ability as primary determinants of spatial and temporal heterogeneity and the biology of the component species if we are to understand the production, composition, and distribution of annual plant assemblages.

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EFFECT OF ELIMINATING SUBTERRANEAN TERMITES ON THE GROWTH OF CREOSOTEBUSH, *LARREA TRIDENTATA*

Several studies in the northern Chihuahuan Desert have shown that subterranean termites affect soil properties (Parker et al., 1982; Brown, 1983; Elkins et al., 1986). Parker et al. (1982) compared annual plants on a series of plots from which termites had been eliminated with those on plots with termites present and found that, although total annual plant diversity and biomass were not different, dominant species on termite-free plots ranked considerably lower than those on plots where termites were present. Parker et al. (1982) attributed these changes in species dominance to increased nitrogen levels in surface soils from which termites had been eliminated. In a subsequent study, Elkins et al. (1986) reported that water infiltration was significantly lower on plots where termites had been removed. Thus, plots without termites are characterized by higher soil nitrogen and lower water availability. Gutierrez and Whitford (1987) demonstrated that the productivity, life span, and species assemblages of annual plants of the Chihuahuan Desert are a function of the interaction between soil nitrogen and water availability. Shifts in annual plant productivity and species composition which resulted from termite removal resulted from increased nitrogen and decreased soil moisture on the termite-free plots.

Soils devoid of termites are more compacted (Elkins et al., 1986), and nitrogen concentrations in the soil surface decrease with depth. This should affect the growth of deep-rooted shrubs. We studied the effects of water supplementation and termite removal on shoot growth of the common Chihuahuan Desert shrub *Larrea tridentata* to test the hypothesis that reduced infiltration by removal of termites would reduce growth rates of the shrub.

The study area was located at the Jornada Long Term Ecological Research site on the New Mexico State University Experimental Ranch, 40 km NNE of Las Cruces, Dona Ana Co., New Mexico. This site was a desert watershed that emptied into an ephemeral lake. The watershed varied in elevation

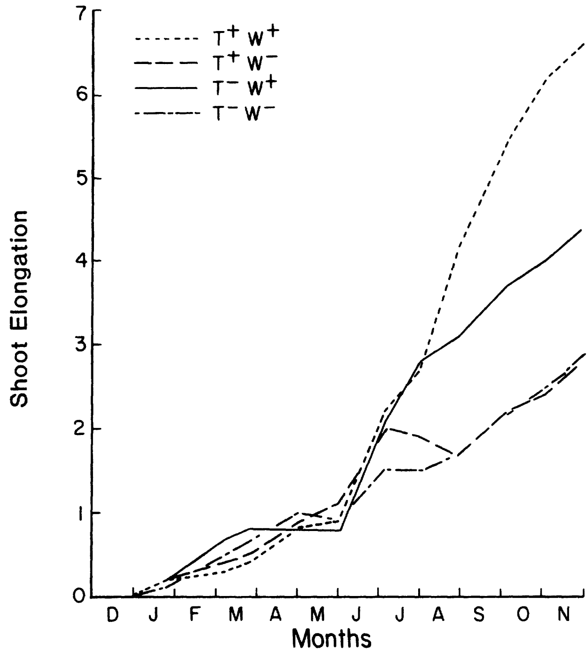

FIG. 1—Average cumulative shoot elongation (cm) in *Larrea tridentata* on plots with termites present (T+) or termites absent (T−) and with supplemental water (W+) or no added water (W−).

from approximately 1,200 to 2,000 m. Our study was conducted on the mid-slope area of the watershed where vegetation was essentially a monotypic cover of *L. tridentata,* with other shrubs limited to the margins of drainages. The 100-year annual precipitation ± 1 *SD* is 211 ± 77 mm, with most rainfall occurring during late summer from convectional storms. Maximum summer temperatures of 40°C and freezing temperatures from October to mid-March have been recorded (Houghton, 1972).

In October and November 1977, eight plots (30 m by 40 m) were treated with chlordane, at an application rate of 10.3 kg/ha, to eliminate termites. Chlordane is a recalcitrant chlorinated hydrocarbon that binds to clay particles in the soil, thereby losing its contact toxicity. Subterranean termites ingest soil, and the chlordane is apparently released in their gut. The only soil animals that did not survive the chlordane treatment or recolonize the treated area were subterranean termites.

In November 1982, 20 randomly chosen shoots were marked at 1 cm from the branch tip on 10 *L. tridentata* present in one of the chlordane-treated plots. The same procedure was repeated with 10 plants growing in a plot of 30 m by 40 m with termites present. On each plot, five plants were sprinkler-irrigated with 13 mm of water every 15 days; the other five plants received only natural rainfalls. Elongation of plant shoots was measured monthly. Due to the presence of termite–water interaction, monthly shoot elongation data were analyzed by stratified one-way analysis of variance tests incorporating time as a variable, and results are reported separately for the effects of termites in the watered and unwatered treatments. The same model was used to test the effects of water for termite and termite-free treatments. For the latter case, we assumed no differences between the two plots to apply the model.

Barbour (1969), Woodell et al. (1969), and Yeaton et al. (1977) reported intraspecific competition for water in *L. tridentata.* This competition may be reflected in plant density (Barbour, 1969; Woodell et al., 1969) or plant size (Yeaton et al., 1977). Our data (Fig. 1) show that, in the termite plot, shoot elongation was higher in watered plants than in unwatered ones ($F = 26.30$; $d.f. = 1,8$; $P < 0.001$). In the termite-free plot, the pooled means of shoot elongation for watered and unwatered plants were not statistically different ($F = 3.15$; $d.f. = 1,8$; $P > 0.10$), but, through time, shoot elongation was higher in the watered plants than in the unwatered ones ($F = 4.48$; *d.f.* = 1,8; $P < 0.001$) in September, October, and November. These results confirm the hypothesis that water limits growth of *L. tridentata.* The lower shoot elongation observed in the watered plants of the termite-free plot relative to the termite plot would be related to the lower soil–water infiltration in this plot (Elkins et al., 1986). Pooled means of monthly shoot elongation for termite and termite-free plots in the watered treatment were marginally different ($F = 4.27$; *d.f.* = 1,8; $P < 0.08$). However, shoot elongation was greater in the termite-present watered plants than in the termite-free watered plants in September, October, and November ($F = 6.72$; *d.f.* = 10,80; $P < 0.01$). No growth-increment differences through time were detected between the unwatered plants on the termite-present and termite-free plots ($F = 0.45$; *d.f.* = 10,80; $P > 0.10$). The total natural rainfall of the growing season was <100 mm, which probably was insufficient to produce differences in soil–water content due to presence or absence of termites. Larger increments of shoots in all treatments were observed June through November (Fig. 1).

As suggested in our initial hypothesis, elimination of termites had a negative effect on growth of *L. tridentata* in the Chihuahuan Desert. The lower growth increment recorded for plants in the termite-free plot is probably the result of reduced soil water or nitrogen at the root surface of plants. Gutierrez and Whitford (1987) reported that soils on termite-free plots at 20 cm were significantly drier than soils on plots with termites. Elkins et al. (1986) showed that termite removal reduced soil–water infiltration for the same site. In this area, roots of *L. tridentata* extend to depths of 2 m passing through the caliche layer (average depth of 90 cm, pers. obser.). The reduced infiltration and lower water content of soils on termite-free plots would significantly reduce the quantity of water and probably nitrogen moving through the soil to the 2-m depth. Water in the shallow soil is quickly removed by evapotranspiration by shallow-rooted grasses, herbaceous plants, and small woody shrubs (Schlesinger et al., 1987). Since incremental growth in length of shoots is an indirect measure of leaf area and flower and fruit production, the fitness of *L. tridentata,* in the long term, could be adversely affected by the absence of termites.

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