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Spatial and temporal variability in relative abundance and foraging behavior of subterranean termites in desertified and relatively intact Chihuahuan Desert ecosystems

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Abstract

The annual feeding activity on paper baits of subterranean termites in desertified (degraded-shrub dominated ecosystems) and relatively undegraded black-grama (*Bouteloua eriopoda*) grasslands was measured over six years on 12 sites. There were no significant differences in mass losses from termite baits among the desertified and undesertified sites. Mass of paper consumed by termites on two sites dominated by creosotebush, *Larea tridentata*, was higher than on the other 10 sites. These sites were characterized by shallow, coarse soils and shrubs that did not retain a below-canopy litter layer. The spatial locations of the highest termite bait removal remained relatively constant over the duration of the study. Interannual variations in mass losses from termite baits were highly correlated with winter–spring rainfall (r^2 between 0.60 and 0.95) except at one site on shallow soils. The relationship between annual rainfall and termite activity was less significant (r^2 between 0.48 and 0.83). Frequency of attack as measured by percent of bait rolls "hit" were not different among sites indicating no differences in densities of subterranean termites. Degradation of Chihuahuan desert grasslands and associated vegetation change has had minimal effect on the activity of subterranean termites. Subterranean termites continue to affect soil properties and processes in both degraded (desertified) and undesertified ecosystems. © 1999 Elsevier Science B.V. All rights reserved.

Keywords: Desertification; Desert grassland; Dunes; Shrub-lands; Subterranean termites

1. Introduction

Desertification has been formally defined as "land degradation in arid, semi-arid and dry sub-humid areas resulting from various factors, including climatic variations and human activities" (Williams and Balling, 1996). Degradation of western rangelands resulting in dramatic changes in vegetation has been documented by a number of investigators (Buffington and Herbel, 1965; Hastings and Turner, 1965; Chew, 1982; Gibbens and Beck, 1988; Grover and Musick, 1990). In the northern Chihuahuan Desert of New Mexico,

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desertification has resulted in the replacement of perennial grasslands by shrub dominated communities. The most degraded landscapes are those where mesquite (*Prosopis glandulosa*) form coppice dunes and where creosotebush (*Larrea tridentata*) occupy gravel pavements.

Desertification has been described primarily in terms of effects on vegetation and soils (Williams and Balling, 1996). There are few studies of the effects of desertification on animal populations (Whitford, 1997). Because of the functional importance of subterranean termites in Chihuahuan Desert ecosystems (Whitford, 1991), it is important to know if and how their abundance and behavior is affected by desertification. We established a long term study to test the hypothesis that desertification has effects on both the relative abundance and foraging behavior of subterranean termites. We examined three hypotheses: (1) variation in mass losses from termite baits will not vary among desertified and relative intact ecosystems among sites and among years, (2) mean mass losses from termite baits will be the same among desertified and relatively intact ecosystems among sites and among years, and (3) spatial patterns of foraging intensity will remain constant on plots over time.

2. Methods

We selected a series of Chihuahuan Desert sites on the Jornada Experimental Range and on the Chihuahuan Desert Rangeland Research Center both of which are located between 40 and 60 km from Las Cruces, NM. The lands of these research stations include two mountain ranges and a large interior drainage basin. The research stations have well documented histories of land use and land cover changes between the 1860s and present (Buffington and Herbel, 1965; Gibbens and Beck, 1988). We used this information to select sites that have undergone large changes in vegetation composition and sites that have had some increase in shrub cover but that retain the vegetation composition characteristic of the area before the establishment of commercial ranching. The minimum distance between plots was 1 km. One group of plots was on a montain piedmont (creosotebush, *L. tridentata*, sites and the grass mosaic site dominated by grasses: black grama, *Bouteloua*

eriopoda, and dropseed, *Sporobolus* spp.). The tarbush (*Flourensia cernua*) dominated sites receive run-off from the mountain piedmont and were approximately 5 km from the piedmont sites. The remaining sites were on a plain approximately 15 km northeast of the piedmont. These sites included the black grama (*B. eriopoda*) grasslands, a site in mesquite (*P. glandulosa*) scrub, and the mesquite (*P. glandulosa*) coppice dune sites.

The subterranean termite fauna of the Jornada Basin is dominated by *Gnathamitermes tubiformans*. *G. tubiformans* accounts for more than 90% of the soldiers collected during field surveys. This species readily utilizes paper baits and builds foraging galleries within baits as well as on dead vegetation. Previous studies of subterranean termites in the Jornada Basin have been conducted in creosotebush dominated shrub communities (Johnson and Whitford, 1975; Schaefer and Whitford, 1981; Whitford et al., 1982).

The most effective method for obtaining estimates of relative abundance of subterranean termites in arid environments is by the use of baits placed on the soil surface. Toilet paper rolls are uniform size cellulose baits which are eaten by North American subterranean termites (LaFage et al., 1973; Johnson and Whitford, 1975). Subterranean termites build foraging galleries within the toilet roll baits and consume variable amounts of paper leaving hollowed areas within the rolls. We established grids of bait units (toilet paper rolls; LaFage et al., 1973) in desertified and relatively undegraded grasslands on the Jornada Experimental Range and Chihuahuan Desert Rangeland Research Center north of Las Cruces, NM. In order to assess variation in the relative abundance of subterranean termites attributable to soil type and not to vegetation change, we established pairs of grids on the same soil units and same vegetation communities (Table 1). Additional plots were established in grassland, creosotebush, and mesquite communities on soils that differed from the replicates.

Each grid of bait units consisted of five rows of baits with five baits per row. The grid spacing was 1.5 m between rows. Bait rolls were held in place by placing the rolls over a piece of steel rebar that was driven into the soil at each station. Bait rolls were covered with 18 cm diameter tin cans to prevent disintegration of the baits during intense rains. Bait grids were established in 1988 and rolls were replaced at the end of

Table 1
Soil characterisitics and desertification status (N – not desertified); (D – desertified) of the termite bait grid sites

Site	Soil series	Texture	Depth to caliche (cm)	Desertification status
Black grama I	Onite Pajarito	Sandy loam	50	N
Black grama II	Onite Pajarito	Sandy loam	50–80	N
Grass Mosaic	Berino Dona Ana	Fine sandy loam	>100	N
Creosotebush I	Nickel Upton	Sand	20–50	D
Creosotebush II	Nickel Upton	Gravelly sand	50–80	D
Creosotebush III	Nickel Upton	Loamy sand	50–100	D
Creosotebush IV	Nickel Upton	Loamy sand	50–100	D
Mesquite	Wink Harrisburg	Loamy fine sand	70–120	D
Coppice Dune I	Onite Pintura	Loamy fine sand	30–300	D
Coppice Dune II	Onite Pintura	Loamy fine sand	30–300	D
Tarbush I	Stellar	Clay loam	>100	D
Tarbush II	Stellar	Clay loam	>100	D

The dominant vegetation in the sites are black grama (*B. eriopoda*), creosotebush (*L. tridentata*), mesquite (*P. glandulosa*) and tarbush (*F. cernua*). Soil data from Bullock and Neher (1980).

each year. Sample years were 1988–1990 and 1993–1995. Bait rolls placed in the field in 1992 remained in place for two years on some of the plots; those data were not included in our analysis. Bait rolls were dried to a constant weight at 60°C and tagged with a grid identification number before being placed in the field. At the end of the sample year, gallery carton and soil were carefully removed from each roll. The cleaned rolls were oven dried at 60°C for 72–96 h and the dry mass recorded.

The data from the paired plots were analyzed by split-plot in time analysis of variance. Spatial patterns were examined by kriging and contour mapping of the relative abundance/foraging intensity as measured by mass losses from baits over time. For kriging and contour mapping we used Surfer software (Golden Software, 809, 14th St., Golden, CO 80401).

3. Results

There were no significant differences in mean mass losses from the termite baits among the desertified and relatively intact black-grama sites ($p > 0.27$–0.97). However, some plots within the same vegetation type but on different soils were significantly different from the paired plots in that vegetation type (Fig. 1). The mean mass losses from baits on the two unpaired creosotebush sites (creosotebush I and creosotebush II) were significantly higher than the mean mass losses from the baits on the black grama grassland grids (black grama I and II–creosotebush II; $t = 9.1$, $p < 0.01$; black grama I and II–creosotebush I; $t = 7.3$, $p < 0.01$). The mean mass losses from baits on the grass mosaic grid and mesquite grid were not significantly different from those recorded on the black grama grassland grids (black grama I and II–grass mosaic; $t = 0.46$, $p > 0.1$ and black grama I and II–mesquite; $t = 0.003$, $p > 0.1$).

The absence of differences in mean mass losses from the baits on the paired plot grids resulted from large within plot variance (Fig. 1). The within plot coefficients of variation ranged from 38.7% to 492.0%. Spatial analysis showed that the locations on the grids subjected to the most intense foraging activity were essentially constant over the period of study (Fig. 2). However, the intensity of activity as measured by mass loss from the bait rolls varied considerably among years. On most plots there were only small differences among years in the percent of bait rolls exhibiting some loss due to termite feeding (Fig. 3). On some plots there were marked reductions in the frequency of attack on bait rolls during the 1990 sample year. Interannual variations in mass losses from termite baits were more closely correlated with winter–spring rainfall than with total annual rainfall (Table 2). The correlation between winter–spring rainfall and average mass losses from termite baits was lowest at the creosotebush I site. The creosotebush I site was on very shallow soils where the depth to the caliche (cemented calcium carbonate) layer is 10–30 cm. (Tables 1 and 2).
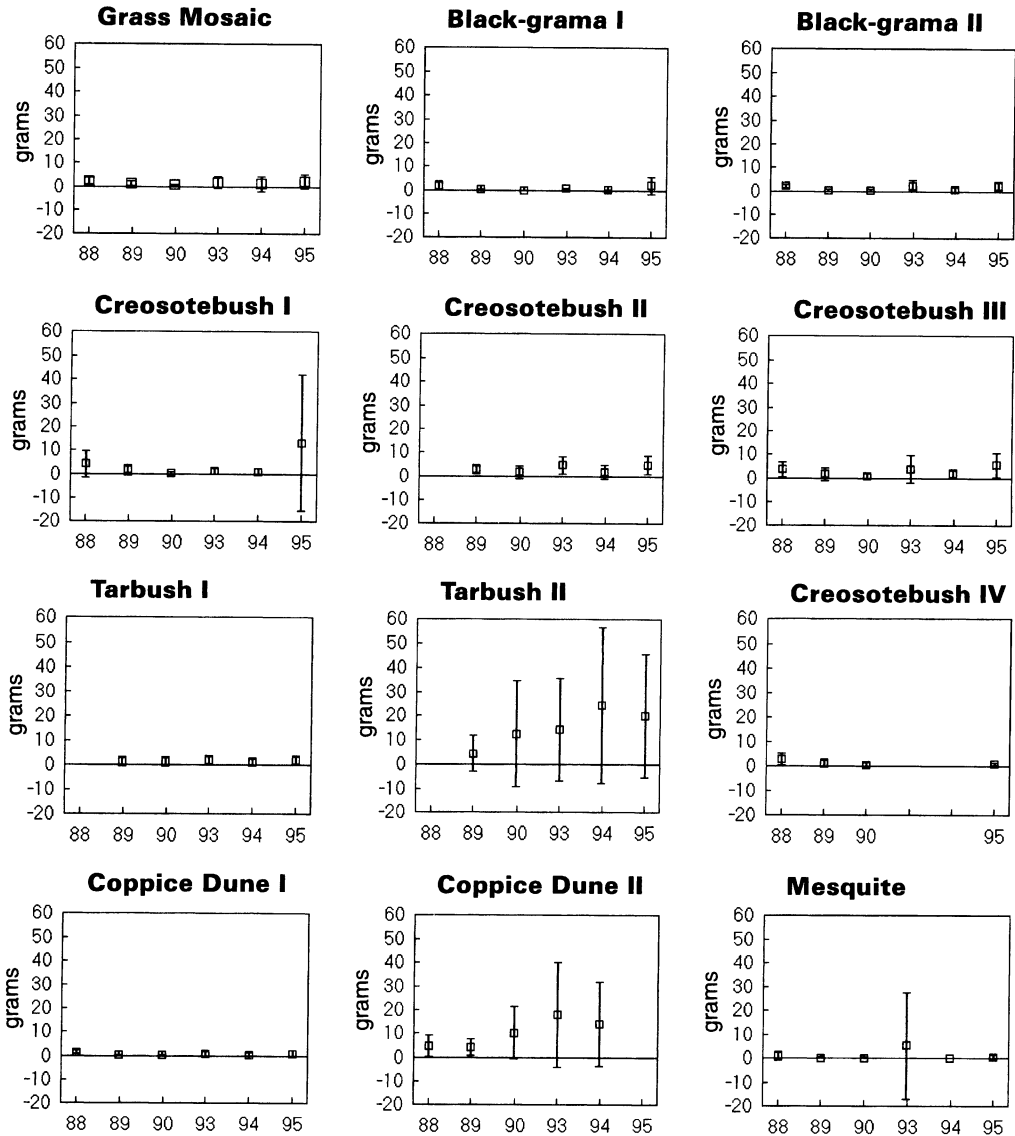
Fig. 1. Interannual patterns of mass of paper consumed by subterranean termites on toilet paper roll bait grids in a variety of desertified and undesertified sites in the northern Chihuahuan Desert. The black grama and grass mosaic sites are not desertified; all of the other sites are desertified.

4. Discussion

The significant differences in relative abundance of subterranean termites were mostly among sites on different soil types and not among sites having experienced small and large changes in vegetation cover and composition. Since *G. tubiformans* uses a wide range of plant materials and dung as food (Whitford et al.,

1982) it is not surprising that there would be few differences among sites on similar soils but with different vegetation. Soil texture and soil depth appear to be more important as variables affecting relative abundance of *G. tubiformans* than are the changes from grass dominated systems to shrub dominated systems. The formation of coppice dunes resulted in transport and loss of soil fines and accumulation of
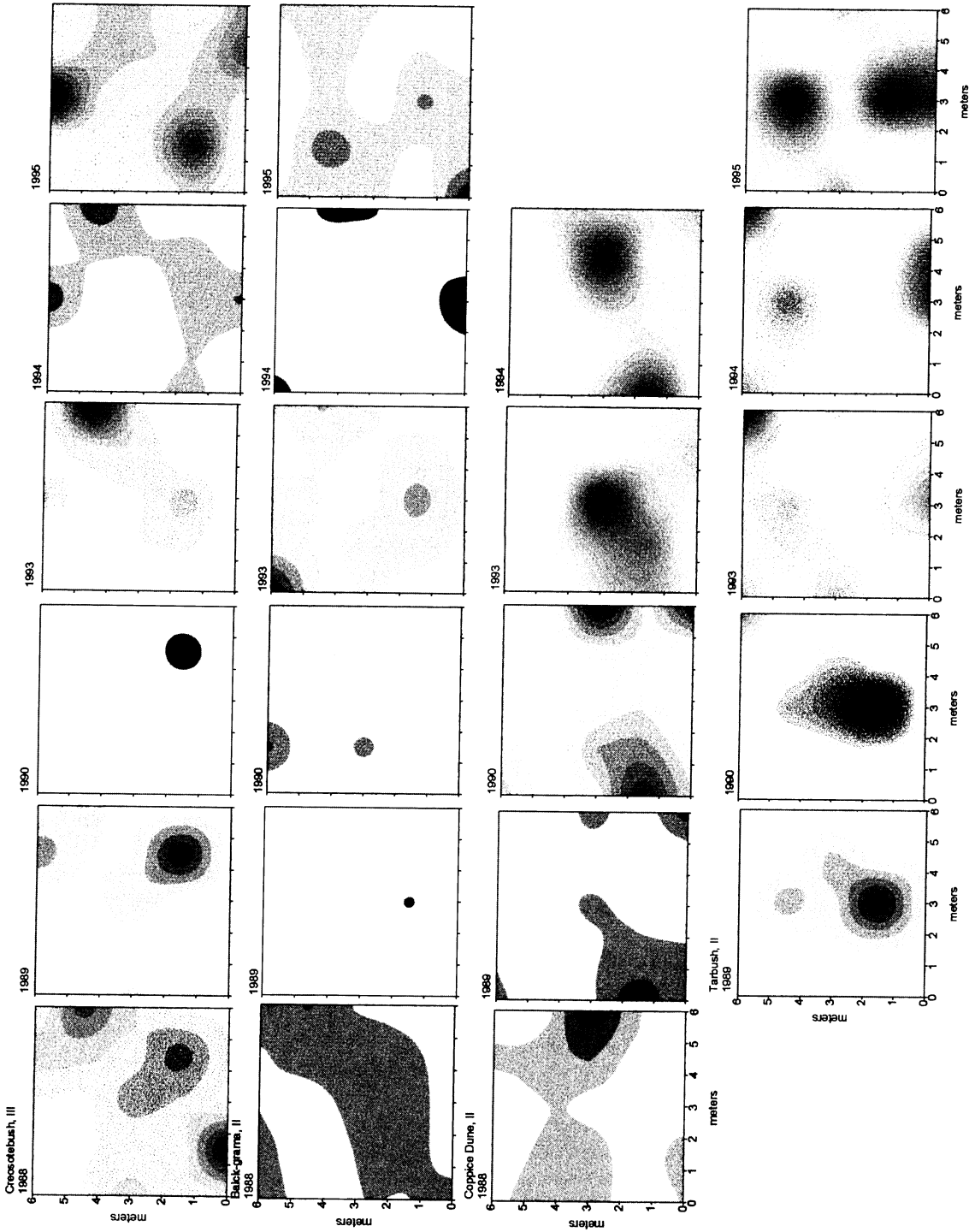
Fig. 2. Interannual variation in spatial patterns of foraging intensity of subterranean termites as measured by mass of paper consumed from toilet paper roll baits on grids in desertified and undesertified sites in the northern Chihuahuan Desert. Increasing mass loss values are from clear–virtually no loss to dark-high to maximum loss. The black grama and grass mosaic sites are not desertified; all of the other sites are desertified.
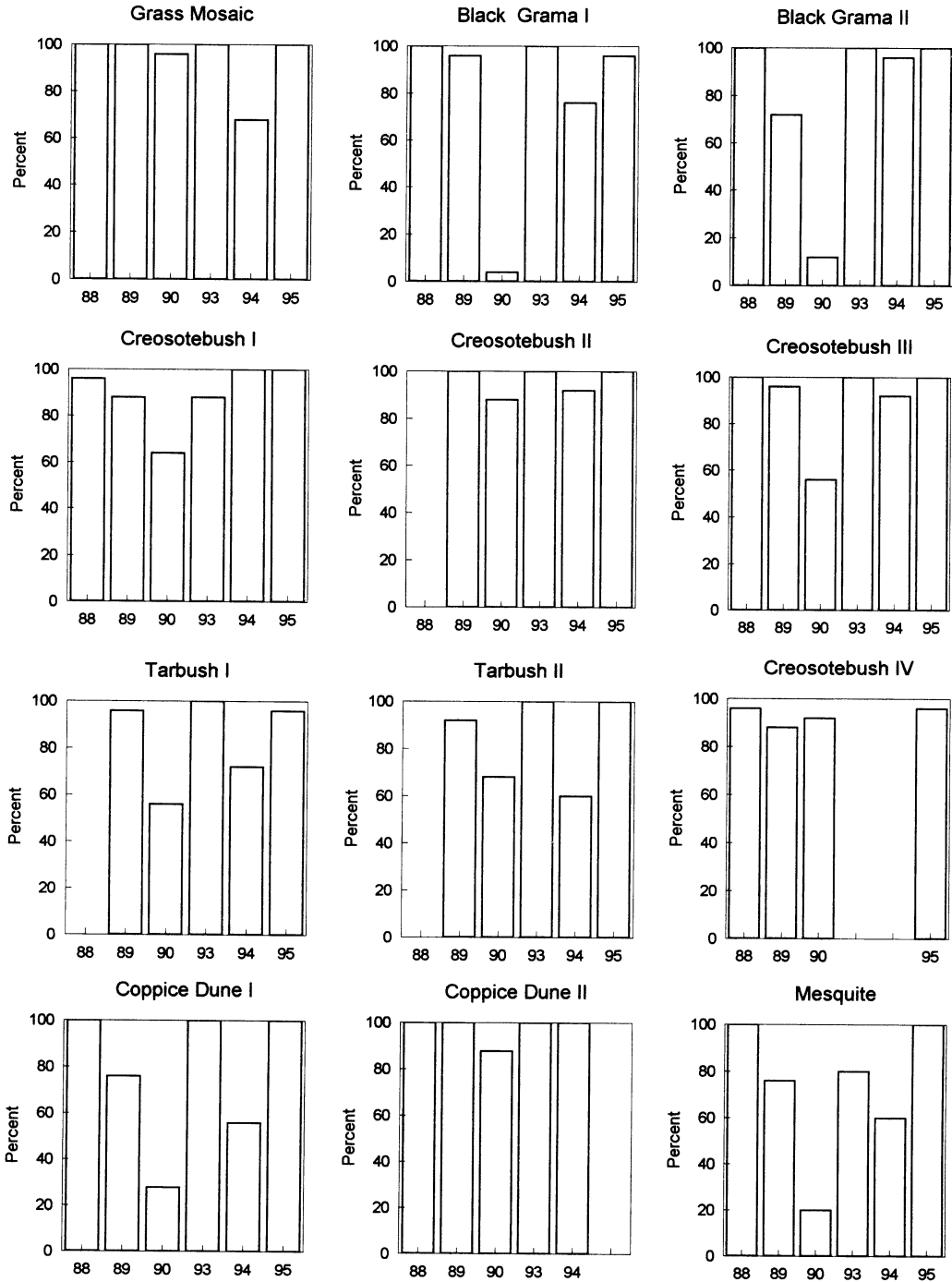
Fig. 3. Interannual variation in the percent of termite baits attacked by subterranean termites on desertified and undesertified sites in the northern Chihuahuan Desert. The black grama and grass mosaic sites are not desertified; all of the other sites are desertified.

Table 2
Regression of mean mass losses for termite baits and winter–spring rainfall (December–March) and total annual rainfall (Y=mean mass loss (g), X=rainfall (mm))

Site	Regression (winter)	Winter (r^2)	Regression (annual)	Annual (r^2)
Grass Mosaic	$Y=0.24X$	0.95	$Y=0.006X$	0.83
Black grama I	$Y=0.01X$	0.67	$Y=0.003X$	0.48
Black grama II	$Y=0.02X$	0.83	$Y=0.006X$	0.64
Creosotebush I	$Y=0.54X$	0.41	$Y=0.128X$	0.30
Creosotebush II	$Y=0.38X$	0.70	$Y=0.010X$	0.65
Creosotebush III	$Y=0.44X$	0.84	$Y=0.011X$	0.67
Creosotebush IV	$Y=0.02X$	0.85	$Y=0.006X$	0.72
Mesquite	$Y=0.14X$	0.60	$Y=0.399X$	0.62
Coppice Dune I	$Y=0.11X$	0.82	$Y=0.003X$	0.64
Coppice Dune II	$Y=0.14X$	0.72	$Y=0.040X$	0.77
Tarbush I	$Y=0.02X$	0.73	$Y=0.005X$	0.72
Tarbush II	$Y=0.14X$	0.60	$Y=0.040X$	0.62

sand in the dunes. The great variation in soil depth and changes in texture of soils in the coppice dunes were predicted to have a negative impact on the subterranean termites. However, there were essentially no differences in relative abundance or foraging intensity in the grama-grassland sites and coppice dune sites on the same soil series. These differences in soil depth and texture between the black-grama grasslands and coppice dunes were not as great as differences in the soils on which creosotebush communities developed compared to the black-grama grassland soils.

The high coefficients of variation in paper consumption on a single grid and the spatial pattern of consumption over the years of this study suggest that *G. tubiformans* has preferred subterranean pathways to food objects on the soil surface. If those objects remain in the same place over a series of years, these termites will continue to feed most intensively in the same area and their use of other materials will vary with availability and soil environmental conditions. The high coefficients of variation contribute to the problem of interpreting mass losses from baits as a measure of relative abundance of subterranean termites.

The data from this study suggest that subterranean termites utilize surface baits with intensity inversely related to the availability of natural foods. Mass losses from bait rolls were greatest on grids in shrub dominated ecosystems during years with little or no annual plant production. The highest rates of mass loss from grids in two of the creosotebush dominated ecosystems (creosotebush I and II) where virtually none of the shrubs had developed a hemispherical morphology. Hemispherical shrubs capture and retain litter below the canopy and sub-canopy soils are characterized by higher water and nutrient status than soils in the intershrub space (deSoyza et al., 1997). The densities of annual plants in the sub-canopy areas in creosotebush communities are greater under hemispherical shaped shrubs than under inverted cone shaped shrubs (deSoyza et al., 1997). Since annual plants contribute most of the annual primary production that is available to termites, subterranean termites in ecosystems with low annual plant production are expected to consume more of the bait roll mass than termites in ecosystems with relatively high biomass of dead annual plants.

In an *Acacia* savanna in Botswana (Dangerfield and Mosugelo, 1997) reported that the proportion of baits attacked was positively associated with rainfall. In this study, mass of paper removed was correlated with rainfall but not proportion of baits attacked. This is attributable to the differences in foraging behavior of the termites in an African savanna and *G. tubiformans* in the Chihuahuan Desert. The high correlation between mass losses and winter–spring rainfall suggest that early growing season soil moisture may be the most important variable affecting the foraging activity of termites in surface baits. Subterranean termites build foraging galleries within the baits rolls. Above ground foraging gallery construction requires moist soil. The absence of moist soil early in the growing season undoubtedly reduces the ability of the termites to feed on the bait rolls. The higher

correlation of mass losses with winter–spring rainfall than with annual rainfall suggests that termites are feeding in materials with large mass and large area of contact with the soil surface more frequently in the spring and early summer than in the late summer. Livestock dung pats and *Yucca* logs are reliable places to find *G. tubiformans* in late spring and early summer. When the soil profile is dry, termites construct foraging galleries in those materials that are structurally similar to the galleries found in toilet roll baits. In the Chihuahuan Desert, late summer monsoon rains are the most predictable and generally result in the germination and establishment of summer annuals. Subterranean termite foraging in baits during the late summer is likely to vary as a function of the quantity of natural food available (i.e. dead summer annuals) and the availability of moist soil for construction of foraging galleries. In late summer above ground foraging galleries are abundant (MacKay et al., 1985). These variables added to variation in mid-summer soil moisture are probably responsible for the lower correlation of baits mass losses and annual rainfall. Since the patterns of mass losses proportion of baits attacked varied in similar ways in our study, our data support this relationship.

The inverse relationship between annual plant production (function of seasonal rainfall) and mass of paper consumed by subterranean termites from the bait rolls demonstrates that data based on termite consumption of surface baits must be interpreted cautiously. Termites may feed intensively on paper baits when alternate food sources are not available or are limited. While toilet paper baits produce thermal shadows similar to those produced by dung on the surface of the soil (Ettershank et al., 1980) termites may switch to other food if available and if the soil environment is conducive to surface foraging. Thus mass of paper removed from baits is only a measure of feeding activity and may not be proportional to the numbers of foragers in a colony. In order to estimate densities of subterranean termite colonies, the frequency of "hits" on baits and spatial patterns of mass removal from baits provide a better indirect measure than mass losses from baits.

Since the grid locations were selected at random within each of the sites to be sampled in this study, it would be expected that one or more of the grids would experience few "hits" by termites, especially if deser-

tification had reduced the densities of termite colonies. The absence of differences in the frequency of "hits" on baits in the different ecosystems is the strongest evidence that desertification has had no effect on the density of subterranean termite colonies. The consistency of spatial distribution of surface foraging and the high frequency of "hits" on all of the grids demonstrates that the keystone activities of subterranean termites such as production of macropores, decomposition of dead plant materials and dung, and modification of soil profiles are conserved in desertified landscapes in the Chihuahuan Desert.

The results of these studies show that in the Chihuahuan Desert, subterranean termites are resistant to the changes in soil and vegetation that have occurred as a result of desertification processes over the past 1.5 centuries. Therefore subterranean termites are present in sufficient numbers in even the most degraded, and unproductive ecosystems (the mesquite coppice dunes) to maintain their keystone role. The abundance of termite colonies in the most degraded rangeland ecosystems suggests that restoration efforts that focus on utilizing the functional roles of these animals are likely to be most successful. Strategic distribution of recalcitrant mulches could induce higher densities of foraging gallery macropores and enhance other soil physical and chemical properties for seedling establishment.

Acknowledgements

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