Effect of Desert Termites on Herbage and Litter in a Shortgrass Ecosystem in West Texas

MICHAEL C. BODINE AND DARRELL N. UECKERT

Highlight: *The desert termite,* Gnathamitermes tubiformans, *is an important insect on rangelands in the southwestern United States. Population densities of this insect averaged 2139/m² in the upper 30 cm of soil in a shortgrass community in West Texas over a 3-year period and reached a peak of 9127/m². The live biomass of termites averaged 5.2 g/m² and reached a peak of 22.21 g/m². In a laboratory study, desert termite workers consumed 2.4% of their live body weight/day of dry buffalograss leaves. In field studies, control of desert termites with insecticide resulted in a 22% increase in standing crop of grass and a 50% increase in litter accumulation by the end of the second growing season after control was initiated. Termite-free plots had almost three times more litter than termite-infested plots after four growing seasons. Desert termites accounted for 55% of the disappearance of litter from the soil surface. Ranchers can expect higher population densities of desert termites and hence greater consumption of forage and litter during wet years.*

Termites are viewed as both beneficial and destructive in many ecosystems. In some instances they are thought to be important in nutrient cycling and soil formation, whereas in others they are regarded as major factors in range deterioration and soil erosion. A number of species of ground-dwelling termites are restricted to the arid and semiarid lands of the southwestern United States. The desert termite, *Gnathamitermes tubiformans* (Buckley)[1], occurs in southern New Mexico, Texas, Arizona, and northern Mexico and has been reported to destroy large areas of growing vegetation on grazing lands (Light, 1934; Snyder, 1949; Weesner, 1970). This species lives in the soil and comes aboveground to feed on grasses, forbs, dead herbage, dry wood, and livestock manure. This insect constructs mud tubes or sheetings around the surfaces of its food (Fig. 1). It does not penetrate wood, but removes only the surface material. When attacking herbs, it often consumes the entire aboveground portions of the plants, leaving intact its earthen tubes with the general shape of the consumed vegetation. The workers and soldiers come above the soil surface at night and during the cooler parts of the day to forage, and are particularly active after rains (Light, 1934; Calaby and Gay, 1959; Weesner, 1970).

The loss of forage and litter from the soil surface to these insects frequently alarms ranchers and range managers, hence this study was undertaken to determine their impact on rangeland herbage and litter, and their role in the energy flow through a shortgrass ecosystem.

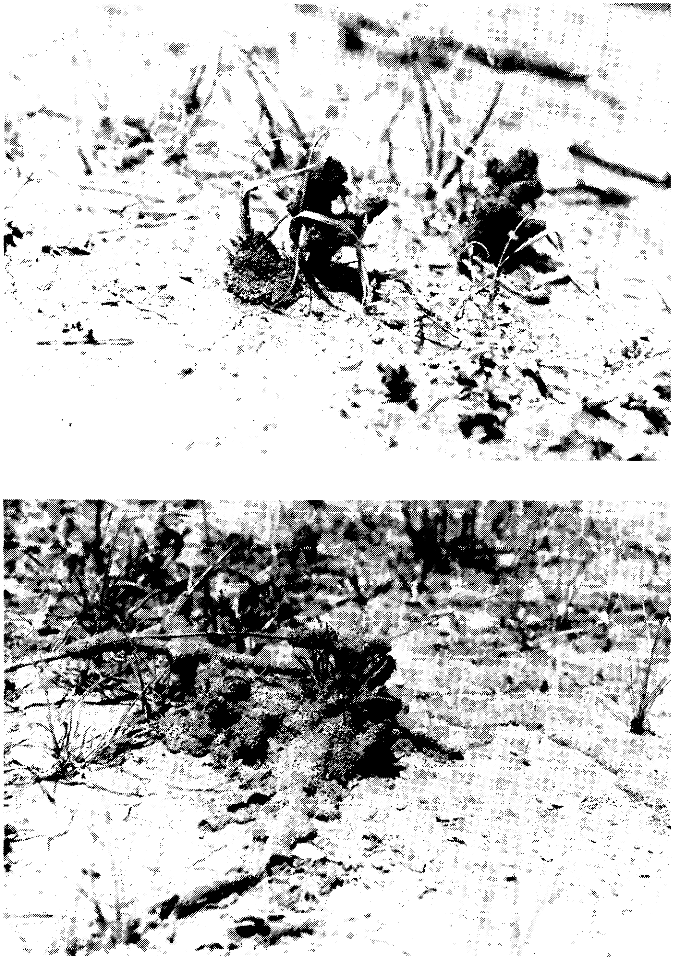

Fig. 1. *Desert termites construct mud tubes and sheetings around their foods, including grasses (A) and plant litter (B).*

Authors are graduate research assistant and associate professor, Range and Wildlife Management Department, Texas Tech University, Lubbock, 79409. Bodine's present address is P.O. Box 695, Sterling City, Tex. 76951.

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[1] Isoptera: Termitidae.

Literature Review

Lee and Wood (1971) listed various foods utilized by termites, including living and dead wood, forbs and grasses, plant debris, fungi, dung, and soil rich in organic matter. Termites feed on plants at all stages of growth, and their feeding damages roots, stems, leaves, and seeds of the host plant (Reddy, 1960; Sankaran, 1960). Harvester termites cut down standing grasses and forbs, while scavengers collect leaves, twigs, seeds, plant litter, dung, and other substrate from the soil surface. Many species are polyphagous or oligophagous (Lee and Wood, 1971).

Many instances of termites feeding on living vegetation have been documented. Krishnamoorthy and Ramasubbiah (1960) reported that termites fed on green house plants, field crops, and forage plants on grazing lands. Reddy (1960) stated that nearly every agricultural crop in the humid tropics is fed upon by termites. Ferrar and Watson (1970) reported that termites feed on grasses, crops, and live wood in Australia. Watson and Gay (1970) determined that *Drepanotermes perniger* (Froggatt) and *D. rubriceps* (Froggatt) were principally responsible for the degradation of a mulga ecosystem in Queensland, Australia. These termites increased in numbers during years when grass was abundant. During ensuing drier conditions, the termites removed the remaining grass and litter, leaving denuded areas which were subject to extensive erosion of the topsoil. Coaton (1954, 1960) discussed the impact of the harvester termites *Hodotermes mossambicus* (Hagen) and *Microhodotermes viator* (Latreille) on grasslands in South Africa. He felt that overgrazing, failure to apply rotational grazing, and burning of the veld in late winter resulted in a denuded condition which was favorable to a progressive increase of termite population levels and consumption of practically all of the grass produced. In Zululand, termites were believed to be responsible for a 25% decrease in carrying capacity of the grasslands.

Many species of termites are believed to compete with grazing animals for forage, to actually damage forage resources, and to interrupt soil nutrient cycles. On the other hand, some termites are thought to be beneficial in their effect on the soil. Lee and Wood (1971) summarized these inconsistencies by stating: "One cannot say, on the basis of present knowledge, whether or not grass-feeding termites can be ranked with kangaroos as low-level competitors to be tolerated and possibly 'managed,' or whether like the rabbit, they should be more or less exterminated." Krishna and Weesner (1970) reported that less than 10% of the known species of termites have actually been recorded as pests, and that they are actually very important in nutrient cycling and soil formation. Lee and Wood (1971) have surveyed the literature on the influence of termites on nutrient cycling and soil properties.

Termites aid in the decomposition of wood and plant litter, thereby contributing to the formation of humus and cycling of nutrients (Adamson, 1943). Hopkins (1966) reported that termites were largely responsible for the decay of wood in certain habitats in Nigeria. Maldague (1964) estimated that *Cubitermes fungifaber* (Sjöstedt) consumed approximately 50% of the annual litter fall in a *Brachystegia* forest near Yangambi, Congo; however, Lee and Wood (1971) believed Maldague's estimate to be too high, and reported that it was actually 10% or less. Lee and Wood (1971) reported that *Nasutitermes exitiosus* (Hill) consumed 16–17% of the woody litter, or 4.9% of the total annual litter fall in a dry sclerophyll forest in Australia.

Maldague (1964) estimated the population density of subterranean and mound-building termites in *Brachystegia* forest in the Congo at $1000/m^2$ with a total biomass of 10 g/m^2 (live weight). Lee and Wood (1971) estimated the population of *N. exitiosus*, a mound-building termite in Australia, at $600/m^2$ with biomass of 3.0 g/m^2. Strickland (1944, 1945) reported population densities of subterranean termites of $3864/m^2$ and $5473/m^2$ in Trinidad rain forest. Lee and Wood (1971) reported population densities of $12/m^2$ in desert grasslands and steppe of Southern Australia and $2000/m^2$ in native grasslands of Northern Australia. They theorized that the biomass of termite populations may approach or exceed that of native mammalian herbivores in some habitats, and may thus result in dietary competition.

Methods and Materials

Study Area

The study was conducted 19.2 km southwest of Post in Garza County, Texas, on the southeastern edge of the Llano Estacado. The climate of the area is semiarid, characterized by low precipitation, high evaporation, hot summer days followed by cool nights, and moderate winter temperatures punctuated by severe cold spells. Annual precipitation in the area ranges from 22 cm to 103 cm, with a mean of 48 cm, about 85% (41 cm) of which falls between March and October. However, high winds and high temperatures contribute to an annual evaporation of 185 cm. The annual snowfall is 19 cm. The frost-free period is about 201 days (Mowery and McKee, 1959).

The soil throughout the study area is an Olton clay loam. The topography of the area is nearly level to gently rolling, with a 0–1% north-facing slope. The vegetation consists primarily of blue grama (*Bouteloua gracilis* H.K.B.), and buffalograss (*Buchloe dactyloides* Nutt.). Minor grass species include red threeawn (*Aristida longiseta* Steud.), sand muhly (*Muhlenbergia arenicola* Buckl.), vine-mesquite (*Panicum obtusum* H.K.B.), tobosagrass (*Hilaria mutica* (Buckly) Benth.), and silver bluestem (*Bothriochloa saccharoides* (Sw.) Rydb.). Honey mesquite (*Prosopis glandulosa* Torr.) is the major shrub species.

Termite Population Density and Biomass

To determine the population density of subterranean termites, 40 randomly selected soil cores ($81.07\ cm^2 \times 30.18$ cm) were taken monthly. Each soil core was sealed in a plastic bag and returned to the laboratory to be manually examined for termites. The termites were counted and a mean number of termites/m^2 was calculated. The average biomass of individual

Table 1. Mean population density (number/m^2) and biomass (g/m^2) (live weight basis) of desert termites in the upper 30 cm of soil in shortgrass rangeland in Garza County, Texas, during 1972, 1973, and 1974 and the growing seasons (March through October) of these years.

Time interval	Population density[1]	Population biomass
Years		
1972	3672 a	8.93
1973	1692 b	4.12
1974	1152 b	2.80
Growing seasons		
1972	4730 c	11.51
1973	2640 d	6.42
1974	1482 e	3.61

[1] Means within a column followed by similar letters are not significantly different at $P < 0.10$.

worker termites, determined by weighing three groups of 100 live specimens, was used as the mean weight of all castes and instars to convert population densities to g/m^2.

Herbage Consumption

Laboratory study.

Laboratory feeding trials using *G. tubiformans* workers were conducted during September, 1972, to determine the mean rate of dry matter consumption. The trials, in which live workers were collected in the field and placed in 3.8-liter glass jars, 1/3 full of moist sand, and covered to exclude light, were replicated five times. Oven-dried buffalograss leaves were placed in each jar with the termites. After 10 days, the contents of each jar were emptied, the remaining termites were counted, and the remaining leaves oven-dried and weighed. Dry matter consumption per termite per day (D) was calculated according to the equation:

$$D = \frac{X_i - X_n}{1/2\,(N_i + N_n)}\ (1/10)\ ,$$

where X_i = initial weight of oven-dried buffalograss leaves,
X_n = final weight of oven-dried buffalograss leaves,
N_i = initial number of termites, and
N_n = final number of termites.

The temperature of the laboratory during these feeding trials was approximately 28°C.

Field Study.

Paired plots (0.6 ha in area) were established during July, 1971, and one plot was sprayed with chlordane (octachloro-4, 7-methanotetrahydroindane) at a rate of 3.37 kg AI/ha to control termites. The insecticide treatment was applied again in April, 1973, to maintain essentially 100% termite control. One exclosure (4.6 m X 4.6 m) was constructed on each plot to eliminate the influence of livestock on herbage production and litter accumulation. Both plots were deferred from grazing during the 1974 growing season.

The standing crop of grasses, forbs, and litter was sampled on June 5 and October 10, 1972, and again on October 18, 1974 (11, 15, and 39 months subsequent to initiation of termite control, respectively). On each plot, 45 randomly selected $0.25\text{-}m^2$ circular quadrats were clipped to ground level to determine standing crop biomass of grasses and forbs. A Devac® insect vacuum was used after clipping to collect the litter from each quadrat. Herbage and litter samples were oven-dried at 63°C for 72 hours and weighed. The litter samples from each plot were combined, and a composite sample was ashed in a muffle furnace at 600°C for 8 hours. The oven-dried weight of each litter sample was then converted to an ash-free weight. During October, 1972, five $0.25\text{-}m^2$ circular quadrats were sampled in each exclosure to determine the standing crop of forage and litter.

Belowground plant biomass was determined during June and October, 1972, by extracting the major roots from 40 randomly selected soil cores ($81.07\ cm^2$ X 30.18 cm) taken from the sprayed plot and from 40 similar cores taken from the unsprayed plot. Each soil core was washed over a No. 40 soil sieve (0.42-mm mesh) to separate the soil and roots. Root samples were oven dried, weighed, and ashed to determine an ash-free weight for each sample.

Standing crop data of grasses, forbs, roots, and litter on termite-infested and termite-free plots were analyzed for significant differences using the *t*-test (Snedecor and Cochran, 1967).

Litter Bag Study.

The rate of removal of organic material from above and below the soil surface by termites was estimated using the litter-bag technique described by Bocock (1964). On April 4, 1972, 240 nylon net bags (30 cm X 30 cm, 3-mm mesh) were filled with 10 g of oven-dried blue grama leaves, and 60 were placed on the soil surface and 60 were placed 15 cm below the soil surface on both termite-infested and termite-free areas. Each month from May through December, five bags were collected at random from each treatment and weighed. Differences in disappearance were attributed to termite consumption.

Results and Discussion

Termite Population Densities

The mean population density of termites on the unsprayed plot was $2139/m^2 \pm 688$ (90% confidence limits) over the 3-year period. The peak in population density occurred in September, 1972 ($9127/m^2$). There were usually no termites in the upper 30 cm of soil during the winter months (November, December, January, and February). Population densities varied significantly between years and between growing seasons (Fig. 2) (Table 1). The population density during 1972 ($3672/m^2 \pm 2076$) was significantly higher than during 1973 ($1692/m^2 \pm 995$) ($P < 0.1$) and 1974 ($1152/m^2 \pm 616$) ($P < 0.02$). The population density during the growing season (March through October) of 1972 ($4730/m^2 \pm 1883$) was also significantly higher than during the 1973 growing season ($2640/m^2 \pm 1194$) ($P < 0.1$) and the 1974 growing season ($1482/m^2 \pm 635$) ($P < 0.01$). These differences in termite population densities were attributed to annual and seasonal fluctuations in air and soil temperatures, precipitation, and soil moisture (Ueckert et al., unpublished data). In years or growing seasons of relatively abundant precipitation, temperature was the most important factor affecting desert termite population densities; under more xeric conditions, soil moisture was the most important factor. Termite population densities were positively correlated with temperatures and soil moisture. Conditions were considerably more mesic in 1972 than during 1973 or 1974.

Termite Population Biomass

The mean weight of a live *G. tubiformans* worker was 2.433 mg and its mean oven-dry weight was 0.584 mg. We used these values as an approximation of weights for all castes of termites

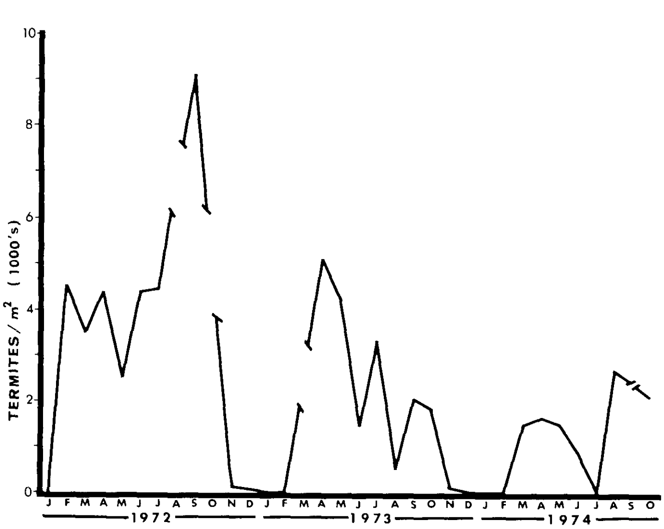

Fig. 2. *Population densities of termites in the upper 30 cm of soil in a shortgrass community in Garza Co., Texas, from January, 1972, through October, 1974.*

in calculating termite biomass in the upper 30 cm of soil, since workers comprised 85% of the sample population. The mean live population biomass in the upper 30 cm of soil was 5.2 g/m^2 (46.4 lb/acre) (1.25 g/m^2 oven-dry basis) over the entire 3-year period. The peak biomass (22.21 g/m^2) (198.2 lb/acre) occurred during September, 1972. The biomass of termites was 2.2 times greater in 1972 than in 1973 and 3.2 times greater in 1972 than in 1974. The biomass of termites during the 1972 growing season was 1.8 and 3.2 times greater than during the 1973 and 1974 growing seasons, respectively (Table 1).

The biomass of cattle grazing the study area and surrounding rangeland is approximately 5.6 g/m^2 (50 lb/acre), live-weight basis, based on an approximate stocking rate of 8.09 ha/animal unit. This value is almost identical to the biomass (live-weight basis) of desert termites occupying this same rangeland over the 3 years of this study. The biomass of termites was 2.1 times greater than that of cattle on the study area during the 1972 growing season and almost 4 times greater during September, 1972. The biomass of *G. tubiformans* in this semiarid shortgrass ecosystem in September, 1972 was twice that reported by Maldague (1964) for subterranean and mound-building termites in *Brachystegia* forest in the Congo (10 g/m^2), and 110 times greater than that reported as the maximum biomass of *G. perplexus* (0.04847 g/m^2) in the Sonoran Desert of Arizona by Nutting et al. (1973).

Dry Matter Consumption

Workers of *G. tubiformans* consumed a mean of 0.058 mg ± 0.02 mg (95% confidence limits) (oven dry weight) of buffalograss leaves per termite per day, or 23.8 mg/g termites/day, or 2.4% of live body weight/day at 28°C in the laboratory feeding study. An indication of the role of *G. tubiformans* in the energy flow through this shortgrass ecosystem can be estimated by extrapolation from the results of this feeding trial. The population of desert termites during the 1972 growing season (11.51 g/m^2) would consume 0.28 g/m^2/day of herbage. There were 5 months during the 1972 growing season during which the soil temperature in the upper 30 cm approached or exceeded 28°C. During this period these termites would consume about 41 g/m^2 (366 lb/acre) of herbage and litter. Assuming that the caloric value of herbage and litter is about 4000 kcal/kg (Cook, 1970), this would be the equivalent of 164 $kcal/m^2$ of gross energy consumed by desert termites.

Impact of Termites on Herbage, Roots, and Litter

By June, 1972, 11 months after termite control was initiated, there were no significant differences in standing crop of grasses, forbs, or roots between grazed, termite-infested (unsprayed) and grazed, termite-free (sprayed) plots (Table 2); however there was 123 kg/ha (110 lb/acre) more litter, ash-free basis, ($P < 0.2$) on the termite-free area. By October, 1972, grazed, termite-free rangeland had 235 kg/ha (210 lb/acre) more grass and 264 kg/ha (236 lb/acre) more litter than the grazed, termite-infested area ($P < 0.01$); however, there were no differences in forb or root biomass. By October, 1972, termite control had resulted in highly significant increases in standing crop of grasses and litter within the grazing exclosure (Table 2). Ungrazed, termite-free rangeland had 22% (401 kg/ha or 358 lb/acre) more grass and 50% (245 kg/ha or 219 lb/acre) more litter than ungrazed, termite-infested rangeland ($P < 0.01$). Ungrazed,

Table 2. Standing crop (kg/ha, oven-dry basis) of grasses, forbs, roots, and litter on termite-infested and termite-free shortgrass rangeland in June and October, 1972, and October, 1974.

Date	Termite-free	Termite-infested	Difference
June, 1972 (grazed)			
Grass	678	644	34
Forbs	79	75	4
Roots[d]	13118	11639	1479
Litter[d]	875	752	123[c]
October, 1972 (grazed)			
Grass	1829	1594	235[b]
Forbs	51	43	8
Roots[d]	8285	8186	99
Litter[d]	701	437	264[b]
October, 1972 (ungrazed)			
Grass	2227	1826	401[b]
Forbs	29	62	−33[c]
Litter[d]	737	492	245[b]
October, 1974 (ungrazed)			
Grass	1246	1163	83
Forbs	121	108	13
Litter[d]	1663	565	1098[a]

[a]Significant at $P < 0.001$.
[b]Significant at $P < 0.01$.
[c]Significant at $P < 0.20$.
[d]Ash-free basis.

termite-infested rangeland had about two times more forbs than the sprayed plot. The decrease of forbs on the termite-free plot was possibly due to increased competition from the grasses and increased litter accumulation, which prevented the establishment of annual forbs.

At the end of the fourth growing season following initiation of termite control (October, 1974), ungrazed, termite-free rangeland had almost three times (1098 kg/ha or 980 lb/acre) more litter than ungrazed, termite-infested rangeland ($P < 0.001$) (Table 2). There were no differences in standing crop of grasses or forbs between treatments.

Termite control resulted in a significant increase in grass production in the 1972 growing season, but the increase during the 1974 growing season was not significant. This difference between years is explained by differences in termite population densities and precipitation. The majority of the 1974 growing season (March through mid-August) was extremely dry (13.36 cm of precipitation; 13 cm below the normal), whereas the 1972 growing season was relatively mesic (78.46 cm of precipitation; 39.32 cm above the normal for March through October). Low soil moisture during the 1974 growing season seriously limited grass production on sprayed and unsprayed plots until late August; thus drought may have overshadowed any treatment effects. Low soil moisture during the 1974 growing season also seriously reduced the population density of desert termites (Table 1) (Fig. 2). The termite population density during the 1974 growing season was less than 1/3 that during the 1972 growing season; thus we expected that termites would consume only about 1/3 as much herbage in 1974. Termites had reduced the standing crop of grass on ungrazed rangeland by about 401 kg/ha at the end of the 1972 growing season; by 20% of this amount (83 kg/ha) at the end of the 1974 growing season (Table 2).

The biomass of litter on termite-free rangeland appears to be increasing each year that termite control is maintained. The increased litter cover may also contribute to increased forage production in years of adequate rainfall, by increasing rainfall infiltration, and lowering soil temperatures and evaporation of

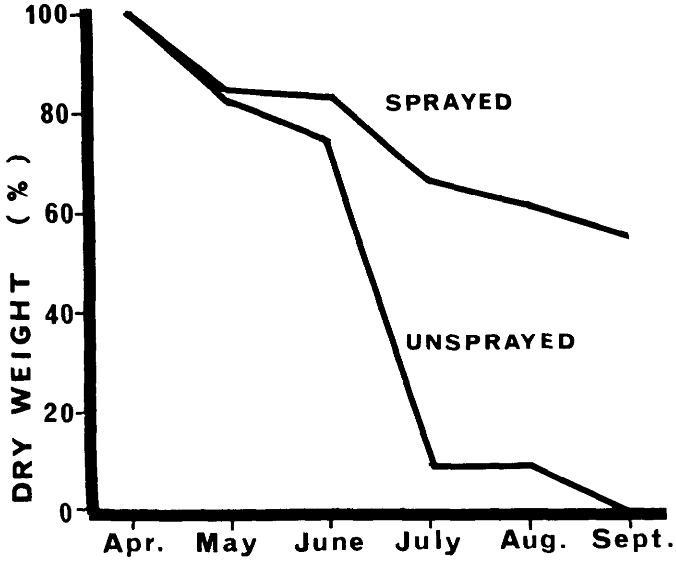

Fig. 3. *Proportions of litter remaining in net bags on the soil surface in termite-infested (unsprayed) and termite-free (sprayed) rangeland, April to September, 1972.*

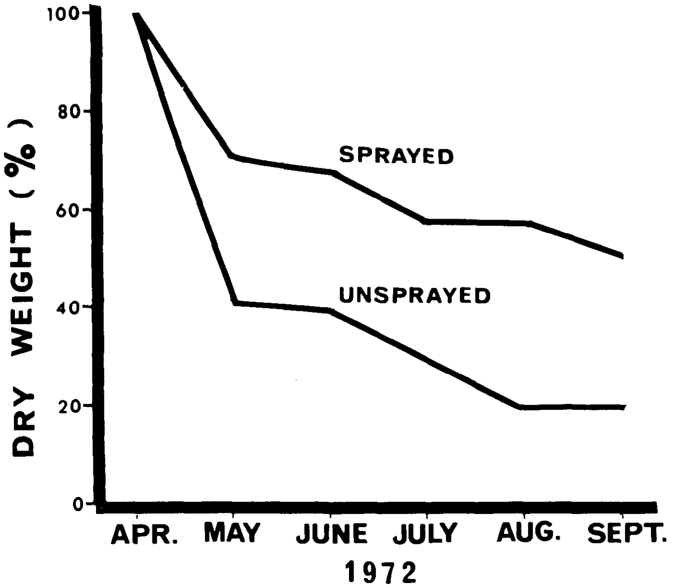

Fig. 4. *Proportions of litter remaining in net bags buried 15 cm beneath the soil surface in termite-infested (unsprayed) and termite-free (sprayed) rangeland, April to September, 1972.*

soil moisture, assuming that microbial decomposition rates will be sufficient to keep soil nutrient levels above limiting levels for plant growth. We are presently studying the effects of desert termites on soil physical properties.

Role of Desert Termites in Litter Decomposition

By September, 1972, all of the blue grama leaves had disappeared from the litter bags on the soil surface in termite-infested rangeland, while 55% of the original 10 g still remained in the bags on the soil surface in termite-free rangeland (Fig. 3). These data indicate that termites account for 55% of the removal of litter from the soil surface, while microbial decomposition accounts for 45%.

In September, 1972, 50.2% of the original 10 g of blue grama leaves remained in the litter bags 15 cm beneath the soil surface on termite-free rangeland, while only 19.4% remained in those 15 cm beneath the soil surface in termite-infested rangeland (Fig. 4). Thus about 38% of the removal of litter incorporated into the soil was attributed to termite consumption, while microbial decomposition accounted for 62%.

Disappearance of litter from litter bags could have been due to termite ingestion, transporting of the litter to underground chambers, or to accelerated decomposition of the leaves due to fragmentation caused by termite feeding. Hopkins (1966) reported that termite feeding increased the surface area of wood and that this was largely responsible for its decomposition. Litter bag contents increased in weight after September due to growth of plant leaves and roots into the bags. This material could not be separated from the original blue grama leaves.

Conclusions

This research has demonstrated that desert termites are an extremely important component of this major rangeland type in the southwestern United States. The magnitude of the ecological role of desert termites can be very significant to the range manager if environmental conditions favor high population densities of these ground-dwelling insects. It should be recognized that termite population densities will vary between years and growing seasons. Ranchers can expect higher population densities of desert termites and hence a greater total loss of forage to these insects during wet years. However, during dry years their aboveground foraging activities may be more noticeable and the detrimental effect of termite feeding on forage plants may be more severe.

Termite control on rangeland resulted in increased forage production as well as a buildup of plant litter. The economic feasibility of controlling desert termites will depend on livestock prices, weather conditions, population densities of termites, and cost of insecticide and its application. The long-term effect of termite control on soil properties and the nutrient cycle are aspects that are unknown and that should be studied before large-scale and long-term desert termite control is attempted.

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