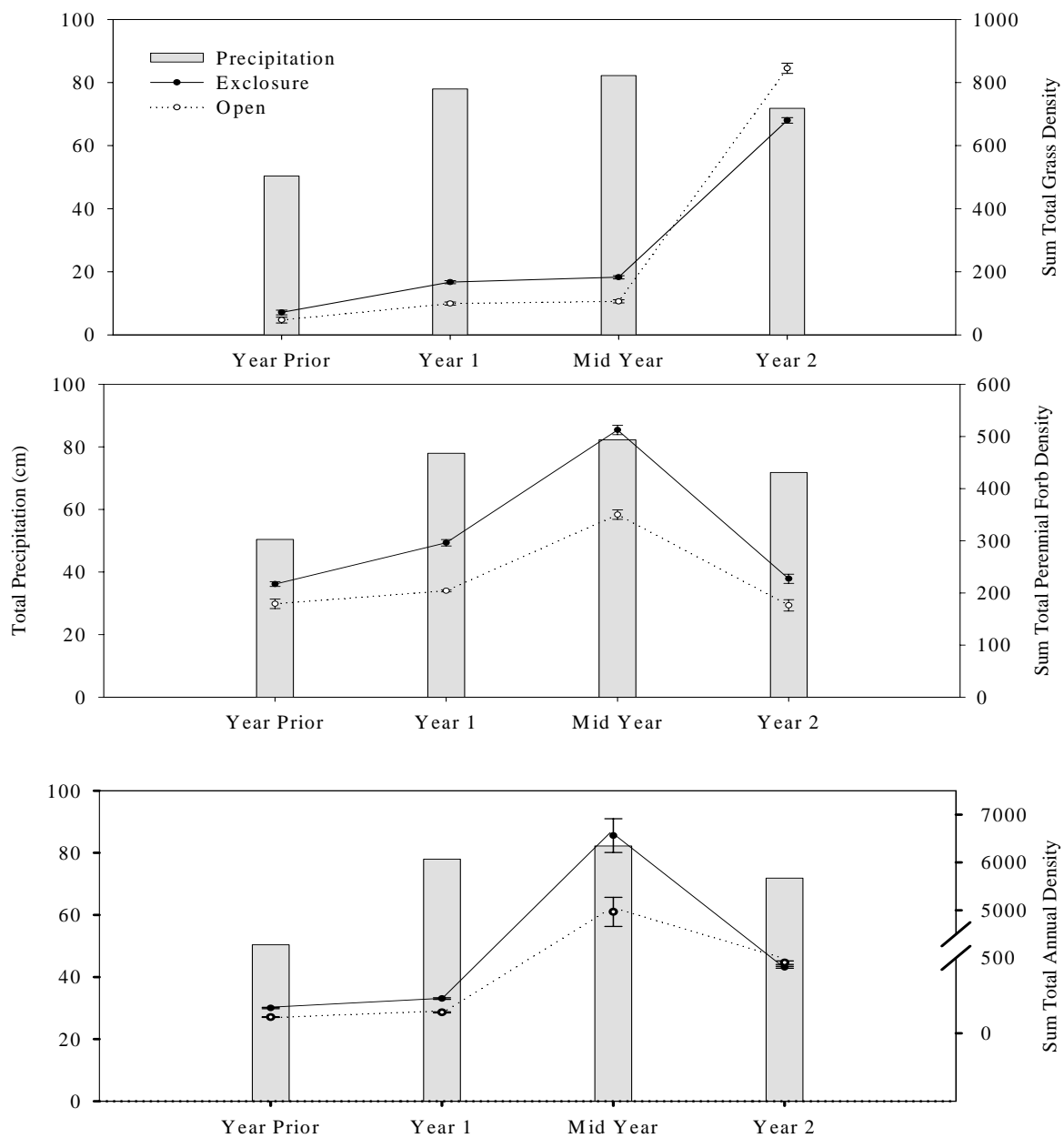


Figure 19. Sum of total perennial grass, perennial dicot and annual dicot density (number m<sup>-1</sup>) in unburned treatments at the Sonora Research Station, 2002-2004. Year Prior is sampling date October 2002, Year 1 is July 2003, Mid Year is May 2004 and Year 2 is November 2004. Note: Density scale varies among graphs.

temperatures and rainfall, with *Plantago helleri* and *P. rhodosperma* the dominant species (Table 17; Figure 19). July 2003 found *Hilaria belangeri* and *Ratibida columnaris* the dominant species. In November 2004, *H. belangeri* remained dominant but co-dominant species emerged including, *Bouteloua trifida*, *Hedyotis acerosa* and *Oxalis drummondii*. Due to plant composition differences between seasons, May 2004 was analyzed separately.

Significantly higher densities of seedlings were found in November 2004 compared with July 2003 for total seedlings, *Hilaria belangeri* and *Sida abutifolia* (Table 18). Seedling survivorship probably occurred after the experiment began because rainfall was above average leading to greater seed production in 2003 and consequently higher numbers of seedlings in May and November 2004. Results were pooled into three functional groups, grasses, perennial dicots and annual dicots to observe establishment patterns between years. Grass density increased slightly the first year and abundantly the second (Figure 19). Perennial dicot density was highest in May 2004, but decreased by November possibly due to July drought conditions or negative competitive effects with perennial grasses. Favorable growing conditions were especially evident in annual dicot densities in May 2004. Compositional differences in annuals between May and November account for the reduction in seedlings in November 2004, but they could also be reduced due to competitive effects with perennial grasses.

A qualitative assessment determined that results of the prescribed burn resembled other winter burns at the Sonora Research Station in patchiness and intensity (Taylor, pers. observation). All seedlings were blackened or destroyed and no further recruitment occurred during the spring season (Table 17). More seedlings occurred in the unburned burn ( $F = 4.36$ ,  $p < .05$ ; Table 17).

Out of a total of 57 species that established seedlings by November, 15 species were analyzed for burn treatment effects because sample sizes were large enough for a nested ANOVA (ant nest density nested in burn treatment). Burn treatment significantly reduced seedling establishment in two dicots, *Verbena canescens* ( $F = 26.65$ ,  $p < .05$ ) and

Table 18. Number of seedlings  $m^{-1}$  of *Hedeoma drummondii*, *Hilaria belangeri*, *Sida abutifolia* and all species for the 2 X 2 X 2 factorial ANOVA randomized block design at the Sonora Research Station in July 2003 and November 2004. None of the burn treatments were significant therefore data were pooled to increase sample sizes. Individual species data were pooled for ant nest density because not all treatment combinations had sufficient sample sizes. Numbers in parentheses are error d.f.

Source of Variation	df	Total of All Species establishment		<i>Hedeoma drummondii</i>		<i>Hilaria belangeri</i>		<i>Sida abutifolia</i>	
		MS	F	MS	F	MS	F	MS	F
Year (Block)	1	23.5	536.99**	0	0	54.8	66.23**	0.71	19.99**
Arena	1	0.27	6.23*	2.05	5.96*	1.38	1.67	0.13	3.76†
Nest Density	1	0	0.22	--	--	--	--	--	--
Nest Density x Arena	1	0	0.05	--	--	--	--	--	--
Error	153	0		0.34 (51)		0.83 (117)		0.003 (71)	

\*  $p < .05$

\*\*  $p < .001$

†  $p = .056$

*Thelesperma simplicifolium* ( $F = 29.86$ ,  $p < .05$ ), and one perennial grass, *Bouteloua trifida* ( $F = 55.94$ ,  $p < .05$ ). Burn treatment did not effect any of the other 12 species analyzed.

No significant difference was detected in establishment between low and high nest density treatments in July 2003 and November 2004 (Table 18). However, in May total species and *Plantago helleri* seedlings were significantly greater in high nest densities compared to low (Table 19).

Exclusion from ant foragers caused significant differences in total seedling establishment only after the first year, in July 2003 (Table 18). This was primarily caused by greater perennial forb establishment in exclosures compared to open arenas (Figure 19). During May 2004, higher establishment occurred inside exclosures but this difference was not significant (Table 19; Figure 19). However, by November 2004 greater grass and annual dicot densities were found in open arenas rather than exclosures. Seedling densities in July 2003 and November 2004 were significantly higher in exclosures for *Hedeoma drummondii* and *Sida abutifolia*, an annual and a perennial dicot, respectively (Table 18). *Scutellaria drummondii* only produced seedlings in July 2003 and had significantly more seedlings inside compared to outside exclosures (Kruskal-Wallis  $H = 11.77$ ,  $p = .001$ ).

In May 2004 data were sufficient for comparisons between nest density and arena treatments for all seedlings and six species. Significantly higher seedling densities of *P. helleri* and *Salvia texana* were recorded inside exclosures (Table 19). Furthermore, a significant interaction was observed for *Verbena canescens*, an annual dicot, with exclosures causing increased seedlings in low nest density compared with high density, but open arenas had the opposite affect.

## Discussion

Seed predation by *Pogonomyrmex barbatus* reduce seed number leading to lower seedling emergence of summer dicots during the first year of drought recovery than during subsequent years, and that the effect of seed predation on seedling establishment is species-dependant. Consequently, the hypothesis that seedling establishment would be comparable between presence and absence of seed predators was rejected. The results of this study

Table 19. Number of seedlings m<sup>-1</sup> species for the 2 X 2 factorial ANOVA randomized block design at the Sonora Research Station in May 2004. All data in the burn treatment were 0, therefore data were pooled in unburned treatment to increase sample sizes. Numbers in parentheses are error d.f.

Source of Variation	df	Total of All Species		<i>Plantago helleri</i>		<i>Daucus pusillus</i>		<i>Verbena canescens</i>		<i>Thelesperma simplicifolium</i>	
		MS	F	MS	F	MS	F	MS	F	MS	F
Arena	1	1.23	1.82	10.06	3.58*	0.36	0.01	0.19	0.30	38.87	0.81
Nest Density	1	16.78	24.88**	34.16	12.14**	9.92	0.36	0.80	1.25	95.45	1.99
Arena x Nest Density	1	0.001	0.02	0.002	0.006	47.15	1.71	3.53	5.49*	21.67	0.45
Error	34	0.67		2.82 (32)		27.58 (24)		0.64 (26)		47.87 (20)	

\*\* p < .001

\* p < .07

Table 19. Continued.

Source of Variation	<i>Astragalus leptocarpus</i>		<i>Salvia texana</i>	
	df	MS	F	Kruskal-Wallis H
Arena	1	25.08	0.70	6.05*
Nest Density	1	0.15	0.004	0.03
Arena x Nest Density	1	0.19	0.005	--
Error	34	35.81 (18)		(10)

\*\*  $p < .001$

\*  $p < .07$

support observations that ant predation effects seedling establishment in grasslands (Hobbs 1985, Reader and Beisner 1991, Peters et al. 2005). However, Brown and Human (1997) found no differences in seedling establishment when ants were excluded due to either low harvest rates or need for longer studies to observe small, cumulative responses. Indeed, this study could have found additional, commutative changes to vegetation dynamics with more time and with more climate variability.

Greater seedling establishment recorded inside exclosures could be due to improved microclimate conditions. Yet, in the zero nest treatments seedling establishment of sown seed was similar between inside and outside exclosures. Higher plant cover was observed just inside the perimeter of the exclosures (approximately 20 cm wide), but these places were eliminated from natural seed counts and were unused for sown seed plots. Thus, seedling recruitment inside exclosures was not likely due to improved conditions for establishment.

Indirect effects of seed predation were observed for grasses and annual dicots due to reduction of intense competition in the open arenas. High densities of dicots found in the exclosures in May 2004 (the result of a mild, wet spring) may have reduced both survivorship and seedling establishment of grasses and annual dicots leading to lower densities inside the exclosures. In open arenas the reduction of seeds by *P. barbatus* alleviated competition between grasses and dicots allowing greater numbers of their seedlings to survive.

This study's findings support two observations, first that high dicot abundance in winter and spring at the Sonora Research Station contributes to decline in grass abundance. Perhaps due to competition with previously established, larger, dicots for limited rainfall in early summer or to nutrients, space and light. Second, the indirect consequence of granivory by competitive release effects agree with studies of harvester ants in deserts. Reduction of the most abundant species of winter annual increased diversity by allowing fewer competitive species to establish (Brown et al. 1979, Samson et al. 1992).

Burn treatments were not significantly different for sown seed indicating that microhabitat conditions were unchanged for seedling germination and establishment, thus



accepting the hypothesis that fire resulted in comparable densities of seedlings. These results agree with research conducted in semi-arid grasslands (Gillespie and Allen 2004, Snyman 2004). In contrast, other studies found more dicot seedlings in burned compared to unburned plots due to increased survival of seedlings (Maret and Wilson 2000, Yates and al 2003). Lesica (1999) showed fire removed grass litter which increased dicot survivorship.

Fire killed naturally occurring seedlings and seedling density remained depressed through November 2004, however seedling abundance in nest density and arena treatments were unaffected. This suggests that ant foraging behavior was unchanged.

The effects of *P. barbatus* seed predation on seedling establishment were overshadowed by weather conditions (Figure 19). Improved recruitment of the sown species was associated with increased rainfall and natural seedling establishment increased during the study due to above-average rainfall and moderate temperatures. These observations are consistent with other studies in semi-arid regions, thus confirming the importance of soil moisture, temperature and season for seedling recruitment of Edwards Plateau dicots (Guterman 1993, Cheplick 1998, Petru and Menges 2003). The results of this study add evidence to the findings of Wilby and Shachak (2004) that changes in harvester ant effects on vegetation dynamics among years are due to varying climatic conditions.

Relative density of *P. barbatus* colonies did not affect seedling establishment, perhaps because foraging areas are disjunct even when nests are closely spaced together. The average distance between nests was roughly 14 meters. Since foragers can travel up to 30 m potential foraging areas overlap (Chapter III). *Pogonomyrmex barbatus* are territorial, often fighting over foraging areas (Gordon 1995, Gordon and Kulig 1996, Gordon 1999) and in this study colonies presumably protected their foraging areas. Seed harvest rates equalized because foraging areas were divided among colonies regardless of local nest density.

Excluding seed predators significantly increased the number of established seedlings for 13% of species either sown or naturally occurring, supporting findings that harvester ants select among seed species and can have larger effects on those they prefer. Harvest was greater than 50% for seeds of all sown species indicting possible selection for them by *P.*

*barbatus* foragers. Two explanations are hypothesized, first sown seed density represents a two-fold increase in the known soil seed bank (Kinucan 1987), thus, seeds were sown as high density patches and might be highly sought by foragers. Intensity of foraging by a colony is affected by seed abundance (Holldobler 1976, Rissing and Wheeler 1976, Gordon 1991, Lopez et al. 1993). Second, these are late-successional species with large seeds. Harvester ants typically select heavier seeds.

Selection among species was possible because species affected by seed predation had no known common traits. Both common (*Sida abutifolia* and *Verbena canescens*) and rare (*Salvia texana*) species were chosen (Table 17). Harvester ants could influence plant community structure by differentially selecting some species over others (Hobbs 1985, Crist and MacMahon 1992). In addition, seed predation may indirectly reduce interspecific competition resulting in increased numbers of rarer species (Brown et al. 1979, Inouye et al. 1980). Thus, reduction of the abundant *S. abutifolia* and *V. canescens* may account for increased densities of other species, however further study is needed to demonstrate this effect or its relative importance to interspecific competition at Sonora Research Station.

Results of exclosure experiments differed from results of seed harvest experiments for sown seed. Although *E. pinnatifida* seedlings were denser inside exclosures, harvest rates did not differ between arena treatments. The discrepancy could be due to the shorter duration seeds were presented in the harvest experiment compared with the longer time seeds were available in the exclosures. The latter allowed greater opportunities for foragers to find *E. pinnatifida* seeds. Discrepancies between the two experiments for *V. bipinnatifida*, *L. dubia* and *T. simplicifolium* were complicated by the lack of seedling establishment in zero nest density where the habitat differed from the remainder of the study site.

Probability of an individual seed surviving to a seedling was estimated to range from 2.6% for *S. calva* to 38.1% for *T. simplicifolium*. However, field results were considerably lower for all species, due to microsite variability for suitable recruitment sites (Harper 1977). Differences in species richness and seedling density were variable between nest locations, probably owing to heterogeneity caused by abrupt changes in soil depth, rockiness and

texture (Smeins and Merrill 1988, Fuhlendorf and Smeins 1998).

*Pogonomyrmex barbatus* seed predation was a small driver on this ecosystem during the study, altering seedling density only after drought and only for 13% of dicot species. However, seed predation may cause notable indirect effects of competitor release. Grasses and annual dicots can coexist in this grassland even under intense competition, but they benefit when seed abundance is reduced by granivory. Nonetheless, spatial variability in seedling densities was high despite forager access. Rainfall drives the germination of seeds, increases survivorship and seed production while competition appears to effect seedling survivorship and establishment. *Pogonomyrmex barbatus* role in seedling establishment may occur under certain climatic conditions and their large-scale and long-range influence could be of equal weight to already existing heterogeneity or could be additive.

## CHAPTER VI

### RED HARVESTER ANT (*POGONOMYRMEX BARBATUS*) EFFECTS ON GRASS DYNAMICS IN A SEMI-ARID SAVANNA

#### Introduction

Biotic interactions between plants and animals at any stage in vegetation dynamics are important in structuring vegetation communities, however the relative influence of these interactions is less understood. Plant populations are the result of a series of population dynamic processes: seed immigration, seed germination, seedling establishment, plant growth and mortality of individuals (Harper 1977, Crawley 1986). Seed-harvesting ants of the genus *Pogonomyrmex* can affect processes in two ways; by the differential collection of seed species and by the creation of nests that become patches of unique soils for plants (Brown et al. 1979, Hobbs 1985, Rissing 1988, Crist and MacMahon 1992, Whitford and DiMarco 1995, Cloudsley-Thompson 1996, Brown and Human 1997, Wagner et al. 1997).

Several species in this genus create bare soil disks of approximately one-meter in diameter by clearing all vegetation on their nests (Rissing 1988, Whitford and DiMarco 1995, Wagner et al. 1997, MacMahon et al. 2000) and plants encircling the disk tend to be larger than those in surrounding habitats (Golley and Gentry 1964, Wight and Nichols 1966, Rissing 1986, Whitford 1988, Soule and Knapp 1996). In addition, nests may act as drought refugia for grasses. During a severe drought, grasses were observed to survive longer near disk margins and, when the drought ended, to recover faster than grasses in nearby habitats (Chapter II).

Seed densities may be greatly reduced by post-dispersal seed harvesters that result in modified plant populations (Harper 1977). Harvester ants collect post-dispersal seeds from herbaceous species as a food source, and, colonies can remove nearly 100% of preferred seed species (Polis 1991, Crist and MacMahon 1992). Seed predation (granivory) influences recruitment and population densities of plants (Brown et al. 1979, Davidson et al. 1984,

Hobbs 1985, Rissing 1986). The combined effect of granivory and nest construction processes is unclear and rarely studied. Brown and Human (1997) found changes in plant communities at the nest, but not in surrounding habitat. Similarly, Peters et al (2005) found differing plant communities at the nest compared to surrounding habitat, but, density of approximately 25% of all species declined as a function of distance (maximum of 210 cm) from the nest and 25% increased. Thus, *Pogonomyrmex* species may cause significant changes in the dynamics of plant communities by creating two types of zones; (1) foraging and (2) nests with disks. The spatial extent and intensity of effect on plant population dynamics from each zone type could vary. Nevertheless, the simultaneous tasks of foraging and nest construction occur in an ant multiple tasks zone at the nest.

A few species of *Pogonomyrmex* occur in North American savannas, which are highly dynamic ecosystems largely controlled by a disturbance regime of extremes and variability of precipitation, frequent fires, and large mammalian herbivory (Amos and Gehlbach 1988, Smeins and Merrill 1988, Bazzaz 1996, Fuhlendorf and Smeins 1997, Frost 1998, Fuhlendorf et al. 2001). Climate extremes are the dominant, large-scale disturbance affecting vegetation change on the Edwards Plateau, Texas (Smeins and Merrill 1988, Fuhlendorf and Smeins 1997). Droughts reduce basal area of individual grasses, reduce populations of large bunchgrasses and perennial forbs, allow early successional species to fill gaps formed by the die-off, and change the dominant species to ones that are more drought-resistant. The extent to which the dynamics of these savannas may be further modified by *Pogonomyrmex* activities is unknown. This study focused on the interaction of granivory and presence of disk margin on the dynamics of grass species subject to a gradient of rainfall amounts. *Pogonomyrmex barbatus*, red harvester ant, is one of the few species of seed harvesting ants that build large, cleared disks on the nest and are capable of harvesting a large number of seeds (Rissing 1988, Whitford and DiMarco 1995, Wagner et al. 1997). It occurs in the grassland matrix of savannas on the Edwards Plateau, Texas. Nests have a grass dominated margin surrounding the disk approximately one m from the nest entrance (Chapter III) This species is known to collect a variety of seeds, including many

species of grasses (Gordon 1993, Tabor 1998). Both activities differ in spatial extent, with nest construction affecting plants within 1 m of the nest and foraging effecting seed populations from nest entrance to 10 m away. As distance from the nest increases preference for seeds change, for example non-preferred seeds are selected less.

The objective of the simulation model is to determine the long-term dynamics of grass populations before, during and after *P. barbatus* colony establishment and hence modified by foraging and nest construction under variable rainfall at three zones from the nest, tasks zone, foraging zone (both with seed harvest) and unoccupied zone (Figures 20 and 21). The model (Figure 22) is used to test the following hypotheses;

- (1) density of *Bouteloua curtipendula* and *Hilaria belangeri* increases at the tasks zone during colony maturity (Figure 20A and B between m and d) and decreases when the colony dies (Figure 20A and B at d) with normal and low rainfall treatments, but remain unchanged in high rainfall (Figure 20A and B). A third species, *Stipa leucotricha*, will decrease at the tasks zone (Figure 20C between m and d). During colony maturity, seed harvest effects are highest at the tasks zone, variable depending on species in the foraging zone (Figure 20D) and nonexistent in the unoccupied zone (Figure 20E), and
- (2) during colony maturity, grass density is higher at the tasks zone compared with the other two zones for *Bouteloua curtipendula* and *Hilaria belangeri* and lower for *Stipa leucotricha*.

## **Background Information**

### ***Study Area***

The study was conducted at the Texas A&M University Agricultural Research Station, Sonora (elevation 735 m), Edwards Plateau, Texas (31 18'N; 100 28'W). Vegetation is potentially a mixed-grass, savanna parkland dominated by groves of *Quercus virginiana*, *Q. pungens* var. *vaseyana*, *Juniperus ashei* and *J. pinchotii* in a matrix of mid- and short-grass species (Kuchler 1964, Smeins and Merrill 1988, Hatch et al. 1990). Grassland at the study site is dominated by the grasses *Bouteloua curtipendula*, *Stipa leucotricha*, *Hilaria*

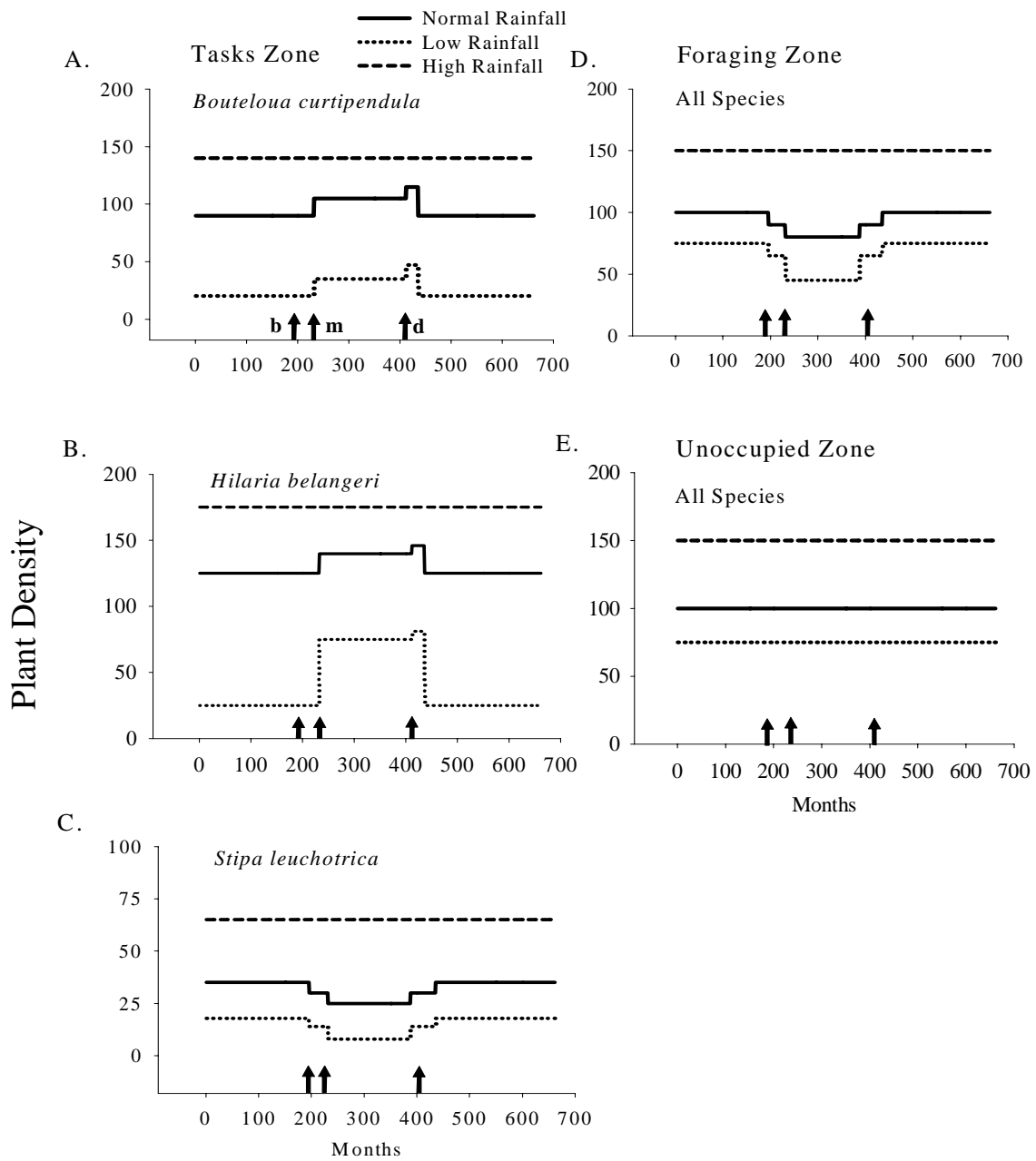


Figure 20. Expected patterns of the effects of *Pogonomyrmex barbatus* on adult number of plants  $\text{m}^{-1}$  of *Bouteloua curtipendula*, *Hilaria belangeri*, and *Stipa leucotricha* at three zones under three rainfall regimes over a time period encompassing colony establishment (b), maturation (m) and death (d). Arrows indicate the month the colony matures and the month dies.

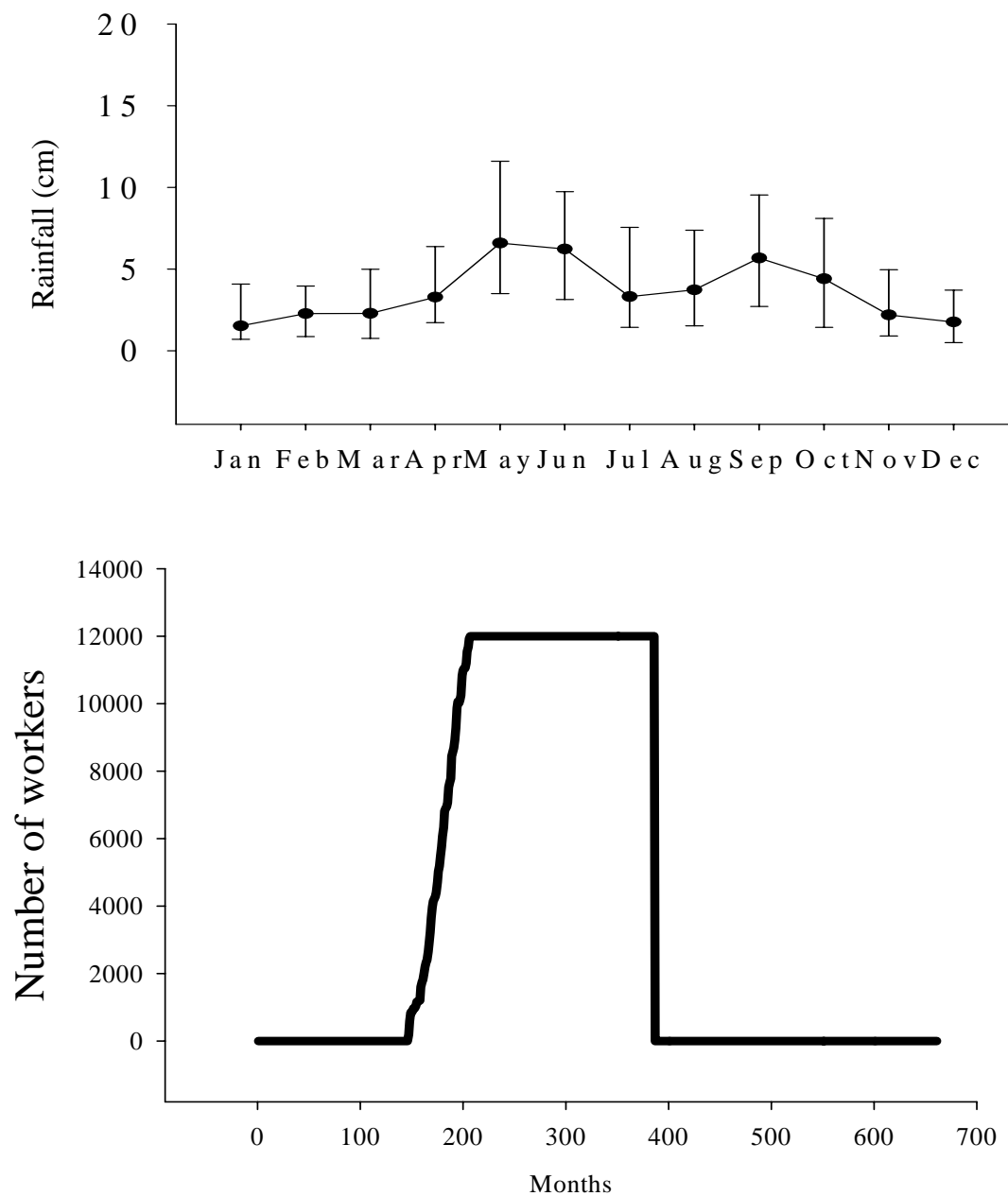


Figure 21. Conceptual pattern of *Pogonomyrmex barbatus* colony growth showing the number of ants varying with colony age (Gordon 1993). Median (inter-quartile range 25% above and 75% below) historical monthly rainfall (cm) patterns at the Sonora Research Station from 1919-2004.



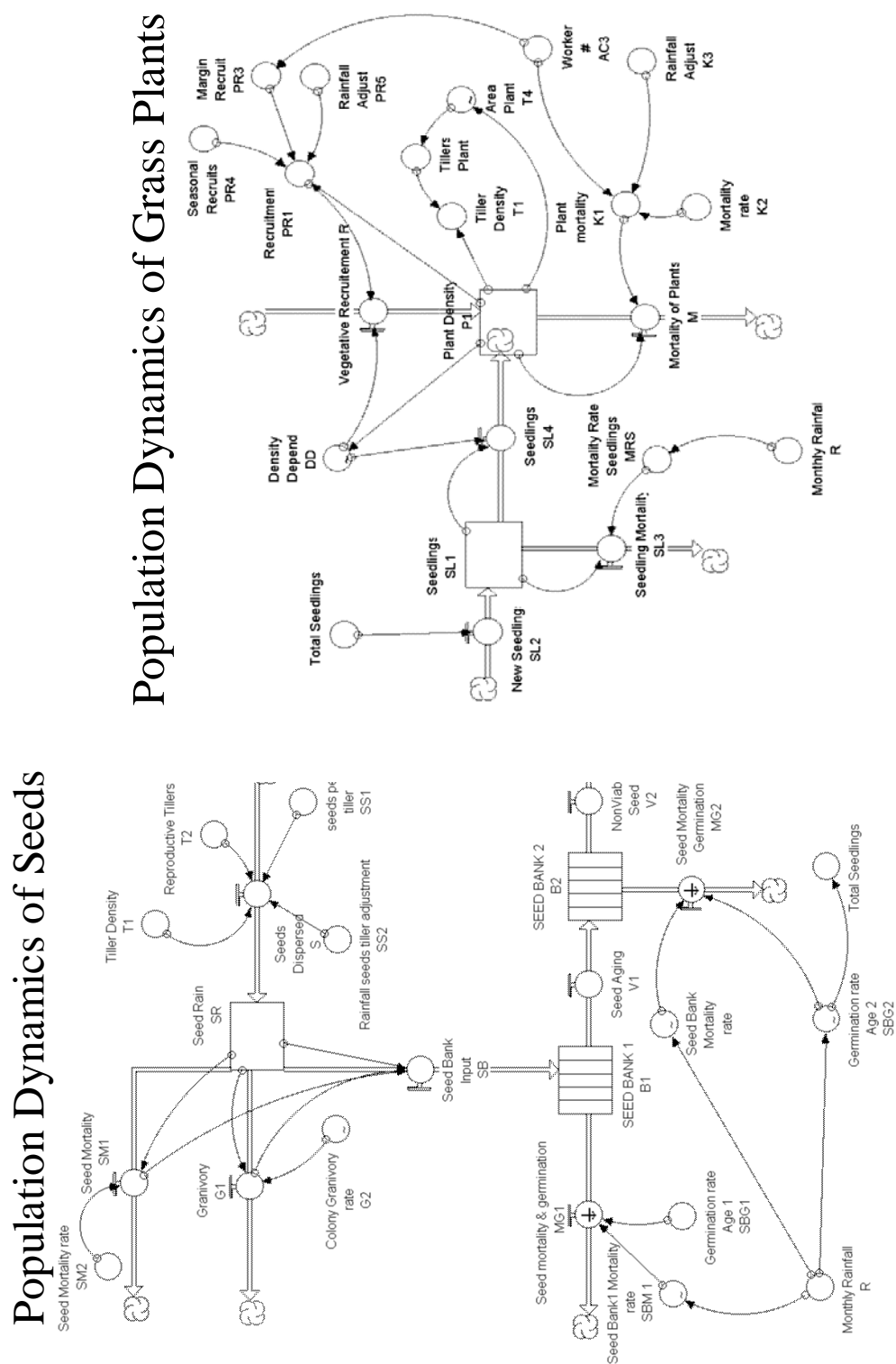


Figure 22. Conceptual model representing the effects of *Pogonomymex barbatus* activity at three zones and under three rainfall treatments on adult density of *Bouteloua curtipendula*, *Hilaria belangeri*, and *Stipa leucotricha*.

*belangeri* and *Bouteloua trifida*. The main periods of grass and dicot seed production occur in June and October.

Grass density data for the study were used from field experiments conducted in 32.0 ha<sup>-1</sup> pastures of two grazing treatments, one treatment with a 55-year history of sheep grazing at light, 16 AUM (one AUM is the monthly demand rate of oven-dry forage for an animal at 12 kg/day (Group 1988)) and another treatment of three replicate pastures at moderate, 32 AUM. In 1983 the entire Sonora Research Station's stocking rates were reduced to 16 AUM. The climate is continental and semi-arid with a bimodal distribution (peaks in May and September) of growing season rainfall (Figure 21A). Average annual precipitation (1919-2004) is 57.5 cm, but variability between years is great with a range of 35.7 cm and standard deviation of 5.1 cm (Station Records). Temperatures average 30<sup>o</sup> C in July and 9<sup>o</sup> C in January (Station Records).

#### ***Data Collection Methods***

Plant density data used to parameterize and evaluate the model were collected intermittently in 22 years from 1949-2002 from the moderate grazing treatment. Data from *P. barbatus* tasks zones and foraging zones were collected from the lightly grazed treatment four times from 2002 to 2003, including one sample for densities of grass seedlings (Chapter IV). Remaining data on plant population demography were collected from the literature and expert opinion (Tables 20, 21 and 22).

Data for the proportion of seeds collected by *P. barbatus* are from a study conducted to determine seed preference at the Sonora Research Station (Chapter IV). Rates of granivory on *S. leucotricha* seeds were assumed to be as high as *B. curtipendula* from observations at the Sonora Research Station. Data on *P. barbatus* life history are from research conducted in the desert (Gordon 1993, Gordon 1995, 1999).

During the drought (June 2002), *B. curtipendula* and *H. belangeri* had twice and three times, respectively, greater densities of adults on *P. barbatus* disk margins compared

Table 20. Parameters for *Bouteloua curtipendula* used in the simulation model. § maximum plants.

Parameters	Mean (S.D.)	Source	Varies W/Rainfall	Source
Number of seeds/tiller (SS1)	33 (17.5)	(Hendon and Briske 1997)	Figure 26	none
Reproductive tillers/tillers (T2)	10%	(Hendon and Briske 1997, Mitchell et al. 1998)	no	N/A
Seed mortality rate (SM2)	92%	(Kinucan 1987)	no	N/A
Seed bank mortality (SBM!)	45%	(Marone et al. 2000)	linear from (0 cm, 0 rate) to (14 cm, 0.45 rate) then level	(Marone et al. 2000)
Seed germination rate (SBG2)	15% (127)	(Kinucan 1987)	0.5% drought 0.0% = 0 cm	(Abbott and Roundy 2003)
Seedling mortality (MRS)	20%	none	Figure 25	none
Seasonal plant recruitment (PR4)	40% (60)	(Hendrickson 1996)	Figure 24	(Briske and Hendrickson 1998)
Density dependant Recruitment (DD)	624 <sup>§</sup> Figure 23	Station Records	no	N/A
Plant mortality (K1)	- 8.0% Tasks Zone -7.8%	none Tasks Zone- Chapter III	linear from (0 cm,0.2 rate) to (4 cm, 0.0 rate) then level	Smeins pers comm
Relative recruitment at Tasks Zone (PR3)	1.3x recruitment	Chapter III	1.0x recruitment <2 cm	none
Granivory Rate (G2)	- Mar-Jul 8 (21) - Aug-Nov 8 (11)	Chapter IV	relative rate = 0.0 + 0.001(worker density)	(Gordon and Kulig 1996)

Table 21. Parameters for *Hilaria belangeri* used in the simulation model. § maximum plants.

Parameters	Mean (S.D.)	Source	Varies W/Rainfall	Source
Number of seeds/tiller (SS1)	5(17.5)	(Scholl 1994)	Figure 26	none
Reproductive tillers/tillers (T2)	10%	(Scholl 1994, Hendrickson 1996)	no	N/A
Seed mortality rate (SM2)	60%	(Kinucan 1987)	no	N/A
Seed bank mortality (SBM1)	45%	(Marone et al. 2000)	linear from (0 cm ,0 rate) to (14 cm, 0.45 rate) then level	(Marone et al. 2000)
Seed germination rate (SBG2)	12% (127)	(Kinucan 1987)	0.1% dry 0.0% =0 cm	(Abbott and Roundy 2003)
Seedling mortality (MRS)	20%	none	Figure 25	none
Seasonal plant recruitment (PR4)	9% (60)	(Scholl 1994)}	Figure 24	(Bullock and al 1994)
Density dependant recruitment (DD)	433 <sup>§</sup> Figure 23	Station Records	no	N/A
Plant mortality (K1)	- 3% Tasks Zone-2.3%	(Busso and Richards 1995) Tasks Zone- Chapter III	linear from (0 cm,0.03 rate) to (4 cm, 0.0 rate) then level	Smeins pers comm
Relative recruitment at Tasks Zone (PR3)	1.6x recruitment	Chapter III	1.0x recruitment <2 cm	none
Granivory rate (G20)	Mar-Jul-7 (6) Aug-Nov- 6 (19)	Chapter IV	relative rate = 0.0 + 0.001(worker density)	(Gordon and Kulig 1996)

Table 22. Parameters for *Stipa leucotricha leucotricha* used in the simulation model. § maximum plants.

Parameters	Mean (S.D.)	Source	Varies W/Rainfall	Source
Number of seeds/tiller (SS1)	4 (25)	(Fowler and Clay 1995)	Figure 26	none
Reproductive tillers/tiller (T2)	40%	(Fowler and Clay 1995)	no	N/A
Seed mortality rate (SM2)	80%	(Kinucan 1987)	no	N/A
Seed bank mortality (SMB1)	45%	(Marone et al. 2000)	linear from (0 cm, 0.0 rate) to (14 cm, 0.45) then level	(Marone et al. 2000)
Seed germination rate (SBG2)	40% (150)	(Kinucan 1987)	0.1% dry 0.0% = 0 cm	(Abbott and Roundy 2003)
Seedling mortality (MRS)	77%	(Fowler and Clay 1995)	Figure 25	none
Seasonal plant recruitment (PR4)	6% (13)	(Busso and Richards 1995, Fowler and Clay 1995)	Figure 24	(Busso and Richards 1995)
Density dependant Recruitment (DD)	178 <sup>§</sup> Figure 23	Station Records	no	N/A
Plant mortality (K1)	- 3% Tasks Zone- 3.25%	(Busso and Richards 1995) Chapter III	linear from (0.0 cm, 0.03 rate) to (4.0 cm, 0.0 rate) then level	Smeins pers comm
Relative recruitment at Tasks Zone (PR3)	0.37x recruitment	Chapter III	0.35x recruitment < 2 cm	none
Granivory rate (G20)	Mar-Jul-18 (21) Aug-Nov-8 (11)	Chapter IV	relative rate = 0.0 + 0.001(worker density)	(Gordon and Kulig 1996)

with adjacent habitat, and *S. leucotricha* had a similar density between the two areas (Chapter III). These relative differences were used to calculate the mortality rates of these species in the tasks zone, otherwise normal rates were used at foraging and unoccupied zones. During a normal rainfall year (August 2003) disk margin densities were 2.5 and 0.5 times greater than the foraging zone for *B. curtipendula* and *H. belangeri*, respectively, but 10 times less for *S. leucotricha* (Chapter III). These relative differences were used to calculate vegetative production rates in the tasks zone.

Normal, monthly stochastic rainfall is selected from the cumulative, historical monthly distribution of rainfall at the Sonora Research Station from 1919-2004 (Station Records; Figure 21A). Variables that are stochastic are normally distributed and truncated to zero.

### ***Grass Ecology***

Important variables in the system include sexual and vegetative reproduction in grasses. Changes in plant density are effected by natality and mortality of seeds and seedlings and these are dependant on rainfall. Three perennial grass species were used in the model, *Bouteloua curtipendula* (sideoats grama), *Hilaria belangeri* (curly mesquite) and *Stipa leucotricha* (Texas wintergrass). They were chosen because of their importance to the rangelands of the Edwards Plateau. *Bouteloua curtipendula* and *S. leucotricha* are late-successional bunchgrasses that are important forage and *H. belangeri* is an early-successional, grazing tolerant short-grass that increases after disturbances. They were also chosen because of the varying preferences for their seeds by ant workers (Chapter IV).

Grasses reproduce by both sexual (seeds) and non-sexual (vegetative) parts. The grass plant is modular, made up of many replications of the above-ground growth from culms, which consists of leaves, branches, new plant buds and adventitious roots. From the new plant buds comes the vegetative reproduction of the plant, called tillers in bunchgrasses and stolons (henceforth called tillers) in the short-grass. These new plants eventually form roots and become new individuals although the distinction is generally blurred. For the purposes of the model, new tillers become new plants within one month and are generated

as the proportion of plants per plant.

Approximately 10% of tillers are reproductive in these species (Scholl 1994, Fowler and Clay 1995, Hendrickson 1996, Hendon and Briske 1997, Mitchell et al. 1998) and they produce seeds as a function of rainfall. At the Sonora Research Station a minimum of 3 cm is necessary to initiate growth and seed production (pers. comm. Taylor 2004). Grasses can remain dormant for extended periods (varying with species) when rainfall is scarce, but prolonged drought increases mortality.

Tiller growth varies seasonally among the three grass species. *Bouteloua curtipendula* and *H. belangeri* are summer grasses and *S. leucotricha* is a winter species. *Bouteloua curtipendula* begins seed production in spring and ends in fall while *H. belangeri* begins earlier in the spring compared to *B. curtipendula*, although it generally produces fewer seeds in the fall. *Stipa leucotricha* generally produces seeds in early spring, but with sufficient rainfall it can continue until June. Seed dispersal occurs in all months that reproductive tillers are grown.

There are seasonal differences in seedling establishment among the species. Perennial grass seeds remain dormant in the seed bank until the following spring in summer species and the following fall in *S. leucotricha* when rains initiate germination (Simpson 1990). Rainfall also affects mortality of dormant seeds in the seed bank. At the Sonora Research Station grass seeds remain dormant for approximately one year, 2.5 years and 3.5 years for *B. curtipendula*, *H. belangeri*, and *S. leucotricha*, respectively (Kinucan 1987). During that time if rainfall during a month is exceptionally high, the seeds will rot. Marone et al. (2000) found mortality rates were 45% for grass seeds in an Argentinian savanna.

### ***Harvester Ant Effects on Grasses***

If *Pogonomyrmex barbatus* granivory affects changes in grass populations it is at the recruitment phase of population dynamics, thus changes in grass density are affected by removal of individuals as propagules in the seed rain. (Granivory occurs at the tasks zone and foraging zone). Conversely, if *P. barbatus* affect population dynamics through improved habitat conditions at the tasks zone, changes in grass density would occur at the recruitment

and mortality rates of change only at this zone. Because foraging and nest margin effects occur differently at the three zones, a comparison of the relative strength of the two effects can be made with each other and with a control, the unoccupied zone.

*Pogonomyrmex barbatus* forages nearly all year, except the coldest months of winter (Gordon 1999, MacMahon et al. 2000). Foraging territories average approximately 10 m from the nest (Gordon 1999); Chapter II}. The number of seeds collected by this species can vary as a function of the number of foraging workers in a colony, which typically contain an average of 12,000 workers in a mature colony (Gordon 1995) (Figure 21B). The number of workers is dependant on colony age; young colonies, from one to two years old, contain roughly 5,000 workers and the number increases linearly until age five years when the colony is mature (Gordon 1993). *Pogonomyrmex barbatus* colonies can live up to 20 years

### **Model Overview**

Conceptually, the modeled system includes the area surrounding a single ant colony over a time period encompassing the establishment, maturation and death of the colony (Figure 22). The model consists of 9 structurally identical modules representing the dynamics of each of three grass species (*Bouteloua curtipendula*, *Hilaria belangeri* and *Stipa leucotricha*) in each of three zones (tasks, foraging and unoccupied). Each module consists of two sub-models representing the dynamics of (1) plants and (2) seeds (Figure 22).

The plant sub-model represents changes in the density of seedlings (SL1) and adult plants (P). Density of seedlings increases as new seedlings sprout (SL2), and decreases due to seedling mortality (SL3) and as seedlings are recruited (SL4) into the adult plant population. The rate at which new seedlings sprout depends on the germination rate of seeds (from the seed sub-model) and seedling mortality (MRS) depends on rainfall. Seedling recruitment depends on rainfall, season, plant density and ant foraging. Density of adult plants changes as the net difference seedling recruitment (SL4) plus new vegetative plants (®) and plant mortality (M). Plant mortality depends on rainfall and level of colony maturation (AC3). Vegetative recruitment (PR1) depends on season, rainfall and level of colony maturation (AC3).



The seed sub-model represents changes in the density of the seed rain (SR) and seed banks (B1) and (B2). Density of the seed rain increases as new seeds are dispersed (S) from plant tillers (T1) and decreases with mortality (SM1), ant granivory (G1) and as seeds are recruited into soil of the seed bank (SB). The number of seeds dispersed depends on the number of tillers that are reproductive which is a constant proportion of tiller density, plant density, season and rainfall. Seed bank density (B1) increases from input of seeds from the seed rain and decreases due to seed mortality (SBM1) which depends on rainfall and aging (V1). At initial stage in the seed bank seeds are not capable of germination and therefore need the next season to become germinatable (B2). Density of seeds increase due to input from the first seed bank stage and decrease due to rainfall dependant mortality (SBM2) and germination (SBG2), and non-viability (V2).

### **Model Description**

The model is formulated as a compartmental model based on difference equations ( $\Delta t = 1$  month) and is programmed in STELLA 7 (High Performance Systems 2002). The forms of the equations in each of the nine modules are identical (Figure 22), but parameters differ by species and zone.

### ***Plant Sub-model***

The dynamics of the state variable, density of plants, is expressed through the system:

$$P(t+1) = P(t) + [R + SL4 - M] * \Delta t \quad (1)$$

where  $N(t)$  represents the density of grasses (number  $m^{-1}$ ) beginning at time  $t$ ,  $R$  represents the density of vegetative plants (number  $m^{-1}$ ) recruited into the population during time  $t$ ,  $SL4$  represents the density of seedlings (number  $m^{-1}$ ) becoming adults during time  $t$ , and  $M$  represents the density of plants (number  $m^{-1}$ ) dying during time  $t$ .

Vegetative recruitment is calculated as:

$$R_t = (PR1 + SR) * Ddt \quad (2)$$

where PR1 represents the number of plants from vegetative recruitment, SR represents the number of seedlings entering the population from germinated seed, and DDt represents the density dependant reduction in recruitment as plant population size (Pt) increases (Figure 23). The form of this relationship was adjusted such that simulated plant population density fluctuates around known field data; half the field data were used to parameterize this relationship and half were used later during model evaluation. Data were divided into random stratified samples based on three total monthly rainfall levels, dry (<3 cm), normal (3 to 10 cm) and wet (>10 cm).

Vegetative recruitment is the production of new plants from the parent and has the form:

$$PR1 = (Pt * PR3) * (PR4 * PR5) \quad (3)$$

where PR3 represents the relative rate of plant recruitment on ant nest margins (Tables 20, 21 and 22). PR4 represents the seasonal proportion of plants recruiting vegetative plants (Tables 20, 21 and 22). PR5 represents relative rates of plant recruitment adjusted by rainfall (Figure 24).

Seedling recruitment, SL4, is calculated as part of the dynamics of the state variable density of seedlings expressed as:

$$SL1(t+1) = SL1(t) + (SL2 - SL3 - SL4) \quad (4)$$

where SL1(t) represents the density of seedlings (number m<sup>-1</sup>) at the beginning of time t, SL2 represents the number of seedlings that germinated out of the seed bank and recruited into the population of seedlings, SL3 represents the number of individuals dying due to drought and was calculated as:

$$SL3 = SL1(t) * MRS \quad (5)$$

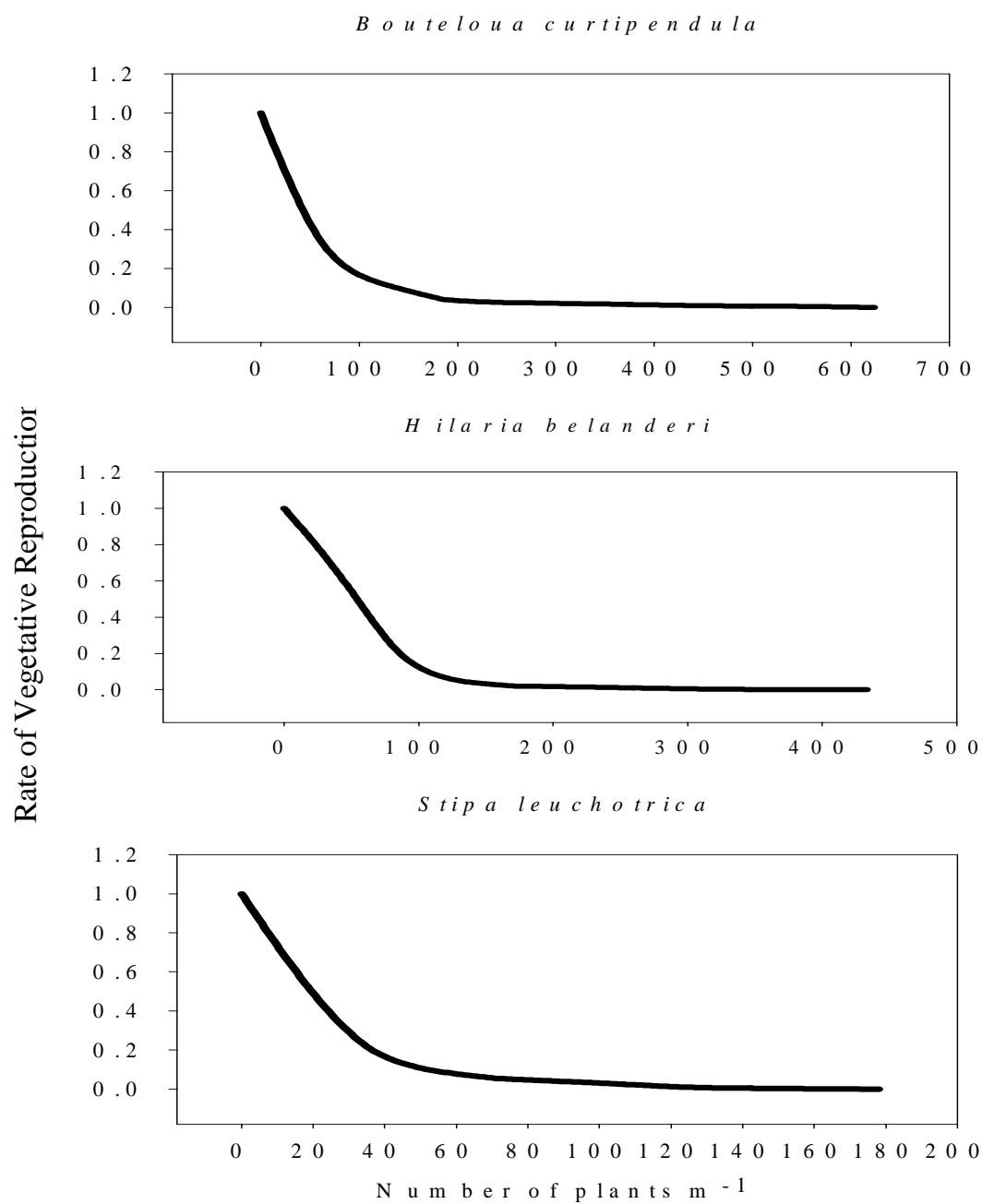


Figure 23. Density dependant functional curve based on half the field data collected at the Sonora Research Station, 1949-2002 for each grass species.

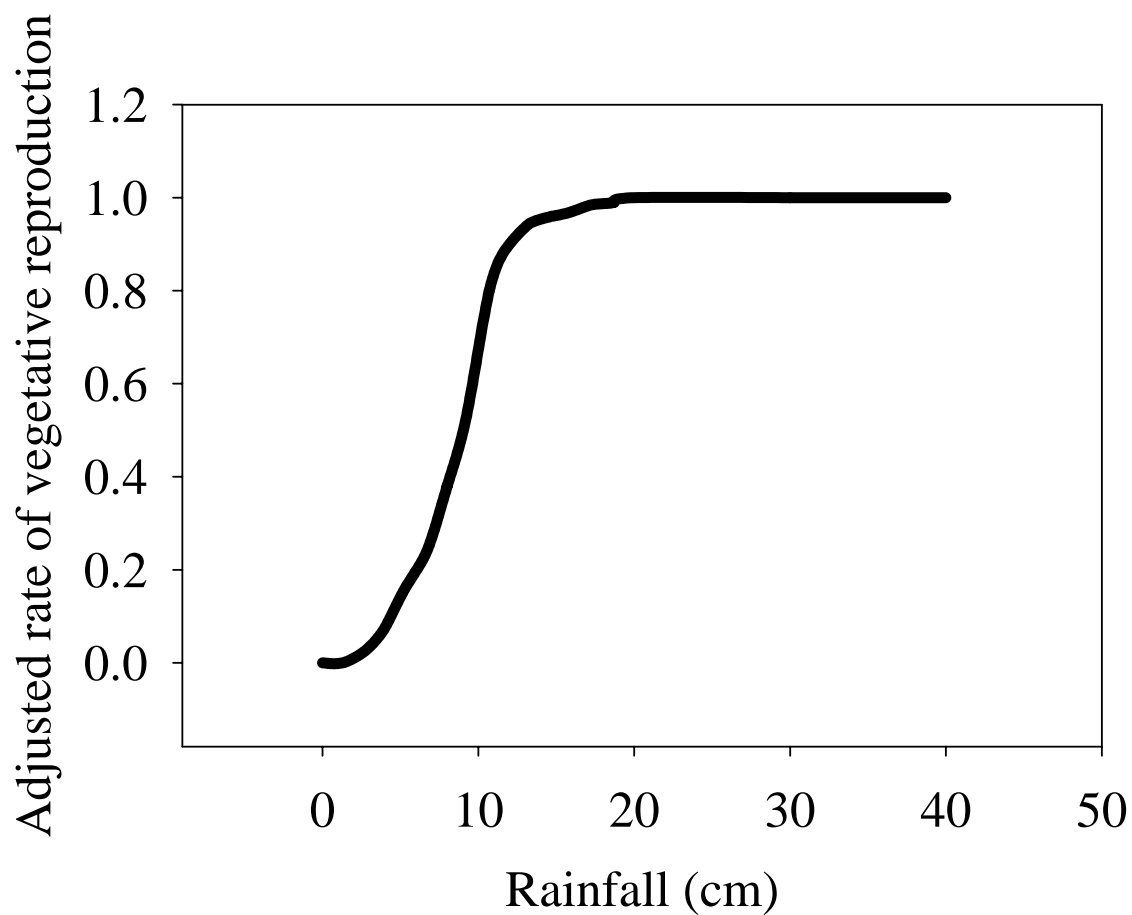


Figure 24. Adjusted rate of vegetative reproduction for all species as a function of the amount of rainfall (cm) each month based on reported rates in the literature (Bullock et al 1994, Busso and Richards 1995, Briske and Hendrickson 1998).

where MRS represents the proportion of seedlings that die as a function of rainfall (Figure 25). No data were available for seedling mortality rates of *B. curtipendula* and *H. belangeri* but field observations suggest that it can be high (Smeins pers comm.). SL4 is the number of surviving seedlings that mature to adults during time t.

Plant mortality is calculated as:

$$M = P(t) * K1 \quad (6)$$

where K1 is proportion of plants dying out of the plant density and is calculated as:

$$K1 = K2 * K3 \quad (7)$$

where K2 is the percentage of plants that die (Tables 20, 21 and 22). No data are available for grass mortality rates for these species, however Busso and Richards (1995) found that the perennial bunchgrass *Pseudoroegneria spicata* had rates of 3%. Grass mortality generally occurs during dry conditions, with increased rainfall mortality is eliminated. Grasses on tasks zones have different mortality rates compared with the other zones (Tables 20, 21 and 22). In this system mortality of individuals only occurs during dry conditions, thus K3 represents the relative proportion of plants that die during droughts due to rainfall amounts (Table 20, 21 and 22).

### ***Seed Dynamics Sub-model***

The number of seeds  $m^{-1}$  is represented by the state variable seed rain, which is the density of seeds dispersed by adult plants onto the soil surface during time t and is calculated using four variables:

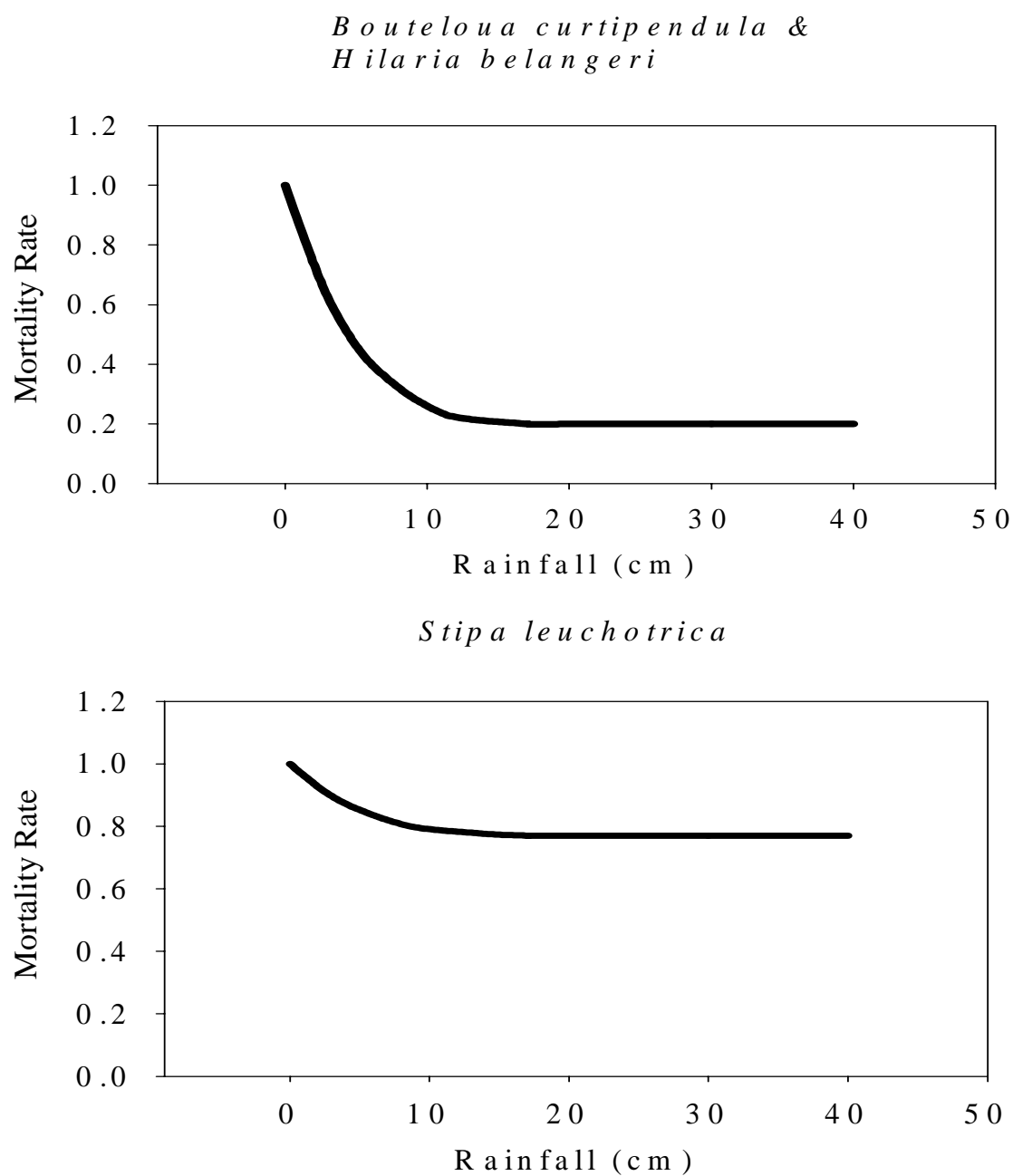


Figure 25. Relationship between the proportion of seedlings dying and amount of rainfall each month for all species. The form of the function is taken from expert opinion.

$$SR(t+1) = SR(t) + S - SB - (G + SM1) \quad (8)$$

where SR represents the number of seeds  $m^{-1}$  on the soil surface during time t. S represents the number of seeds dispersed by adult plants, SB represents the number of seeds that survive and enter the soil seed bank each month, G represents the number of seeds harvested by *P. barbatus* workers, and SM1 represents mortality of seeds once they are dispersed but before entering the seed bank. The number of seeds dispersed by plants is calculated as:

$$S = (T1 * T2) * (SS1 * SS2) \quad (9)$$

where T1 represents the number of tillers  $m^{-1}$  derived from the plant density by:

$$T1i = Pi(t) * T3 \quad (10)$$

where T3 represents the number of tillers per basal area of one grass plant. It is assumed that each species has a characteristic number of tillers per  $2 \text{ cm}^2$  of basal area (*B. curtipendula* = 0.5 tillers, *H. belangeri* = 6 tillers, and *S. leucotricha* = 4 tillers). T3 is estimated as:

$$T3 = T4 * \text{characteristic number of tillers}/2 \quad (11)$$

where T4 represents the basal area of plant individuals, which are inversely related to plant density. The proportion of tillers, T2, that produce seeds varies with species and they each produce a varying number of seeds per tiller (Tables 20, 21 and 22). Production of seeds is seasonal, and SS1 represents the number of seeds dispersed per tiller (*B. curtipendula* June -October; *H. belangeri* June - October; *S. leucotricha* January - June). SS2 represents the relative rate of seed production by tillers based on rainfall amounts (Figure 26).

Granivory is calculated as:

$$G1 = SR * G2 \quad (12)$$

where G2 represents the proportion of the seed rain density harvested by ants (Tables 20, 21 and 22). The proportion of the seed rain harvested is dependant on the number of workers in the colony, AC3, and varies with colony age (Figure 21A).

Seed rain mortality is calculated as:

$$SM1 = (SR - G1) * SM2 \quad (13)$$

Where SM2 represents the proportion of seeds that die due to factors other than harvester ant granivory such as disease, lack of suitable microsites, or other species harvesting seeds. SM2 is assumed to be 0.10.

The seed bank is formulated as two state variables with the first seed bank (B1) standing for seed dormancy from the time seeds enter the seed bank until the following germination season. This state variable is represented as:

$$B1(t+1) = B1(t) + (SB - MG1 - V1) \quad (14)$$

where MG1 represents the fraction of seed density lost due to either mortality or germination and V1 represents moving into the next seed bank generation when the appropriate time of year arrives. Length of time in the dormant state is eight months.

Loss of seeds in the seed bank is calculated as:

$$MG1 = SBM1 + SBG1 \quad (15)$$

where SBM1 are the proportion of seeds (0.45) in the seed bank density that die due to



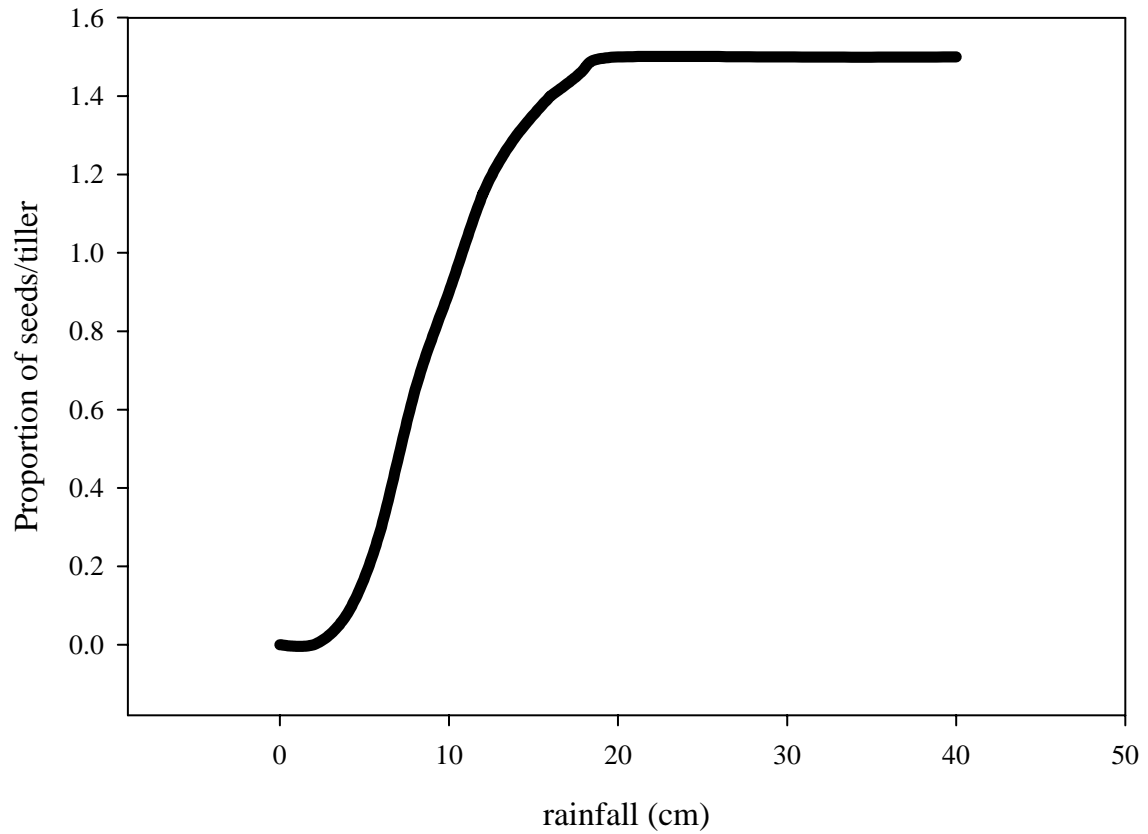


Figure 26. Relationship between the number of seeds produced per tiller and amount of rainfall each month for all species. The form of the function is taken from expert opinion.

rotting and is dependant on the amount of rainfall. As rainfall increases mortality rate increases linearly from a minimum of  $(x_1, y_1)$  to a maximum of  $(x_2, y_2)$  where it then remains stable despite rainfall amounts (Tables 20, 12 and 22). At this seed bank stage SBG1 is zero because seeds are unable to germinate.

The next stage in the seed bank has the form:

$$B2(t + 1) = B2(t) + (V1 - V2 - MG2) \quad (16)$$

where MG2 represents the fraction of seed bank density lost due to mortality and germination and V2 represents seeds that lose their viability thus exiting the seed bank. Loss of the number of seeds  $m^{-1}$  in the seed bank is calculated as:

$$MG2 = SBM2 + SBG2 \quad (17)$$

where SBM2 represents the proportion of seeds that die due to rotting and is identical to SBM1. SBG2 represents proportion of seeds that germinate (Tables 20, 21 and 22). Germination rate is dependant on the amount of precipitation, thus rainfall less than 2 cm results in zero germination. Abbott and Roundy (2003) demonstrated that grass seeds of *B. curtipendula* germinated 0.5% of maximum germination rates under very dry conditions. This rate was used for the other species because no data were found on natural germination rates under varying rainfall levels. Sprouted seeds result in seedlings (See Plant Sub-model).

### **Model Evaluation**

Model evaluation consisted of (1) comparing simulated dynamics of seedling (SL), seed bank (B2) and plant (P) densities in the foraging zone to field data, (2) examining the sensitivity of simulated dynamics of plant densities in the foraging zone to changes in number of seeds per tiller (SS1), rates of seasonal plant recruitment (PR4), seedling mortality (MRS) and seed mortality (SM2), (3) examining the sensitivity of simulated dynamics of densities in the tasks zone to changes in rates of granivory (G2), plant mortality (K1) and

plant vegetative recruitment (PR1), and (4) examining the sensitivity of simulated dynamics of densities in the foraging zone to changes in the functional form between rainfall and number of seeds per tiller ((SS2), rates of seedling mortality (MRS) and vegetative recruitment (PR5) (Figure 22).

### ***Comparison to Field Data***

The model was evaluated for performance of the temporal dynamics of adult grass, seed bank and seedling density from 20 replicate stochastic simulations representing historical rainfall conditions. Simulated adult density data were sampled in September of each simulated year for comparison with field data collected at the same time each year. Simulated seed bank data were compared in March and July when seed bank densities were collected at the Sonora Research Station (Kinucan 1987). Simulated seedling data were sampled in June 2003 when field data were collected (Chapter III). Twenty replications allow detection of a 10 individual difference between simulation and field results at 0.05 and 0.80 Type I and Type II error rates, respectively.

Simulated adult plant dynamics fall within the range of the field data for all three species (Figure 27). As years progressed a noticeable decline in correspondence was observed, due possibly to *Bouteloua curtipendula* out-competing *Stipa leucotricha*, or due to juniper encroachment that reduces grass density (Smeins and Merrill 1988, Dye II et al. 1995, Breshears et al. 1997a, Fuhlendorf and Smeins 1997, Yager and Smeins 1999). Simulated seedling densities were consistently lower than field results for *B. curtipendula* and *S. leucotricha* and corresponded less well than adult grasses (Figure 28). In contrast, *H. belangeri* fell within the range of the field data. Simulated seed bank densities fell within the range of results reported for all species (Figure 29).

### ***Sensitivity of Plant Dynamics***

A sensitivity analysis was conducted to determine the degree of confidence in the simulated results being able to predict temporal dynamics of grass populations. It was conducted with a deterministic version of the model and stochastic variables were held constant at their means while varying, one at a time, the values of seeds/tiller, rate of

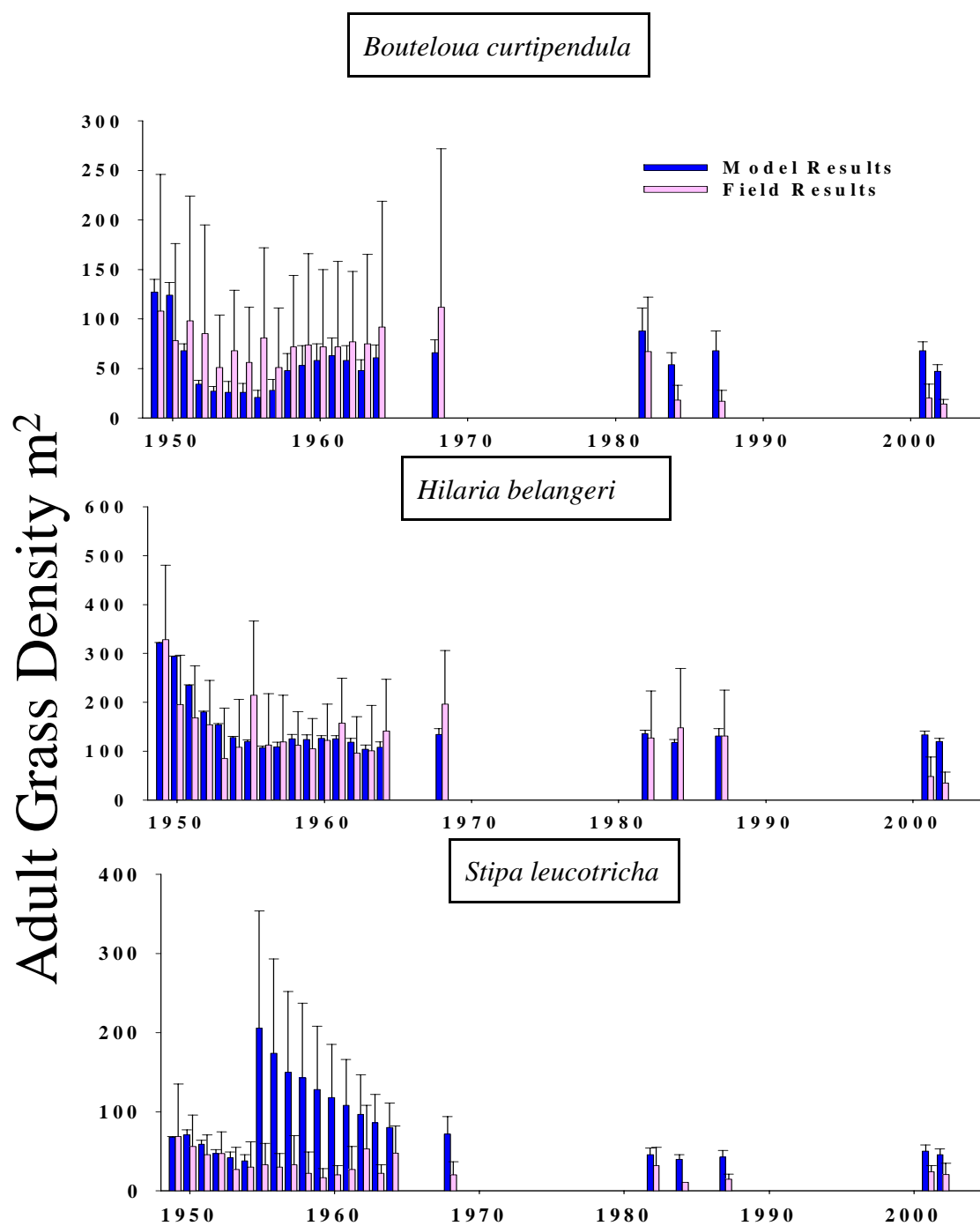


Figure 27. Average number of *Bouteloua curtipendula*, *Hilaria belangeri* and *Stipa leucotricha* adult plants  $\text{m}^{-1}$  (S.D.) simulated and field collected in September of each year under historical rainfall, 1949-2002. Note: scales differ between species.  $n = 20$ .

seasonal plant recruitment, and seed mortality at the foraging zone, and granivory, plant mortality and plant recruitment in the tasks zone. In addition, the functional forms of variables adjusted due to amount of rainfall were held constant while the forms of seeds/tiller, seedling mortality and vegetative recruitment were varied.

The results of the sensitivity analysis at the foraging zone indicate that final *B. curtipendula* density is sensitive to changes in seasonal plant recruitment rate (PR4) (Table 23). As rates were increased or decreased from baseline values plant densities changed up to 100% from baseline density. Sensitivity analysis indicates that at foraging zone final plant densities for *B. curtipendula* are sensitive to changes in the functional relationship between amount of rainfall and plant recruitment (PR5) (Table 24). Plant densities dropped 97% for *B. curtipendula* when the function was exponential. *Bouteloua curtipendula* dropped 52% with linear. . The results of the sensitivity analysis at the tasks zone found final densities were sensitive to changes in rates of plant mortality and recruitment (Table 25).

Sensitivity analyses results for *H. belangeri* showed that seeds/tiller (SS1) were moderately sensitive, nearly 19% of baseline values. *Hilaria belangeri* density is reduced 20% when the functional form of the proportion of seeds per tiller and rainfall is sigmoid.

Final *S. leucotricha* plant density is sensitive to rates of seasonal plant recruitment (up to 58% change from baseline density), seedling mortality (MRS) (up to 35% change) and seed mortality (SM2) ( up to 36% change) and to number of seeds per tiller (23% change at roughly 250% of baseline number). The results of the sensitivity analysis at the asks zone found densities were sensitive to changes in rates of plant mortality, granivory and recruitment (Table 25).

Confidence in the model's ability to address the hypotheses lies in our confidence in which the tasks zone values (both mortality and plant recruitment) were specified, which were collected during and immediately after a severe drought and may not reflect normal rainfall responses and are least confident during wet rainfall. All other values are reasonably

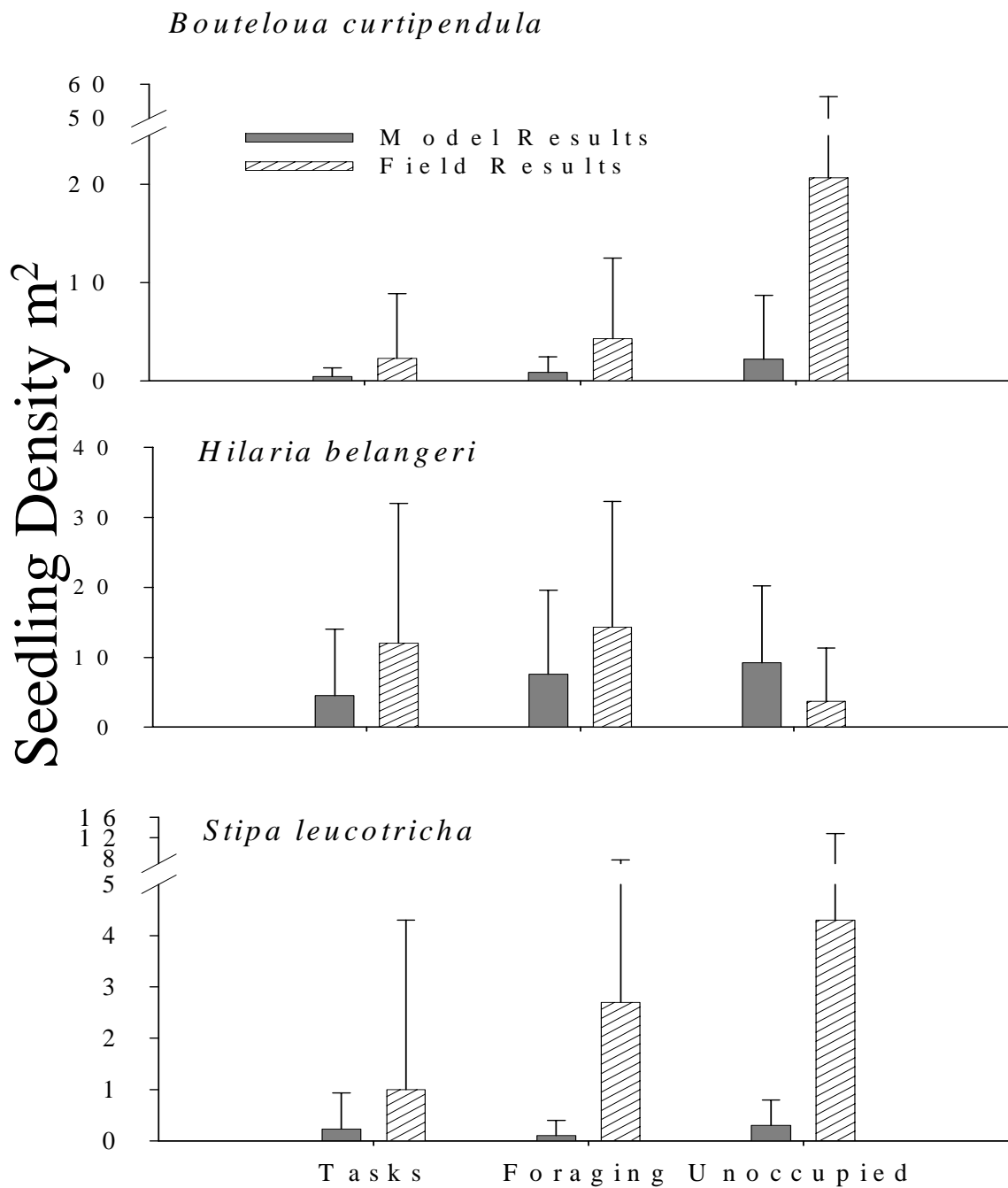


Figure 28. Average number of *Bouteloua curtipendula*, *Hilaria belangeri* and *Stipa leucotricha* seedlings m<sup>-1</sup> (S.D.) simulated and field collected in June 2003 at three zones surrounding the ant nest, tasks, foraging and unoccupied, under historical rainfall, 1949-2002. Note: scales differ between species. n = 20.

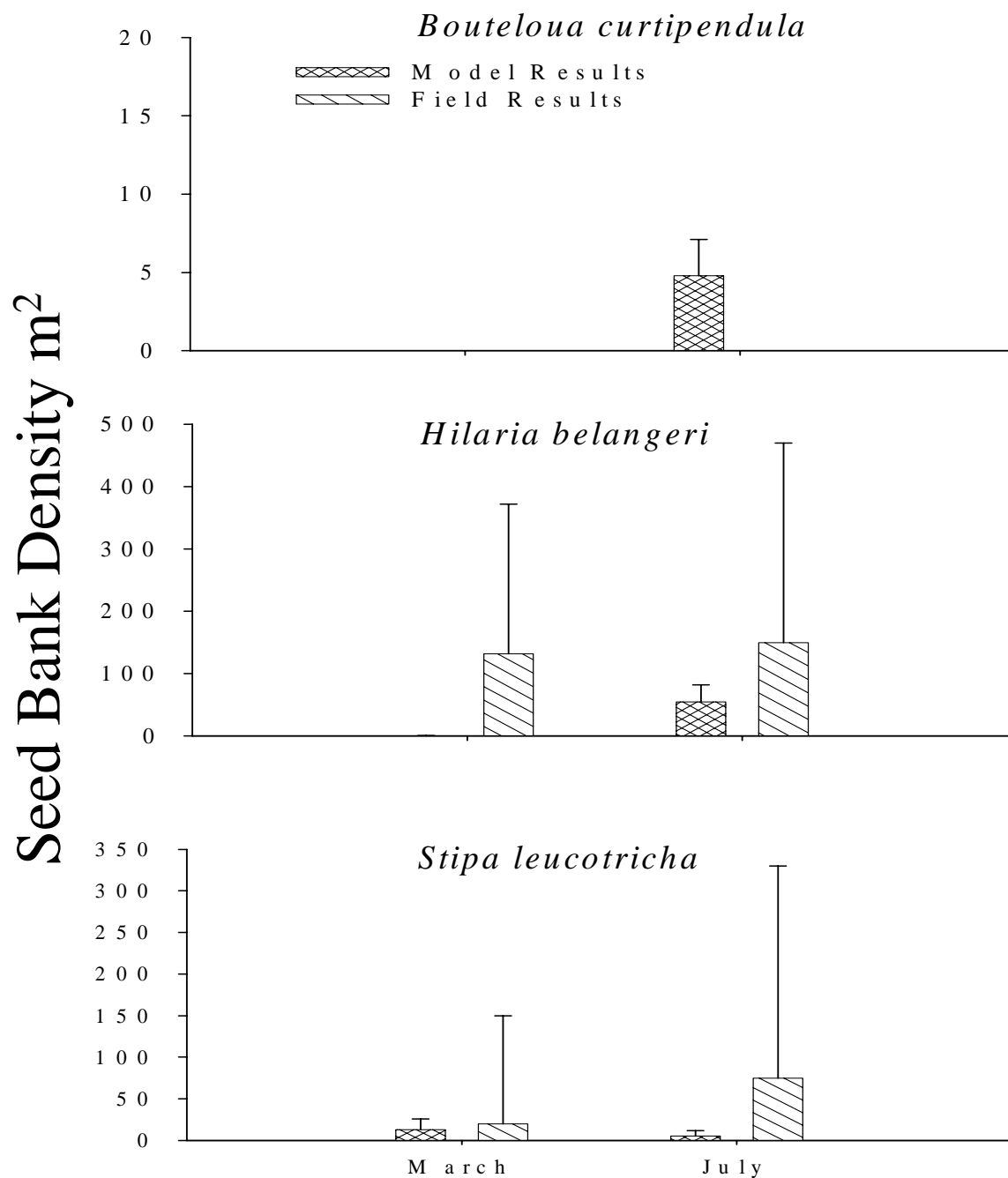


Figure 29. Model evaluation of average (S.D.) simulated seed bank numbers m<sup>-1</sup> of *Bouteloua curtipendula*, *Hilaria belangeri* and *Stipa leucotricha* compared to field data at the foraging zone. Data were evaluated in March and July of each year. Note: scales differ between species. n = 10.

Table 23. Sensitivity analyses of the baseline version of the model indicating changes in final (after 660 months of simulated time) number of plants  $\text{m}^{-1}$  of *Bouteloua curtipendula*. At foraging zone results are from the indicated changes in number of seeds per tiller, rates of seasonal plant recruitment (plants/plant/month) and proportion of seeds that die/month; in the functional forms relating rainfall to relative rate of seeds per tiller, plant recruitment (plants/plant/month) and proportion of seedlings dying per month; and at tasks zone resulting from the indicated changes in rates of plant recruitment (plants/plant/month), plant mortality, and granivory.

Foraging Zone Constant/Rate	Values	% of baseline	Density	% change from baseline
Number of seeds/tiller (SS1)	1	3	63.1	1
	35	100	63.8	0
	78	223	64.6	2
	300	857	71.0	11
Seasonal Plant Recruitment Rate (PR4)	0.1	75	0	100
	0.3	75	45	30
	0.4	100	64	0
	0.5	125	80	25
	0.9	225	125	95
Seed Mortality Rate (SM2)	0.5	54	67.0	5
	0.9	100	63.9	0
	1.0	111	63.1	1
Foraging Zone Functional Forms	Functional Form	N/A	Density	% change from baseline
Relative proportion of seeds/tiller (SS2)	hyperbolic (baseline)		64.2	0
	linear		64.4	0.3
	sigmoidlike		63.3	1.4
Seedling mortality (MRS)	exponential (baseline)		63.8	0
	sigmoidlike		63.2	0.9



Table 23 Continued

Foraging Zone Constant/Rate	Values	% of baseline	Density	% change from baseline
Plant Recruitment (PR5)	linear		63.3	0.8
	concave (baseline)		63.6	0
	exponential		0.2	97
	hyperbolic		80.8	21
	linear		30.5	52
Tasks Zone Rate	Values	% of baseline	Density	% change from baseline
Granivory (G2)	0.09	50	59.9	0.2%
	0.18	100	59.8	0
	0.27	150	59.8	0
	0.90	500	59.1	1
Plant mortality (K1)	0.1	53	105	28
	0.19	100	82	0
	0.3	158	13	84
	0.5	263	0	100
Plant recruitment (PR1)	0.5	36	0	100
	1	73	29	49
	1.37	100	57	0
	2	146	96	68
	6	438	188	230

Table 24. Sensitivity analyses of the baseline version of the model indicating changes in final (after 660 months of simulated time) number of plants  $\text{m}^{-1}$  of *Hilaria belangeri*. At foraging zone results are from the indicated changes in number of seeds per tiller, rates of seasonal plant recruitment (plants/plant/month) and proportion of seeds that die/month; in the functional forms relating rainfall to relative rate of seeds per tiller, plant recruitment (plants/plant/month) and proportion of seedlings dying per month; and at tasks zone resulting from the indicated changes in rates of plant recruitment (plants/plant/month), plant mortality, and granivory.

Foraging Zone Constant/Rate	Values	% of baseline	Density	% change from baseline
Number of seeds/tiller (SS1)	1	17	80	19
	5.9	100	99	0
	15	254	117	18
	25	424	126	27
	59	1000	189	91
Seasonal Plant Recruitment Rate (PR4)	0.05	44	88	8
	0.09	100	96	0
	0.2	222	115	19
	0.4	444	128	33
Seed Mortality Rate (SM2)	0.2	50	101	5
	0.4	100	96	0
	0.6	150	90	6
	1.0	250	72	25
Foraging Zone Functional Forms	Functional Form	N/A	Density	% change from baseline
Relative proportion of seeds/tiller (SS2)	hyperbolic (baseline)		105	0
	linear		110	4.5
	sigmoidlike		84	20.0
Seedling mortality (MRS)	exponential (baseline)		96.2	0
	sigmoidlike		80.2	17

Table 24 Continued

Foraging Zone Functional Form	Values	N/A	Density	% change from baseline
Plant Recruitment (PR5)	linear		82.6	14
	concave (baseline)		63.6	0
	exponential		0.2	97
	hyperbolic		80.8	21
	linear		30.5	52
Tasks Zone Rate	Values	% of baseline	Density	% change from baseline
Granivory (G2)	0.01	20	89.0	0.1%
	0.05	100	88.9	0
	0.10	200	88.9	0
	0.90	1800	88.6	0.3
Plant mortality (K1)	0.01	33	119	35
	0.03	100	88	0
	0.10	333	54	39
	0.20	667	0	100
Plant recruitment (PR1)	0.50	31	73	17
	1.6	100	88	0
	4	250	115	31
	6	375	129	47
	8	500	139	58

Table 25. Sensitivity analyses of the baseline version of the model indicating changes in final (after 660 months of simulated time) number of plants  $\text{m}^{-1}$  of *Stipa leucotricha*. at foraging zone results are from the indicated changes in number of seeds per tiller, rates of seasonal plant recruitment (plants/plant/month) and proportion of seeds that die/month; in the functional forms relating rainfall to relative rate of seeds per tiller, plant recruitment (plants/plant/month) and proportion of seedlings dying per month; and at tasks zone resulting from changes in rates of plant recruitment (plants/plant/month), plant mortality, and granivory.

Foraging Zone Constant/Rate	Values	% of baseline	Density	% change from baseline
Number of seeds/tiller (SS1)	1	27	19	14
	3.67	100	22	0
	9	245	27	23
	25	681	34	55
	40	1090	46	92
Seasonal Plant Recruitment Rate (PR4)	0.01	17	4	17
	0.06	100	23	0
	0.11	183	33	43
	0.4	667	63	58
	1.0	130	17	35
Seed Mortality Rate (SM2)	0.2	25	30	36
	0.6	75	26	18
	0.8	100	22	0
	1.0	125	17	23
Foraging Zone Functional Forms	Functional Form	N/A	Density	% change from baseline
Relative proportion of seeds/tiller (SS2)	hyperbolic (baseline)		25.8	0
	linear		27.9	8
	sigmoidlike		27.9	8
Seedling mortality (MRS)	exponential (baseline)		22.2	0
	sigmoidlike		22.2	0

Table 25 Continued.

Foraging Zone Functional Form	Values	N/A	Density	% change from baseline
Plant Recruitment (PR5)	linear		22.8	3
	concave (baseline)		15.9	0
	exponential		8.7	45
	hyperbolic		16.1	1
	linear		13.7	14
Tasks Zone Rate	Values	% of baseline	Density	% change from baseline
Granivory (G2)	0.09	50	0.45	22
	0.18	100	0.37	0
	0.27	150	0.29	22
	0.90	500	0.03	92
Plant mortality (K1)	0.01	33	19	96
	0.03	100	0.7	0
	0.05	167	0	100
Plant recruitment (PR1)	0.2	54	0.1	72
	0.37	100	0.36	0
	0.6	162	1.6	29
	0.9	243	5.9	154

confident because of the high spatial and temporal variability of the Sonora Research Station as demonstrated in the several years of field collection (Figures 27-29).

### **Simulation Results**

The hypothesis that the tasks zone creates an increase in grass density only while the colony is mature with normal and low rainfall treatments, but not in the high rainfall treatment, was tested by comparing rainfall levels at the three zones from the ant nest, tasks zone, foraging zone and unoccupied zone beginning with no colony present through the establishment and death of the colony and finally for several years after for a total of 55 years (Figure 20). Thirty replications allowed detection of a 30 plant difference in predictions of numbers of grasses  $\text{m}^{-1}$  at 0.05 and 0.80 Type I and Type II errors, respectively.

#### **Tasks Zone**

At the tasks zone *P. barbatus* granivory rates are at their highest for all grass species and grasses develop higher densities on the disk margin during the life of the colony. *Bouteloua curtipendula* results indicate that adult numbers before the colony matures are approximately 100 plants  $\text{m}^{-1}$ . Beginning with the year the colony establishes density increases sigmoidally to a carrying capacity of approximately 125 plants  $\text{m}^{-1}$  when the colony matures. Plant density returns to pre-colony densities (approximately 5 years after the colony dies) under normal rainfall (Figure 30). During simulations of rainfall higher than normal (wet treatment), results show that numbers are approximately 200 to 225 plants  $\text{m}^{-1}$  pre and during colony maturity, respectively, and densities are reached about 4 years after the colony matures. densities return to pre-colony densities 8 years after the colony dies. When simulated rainfall is low (dry treatment), numbers decline to approximately 20 plants  $\text{m}^{-1}$ . Beginning with the year the colony matures, plant density stabilizes, but on colony death densities slowly decline to the final month.

*Hilaria belangeri* results show that before colony establishment numbers were 125 plants  $\text{m}^{-1}$  which increases sigmoidally to near 150 plants  $\text{m}^{-1}$  about 5 years after the colony matures, and decreases to pre-colony densities approximately 5 years after the colony dies

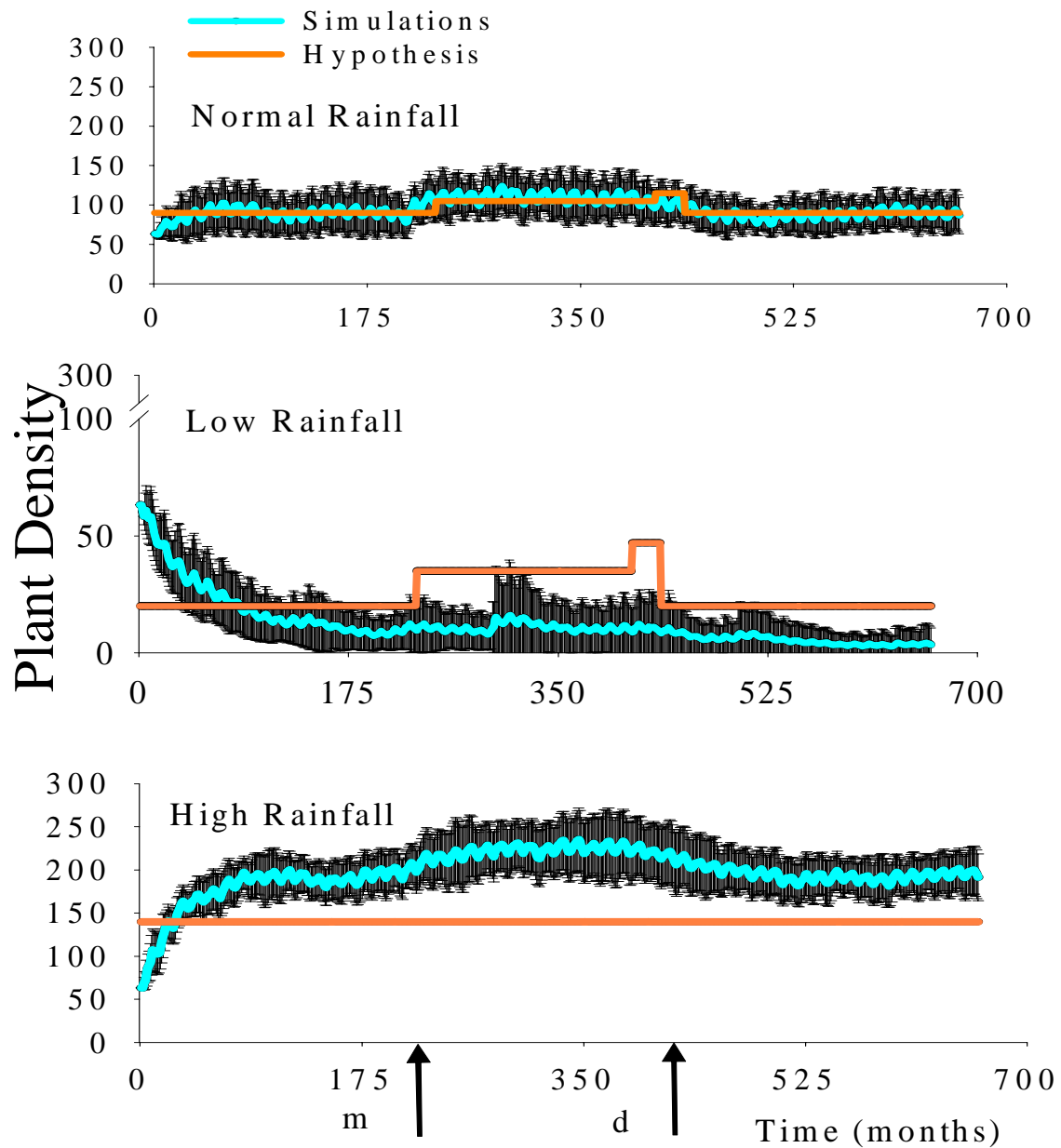


Figure 30. Population dynamics of the average (S.D.) number  $\text{m}^{-1}$  of *Bouteloua curtipendula* adults under three rainfall treatments at the tasks zone. Arrows indicate the month the *P. barbatus* colony matures (m) and the month it dies (d).  $n = 30$ .

(Figure 31). During wet treatments grass numbers are higher at 175 plants  $\text{m}^{-1}$  increasing linearly to 210 plants  $\text{m}^{-1}$  after colony maturity. Unlike *B. curtipendula*, plant density returns to a new higher density about 12 years after the colony dies, approximately 190 plants  $\text{m}^{-1}$ . Dry treatment simulations are similar to normal years with approximately 80 plants  $\text{m}^{-1}$  increasing, in nearly 2 years, to 120 plants  $\text{m}^{-1}$  during colony maturity and then decreasing to pre-colony densities about 3 years after colony death.

In normal rainfall years, *S. leucotricha* decreases from approximately 35 to 25 plants  $\text{m}^{-1}$  before and during colony maturity respectively (Figure 32). The decrease reaches carrying capacity about 6 years after maturity and takes about 16 years to recover after colony death. During wet treatments numbers are higher at 57 plants  $\text{m}^{-1}$  decreasing linearly during the life of the colony and returning to pre-colony densities about 15 years after the colony dies. During dry simulations, plant density is reduced from 35 plants  $\text{m}^{-1}$  to approximately 15 plants  $\text{m}^{-1}$ . During colony maturity density continues to decrease to approximately 9 plants  $\text{m}^{-1}$  and does not recover after the colony dies.

### **Foraging Zone**

At the foraging zone *B. curtipendula* results (Figure 33) are similar to pre-colony densities during normal rainfall (100 plants) and wet treatments (170 plants) for the entire simulation (Figure 31). However, during dry treatments densities decrease linearly from near 20 to approximately 5 plants  $\text{m}^{-1}$  during the final year. *Hilaria belangeri* reaches carrying capacity and remains at roughly the same numbers during the entire simulation for normal (125 plants  $\text{m}^{-1}$ ), wet (175 plants  $\text{m}^{-1}$ ) and dry rainfall treatments (80 plants  $\text{m}^{-1}$ ) (Figure 34).

*Stipa leucotricha* reaches pre-colony carrying capacity and remains at this density for normal (38 plants  $\text{m}^{-1}$ ) and wet (57 plants  $\text{m}^{-1}$ ) rainfall treatments (Figure 35). In contrast to the other species, during dry simulations, plant numbers decline linearly from approximately 15 plants  $\text{m}^{-1}$  during the life of the colony, and returns to pre-worker densities about 3 years after the colony dies.

### **Unoccupied Zone**

*Bouteloua curtipendula* repeated the pattern found at foraging zone for the three



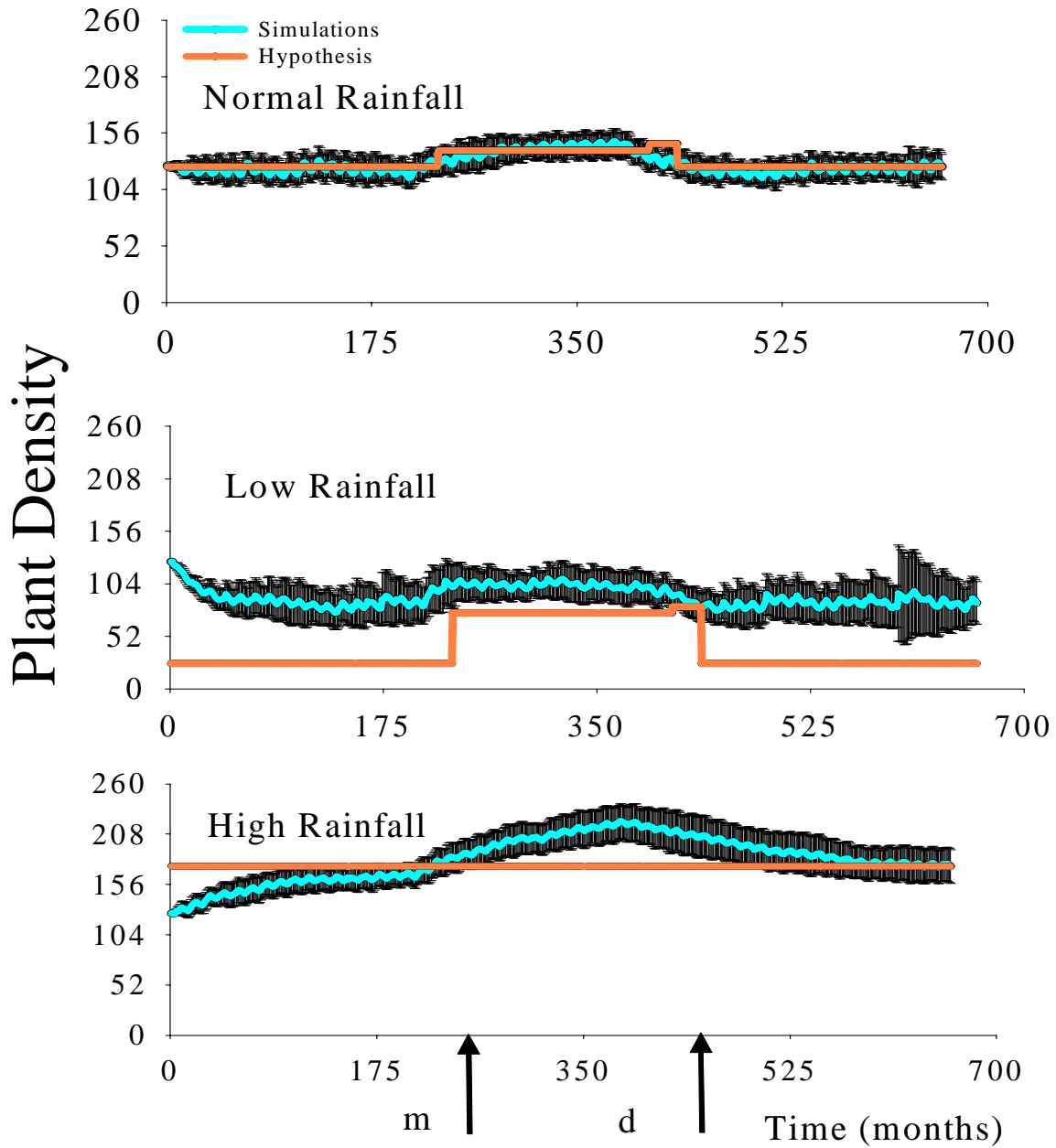


Figure 31. Population dynamics of the average (S.D.) number  $m^{-1}$  of *Hilaria belangeri* adults under three rainfall treatments at the tasks zone. Arrows indicate the month the *P. barbatus* colony matures (m) and the month it dies (d).  $n = 30$ .

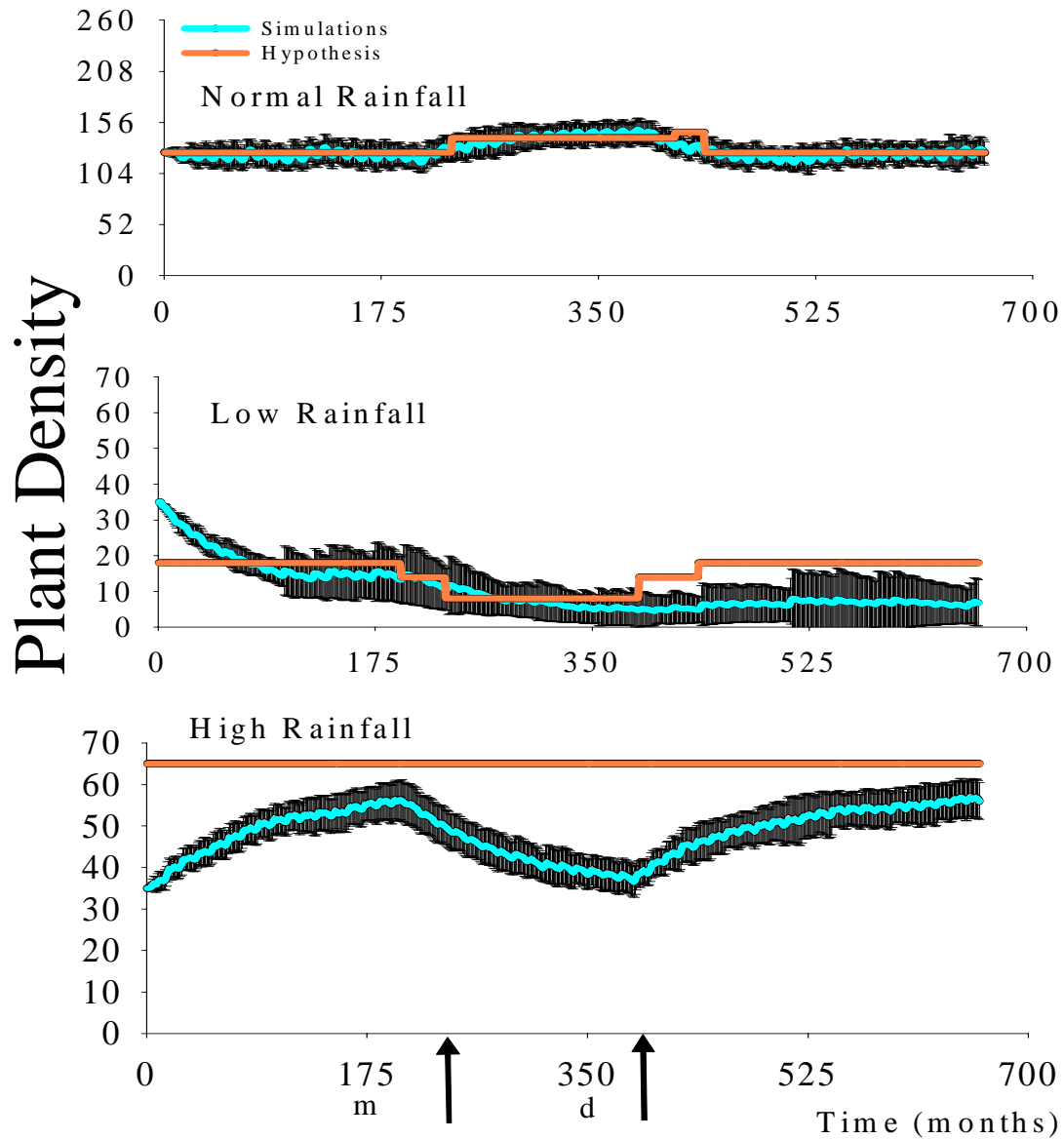


Figure 32. Population dynamics of the average (S.D.) number  $m^{-1}$  of *Stipa leucotricha* adults under three rainfall treatments at the tasks zone. Arrows indicate the month the *P. barbatus* colony matures (m) and the month it dies (d).  $n = 30$ .

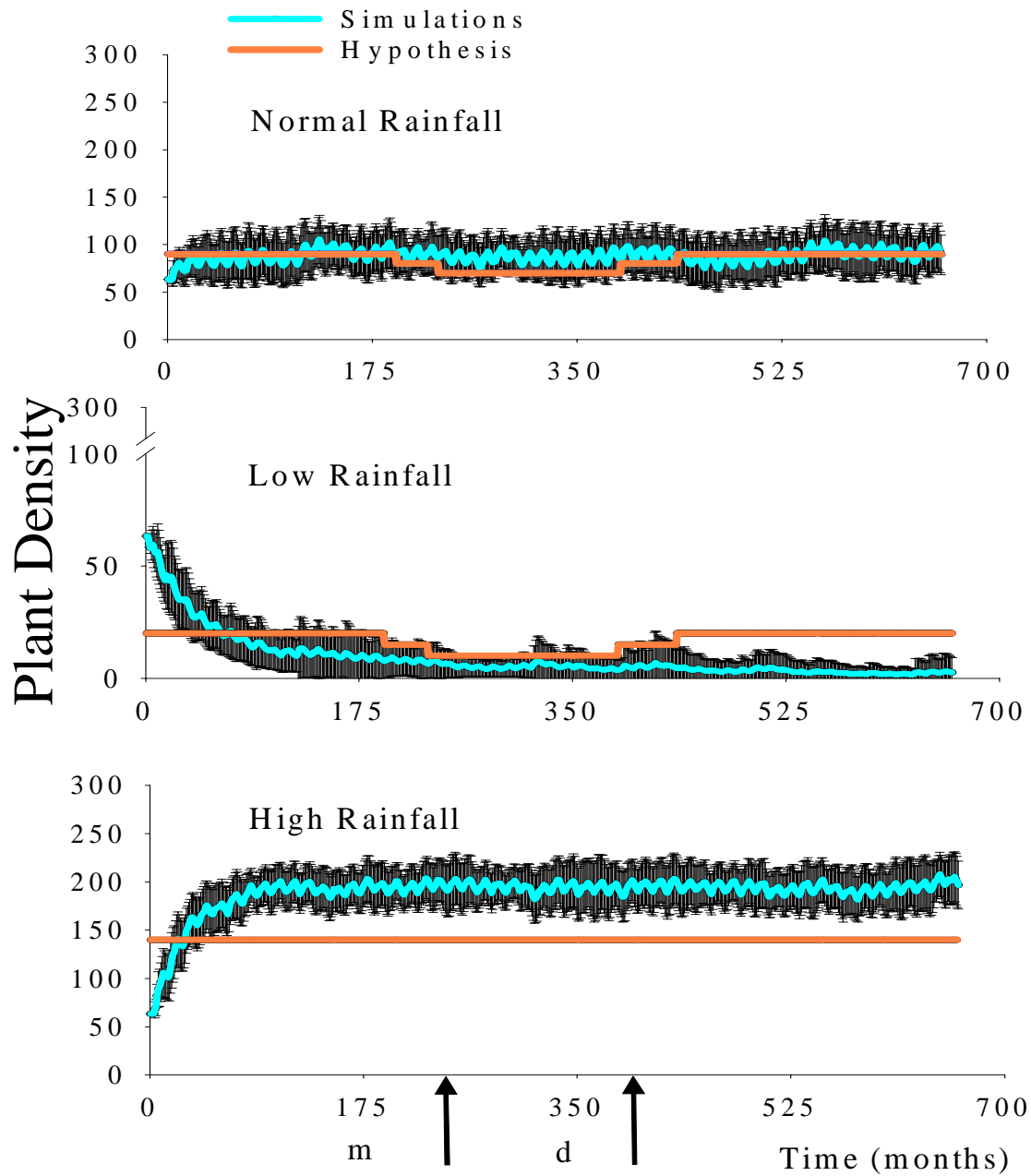


Figure 33. Population dynamics of the average (S.D.) number  $m^{-1}$  of *Bouteloua curtipendula* adults under three rainfall treatments at the foraging zone. Arrows indicate the month the *P. barbatus* colony matures (m) and the month it dies (d).  $n = 30$ .

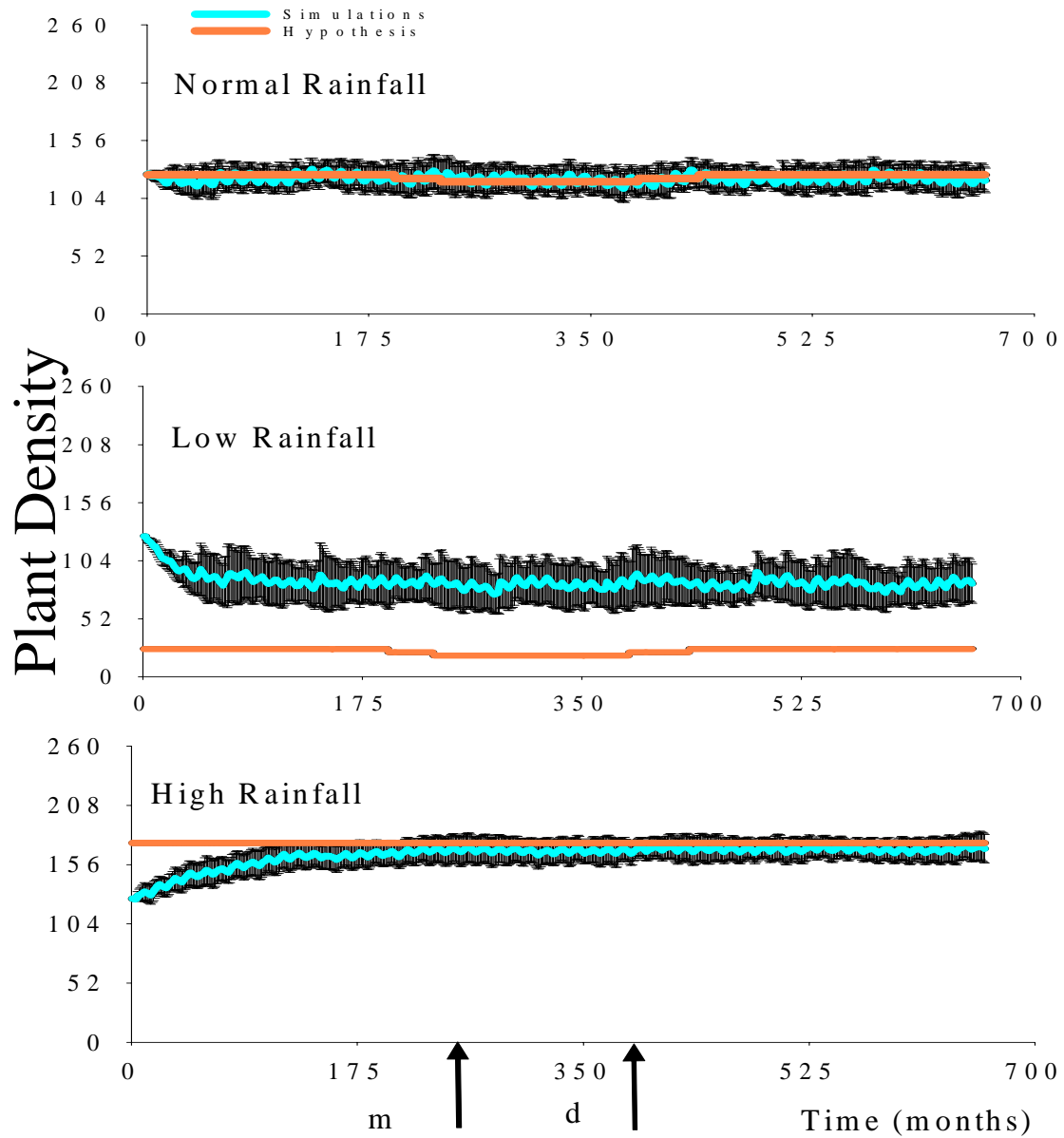


Figure 34. Population dynamics of the average (S.D.) number  $m^{-1}$  of *Hilaria belangeri* adults under three rainfall treatments at the foraging zone. Arrows indicate the month the *P. barbatus* colony matures (m) and the month it dies (d).  $n = 30$ .

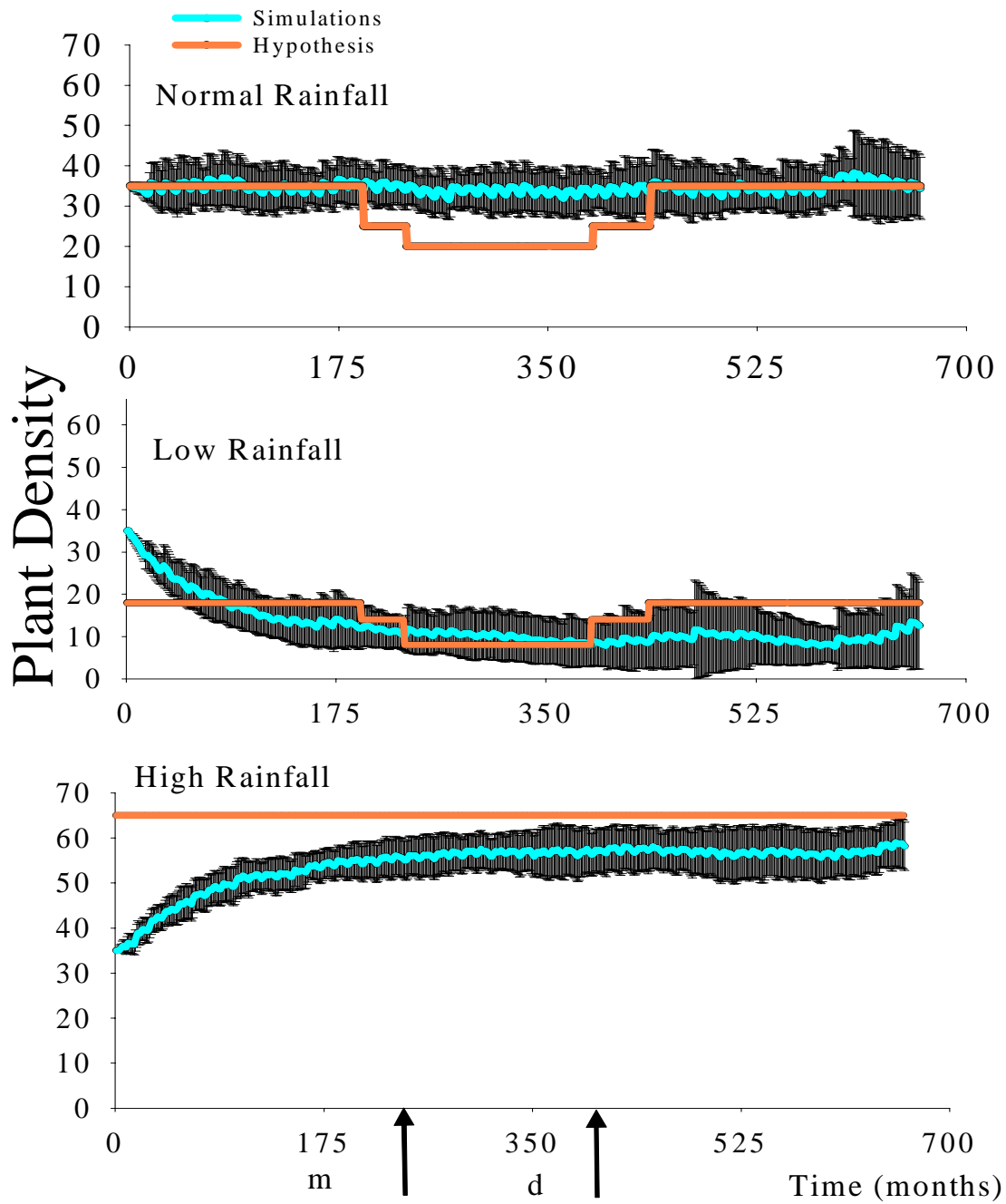


Figure 35. Population dynamics of the average (S.D.) number  $\text{m}^{-1}$  of *Stipa leucotricha* adults under three rainfall treatments at the foraging zone. Arrows indicate the month the *P. barbatus* colony matures (m) and the month it dies (d).  $n = 30$ .

( rainfall treatments (Figure 36). In addition, *H. belangeri* repeats the patterns observed at normal, wet and dry rainfall treatments (Figure 37). *Stipa leucotricha* remains at roughly the same density during the entire simulation for normal (38 plants m<sup>-1</sup>), wet (57 plants m<sup>-1</sup>) and dry rainfall treatments (20 plants m<sup>-1</sup>) (Figure 38).

The tasks zone was important in dry rainfall treatments for *B. curtipendula* with significantly higher plant densities at tasks zone compared to foraging and unoccupied zones (Table 26). Bonferroni post-hoc tests showed that significance occurred during the dry rainfall treatment only (Test = 0.84,  $p < .001$ ; Figure 39). *Hilaria belangeri* has significantly higher densities on the tasks zone compared to the other zones. *Stipa leucotricha* had a significant interaction between rainfall treatment and zones. During dry simulations similar densities occurred between tasks zone and foraging zone, but in wet simulations similar densities occurred between foraging zone and unoccupied zone.

## Discussion

Rainfall levels and presence at tasks zones during colony maturation strongly affect grass population dynamics in this model. High and low rainfall treatments overwhelm the system by rapidly increasing or reducing numbers of plants from normal rainfall numbers. Nevertheless, a large increase in grass populations occurs at the tasks zone during a mature colony for *Bouteloua curtipendula* and *Hilaria belangeri*. This may be due to the establishment of soil conditions or decreased competition in the nest that promotes better conditions for grasses at the tasks zone than away from them. These findings concur with other studies that demonstrate larger densities and greater sizes of grasses on nest margins (Golley and Gentry 1964, Wight and Nichols 1966, Rissing 1986, Whitford 1988, Soule and Knapp 1996), although the mechanisms have not been determined.

It is unclear why *Stipa leucotricha* populations are reduced at the tasks zone, although the results of the simulations show that in the foraging zone, where only seed harvest is occurring, densities are reduced in conjunction with dry treatments. Seeds of this species may

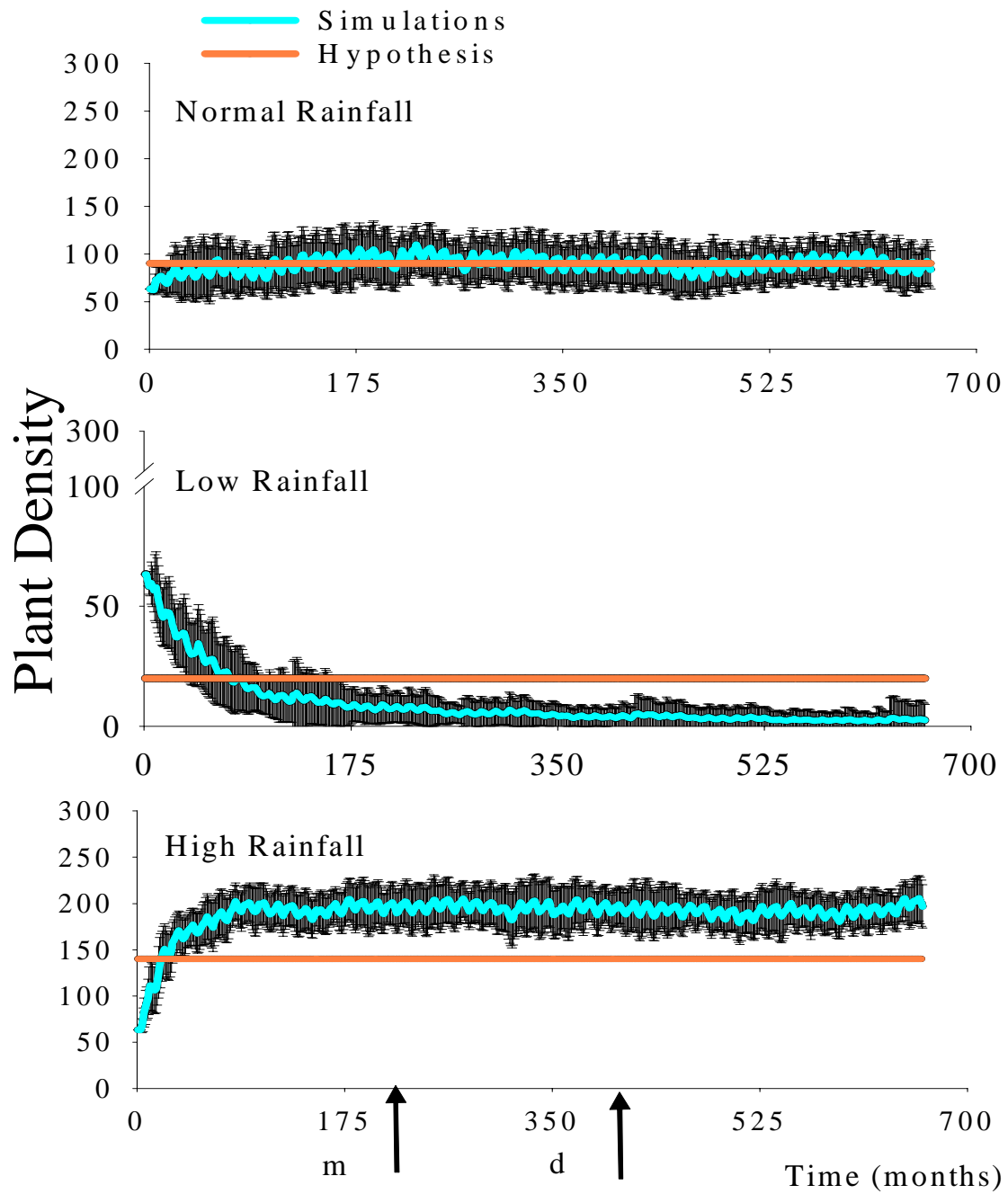


Figure 36. Population dynamics of the average (S.D.) number  $m^{-1}$  of *Bouteloua curtipendula* adults under three rainfall treatments at the unoccupied zone. Arrows indicate the month the *P. barbatus* colony matures (m) and the month it dies (d).  $n = 30$ .

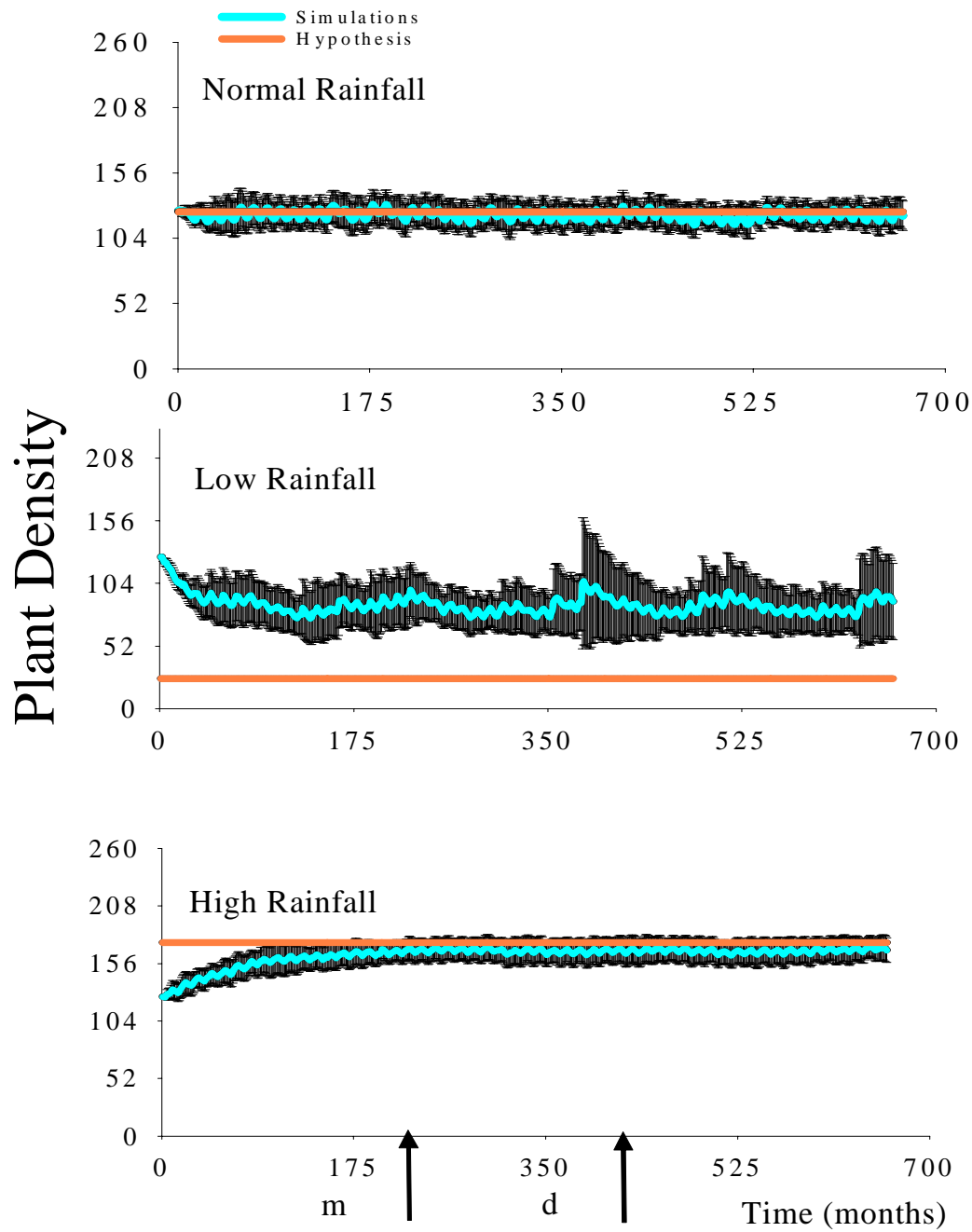


Figure 37. Population dynamics of the average (S.D.) number  $m^{-1}$  *Hilaria belangeri* adults under three rainfall treatments at the unoccupied zone. Arrows indicate the month the *P. barbatus* colony matures (m) and the month it dies (d).  $n = 30$ .



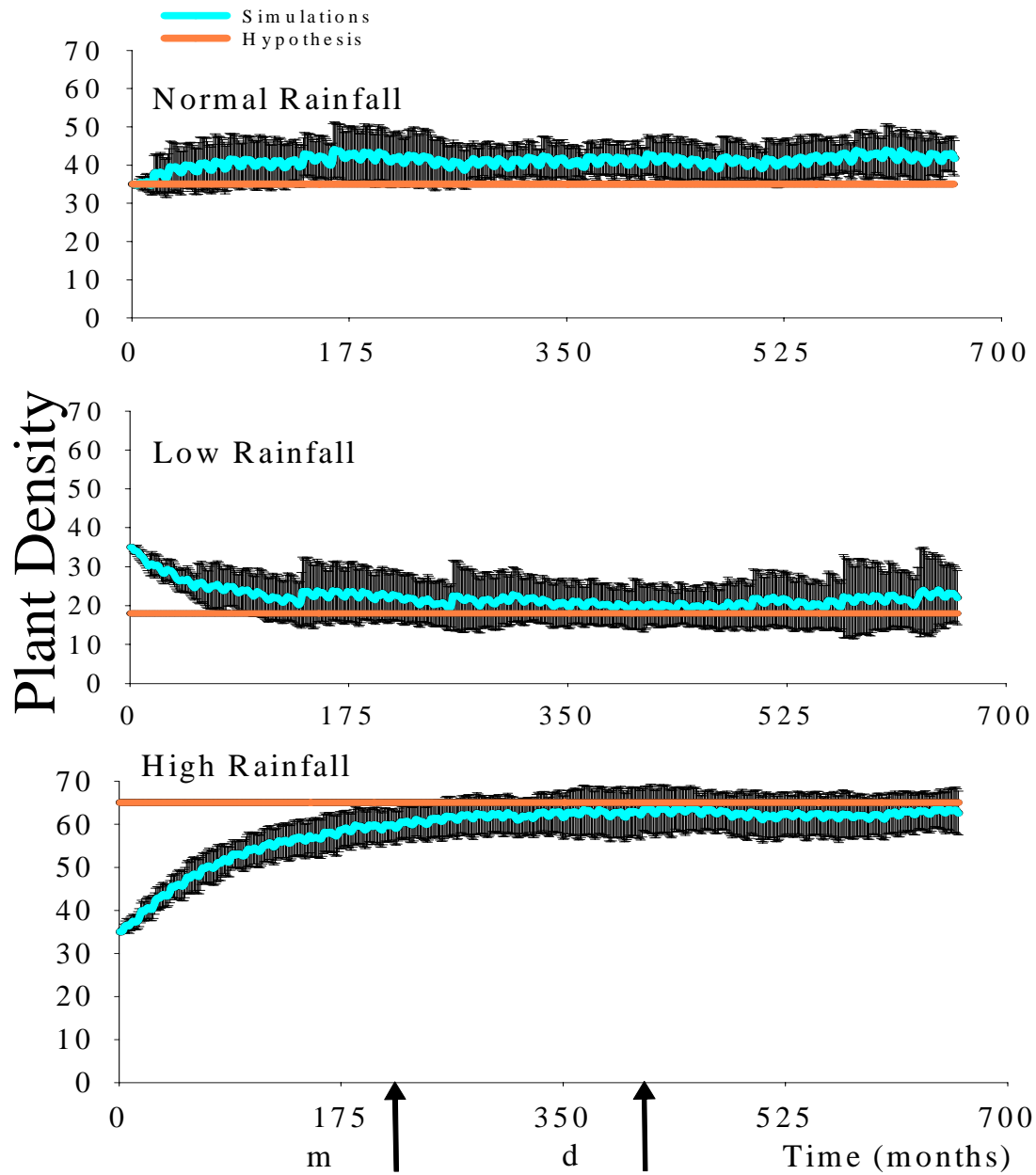


Figure 38. Population dynamics of the average (S.D.) number  $\text{m}^{-1}$  *Stipa leucotricha* adults under three rainfall treatments at the unoccupied zone. Arrows indicate the month the *P. barbatus* colony matures (m) and the month it dies (d).  $n = 30$ .

Table 26. Results of a two-way ANOVA for the effects of three zones surrounding the *P. barbatus* nest, (tasks, foraging and unoccupied), three rainfall treatments (normal, wet and dry) and their interaction during 55 year simulation model on number of plants <sup>-1</sup> of *Bouteloua curtipendula*, *Hilaria belangeri* and *Stipa leucotricha* at the Sonora Research Station. Mean historical rainfall (cm) during normal (3-10 cm), dry (<3 cm) and wet (>10 cm) years from 1919-2004 was utilized as covariate.

Source of Variation	<i>Bouteloua curtipendula</i> <sup>1</sup>			<i>Hilaria belangeri</i> <sup>2</sup>		<i>Stipa leucotricha</i> <sup>2</sup>	
	df	MS	F	MS	F	MS	F
Zone (covariate Historical Rainfall)	2	41.3	8.5***	1.3	1.5	0.4	0.5
Rainfall	2	6288.1	538.0***	6288.1	538.0***	3.6	4.1*
Zone x Rainfall	4	0.5	0.4	0.5	0.4	2	2.2
Error	531	1.2		1.2			

1 = Square root transformation of the data

2 = arcsin transformation of the data

\* p < .05

\*\* p = .06

\*\*\* p < .001

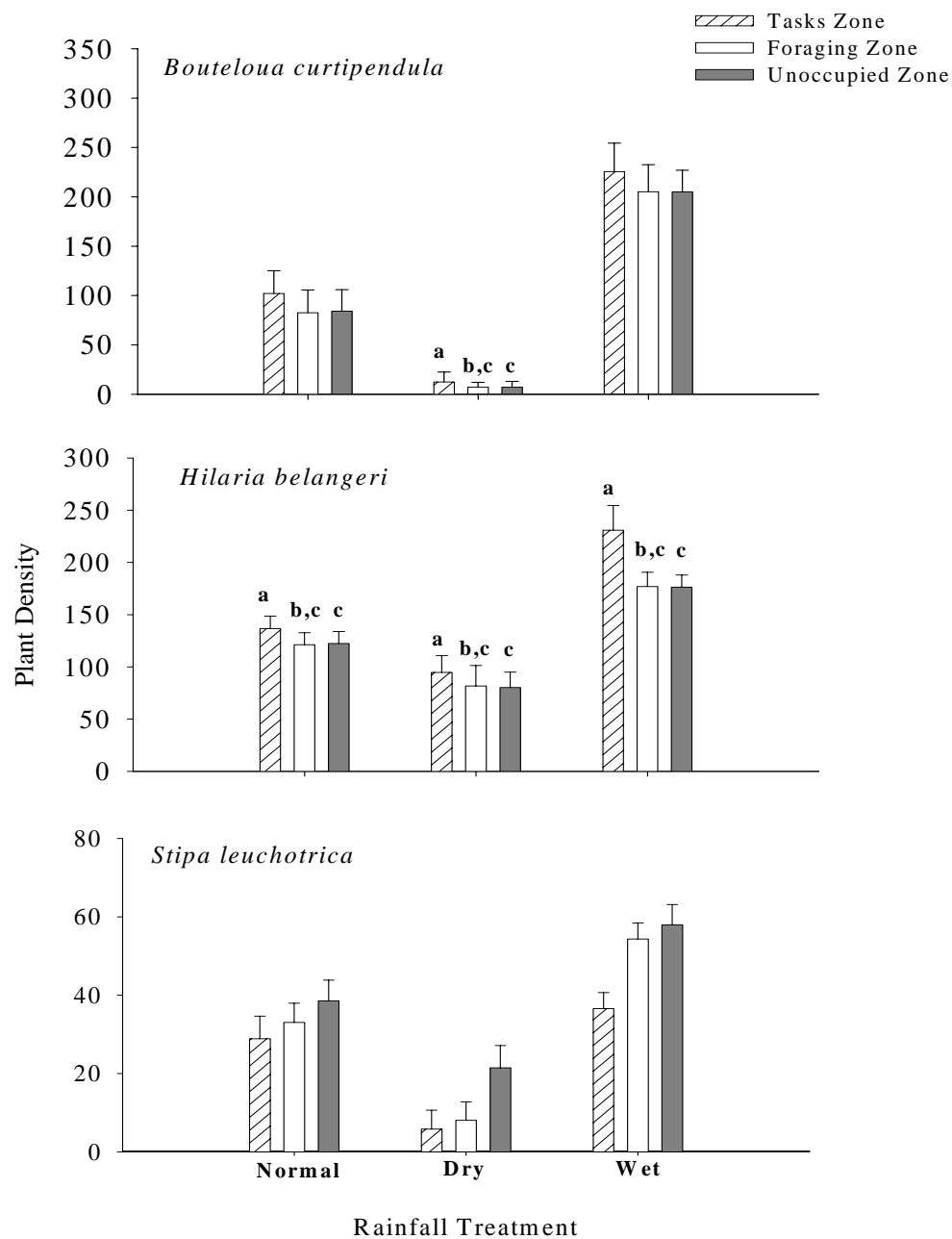


Figure 39. The effect of zone and rainfall treatment on the average (S.D.) number of adult plants m<sup>-1</sup> of *Bouteloua curtipendula*, *Hilaria belangeri* and *Stipa leucotricha* 11 years after colony maturity. Different letters above bars show significant differences using Bonferroni test *a posteriori*,  $p < .001$ . Note: scales differ between species.  $n = 30$ .

be harvested at the tasks zone at greater rates than previously thought. Although no significant differences were found among zones, prolonged drought with high seed removal may contribute to the species decline. In addition, competition with the other grasses may reduce densities at the tasks zone.

The tasks zone appears to act as a drought refugia for *Bouteloua curtipendula* which only maintains its densities there during dry treatments. Similarly, the tasks zone facilitates *H. belangeri* populations during wet treatments, by increasing densities that stay at the new, high numbers years after the colony has died. Field observations agree; when *Hilaria belangeri* becomes established due to environmental conditions or grazing pressure its population is high and continues to grow. These model results indicate a promising hypothesis that communities may be modified by ant presence due to differential responses of the grass species to the interaction of rainfall amount and ant activity.

Granivory appears to be least important, except for a few species under particular environmental conditions. Seedling mortality is high and could be more important than seed loss to grass demographics. In addition, it appears that population dynamics is driven more by vegetative reproduction than seedling establishment in this model. It is uncertain under what conditions seedling establishment would become important. Studies demonstrate that species switch reproductive strategies depending upon competition or environmental conditions (Grime 1974, Kays and Harper 1974). Nonetheless, sexual reproduction is important for grasses in three ways, the continued genetic diversity of the population, expansion into new habitats, and rapid population recovery after large-scale disturbances.

The simulation model allows a simple, but realistic and dynamic attempt to determine the influence of *P. barbatus* activities on populations of grasses on the Edwards Plateau. Rainfall, the major driver in this system, was used to observe the interaction of harvester ant activity due to possible drought refugia effects observed during the field study (Chapter III) and differential selection of seeds by workers that has led to significant repression of seedling establishment (Chapter V). Harvester ants were found to contribute directly to the productivity and spatial heterogeneity of the grassland ecosystem at the Sonora Research

Station. Intriguingly, a spatial dimension to the model, either varying levels of colony density or varying colony dispersion patterns, might reveal whether the results observed during simulations would be important mechanisms for community dynamics and at which spatial scales.

## CHAPTER VII

### CONCLUSIONS

Results indicate that cleared disks and nests constructed by *Pogonomyrmex barbatus* are important to grass population dynamics because they provide a refuge from droughts and could serve as a seed source for nearby areas following resumption of normal rainfall. Nevertheless, differential seed harvest reduces seedling establishment for some species of grasses and dicots. Areas excluded from foragers have higher numbers of grass and dicot seedlings following drought, but in normal rainfall years, competition with spring dicots reduces grass establishment. *Pogonomyrmex barbatus* indirectly changes competitive outcomes between grass and dicot seedlings by reducing dicot seeds, thus lessening the strength of seedling competition with grasses. The experimental studies and simulation modeling demonstrate that *P. barbatus* activities and large-scale disturbances of weather variability, fire and large-mammalian herbivory interact to drive dynamics in the grassland matrix of the semiarid savanna parkland on the Edwards Plateau, Texas.

The hypothesis was rejected that cover of perennial and annual grass and dicot species are comparable between nests and adjacent habitats recovering from a recent drought due to significantly more grass cover, and less dicots, in a roughly 45 cm-wide area surrounding cleared nest disks (Chapter III). These findings agree with others that vegetation structure often differs between harvester ant disk margins and surrounding vegetation (Golley and Gentry 1964, Wight and Nichols 1966, Rissing 1986, Nowak et al. 1990, Soule and Knapp 1996, Lei 1999). Previous studies suggest that the higher moisture and nutrient content of harvester ant nests compared to surrounding soils may promote grass production and reproductive output (Carlson and Whitford 1991, McGinley et al. 1994, Whitford and DiMarco 1995). Nests may retain moisture longer or provide better conditions during drought allowing grasses to survive in this refugia and to recover faster compared with adjacent habitat following drought.

Of all grass and dicot species collected by *P. barbatus* foragers, 69% were gathered

regardless of their abundance and availability in natural conditions, thus rejecting the hypothesis of Chapter IV that foragers will collect species of seeds in relation to their availability. This study is comparable to patterns of seed collection that were found to occur only when overall seed abundance is high (Davidson 1978, Whitford 1978, Hobbs 1985, Wilby and Shachak 2000). In addition, although seed abundance was observed to be similar in the spring and fall, experimental results on seed preference found that significantly more seeds were collected in the spring compared with the fall (Chapter IV). Thus, when *P. barbatus* raises their brood in the spring, they may have higher requirements than in the fall when they are storing seed for winter inactivity.

Seed selection was evident in forager exclusion experiments (Chapter V). Seed harvest altered density of establishing seedlings for only 13% of dicot species. However, during above-normal rainfall the density of grasses was lower where predators were excluded compared with where granivory could occur, suggesting that seed predation may have caused notable indirect effects of competitor release between annual dicots and grasses.

The effects of *P. barbatus* activities were overshadowed by weather conditions during field studies. These results were confirmed in a simulation model that accepted the hypothesis that rainfall levels drive grass density (Chapter VI). Improved recruitment of seedlings during the forager exclusion experiment was associated with increased rainfall and moderate temperatures (Chapter V). These observations are consistent with other studies in semiarid regions, thus affirming the importance of soil moisture, temperature and season for seedling recruitment of Edwards Plateau plants (Guterman 1993, Cheplick 1998, Petru and Menges 2003). Seed harvest altered density of establishing seedlings only after drought.

Simulated interactions between *P. barbatus* activities and rainfall found that low amounts of rainfall reduced the common perennial grass *Stipa leucotricha* under granivory and maintained densities of *Bouteloua curtipendula* at drought refugia at disk margins while populations in nearby areas nearly went extinct (Chapter VI). High rainfall treatments found *Hilaria belangeri* densities high at disk margins and they stayed elevated even after the colony was gone. Thus, the results of these studies add evidence to the findings of Wilby and

Shachak (2004) that changes in harvester ant effects on vegetation dynamics among years are due to varying climatic conditions.

Historical grazing levels alter herbaceous species structure and composition (Smeins and Merrill 1988, Fuhlendorf 1996, Hendrickson 1996, Briske and Hendrickson 1998). Disk margin and adjacent habitat composition also reflected historical grazing treatments agreeing with the hypothesis that grazing levels would determine herbaceous species composition (Chapter III). The effectiveness of the drought refugia for grasses was controlled by grazing treatment because ungrazed had fewer, but larger grasses due to the greater diversity of late-successional species compared with grazed treatments and thus recovered faster. Heavily grazed treatments had smaller disk margins and, due to small, early-successional grasses that died during the severe drought, this treatment recovered slowest.

Seed species selection in this study was not based on successional status of the species, although the common, late-successional grass *Bouteloua curtipendula* was preferred in the spring. Thus, the hypothesis that foragers would prefer late successional species was rejected whatever their habitat's grazing history (Chapter IV). Recovery from disturbances may not be greatly hindered by *P. barbatus* seed preference for late-successional species.

Granivory influences the structure of grassland communities through differential seed selection and reduction of seed abundance. Foraging areas cover from 17.3 to 73.6%, depending on colony density and foraging range, of the grassland community surface area, thus granivory effects could be extensive. This results in an altered community composition from that created by a large-scale disturbance regime and by other factors such as soil type and depth (Figure 40). However harvester ant influences may occur only under certain climatic conditions and grazing histories and their large-scale influence could be of equal weight to already existing heterogeneity or could be additive.

Semiarid savannas are highly variable and the factors and processes that drive their dynamics vary in time and space. Nevertheless, the results of this research show that harvester ant granivory and nest construction shape grasslands communities under drought conditions and alter recovery across a gradient of grazing treatments.



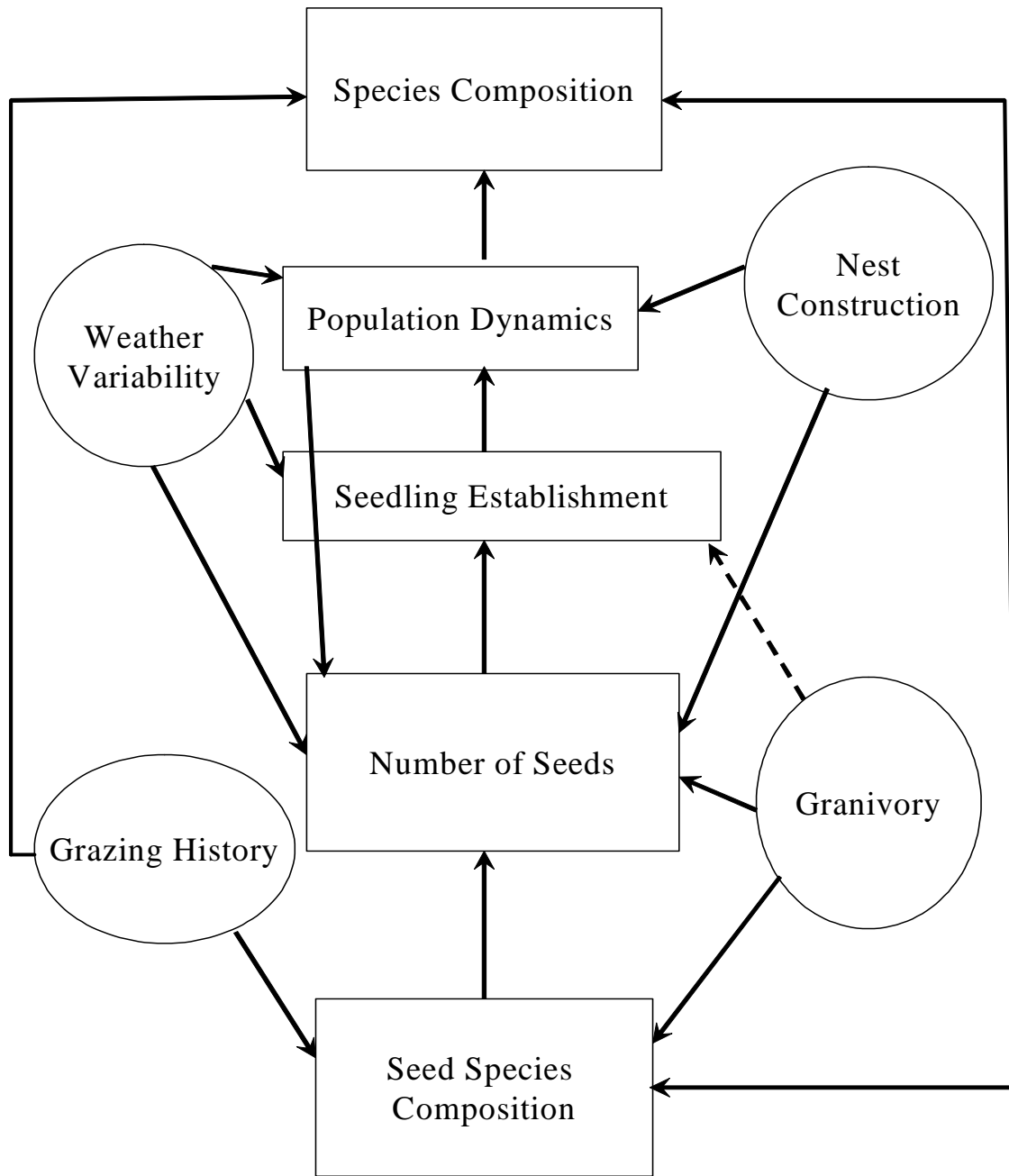


Figure 40. Simplified diagram of potential interactions between *Pogonomyrmex barbatus* nest construction and seed harvest and the large-scale processes of weather variation and grazing history, on the structure and dynamics of savanna communities. Dashed arrow represents an indirect effect.

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